

## A new early Oligocene mammal fauna from the Sirt Basin, central Libya: Biostratigraphic and paleobiogeographic implications



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### ABSTRACT

We report the discovery of a new early Oligocene vertebrate fauna from the vicinity of Zallah Oasis in the Sirt Basin of central Libya. The Zallah Incision local fauna has been recovered from the base of a fluvial channel within a rock unit that has been mapped as “Continental and Transitional Marine Deposits.” This rock unit has produced fossil vertebrates sporadically since the 1960s, but the Zallah Incision local fauna is the most diverse assemblage of fossil mammals currently known from this unit. In addition to lower vertebrates, the fauna includes an indeterminate sirenian, the anthracothere *Bothriogenys*, a new species of the hyracoid genus *Thyrohyrax*, new species of the hystricognathous rodent genera *Metaphiomys* and *Neophiomys*, *Metaphiomys schaubi*, and a new species of the parapithecoid primate genus *Apidium*. The Zallah Incision local fauna from Libya appears to be close in age to Fayum quarries V and G in the Jebel Qatrani Formation of Egypt and the Taqah locality in the Ashawq Formation of Oman. Considered together, these early Oligocene faunas support a modest level of faunal provincialism across the northern part of Afro-Arabia during the early Oligocene.

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### 1. Introduction

The early part of the Oligocene Epoch is a key interval that witnessed the coolest temperatures and most pronounced seasonality of the entire Paleogene (Coxall et al., 2005; Lear et al., 2008; Liu et al., 2009; Hren et al., 2013). The transition from the warm, equable climate that prevailed during the Eocene to the cooler, drier, and far more seasonal world of the Oligocene was accompanied by dramatic changes in faunal composition, which are particularly well documented on the northern continents (Rasmussen et al., 1992; Prothero and Emry, 1996; Meng and McKenna, 1998). In contrast, this transition remains poorly documented in Africa because of a general dearth of fossil localities spanning this interval and because of the restricted geographic distribution of those localities that are currently known. Current knowledge of early Oligocene Afro-Arabian mammal faunas is mainly derived

from localities found in the Fayum Depression of Egypt and Dhofar Province in Oman (e.g., Seiffert, 2010).

The Jebel Qatrani Formation, which outcrops in the Fayum region of northern Egypt, is renowned for its rich and diverse late Paleogene mammal faunas, making it the primary record of late Eocene and early Oligocene mammal evolution in Africa (Gagnon, 1997; Seiffert, 2010). Despite this fundamental role, the Fayum record also raises some important questions. For example, the correlation of the Fayum magnetostratigraphic record published by Seiffert (2006) has recently been challenged by Underwood et al. (2013), who argue that the Jebel Qatrani Formation is entirely Oligocene in age. In addition to the ongoing debate over its correlation, the faunal content of the Jebel Qatrani Formation differs in some ways from that of other broadly contemporary rock units in Afro-Arabia. This is exemplified by the presence of cricetid and anomaluroid rodents, strepsirhine primates, and the unusual proboscidean *Omanitherium* in early Oligocene sites in Oman, taxa that have yet to be reported from the more thoroughly sampled and studied early Oligocene faunas known from Egypt (Gheerbrant et al., 1993; Thomas et al., 1999; Seiffert et al., 2012). Despite important recent progress in documenting later Oligocene faunas in Afro-Arabia (e.g., Kappelman et al., 2003; Stevens et al., 2008,

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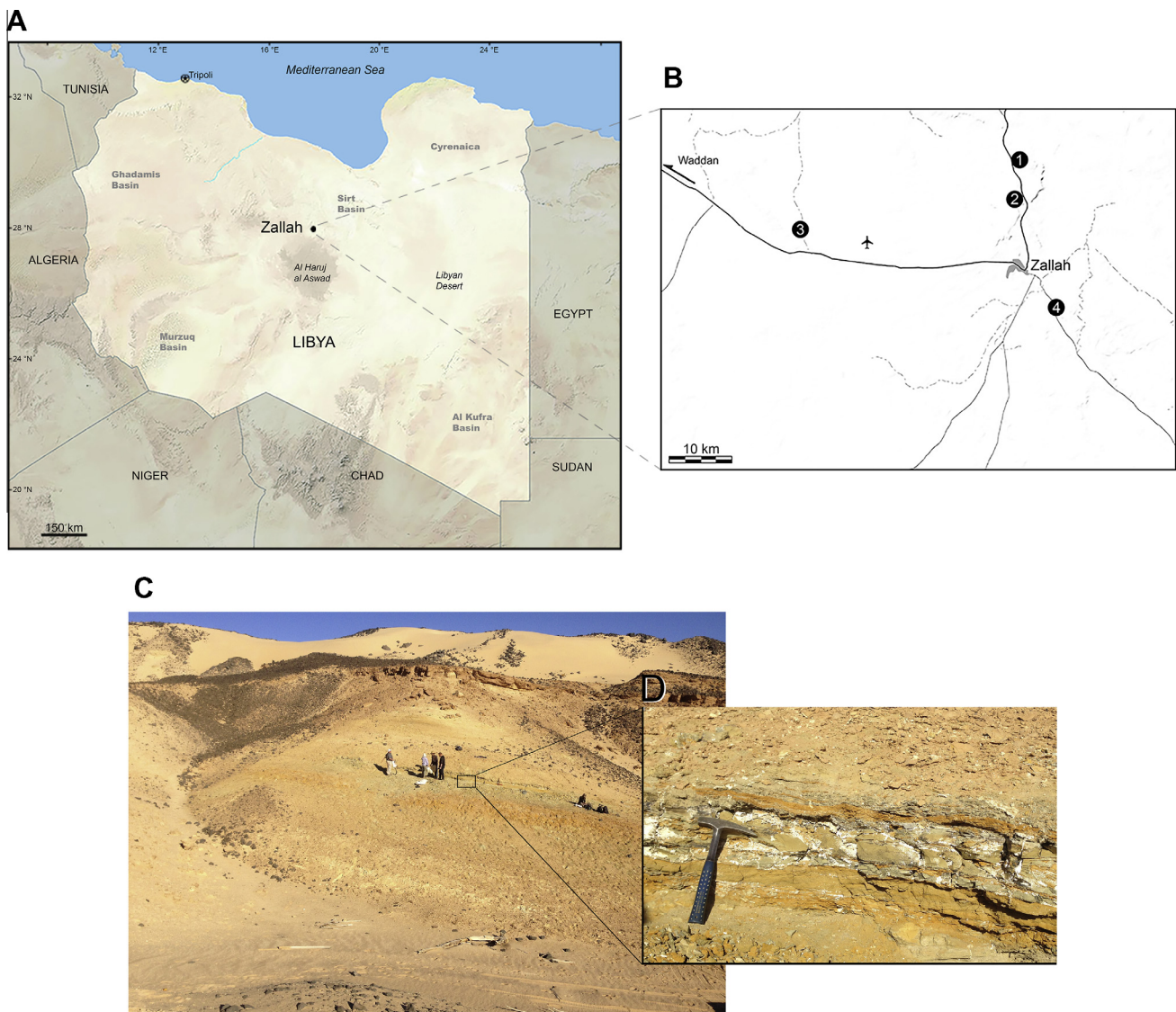
2013; Rasmussen and Gutierrez, 2009; Ducrocq et al., 2010, 2011; Zalmout et al., 2010), the African early Oligocene record remains inadequately sampled, especially from a biogeographic and biostratigraphic perspective.

Fossil vertebrates from the vicinity of Zallah Oasis in the Sirt Basin of central Libya were first reported from deltaic and fluvial deposits in a unit mapped as “Continental and Transitional Marine Deposits” or CTMD (Arambourg and Magnier, 1961; Arnould-Saget and Magnier, 1961; Arambourg, 1963; Vesely, 1985; Fejfar, 1987). Our recent work in this area has led to the discovery of several new early Oligocene vertebrate localities (Fig. 1), one of which has yielded a rich assemblage of early hystricognathous rodents (Coster et al., 2010, 2012). In January 2013 we discovered a promising new site, the Zallah 7 Incision (Z7I) locality, which has yielded a vertebrate fauna including sharks, rays, bony fishes, crocodylians, a sirenian, a hyracoid, early hystricognathous rodents, an anthracothere, and anthropoid primates. Hereafter, we refer to the fauna derived from Z7I as the Zallah Incision local fauna, which is the most diverse assemblage of vertebrates currently known from the CTMD in the Sirt Basin.

The purpose of this paper is to provide a preliminary report on the mammalian component of the Zallah Incision local fauna. Pending the recovery of additional material, we refrain from describing some of its poorly documented taxa at this time. Additionally, a new species belonging to the parapithecoid primate genus *Apidium* from Z7I will be described elsewhere. These new data increase our knowledge of the early Oligocene record of Africa, which is necessary for understanding the potential impacts of paleogeography and paleoenvironmental changes on African faunal composition during this interval. The fossils described here are deposited in the collections of the Geology Department of the Faculty of Science, University of Tripoli, Libya.

## 2. Geological context

The Sirt Basin in central Libya is a Tethyan rift basin consisting of a NW–SE trending system of horsts and grabens that was initiated during the Early Cretaceous (e.g., Van der Meer and Cloetingh, 1993; Baird et al., 1996; Schroter, 1996). The Sirt Basin



**Fig. 1.** (A) Map of Libya and adjacent areas showing the location of Zallah Oasis in the Sirt Basin. (B) Higher resolution map showing Zallah Oasis and the surrounding vicinity. Fossil sites depicted on the map are as follows: 1, Zallah 5 Rodent locality (Z5R locality) (see Coster et al., 2010, 2012); 2, Zallah 7 Incision locality (Z7I locality); 3, fossil site located west of Zallah in Wadi Umm al Laban (see Fejfar, 1987); 4, fossil site located southeast of Zallah reported by Arambourg (1963). (C) Broad perspective of Z7I locality. (D) Detailed view of fossiliferous horizon at Z7I locality.

comprises five main grabens, including the Zallah Trough in its southwestern part. Late Paleogene CTMD strata exposed in the vicinity of Zallah Oasis include estuarine, lagoonal and deltaic facies (Conant and Goudarzi, 1967; Bezan and Malak, 1996). The CTMD is dominated by cross-bedded channel sandstones and mudstones with silt intercalations overlying the marine Eocene Wadi Thamat Formation (Schroter, 1996). The Wadi Thamat Formation is generally represented by greenish/grey mudstones, bioclastic marly limestones, oyster mounds and coquinas dating from the late middle to late Eocene (Goudarzi, 1970; Jurak, 1985; Vesely, 1985). Locally, the CTMD is generally covered by Neogene basalts pertaining to the Jabal Al Haruj volcanic complex, although the Miocene Maraddah Formation caps the CTMD to the south and west of Zallah (Vesely, 1985; Fejfar, 1987).

The first fossil vertebrates from the vicinity of Zallah were described during the early 1960s (Arambourg and Magnier, 1961; Arnould-Saget and Magnier, 1961; Arambourg, 1963). Arambourg's original fossil site, located southeast of Zallah (Fig. 1B), occurs in a conglomerate with well-rounded clasts in a matrix of sand and clay in the upper part of the CTMD. A second mammal-bearing site, located west of Zallah, was reported by Fejfar (1987) as occurring in coarse cross-bedded sandstones and mudstones deposited near the ancient shoreline under deltaic-estuarine conditions.

Our work to date has concentrated on outcrops of CTMD strata located north of Zallah. The Zallah 5 Rodent locality (Z5R) occurs in a muddy sandstone bed capping a succession of laminated red and green mudstones interbedded with siltstone and gypsum, reflecting an estuarine-lagoonal to deltaic depositional environment (Coster et al., 2012). The newly discovered Z71 locality, situated approximately 10 km north of Zallah Oasis, occurs in a level of light greenish to reddish gypsiferous fine to coarse-grained sandstones (Figs. 1C and D and 2). Approximately one ton of friable sediment collected from the site was screenwashed to produce the mammalian fauna described here.

An early Oligocene age has been proposed for the CTMD based on foraminiferal (*Bolivina meletica*, *Nummulites fichtelli*), selachian and mammalian assemblages (e.g., Vesely, 1985; Fejfar, 1987; Coster et al., 2012). The enhanced diversity of the Zallah Incision local fauna enables us to reassess and refine earlier efforts to correlate the CTMD with later Paleogene faunas known from the Jebel Qatrani Formation in the Fayum region of northern Egypt and the Thaytiniti and Taqah local faunas from Dhofar Province in Oman.

### 3. Systematic paleontology

RODENTIA Bowdich, 1821

CTENOHYSTRICA Huchon, Catzefflis, and Douzery, 2000

HYSTRICOGNATHI Tullberg, 1899

METAPHIOMYS Osborn, 1908

**Type species**—*Metaphiomys beadnelli* Osborn, 1908

**Included species**—*Metaphiomys schaubi* Wood, 1968; *Metaphiomys zallahensis* sp. nov.

**Known distribution**—Early Oligocene of Egypt, Oman and Libya; Late Oligocene of Tanzania.

**Emended diagnosis**—Lophodont cheek teeth, moderately high crowned. Pentolophodont upper molars characterized by an anteroloph, a protoloph, a mesolophule, a metaloph and a posteroloph. The mesolophule is variably developed. The paracone is the highest cusp of the upper molar. The metaloph is transverse; a short spur links the lingual extremity of the metaloph to the posteroloph. Tetralophodont lower molars characterized by a metalophulid I, a strong posterior arm of protoconid bearing a backwardly directed protospur, a hypolophid and a posterolophid. Lower molars with no trace of mesoconid or mesolophid. Deciduous premolars retained through life.

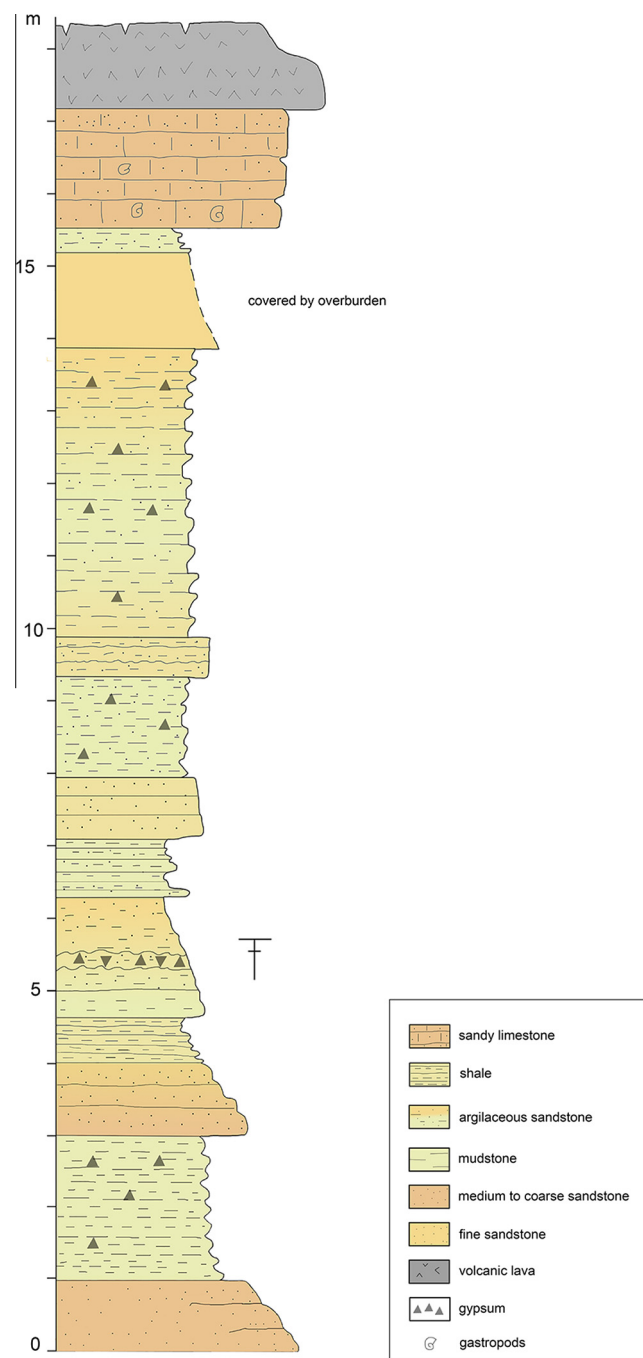


Fig. 2. Lithostratigraphic log of the section at Z71 locality.

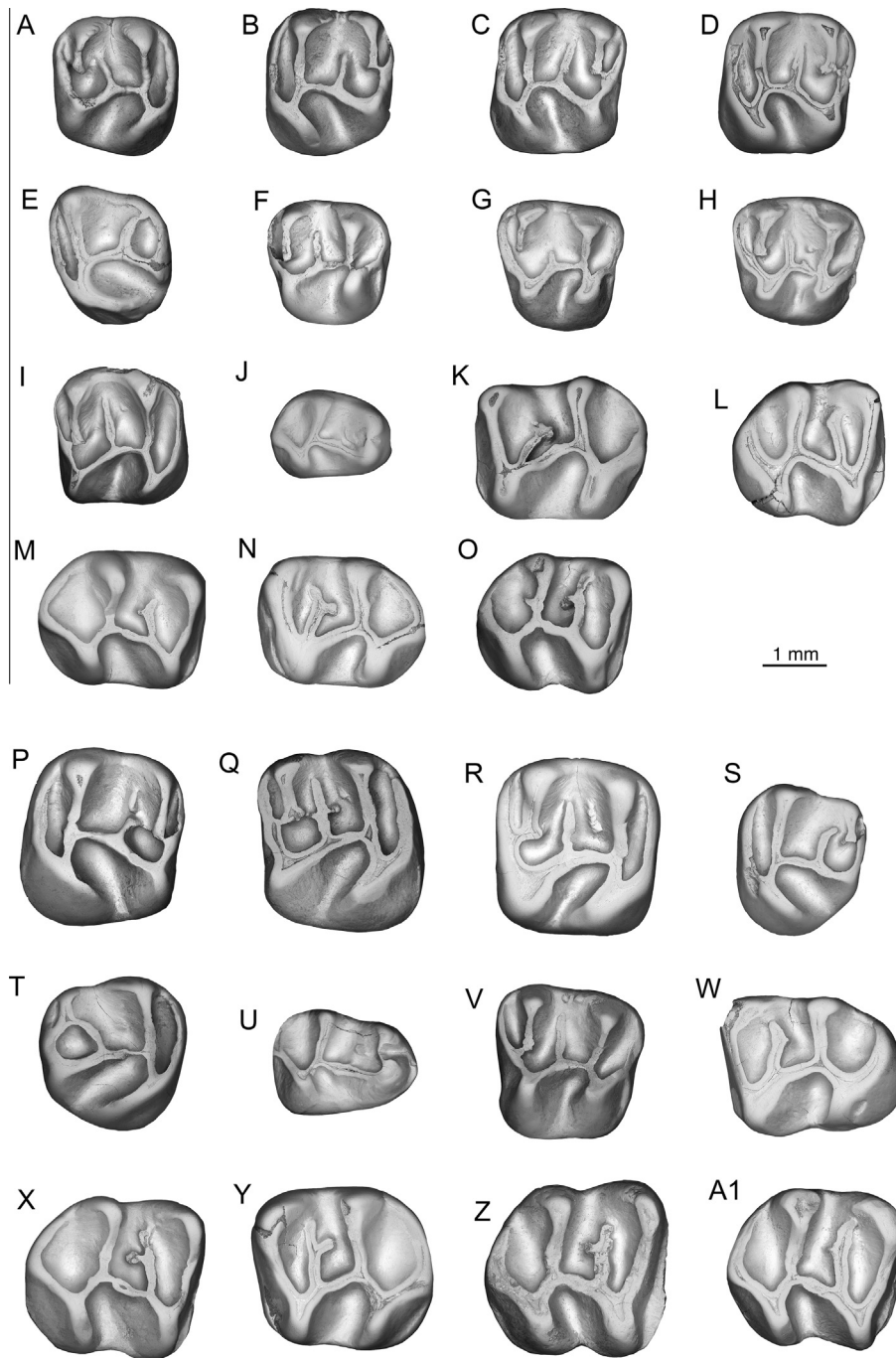
**METAPHIOMYS ZALLAHENSIS**, sp. nov.  
(Fig. 3A–O)

**Holotype**—Z71-122, left M2 (Fig. 3B).

**Etymology**—The species name reflects the geographic provenance of the available hypodigm.

**Hypodigm**—Z71-89, left m1; Z71-90, left m1; Z71-91, left m1 (Fig. 3N); Z71-92, right m1; Z71-93, left m1; Z71-94, right m1; Z71-95, right m1; Z71-96, right m1 (Fig. 3M); Z71-97, right m1 (Fig. 3O); Z71-98, left m1; Z71-99, right m1; Z71-100, left m1; Z71-101, left m1; Z71-102, left m1; Z71-103, right m1; Z71-104, left m1; Z71-105, left m1; Z71-106, right m1; Z71-107, right m1; Z71-108, left m2 (Fig. 3K); Z71-109, right m2; Z71-110, right m2; Z71-111, left m3; Z71-112, right m3 (Fig. 3L); Z71-113, right M1; Z71-114, right M1 (Fig. 3I); Z71-115, left M1; Z71-116, left M1;





**Fig. 3.** (A–O) *Metaphiomys zallahensis*; (A) right M1 (Z71-117); (B) left M2 (Z71-122); (C) left M2 (Z71-121); (D) left M2 (Z71-124); (E) left M3 (Z71-135); (F) right DP4 (Z71-138); (G) right DP4 (Z71-136); (H) right DP4 (Z71-139); (I) right M1 (Z71-114); (J) right dp4 (Z71-149); (K) left m2 (Z71-108); (L) right m3 (Z71-112); (M) right m1 (Z71-96); (N) left m1 (Z71-91); (O) right m1 (Z71-97). (P–A1) *Metaphiomys schaubi*; (P) left M2 (Z71-41); (Q) right M2 (Z71-49); (R) right M2 (Z71-16); (S) left M3 (Z71-54); (T) right M3 (Z71-14); (U) right dp4 (Z71-67); (V) right DP4 (Z71-15); (W) left m3 (Z71-35); (X) right m2 (Z71-29); (Y) left m2 (Z71-28); (Z) right m2 (Z71-18); (A1) right m1 (Z71-17).

Z71-117, right M1 (Fig. 3A); Z71-118, right M1; Z71-119, left M1; Z71-120, left M1; Z71-121, left M2 (Fig. 3C); Z71-123, right M2; Z71-124, left M2 (Fig. 3D); Z71-125, right M2; Z71-126, left M2; Z71-127, right M2; Z71-128, left M2; Z71-129, left M2; Z71-130, left M3; Z71-131, right M3; Z71-132, right M3; Z71-133, right M3; Z71-134, left M3; Z71-135, left M3 (Fig. 3E); Z71-136, right DP4 (Fig. 3G); Z71-137, left DP4; Z71-138, right DP4 (Fig. 3F); Z71-139, right DP4 (Fig. 3H); Z71-140, left DP4; Z71-141, left DP4; Z71-142, left DP4; Z71-143, left DP4; Z71-144, left DP4; Z71-145, right DP4; Z71-146, left DP4; Z71-147, right dp4; Z71-148, left dp4; Z71-149, right dp4 (Fig. 3J); Z71-150, right dp4; Z71-151, left dp4; Z71-152,

left dp4; Z71-153, left dp4; Z71-154, right dp4; Z71-155, left dp4; Z71-156, right dp4; Z71-157, left dp4; Z71-158, left dp4; Z71-159, right dp4.

**Type locality**—Z71 locality, CTMD, Sirt Basin, Libya.

**Measurements**—Table 1.

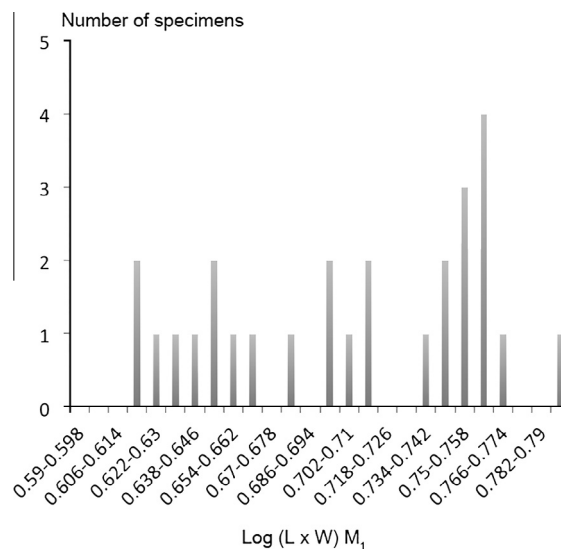
**Diagnosis**—Similar in morphology to *Metaphiomys schaubi* but differs in being smaller. Differs from *M. beadnelli* in being smaller and in showing a lesser degree of crown elevation. Lower molar pattern more specifically differs from *M. beadnelli* in exhibiting a less prominent posterior arm of the protoconid, a less developed protospur and no forward displacement of the buccal tip of the

**Table 1**  
Measurements (in mm) for upper and lower teeth of *Metaphiomys zallahensis*.

Tooth locus	n (number of specimens)	OR (observed range)	x (mean)
DP4			
L	6	1.78–1.99	1.89
W		1.86–2.017	1.94
M1			
L	9	1.85–2.11	1.94
W		1.99–2.27	2.15
M2			
L	10	1.99–2.25	2.13
W		2.26–2.54	2.41
M3			
L	5	1.98–2.08	2.04
W		2.16–2.51	2.33
dp4			
L	6	2–2.8	2.19
W		1.45–1.61	1.57
m1			
L	9	2.08–2.35	2.26
W		1.86–2.03	1.94
m2			
L	4	2.51–2.59	2.54
W		2.22–2.39	2.3
m3			
L	2	2.09–2.28	2.18
W		2–2.05	2.02

posterior arm of the protoconid. Differs from *M. beadnelli* in having the posterior arm of protoconid and posterolophid of lower molars not connected with metaconid and entoconid until after considerable wear.

**Description**—Lower cheek teeth are moderately high-crowned, rectangular and display a well-developed tetralophodont pattern with cusps still distinguishable. The anterocingulid on m1–2 is low, weak and enlarged buccally. The metaconid is slightly more mesial than the protoconid and the metalophulid I is complete. The posterior arm of the protoconid is strong and extends lingually, but its lingual tip does not usually reach the metaconid. In this respect, lower molars of *M. zallahensis* differ from those of *Metaphiomys* known from the nearby Z5R in having a slightly shorter posterior arm of the protoconid (Coster et al., 2012: fig. 4). The lingual wall is poorly developed, leaving the anterofossetid open. A short crest (protospur) extends distally from the posterior arm of the protoconid. Occasionally, a similar crestule extends distally from the middle of the hypolophid. These protospurs are variably developed within the current sample from Z71. The entoconid is slightly more mesial than the hypoconid. The hypolophid parallels the metalophulid I and connects buccally to the anterior arm of the hypoconid and the ectolophid. The posterolophid extends from the hypoconid toward the base of the entoconid and bears a small hypoconulid, which is barely visible in some of the teeth. In some specimens, the posterolophid reaches the entoconid, so that the metafossetid is closed lingually by a low crest. The m3 is shorter than the other molars, and its talonid is pinched buccolingually. The dp4s are oval in occlusal outline, with the talonid being wider than the trigonid. They exhibit a trilophodont pattern with distinct metalophulid II, hypolophid and posterolophid. The metaconid is transverse to the protoconid. There is no metalophulid I. The anterocingulid is present but weak. There is no anteroconid. The ectolophid runs distally from the protoconid to connect the anterior arm of the hypoconid. The mesolophid is generally absent but some of the teeth exhibit an incipient mesolophulid that extends lingually from the ectolophid. The hypoconulid is distinct on the posterolophid.



**Fig. 4.** Histogram showing log (L × W) of the lower first molar (m1) in two species of *Metaphiomys* at Z71 locality.

The upper molars are essentially pentalophodont, with well-developed antero-, proto-, meta-, posteroloph and a mesolophule. The anteroloph and posteroloph end at the base of the paracone and metacone, respectively, but are not connected to these cusps. The protoloph is straight and runs parallel to the anteroloph. The mesolophule on M1–2 is variable in length, but it never reaches the buccal margin of the tooth. There is no metaconule. The hypocone is widely separated from the protocone. The lingual internal sinus is closed buccally by the presence of a complete mure. The metaloph runs lingually from the metacone and connects distally to the middle of the posteroloph. In a few specimens, the metaloph displays a mesial connection to the mesolophule. The hypocone of M3 is displaced buccally and the metacone is strongly reduced, being crestiform. The protocone displays a posterior outgrowth, reducing the opening of the lingual sinus as a result. The lingual sinus displays a mesiodistal orientation. The metaloph of M3 usually displays a double connection with the mesolophule and the posteroloph. The DP4 generally resembles the upper molars in morphology, except for having an anterior cingulum that is much lower and a more mesiodistally constricted lingual part of the tooth.

#### METAPHIOMYS SCHAUBI Wood, 1968

(Fig. 3P–A1)

**Referred material**—Z71-14, right M3 (Fig. 3T); Z71-15, right DP4 (Fig. 3V); Z71-16, right M2 (Fig. 3R); Z71-17, right m1 (Fig. 3A1); Z71-18, right m2 (Fig. 3Z); Z71-19, left m1; Z71-20, left m1; Z71-21, right m1; Z71-22, right m1; Z71-23, right m1; Z71-24, right m1; Z71-25, left m1; Z71-26, left m1; Z71-27, right m1; Z71-28, left m2 (Fig. 3Y); Z71-29, right m2 (Fig. 3X); Z71-30, left m2; Z71-31, right m2; Z71-32, right m2; Z71-33, left m2; Z71-34, right m2; Z71-35, left m3 (Fig. 3W); Z71-36, right m3; Z71-37, right m3; Z71-38, right m3; Z71-39, right M1; Z71-40, left M1; Z71-41, left M2 (Fig. 3P); Z71-42, right M1; Z71-43, right M1; Z71-44, left M1; Z71-45, left M1; Z71-46, left M1; Z71-47, right M1; Z71-48, left M2; Z71-49, right M2 (Fig. 3Q); Z71-50, right M2; Z71-51, right M2; Z71-52, right M2; Z71-53, right M2; Z71-54, left M3 (Fig. 3S); Z71-55, left M3; Z71-56, left DP4; Z71-57, right DP4; Z71-58, left DP4; Z71-59, left DP4; Z71-60, left DP4; Z71-61, left DP4; Z71-62, left DP4; Z71-63, right DP4; Z71-64, left DP4; Z71-65, right DP4; Z71-66, right DP4; Z71-67, right dp4 (Fig. 3U); Z71-68, right dp4; Z71-69, right dp4; Z71-70, right dp4; Z71-71, right dp4; Z71-72, right dp4; Z71-73, left dp4.

**Known Distribution**—Jebel Qatrani Formation (Quarries B, E, and V), Fayum Depression, Egypt; possibly the Ashawq Formation, Oman; CTMD (Fejfar locality and Z71 locality), Sirt Basin, Libya.

**Measurements—Table 2.**

**Description**

This species is larger than *M. zallahensis* but displays a similar similar dental morphology (Fig. 3P–A1). The cheek teeth are lophodont and moderately high-crowned. The lowers display a complete metalophulid I and a prominent posterior arm of the protoconid bearing a backwardly directed protospur (Fig. 3W–A1). The lingual tip of the posterior arm of the protoconid comes close to the metaconid but there is no complete metalopulid II. The anterocingulid is enlarged buccally. There is no mesoconid or mesolophid. The ectolophid connects the protoconid to the anterior arm of hypoconid, delimiting lingually a wide buccal sinusid. The entocoid is slightly more mesial than the hypoconid. The posterolophid, exhibiting a small distinct hypoconulid, runs from the hypoconid toward the base of the entocoid but does not connect this latter cusp. The uppers display a pentalophodont pattern characterized by an anteroloph, a protoloph, a mesolophule, a metaloph and a posteroloph (Fig. P–T). The conules are indistinct. The mesolophule is variably developed. The lingual tip of the metaloph is connected distally to the posteroloph. The posteroloph runs from the hypococone toward the buccal margin of the tooth but does not connect the metacone.

**Comparison**

The Z71 locality has yielded hundreds of isolated teeth of *Metaphiomys*. Examination of these specimens reveals a similar morphology but a wide range of variation in terms of size. A bivariate plot (length versus width) and a histogram of m1 occlusal area were produced for all available specimens of *Metaphiomys* from Z71 (Fig. 4). Summary statistics quantifying the metric variation shown by the sample of *Metaphiomys* from Z71 are provided in Table 3. The coefficient of variation for the length of m1 in all specimens of *Metaphiomys* from Z71 is 6.9. This is higher than average for living rodent species (Gingerich, 1974) and higher than the coefficient of variation for *Metaphiomys* from the entire stratigraphic range of

**Table 3**

Means, standard deviation and coefficient of variation of tooth length (L) and width (W) of *Metaphiomys* from Zallah 7 locality.

Tooth locus	OR (observed range)	x (mean)	s (standard deviation)	V (coefficient of variation)
DP4				
L	1.78–2.28	2.05	0.15	7.18
W	1.86–2.44	2.11	0.17	7.85
M1				
L	1.85–2.40	2.02	0.13	6.68
W	1.99–2.58	2.25	0.17	7.48
M2				
L	1.99–2.62	2.53	0.2	8.98
W	2.26–3.01	2.57	0.23	8.93
M3				
L	1.98–2.49	2.15	0.15	6.86
W	2.16–2.96	2.47	0.22	9.07
dp4				
L	2–3.07	2.39	0.23	9.54
W	1.45–2.26	1.72	0.18	10.86
m1				
L	2.08–2.79	2.44	0.17	6.91
W	1.86–2.52	2.11	0.16	7.44
m2				
L	2.51–2.98	2.7	0.14	5.33
W	2.22–2.75	2.46	0.16	6.66
m3				
L	2.09–2.97	2.48	0.31	12.39
W	2–2.49	2.28	0.21	9.12

the genus in the Jebel Qatrani Formation, which is ~5.5 based on measurements provided by Holroyd (1994). The large coefficient of variation shown by the Z71 sample suggests that more than one species of *Metaphiomys* is represented there. Moreover, the bivariate plot and histogram for *Metaphiomys* m1 specimens from Z71 do not show unimodal distributions.

These results suggest that two closely related species, *Metaphiomys zallahensis* and *Metaphiomys schaubi*, co-occur in the Zallah Incision local fauna.

THRYONOMYIDAE Pocock, 1922

*NEOPHIOMYS* Coster et al., 2012

*NEOPHIOMYS DAWSONAE*, sp. nov.

(Fig. 5)

**Holotype**—Z71-87, left m2 (Fig. 5G)

**Etymology**—For Mary R. Dawson, in recognition of her numerous contributions to our knowledge of Paleogene rodents.

**Hypodigm**—Z71-74, right DP4 (Fig. 5D); Z71-75, left DP4 (Fig. 5E); Z71-76, right M1; Z71-77, right M1; Z71-78, left M1; Z71-79, left M1 (Fig. 5C); Z71-80, left M2 (Fig. 5A); Z71-81, right M1/2 (Fig. 5B); Z71-82, right M1; Z71-83, right m1 (Fig. 5F); Z71-84, left m1 (Fig. 5H); Z71-85, right m1; Z71-86, left m1; Z71-88, left m3 (Fig. 5I).

**Type locality**—Z71 locality, CTMD, Sirt Basin, Libya.

**Measurements**—Table 4.

**Diagnosis**—Slightly larger than *N. paraphiomys*, with upper cheek teeth slightly longer in proportion. Differs from the other species of *Neophiomys* in having more bunodont cheek teeth, and a weaker development of crests. Differs in having a more bulbous and rounded protocone on upper molars, and in developing a mesiolingual cingulum on uppers and a posterior cingulid distal to the hypoconid on the lowers.

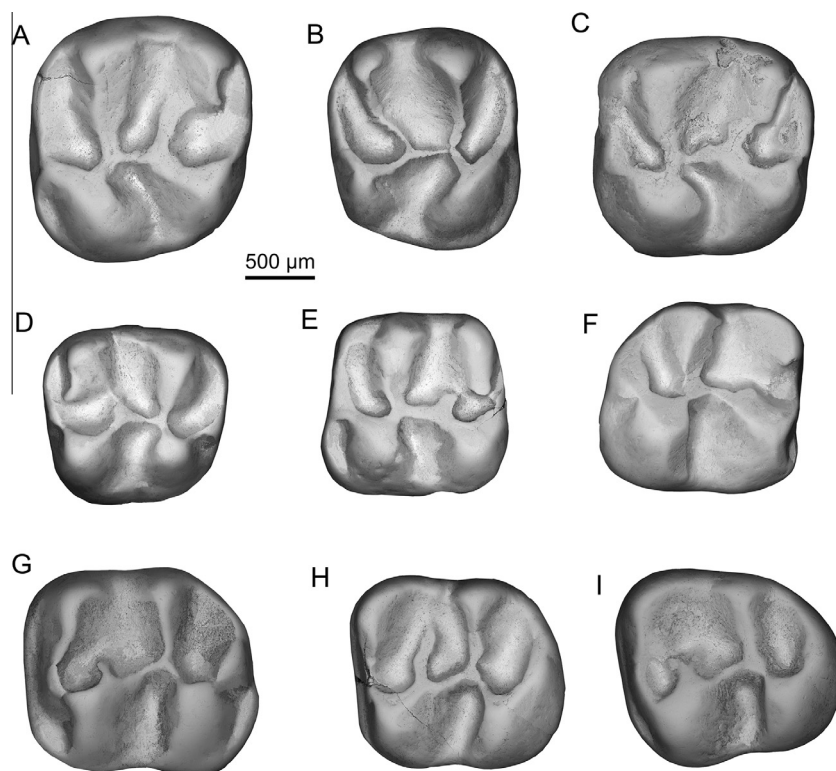
**Description**

The cheek teeth of *Neophiomys dawsonae* are slightly larger and bear weaker crests than those of *N. paraphiomys* from the Z5R locality (Coster et al., 2012) and Fayum Quarry G.

**Table 2**

Measurements (in mm) for upper and lower teeth of *Metaphiomys schaubi*.

Tooth locus	n (number of specimens)	OR (observed range)	x (mean)
DP4			
L	9	1.96–2.28	2.13
W		2.1–2.44	2.21
M1			
L	5	2.05–2.40	2.15
W		2.39–2.58	2.47
M2			
L	5	2.32–2.62	2.5
W		2.64–3.01	2.86
M3			
L	1	2.49	
W		2.96	
dp4			
L	6	2.49–3.07	2.61
W		1.79–2.26	1.93
m1			
L	11	2.4–2.79	2.6
W		2.15–2.52	2.25
m2			
L	8	2.66–2.98	2.78
W		2.38–2.75	2.54
m3			
L	4	2.44–2.97	2.63
W		2.32–2.49	2.4



**Fig. 5.** (A–I) *Neophiomys dawsonae*; (A) left M2 (Z71-80); (B) right M1/2 (Z71-81); (C) left M1 (Z71-79); (D) right DP4 (Z71-74); (E) left DP4 (Z71-75); (F) right m1 (Z71-83); (G) left m2 (Z71-87); (H) left m1 (Z71-84); (I) left m3 (Z71-88).

*N. dawsonae* exhibits bunolophodont cheek teeth that are characterized by moderately developed transverse lophs and cusps that remain discrete. The morphology of m1–2 is basically trilophodont with a metalophulid I, a hypolophid and a posterolophid. The posterior arm of the protoconid shows different patterns of development. It is generally reduced and never forms a complete metalophulid II. The anterior cingulid is low. The ectolophid runs distally from the protoconid to join the short anterior arm of the hypoconid. There is no indication of a mesolophid or a mesoconid. The posterolophid bears a small hypoconulid that is barely distinguishable in some specimens. On m2, a distobuccal cingulid develops distal to the hypoconid; this feature is absent in *N. paraphiomysoides*. The upper molars are bunolophodont and quadrangular. The M1 is more bunodont than M2, with lingual cusps that are more rounded. The anteroloph on the upper molars is lower than the protoloph. The protocone in *N. dawsonae* is more nearly conical and the anteroloph is relatively lower than what is observed in *N. paraphiomysoides*. A weak mesiolingual cingulum is present on the upper molars of *N. dawsonae*, while this character is absent in *N. paraphiomysoides*. The mure is complete. The metacone is variably developed, being small (on M1) to indistinct (on M2). The mesolophule is short and joins the lingual end of the metaloph. There is no indication of a mesostyle or a mesoloph. A short metaloph extends lingually from the metacone. Its lingual terminus is connected mesially to the mesolophule. In some specimens, the mesolophule merges seamlessly with the lingual part of the metaloph, so that the metaloph lacks any distal connection to the posteroloph. The DP4 have an oblong occlusal outline, being slightly longer than wide. These teeth display a very bunodont pattern with rounded cusps and poorly developed lophs. The anteroloph on DP4 is weaker than its counterpart on the molars.

HYRACOIDEA Huxley, 1869

SAGHATHERIIDAE Andrews, 1906

THYROHYRAX Meyer, 1973

THYROHYRAX LIBYCUS, sp. nov.

(Fig. 6A–H)

**Holotype**—Z71-9, left M3 (L, 8.18 mm; W, 9.61 mm) (Fig. 6G).

**Etymology**—The species name recognizes the geographic provenance of this species.

**Hypodigm**—Z71-162, right P2 (L, 6.10; W, 6.36) (Fig. 6D); Z71-163, left P4 (L, 6.84; W, 7.67) (Fig. 6C); Z71-164, left DP4 (L, 6.37; W, 5.77) (Fig. 6E); Z71-165, fragmentary left M1 (L, ~6.79; W, ?) (Fig. 6H); Z71-8, right dentary fragment with dp2–dp3 (L, 6.79; W, 3.79/L, 7.23; W, 4.32) (Fig. 6A); Z71-160, right m3 (L, 11.4; W, 6.15) (Fig. 6F); Z71-161, left m1 (L, 7.06; W, 4.71) (Fig. 6B).

**Type locality**—Z71 locality, CTMD, Sirt Basin, Libya.

**Diagnosis**—Medium-sized member of the genus *Thyrohyrax* with selenolophodont molars. Resembles *T. domorictus* but differs in having higher-crowned upper molars bearing smaller parastyles and larger mesostyles, and in having the apices of the hypocone and metacone more closely approximated. Further differs from *T. domorictus* in having more simplified permanent upper premolars with a more nearly transverse occlusal outline. Upper premolars further differ from those of *T. domorictus* in having the paracone and metacone closely spaced, without a distinct mesostyle and with lesser development of the hypocone and prehypocrista, the protocone being the dominant lingual cusp. Differs from *T. kenyaensis* in being slightly smaller and in having relatively wider upper premolars. Differs from *T. pygmaeus* in its notably smaller size and less molariform upper premolars. Differs from *T. meyeri* in having upper molars with a smaller and less inflated parastyle, and lower molars with a stronger postmetacristid. Differs from *T. litholagus* in being smaller and having upper molars with smaller styles and without strong mesial and lingual cingula.

#### Description

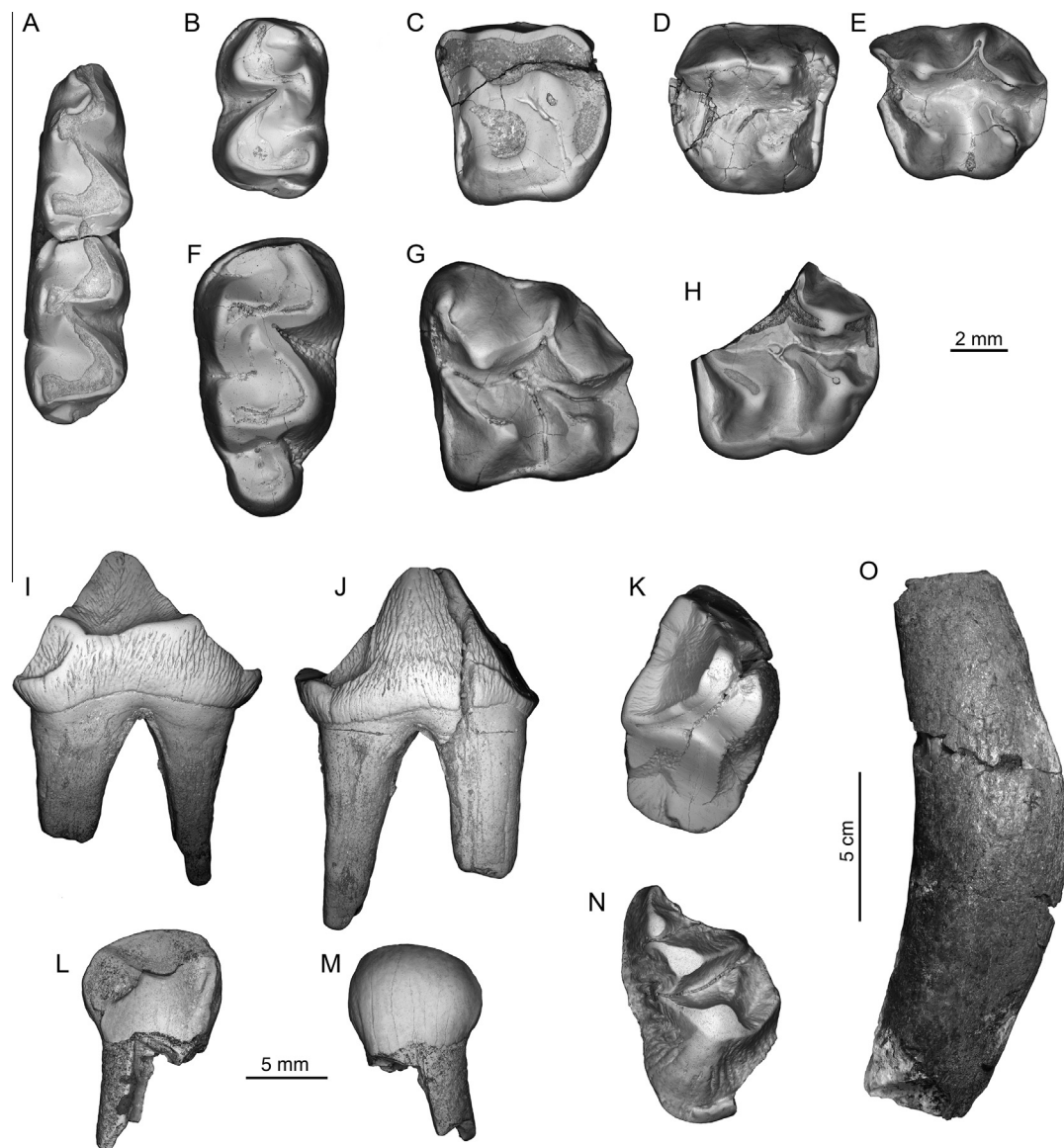
Our description of upper molar morphology is mainly based on the holotype M3 (Fig. 6G). This tooth is trapezoidal in occlusal outline. The buccal cusps are connected by a W-shaped ectoloph and are marginally higher than their lingual counterparts. The apices of the buccal and lingual pair of upper molar cusps closely



**Table 4**  
Measurements (in mm) for upper and lower teeth of *Neophiomys dawsonae*.

Tooth locus	n (number of specimens)	OR (observed range)	x (mean)
DP4			
L	2	1.3–1.34	1.32
W		1.19–1.34	1.26
M1/2			
L	6	1.71–1.44	1.59
W		1.89–1.46	1.72
m1/2			
L	3	1.51–1.68	1.57
W		1.42–1.61	1.49
m3			
L	1	1.51	
W		1.61	

approximate each other, the hypocone and metacone being especially close. This condition differs from that observed in Fayum species of *Thyrohyrax*, and the Zallah taxon resembles *T. kenyaensis* in this respect. The paracone is larger than the metacone. The preparacrista extends mesiobuccally from the paracone to join the parastyle. The postparacrista and the premetacrista meet at the apex of the mesostyle. The parastyle and mesostyle are prominent, apically trenchant and basally rounded. The parastyle is positioned mesiobuccal to the paracone and it is smaller than that of other *Thyrohyrax* species. The mesostyle, located midway between the paracone and metacone, is slightly smaller than the parastyle. Parastyle and mesostyle are lower than the paracone and metacone. A short postmetacrista descends in a distal and slightly buccal direction from the summit of the metacone. Neither a metastyle nor a buccal cingulum is evident. Lingually, the surfaces of the buccal cusps are almost vertical. There is no prominent



**Fig. 6.** Selected fossil mammals from Z71 locality. (A–H) *Thyrohyrax libycus*: (A) right lower jaw fragment with dp2-dp3 (Z71-8); (B) left m1 (Z71-161); (C) left P4 (Z71-163); (D) right P2 (Z71-162); (E) left DP4 (Z71-164); (F) right m3 (Z71-160); (G) left M3 (Z71-9); (H) fragmentary left M1 (Z71-165); (I–K) Right p4 in lingual (I), buccal (J), and occlusal (K) views (Z71-10); (L–M) left i1/2 in lingual (L) and labial (M) views (Z71-168); (N) fragmentary left M1/2 in occlusal view (Z71-169); (O) Sirenia indet., fragment of an anterior rib (Z71-170).



rib or fold on the buccal faces of the paracone and metacone. The buccal and lingual cusps are separated by a longitudinal furrow. The protocone is the dominant lingual cusp. It is situated slightly farther distally than the paracone. A faint lingual cingulum occupies the notch between protocone and hypocone, but this structure is absent around the bases of the protocone and hypocone. In *T. kenyaensis*, the cingulum is much stronger around the protocone. The mesial cingulum is restricted to a faint shelf at the mesial bases of the protocone and paracone. The preprotocrista extends mesiobuccally from the apex of the protocone to the mesiolingual base of the paracone. It is better developed than the postprotocrista, which is extremely short and oriented distolingually. The hypocone is smaller but the same height as the protocone. It is situated directly opposite the metacone. The prehypocrista runs parallel to the preprotocrista and extends to the mesiolingual base of the metacone. The prehypocrista is not as trenchant as the preprotocrista. The posthypocrista is weak. The distocrista forms a convex distal border of the tooth. The upper premolars are simpler than the upper molars (Fig. 6C and D). The paracone and metacone are close together. The parastyle is small and there is no mesostyle. Parastyle, paracone and metacone are positioned in a straight line along the buccal side of the tooth and connected by short crests. The protocone is lingual to the paracone, and it is large. The hypocone is small. The preprotocrista extends to the base of the paracone. A mesial cingulum extends from the base of the protocone to the parastyle. One upper deciduous premolar has been identified as a DP4 (Fig. 6E). Its morphology is similar to the molars, but it differs in being notably smaller and relatively longer. The mesostyle on DP4 is stronger than its counterpart on the upper molars. Likewise, the mesial cingulum on DP4 is better developed and its preparacrista is more mesially oriented than is the case on the upper molars.

The lower dentition is known from a fragmentary mandible with dp2–3 and isolated teeth. *Thyrohyrax* has selenolophodont molars and relatively molariform deciduous premolars. A left molariform lower tooth is interpreted here as m1. The paracristid extends mesially from the protoconid before turning lingually. All cingulids are absent or very weak except for the precingulid, which is present both buccally and lingually, although its mesial part is truncated by the paracristid and an interproximal wear facet. The metaconid is well developed and situated slightly distal to the protoconid. The postmetacristid extends distally from the apex of the metaconid, but there is no development of a metastylid. The cristid obliqua runs mesiolingually from the hypoconid and reaches the distal wall of the trigonid near its midline. There is no mesoconid. The hypoflexid is relatively deep and narrow. The entoconid is positioned lingual to the hypoconid. The hypocristid connects the hypoconid to the entoconid, while the preentocristid is poorly developed, leaving the talonid basin open lingually. There is no posthypocristid and the distal cingulid is salient on the distolingual edge of the tooth. The m3 is essentially similar to m1 but considerably larger. There is no trace of a paraconid. The posthypocristid descends distally from the midpoint of the hypocristid to join a large, lobate hypoconulid.

The lower deciduous premolars are smaller and relatively narrow when compared with the molars. On dp2 (and dp3 to a lesser extent) the metaconid and protoconid are positioned closer together than the hypoconid and entoconid. The paraconid on dp2 is centrally positioned on the mesial edge of the tooth and larger than that observed on dp3.

ARTIODACTYLA Owen, 1848

ANTHRACOTHERIIDAE Leidy, 1868

BOTHRIODONTINAE Scott, 1940

*BOTHRIOGENYS* Schmidt, 1913

*BOTHRIOGENYS* sp.

(Fig. 6I–N)

**Referred material**—Z71-10, right p4 (L, 17.71; W, 10.56) (Fig. 6I–K); Z71-168, left i1/2 (Fig. 6L–M); Z71-169, mesiolingual fragment of left M1/2 (Fig. 6N).

**Known distribution**—Jebel Qatrani Formation, Fayum Depression, Egypt; Krabi Basin, Thailand; CTMD (Arambourg locality, Z71 locality), Sirt Basin, Libya.

#### Description

Anthracothers in the Zallah Incision local fauna are represented by a few fragmentary upper and lower teeth. Z71-10, a right p4, is the only well-preserved tooth pertaining to this group currently known from the Zallah Incision local fauna. It is elongated mesiodistally and triangular in buccal view. The Zallah specimen is about the size of p4 in *Bothriogenys gorringei* from the Fayum. Its overall morphology resembles that of Fayum species of *Bothriogenys*, but the mesial part of the tooth is less elongated. As a result, the Zallah anthracothere has a shorter p4 trigonid because its mesiobuccal margin is more convex than that of other species of the genus. Compared to Fayum species of *Bothriogenys*, the Zallah p4 can be distinguished by its less elongated and transversely compressed crown, a steeper preprotocristid and a higher and more prominent lingual cingulid. The protoconid is the largest and tallest cusp. There are well-developed wear facets on the mesiobuccal and distal faces of the protoconid (or trigonid). Small but distinct paraconid and metaconid cusps are present. The paraconid is somewhat taller than the metaconid. The paraconid is located at the lingual extremity of the preprotocristid. Two crests emanate from the protoconid distally. The more lingual of these joins the metaconid, which lies distolingual to the protoconid. The postprotocristid, which bears a strong wear facet, extends to the abbreviated talonid, where it connects to the small hypoconid. Cingulids occur on the mesiobuccal, lingual, and distobuccal margins of the crown. The buccal cingulid is weak and discontinuous, being absent near the midpoint of the tooth at the level of the protoconid. Mesially, the buccal cingulid is scored by the prominent wear facet on the preprotocristid. The lingual cingulid forms a high shelf midway up the lingual side of the crown. This ledge-like structure connects the metaconid and paraconid. In this respect, *Bothriogenys* sp. from Z71 resembles *Bothriogenys orientalis* from the late Eocene of Krabi, Thailand (Ducrocq, 1999). The Thai species is larger than its congener from Zallah, but these species are morphologically close in displaying a broad p4 crown with a well-developed lingual cingulid bearing a small paraconid at its mesial terminus.

The incisor is spatulate in shape. The lingual and labial surfaces of the incisor are convex. The crown is moderately worn, with some dentine exposure along the apical margin of the tooth. A distinct mesial cingulid reaches the apical margin of the crown.

A fragment of upper molar has been identified. Only the mesiolingual part of the tooth is preserved, which bears two main cusps (protocone and paraconule) and a third smaller cusplule on the preparaconule crista. The conical protocone is the largest cusp preserved on the tooth fragment. The preprotocrista is mesiobuccally directed and stops at the mesial base of the paraconule while a stronger postprotocrista extends distobuccally from the apex of the protocone. The paraconule is mesiobuccal to the protocone. A short preparaconule crista runs mesially from the apex of the paraconule, while a longer and more trenchant postparaconule crista runs distobuccally. The tooth exhibits a small but distinct cusplule located mesiobuccal to the paraconule on the mesial margin of the tooth. A distinct cingulum occurs on the lingual margin of the tooth near the base of the protocone.

SIRENIA Illiger, 1811

SIRENIA indet.

(Fig. 6O)

**Referred material**—Z71-170, fragment of an anterior rib (Fig. 6O).

### Description

A single partial rib of a sirenian has been recovered from the Zallah Incision local fauna. It is broken on both sides; the neck and the head are missing. There is variation in thickness and cross-sectional area along the shaft. The proximal and distal ends are virtually oval in cross-section while the midshaft is more or less triangular and swollen laterally.

### 4. Biostratigraphic correlation

The fossiliferous horizon yielding the Zallah Incision local fauna occurs in the CTMD, a unit that is sandwiched between the marine late middle-late Eocene Wadi Thamat Formation and either the marine early Miocene Maraddah Formation or Neogene basalts pertaining to the Jabal Al Haruj volcanic complex (Vesely, 1985). The CTMD is bounded above and below by unconformities, and composite sections of the CTMD have yet to be constructed because of the wide areal extent of CTMD outcrops, which are frequently separated by cover. Local sections of the CTMD are variable in thickness, ranging from ~11 m at the Arambourg locality south-east of Zallah (Fejfar, 1987) to >50 m at the Z5R locality to the north of Zallah (Coster et al., 2012). Accordingly, there is no reason to believe that all of the mammalian faunas currently known from the CTMD are strictly coeval. Based on its mammalian fauna and its foraminiferal assemblage, which includes *Bolivina melettica* and *Nummulites fichteli*, the CTMD is widely regarded as early Oligocene in age, making it roughly contemporaneous with the Jebel Qatrani Formation in the Fayum Depression of Egypt (Arambourg, 1963; Savage, 1969, 1971; Wight, 1980; Vesely, 1985; Fejfar, 1987; Rasmussen et al., 1992; Seiffert, 2010; Coster et al., 2010, 2012). Here, we review biostratigraphic evidence from fossil mammals bearing on the age of the CTMD in general as well as its major sites.

Proboscidean remains from the Arambourg locality were originally assigned to *Palaeomastodon intermedius* and *Phiomia wintoni* (Arambourg and Magnier, 1961; Arnould-Saget and Magnier, 1961; Arambourg, 1963; Savage, 1971). Sanders et al. (2010) synonymized *P. wintoni* under *P. serridens* and recognized Zallah specimens of *Palaeomastodon* as being indeterminate at the species level. *Phiomia serridens* and *Palaeomastodon* are best known from the early Oligocene Jebel Qatrani Formation in the Fayum Depression of Egypt (e.g., Sanders et al., 2010), while proboscidean assemblages from late Oligocene sites in Afro-Arabia include primitive deinotheres and gomphotheres alongside larger species of *Phiomia* and *Palaeomastodon* (Kappelman et al., 2003; Sanders et al., 2004; Shoshani et al., 2006; Rasmussen and Gutierrez, 2009; Ducrocq et al., 2010; Zalmout et al., 2010). In addition to paleomastodontids, the mammalian fauna from the Arambourg locality includes *Titanohyrax angustidens* and *Bothriogenys* sp., cf. *B. gorringei*. The hyracoid *Titanohyrax angustidens* also occurs in the Upper Sequence of the Jebel Qatrani Formation in the Fayum, where it first appears at Quarry V (Rasmussen and Simons, 1988). Species of *Bothriogenys* apparently occur throughout the Jebel Qatrani Formation, but there is no published information regarding their local stratigraphic ranges there (Ducrocq, 1997).

The first Zallah microvertebrate fossils were described from a small outcrop of cross-bedded sandstone reportedly located ~35 km west of Zallah Oasis (Fejfar, 1987). The exact position of this locality has been difficult to relocate, and several attempts to revisit the site have been unsuccessful. Nevertheless, the site originally yielded an assemblage of three early hystricognathous rodents (*Metaphiomys schaubi*, *Phiomys andrewsi* and *Neophiomys paraphiomyoides*). Most of the recovered specimens were referred to *M. schaubi*. Fejfar's (1987) study of the Zallah rodents and the previously described large mammals led him to correlate the CTMD in Libya with Quarry G in the Upper Sequence of the Jebel Qatrani Formation in Egypt.

A second microvertebrate site, the Z5R locality, was recently discovered approximately 15 km north of Zallah (Coster et al., 2010, 2012). This locality has yielded a substantial quantity of microvertebrate fossils, but the only mammal remains found there to date are five species of early hystricognathous rodents. These include *Metaphiomys* aff. *schaubi*, *Neophiomys paraphiomyoides*, *Talahphiomys lavocati*, *Phiocricetomys atavus*, and *Gaudeamus lavocati*, the latter of which is by far the most abundant taxon in the fauna (Coster et al., 2010, 2012). The Z5R locality occurs in strata showing reversed magnetic polarity (Coster et al., 2012: fig. 8). Based on the assemblage of early hystricognathous rodents known from the Z5R locality and its occurrence in rocks of reversed magnetic polarity, Coster et al. (2012) advocated a correlation with either Chron C13r or Chron C12r. With respect to the well-documented sequence of faunas from the Fayum in Egypt, Z5R correlates best with sites in the Lower Sequence of the Jebel Qatrani Formation. The co-occurrence of *Gaudeamus* and *Talahphiomys lavocati* at Z5R suggests that this fauna is close in age to that known from Quarry E in the Jebel Qatrani Formation. However, the presence of *Neophiomys paraphiomyoides* in the fauna from Z5R could indicate a slightly younger age, given that the latter taxon remains unknown below the level of Quarry G in the Upper Sequence of the Jebel Qatrani Formation (Fig. 7).

The early hystricognathous rodents known from the Zallah Incision local fauna include three taxa, two of which are new at the species level. *Metaphiomys schaubi* from Z71 has also been reported from the locality west of Zallah by Fejfar (1987). The species of *Metaphiomys* from Z5R, which has been described as *Metaphiomys* aff. *schaubi*, is smaller than *M. schaubi* and about the same size as *M. zallahensis* from Z71. *Metaphiomys* aff. *schaubi* from Z5R appears to be more primitive than either *M. schaubi* or *M. zallahensis* from Z71 in having less crested cheek teeth, and upper cheek teeth that retain a connection between the metaloph and the mesolophule that has been lost in *M. schaubi* and *M. zallahensis*. *Neophiomys dawsonae* from Z71 is larger and displays more inflated cusps than *N. paraphiomyoides*, which is recorded from Quarry G in the Jebel Qatrani Formation in Egypt and from Fejfar's microvertebrate site and Z5R in the CTMD near Zallah. The absence of *Gaudeamus* and *Talahphiomys lavocati* and the seemingly derived morphology of *Metaphiomys schaubi* and *M. zallahensis* compared to *Metaphiomys* aff. *schaubi* from Z5R indicate that Z71 is slightly younger than Z5R. Unfortunately, these two sites cannot be physically tied to the same stratigraphic section, because they lie on opposite sides of a large area covered by the Neogene Jabal Al Haruj volcanics. The presence of *Metaphiomys schaubi* and the absence of *Paraphiomys simonsi* and *Phiocricetomys minutus* at Z71 suggest that the Zallah Incision local fauna is close in age to Fayum quarry G, which is a productive site in the Upper Sequence of the Jebel Qatrani Formation in Egypt (Fig. 7). In contrast, the highest fossiliferous Upper Sequence quarries (I and M) in the Jebel Qatrani Formation in Egypt lack *Metaphiomys schaubi* but yield *Paraphiomys simonsi* and *Phiocricetomys minutus* (Wood, 1968; Sallam et al., 2011).

A striking array of members of the endemic afrotherian mammal order Hyracoidea has been described from Paleogene strata across northern Afro-Arabia. The new species of *Thyrohyrax* known from Z71 is close in size to *T. domorictus*, which is the most common hyracoid found in the Jebel Qatrani Upper Sequence quarries I and M (Rasmussen and Gutierrez, 2010). However, in terms of its morphology and likely relationships, *T. libycus* from the Zallah Incision local fauna more closely resembles *T. kenyaensis* from the late Oligocene Kenyan Losodok locality (~24–27 Ma, Rasmussen and Gutierrez, 2009). Other Oligocene hyracoidea have been described from Thaytiniti and Taqah, Oman (Pickford et al., 1994), Chilga, Ethiopia (Kappelman et al., 2003), Losodok, Nakwai and Lokone, Kenya (Rasmussen and Gutierrez, 2009; Ducrocq et al., 2010),

Rock unit		Hystricognathous rodents from the Fayum Depression	Rock unit		
Quarries			Hystricognathous rodents from Zallah localities		
Jebel Qatrani Formation	Upper Sequence	<p>M I G V</p> <p><i>Gaudeamus hylaeus</i> <i>Gaudeamus asilus</i> <i>Gaudeamus aff. asilus</i> <i>Gaudeamus aegyptius</i> <i>Phiomys andrewsi</i> <i>Talaphiomys lavocati</i> <i>Metaphiomys schaubi</i> <i>Metaphiomys beadnelli</i> <i>Neophiomys paraphiomysoides</i> <i>Phiocricetomys minutus</i> <i>Neophiomys aff. paraphiomysoides</i> <i>Paraphiomys simonsi</i></p>	Continental and Transitional Marine Deposits		
	Lower Sequence		<p>A &amp; B E L-41</p>	Z5R	Z71
			<p><i>Gaudeamus lavocati</i> <i>Talaphiomys lavocati</i> <i>Neophiomys paraphiomysoides</i> <i>Phiocricetomys atavus</i> <i>Metaphiomys aff. schaubi</i></p>	<p><i>Metaphiomys schaubi</i> <i>Metaphiomys zallahensis</i> <i>Neophiomys dawsonae</i></p>	<p><i>Metaphiomys schaubi</i> <i>Phiomys andrewsi</i> <i>Neophiomys paraphiomysoides</i></p>

Fig. 7. Distribution of hystricognathous rodents in the Jebel Qatrani Formation (after Wood, 1968 and Sallam et al., 2011) and in the Zallah area (after Coster et al., 2010, 2012, this paper). Proposed correlation of the Zallah localities with the Jebel Qatrani quarries based on hystricognathous rodent assemblages.

Mbeya, Tanzania (Stevens et al., 2009) and Harrat Al Ujayfa, Saudi Arabia (Zalmout et al., 2010).

Anthracotheriid artiodactyls identified as *Bothriogenys* are known from the Jebel Qatrani Formation in the Fayum, Egypt (Black, 1978; Ducrocq, 1997) and the Krabi Basin in southern Thailand (Ducrocq, 1999). The lower premolar assigned to *Bothriogenys* sp. from Z71 does not perfectly match its counterpart in any of the described Fayum species. Elsewhere, a *Bothriogenys*-like form has been described from the late Oligocene of Lokone in Kenya (Ducrocq et al., 2010) and a species of *Bothriogenys* also occurs in the late Oligocene fauna known from Chilga in Ethiopia (Sanders et al., 2004), but the genus is replaced at Losodok, Kenya by the more advanced anthracotheriid *Brachyodus* (Rasmussen and Gutierrez, 2009).

Other biostratigraphically important data regarding the Zallah Incision local fauna are provided by its fossil primates. Beard et al. (in press) mentioned a new species of the parapithecoid *Apidium* from the Zallah Incision local fauna. In the Jebel Qatrani Formation in Egypt, species of *Apidium* range throughout the Upper Sequence, from Quarries G and V to Quarries I and M. The new species of *Apidium* from the Zallah Incision local fauna in Libya is closely related to *A. phiomense* from the highest fossiliferous strata in the Jebel Qatrani Formation, but it resembles the slightly older species *A. bowni* and *A. moustafai* in terms of size and certain aspects of dental morphology. Elsewhere, fossils cited as cf. *Apidium* sp. have been reported from the early Oligocene Taqah locality in Oman (Thomas et al., 1999). To date, oligopithecids and proteopithecids, which are the most common anthropoids encountered in the Lower Sequence of the Jebel Qatrani Formation (e.g., Seiffert et al., 2010) have not been recorded from the Zallah Incision local fauna. Late Oligocene sites in Afro-Arabia lack *Apidium* and are generally characterized by the presence of stem catarrhines (*Kamoyapithecus*, *Saadanius*) and/or crown catarrhines (*Rukwapithecus*, *Nsungwepithecus*) (Madden, 1980; Leakey et al., 1995; Rasmussen and Gutierrez, 2009; Zalmout et al., 2010; Stevens et al., 2013).

### 5. Summary

The newly discovered Zallah Incision local fauna includes a variety of small- and medium-sized mammals that show clear affinities with other early Oligocene Afro-Arabian faunas, particularly those from the Jebel Qatrani Formation in the Fayum region of Egypt and the Ashawq Formation in Oman. The closest relatives of most taxa known from the Zallah Incision local fauna occur in quarries V and G in the Upper Sequence of the Jebel Qatrani Formation in Fayum, Egypt and the Taqah locality in the Ashawq Formation of Oman. If we follow the correlation of the Jebel Qatrani Formation to the GPTS proposed by Seiffert (2006) and assume a tight correlation between the Zallah Incision local fauna and quarries V and G in the Fayum, then the Zallah Incision local fauna would date to ~31 Ma (upper part of Chron C12r), or approximately the middle part of the early Oligocene. Following the correlation to the GPTS proposed by Underwood et al. (2013), the Zallah Incision local fauna would be slightly younger, or ~30 Ma (upper part of Chron C11r). Biostratigraphic evidence from early hystricognathous rodents indicates that the fossiliferous part of the CTMD near Zallah in the Sirt Basin of Libya spans at least a short interval of early Oligocene time. The Z5R locality appears to be the oldest fossiliferous site currently known from the CTMD, because it yields taxa including *Gaudeamus* and *Talaphiomys lavocati* that suggest correlation with the Lower Sequence of the Jebel Qatrani Formation in Egypt. The Z5R locality is known to occur in strata of reversed magnetic polarity. Assuming a close correlation between the Z5R locality and Quarry E in the Lower Sequence of the Jebel Qatrani Formation, the age of the Z5R locality would either be ~32.5 Ma (lower part of Chron C12r; Seiffert, 2006) or ~30.5 Ma (lower part of Chron C11r; Underwood et al., 2013).

The Zallah Incision local fauna includes sharks, rays, bony fishes, crocodylians, a sirenian, a hyracoid, an anthracothere, anthropoid primates, and hystricognathous rodents as well as other taxa that remain poorly documented at present. The mammalian taxa known from the Zallah Incision local fauna



include groups that were previously documented from the early Oligocene of the Fayum Depression in Egypt and Dhofar Province, Oman. This includes endemic African groups (Hyracoidea and Sirenia) along with clades that are not members of Afrotheria (Hystricognathi, Anthropoidea and Anthracotheriidae). Paleontological evidence indicates that these non-afrotherian mammal groups dispersed from Asia to Africa sometime during the middle-late Eocene, after which they experienced broad evolutionary radiations (e.g., [Werdelin and Sanders, 2010](#)). By the early Oligocene, four anthropoid clades (afrotarsiids, oligopithecids, parapithecids, and propliopithecids) were present in Afro-Arabia (e.g., [Jaeger et al., 2010a](#); [Seiffert et al., 2010](#)). The distribution of parapithecids during the early Oligocene, ranging from Oman into northern Egypt and central Libya, indicates that parapithecids were flourishing across at least the northern part of Afro-Arabia at this time. Hystricognathous rodents colonized Africa during the latter part of the Eocene ([Wood, 1968](#); [Jaeger et al., 1985, 2010b](#); [Sallam et al., 2009](#); [Marivaux et al., 2002, 2014](#)), and their subsequent adaptive radiation on that continent gave rise to the Hystricidae, the South African Petromuridae, the sub-Saharan Bathyergidae and the West African Thryonomyidae. The early Oligocene Libyan hystricognathous rodents record the initial stages of an evolutionary explosion by the descendants of these Eocene immigrants. The hystricognathous taxa known from the Zallah Incision local fauna are considered to be early members of a clade that embraces the extant Thryonomyidae and their fossil relatives (e.g., [Sallam et al., 2009](#); [Coster et al., 2012](#)).

Regardless of precisely how the Zallah Incision local fauna is correlated to similar faunas from Egypt and Oman, the Libyan site supports at least a modest degree of faunal provincialism across the northern margin of Afro-Arabia during the early Oligocene. Among the mammalian taxa discussed here, the Zallah Incision local fauna includes two new species of hystricognathous rodents, a new species of hyracoid, and a new species of parapithecoid anthropoid. We anticipate that additional data will reinforce this pattern as the early Oligocene faunas of Libya and Oman become better documented. As recently reviewed by [Beard et al. \(in press\)](#), the apparent provincialism shown by the early Oligocene faunas of northern Afro-Arabia probably reflects the development of geographic barriers to dispersal in this region during this interval. Habitat fragmentation promoting higher rates of allopatric speciation than occurred during the more equable Eocene may be a consequence of the increasing seasonality and the cooler, drier climatic conditions of the Oligocene. However, given the coarse state of our current knowledge of Afro-Arabian Paleogene faunas, this hypothesis remains conjectural and requires further paleontological data to enable a better understanding of this open question.

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