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PEABODY MUSEUM

YALE UNIVERSITY

NUMBER 163 31 DECEMBER 1973

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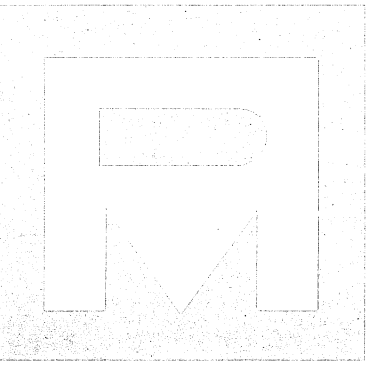
GRANT E. MEYER



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A NEW OLIGOCENE HYRAX FROM THE JEBEL EL QATRANI FORMATION, FAYUM, EGYPT

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(Received 5 June 1973)

ABSTRACT

A fossil hyrax from the Upper Fossil Wood Zone, Jebel el Qatrani formation is described. It represents a new genus and species *Thyrohyrax domorictus*. The type specimen as well as two referred specimens exhibit an internal mandibular fenestra whereas four referred mandibular fragments do not. One nearly complete mandible with an internal mandibular fenestra has extremely inflated horizontal rami which enclose swollen ovoid chambers opening at the fenestra. This inflated ramus, which is believed to be unique among all mammals, and the internal mandibular fenestra are thought to be sexual characters. Evidence from other genera of the Saghatheriinae suggests these characters are found in females; not in males.

INTRODUCTION

Yale University expeditions to the Fayum Province, Egypt, during 1961 to 1967 located fossil vertebrates in the Upper Fossil Wood Zone of the Jebel el Qatrani formation. Rich faunas were found at several localities in the strata of the upper part of the formation and seven Yale quarries were opened. The small hyracoid reported in this paper was found at Yale Quarry G near the base of the upper member of the Jebel el Qatrani formation and at Quarries M and I, near the middle of the upper member. The fauna found at Quarry G consists entirely of small-sized mammals or of small fragments of larger species and included *Apidium moustafai, Propliopithecus* cf. *haeckeli, Phiomys andrewsi, Phiomys paraphiomyoides, Metaphiomys schaubi, Apterodon cf. altidens,* proviverrid (new gen. and sp.). In Quarry I the hyracoid was found with *Parapithecus* sp., *Apidium phiomense, Propliopithecus* sp., *Aegyptopithecus zeuxis, Aeolopithecus chirobates, Paraphiomys simonsi, Metaphiomys beadnelli, Apterodon* cf. *altidens, Apterodon macrognathus, Pachyhyrax crassidentatus, Bunohyrax fajumensis, Megalohyrax eocaenus, Titanohyrax ultimus* and *Bothriogenys gorringei.*

ABBREVIATIONS

Abbreviations used in this paper are as follows:

I	incisor (I^1 = first upper incisor, I_2 = second lower incisor)
C	canine (C^1 = upper canine, C_1 = lower canine)
M	molar (M^1 = first upper molar, M_2 = second lower molar)
P	premolar (P^3 = third upper premolar, P_4 = fourth lower premolar)

CGM	Cairo Geological Museum, Cairo, Egypt
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut

SYSTEMATICS

ORDER HYRACOIDEA Huxley, 1869

FAMILY PLIOHYRACIDAE Osborn, 1899

SUBFAMILY SAGHATHERIINAE Andrews, 1906

Thyrohyrax, new genus

TYPE. *Thyrohyrax domorictus,* new species.

KNOWN DISTRIBUTION. Upper Fossil Wood Zone, Jebel el Qatrani formation, Fayum, Egypt.

DIAGNOSIS. Small Saghatheriinae with a long narrow symphysis and brachyodont, selenolophodont dentition. The dental formula is $\frac{?.?.4.3.}{3.1.4.3.}$. I_2 is slightly larger than I_1 and its root is more rounded. Diastemata are between I_2 and I_3 and the lower canine. The lower canine is two-rooted. P_2-P_4 molariform. M_3 with a small, low hypoconulid. All cingula absent or very weak on lower teeth. P^2-P^4 molariform, lophodont with well-developed preprotocristae and prehypocristae which often come in contact with the ectoloph. Internal mandibular fenestra present on some specimens, absent on others. Those specimens with fenestra have greatly expanded ramus with large inflated chamber within walls of ramus.

ETYMOLOGY: from *Thyra,* Greek, a door, a window; *hyrax,* a term referring to the internal mandibular fenestra in the ramus.

Thyrohyrax domorictus, new species

TYPE. CGM 40001. Collected by G. E. Meyer in February, 1967 from Quarry M, Jebel el Qatrani formation, Egypt. Fragment of right horizontal ramus with P_1-P_4, roots of M_1 and $\frac{1}{2}M_2$-M_3. On the lingual side of the ramus approximately 5.5 mm below M_3, the top half of an internal mandibular fenestra is present. The roof of the internal chamber can be seen below, separate from the dentition.

HYPODIGM.

Quarry M:

1967 CGM 40001 (Type specimen).

Quarry G:

1962 YPM 23886, left ramus with P_2-M_3 and part of the symphysis.
YPM 18086, left M^1.
YPM 18037, left M^2.
YPM 23827, left P^4.
CGM 40004, right P_2, I^1 and M^2.
YPM 23904, ?DP_3 ?DP_4
CGM 40005, right I^3, C and ?P^1 in three associated fragments of maxillae.
YPM 33153, ?DP^3.

1963 YPM 23815, right M_3.
YPM 23817, right M_2.

1964 YPM 33149, right ?P^4, M^1 and P_4.
YPM 33150, left M^3.

1965 YPM 23823, left P^2 and ¼ P^3 in maxillary fragment.

Quarry I:

1963 YPM 23825, fragment of left ramus with P_2-½ P_3.
YPM 23824, fragment of right ramus with M_3.
YPM 33149, left ramus with P_2-M_3.
YPM 33152, 13 tooth fragments.

1964 YPM 23832, fragment of right ramus with M_1-M_2.
YPM 21488, fragment of left maxilla with P^4-M^3.
YPM 33151, right M^2 and P_4.
YPM 33148, mandible with left I_1-I_2, P_2-M_1 and right P_2-M_3, ascending ramus missing.
YPM 23828, fragment of left ramus with M_2-M_3.

1965 YPM 23829, right M_3.
CGM 40002, left M_1 and M_2.
YPM 23858, fragment of right ramus with M_1-M_2, right tibia, five metatarsals, five phalanges and one distal phalanx of right pes, proximal end of one metacarpal and five phalanges of right manus, one lumbar vertebra and several indeterminate fragments.
YPM 23833, symphysis with left I_1-I_2 and right I_2 and C.

1966 YPM 23939, nearly complete mandible, edentulous except for left ½ M_2 and M_3, jaw greatly expanded.

LOCALITY AND HORIZON. YPM Quarries G, M and I, Upper Fossil Wood Zone, Jebel el Qatrani formation, Fayum, Egypt. Late Oligocene.

DIAGNOSIS. Only known species of the genus.

ETYMOLOGY: from *domos,* Greek, a house, a structure; *rictus,* Latin, jaws, a term referring to the chamber within the jaws.

DESCRIPTION. Small Saghatheriinae with brachyodont, selenolophodont dentition. The symphysis is long and fairly narrow with a narrow shelf or ridge at its ventral border. I_1 and I_2 are procumbent, tricuspid when unworn; I_2 is slightly larger than I_1. I_3 is separated from I_2 by a diastema and must be a small tooth, as determined by the alveolus. The lower canine is two-rooted, a feature that is unique to this species among the Saghatheriinae, but typical of the Pliohyracinae. The tooth is small, with a rudimentary paraconid and a large protoconid. The lower canine is in contact with P_1. P_1 is submolariform, with a centrally-positioned paraconid, separated from the protoconid by a short paracristid. The hypoconid is not V-shaped and there is an unusually deep, narrow hypoflexid. P_2-P_4 are molariform with differentiated metaconids and entoconids. The metaconid exhibits a slight metastylid on its distal edge. There is a preparacristid on P_2. The protocristids and hypocristids form complete lophs. The lower molars have a small paraconid, slightly buccal to the centerline, near the protoconid. The metastylid is better

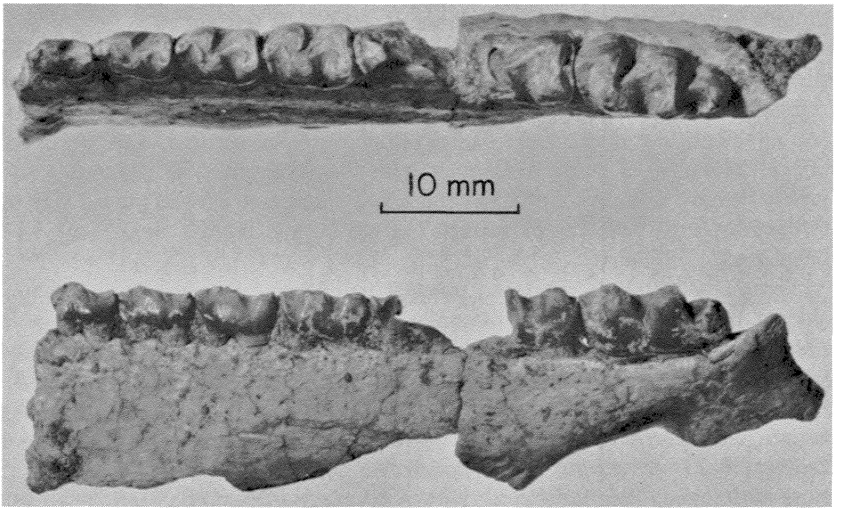

FIG. 1. Occlusial and medial views of the type specimen of *Thyrohyrax domorictus,* CGM-40001. The internal mandibular fenestra can be seen beneath M_3 in the medial view.

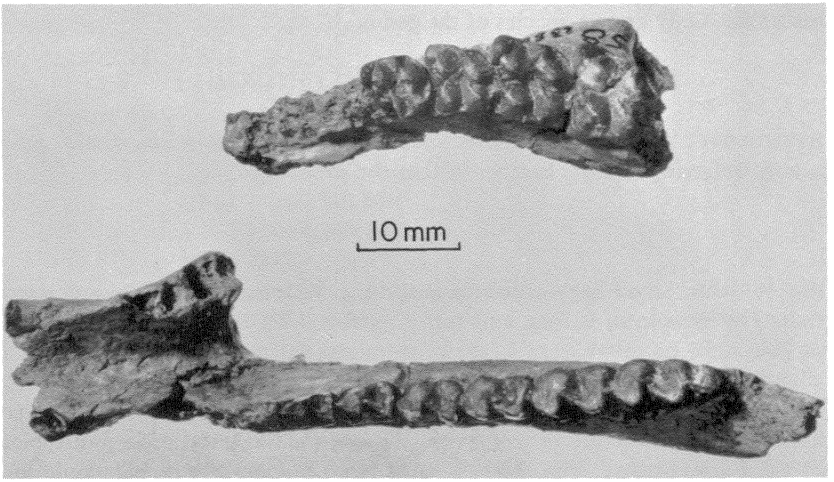

FIG. 2. Occlusial views of *Thyrohyrax domorictus*, above, YPM-23886, a maxilla with P^4-M^3 and below, YPM-21488, a ramus with the symphysis, roots of both I_2 and P_1, and P_2 to M_3. This ramus does not have an internal mandibular fenestra nor is it inflated.

developed than in the premolars and the entoconid projects mesially, partly closing the valley between it and the metastylid. The protocristids and hypocristids are complete, forming lophs. M_3 has a small, low hypoconulid. All cingula are absent or very weak in the lower cheek teeth.

P^2 has a very small mesostyle and is much longer than broad, whereas P^3 possesses a well-developed mesostyle and is slightly longer than broad. The remainder of the upper cheek teeth are broader than long. P^2-M^3 are molariform, selenolophodont with well-developed preprotocristae and prehypocristae which often come in contact with the ectoloph. The parastyles and metastyles are well developed and there is a slight fold on the buccal side of the ectoloph opposite the paracone. The mesial and lingual cingula are well developed.

There is a round to subround internal mandibular fenestra on the lingual side of the ramus below M_3 in some of the specimens; this occurs also in *Megalohyrax* and *Pachyhyrax*. Each of these specimens has a greatly inflated ramus with a large swollen chamber in the horizontal ramus, beneath the dental series, which continues at least into the base of the inflated ascending ramus. There are three specimens known that possess the internal mandibular fenestra and four specimens that possess no fenestra and do not have inflated rami. Other than this difference, there is no morphological difference that can be used to separate the fenestrated and nonfenestrated specimens into different species. New collections made by Yale University in the Upper Fossil Wood Zone have confirmed that there are also specimens of two species of

TABLE 1. Statistical data on teeth of *Thyrohyrax domorictus*. Abbreviations: L = length, M = molar (M^1 = first upper molar, M_2 = second lower molar), n = sample size, OR = observed range, P = premolar (P_3 = third lower premolar, P^4 = fourth upper premolar), s = standard deviation, V = coefficient of variation, W = width, $\bar{x}$ = mean. Measurements for length and width are in mm.

	n	OR	$\bar{x}$	s	V
P_1L	1	4.7	4.7	—	—
W	1	3.1	3.1	—	—
P_2L	5	5.6-6.0	5.82	.1658	2.85
W	6	3.5-4.2	3.82	.2720	7.12
P_3L	5	6.1-7.1	6.58	.4153	6.31
W	5	4.2-4.8	4.46	.2179	4.89
P_4L	5	6.5-7.3	6.82	.3428	5.02
W	5	4.8-5.5	5.20	.3240	6.23
M_1L	7	7.4-8.4	7.73	.3536	4.57
W	7	4.6-5.8	5.14	.5099	9.92
M_2L	12	7.9-9.3	8.65	.4253	4.92
W	12	5.0-6.5	5.66	.5018	8.87
M_3L	9	10.7-12.8	11.85	.8515	7.19
W	9	5.3-6.7	6.15	.4637	7.54
P^2L	1	5.8	5.8	—	—
W	1	5.3	5.3	—	—
P^3L	1	6.4	6.4	—	—
W	1	6.1	6.1	—	—
P^4L	2	6.4-7.0	6.70	.4243	6.33
W	2	7.0	7.0	—	—
M^1L	3	7.1-7.6	7.33	.2550	3.48
W	3	7.7-8.2	7.93	.4183	5.27
M^2L	3	7.9-8.8	8.46	.4950	5.85
W	3	8.6-9.2	8.93	.3082	3.45
M^3L	2	9.9-10.0	9.95	—	—
W	2	9.8-10.0	9.90	.1414	1.42

Bunohyrax and one species of *Megalohyrax* that possess an internal mandibular fenestra and specimens that do not. It therefore seems more logical to consider the possession of an internal mandibular fenestra as a sexual character than to construct a phylogeny of twinned species, with and without fenestrae.

From the known specimens of *Thyrohyrax domorictus* it cannot be determined which sex possesses the fenestra since none of those specimens with the fenestra also possesses the sexually diagnostic incisors. In *Bunohyrax fajumensis* and *Megalohyrax eocaenus* however, those specimens without the

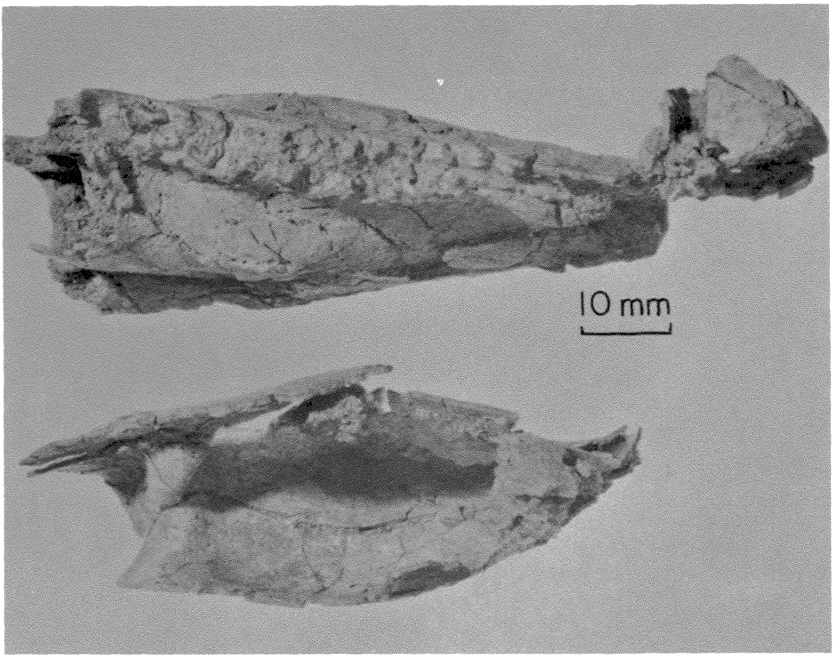

FIG. 3. Occlusial and basal view of *Thyrohyrax domorictus,* YPM-23939, showing the greatly inflated rami and in the basal view, the expanded chamber within the ramus.

fenestra have large procumbent tusk-like incisors typical of extant males whereas specimens that do possess the fenestra have smaller more rounded incisors typical of extant females. These latter specimens are also 10 to 15 percent smaller than the specimens without the fenestra. It is therefore suggested that the females of *Thyrohyrax domorictus* possess an internal mandibular fenestra and inflated ramus; the males do not.

The functional significance of this fenestra and chamber is unknown. A fenestra and chamber enclosed within the ramus are known in *Bunohyrax, Megalohyrax* and *Pachyhyrax* as well as in *Thyrohyrax.* A fossa, roughly similar in shape to the internal chamber, is found on the lingual side of the ramus of *Geniohyus, Meroehyrax* and *Pliohyrax.* No such structure is known in *Saghatherium, Titanohyrax, Gigantohyrax* or the living hyraxes. No analogous feature is to be observed among other mammals nor has any other clue been found in the living hyraxes that has shed any light on this unique and bizarre feature.

Andrews (1907) suggested that the cavity formed by this hollow was used as a resonating chamber for sound production. It seems odd, however, if this were the case, that the feature would have been located under the tongue. There is a guttural pouch in the Eustachian channel in living hyraxes that is

used in sound production but it is not restricted to females. One fossil specimen, a juvenile *Pachyhyrax crassidentatus* shows a very deep round fossa which, however, does not connect with the internal cavity as it does in the adults. This character may suggest that the fenestra is formed by the invagination of the structure it housed causing resorption of the bone of the ramus with its enlargement during adolescent growth. If this is the case, then the fenestra cannot act as a place of entrance for blood vessels or nerves. There are no holes or perforations of the chamber other than the one internal mandibular fenestra, and this chamber is not connected in any way to the dental battery. There is, however, a beveled edge at the dorsolateral side of the fenestra in all species that show fenestrae and there is a similar angulation at the same position of the sulcus of *Pliohyrax*. This beveled edge can only be interpreted as a passageway for something that entered the fenestra. If the fenestra was indeed formed by resorption of the wall of the ramus, then only something of a glandular nature that enlarged as the female reached sexual maturity could have passed through the fenestra into the chamber. No such organ is otherwise known.

The tibia measures 97.4 mm in length and except for its larger size is virtually identical to the tibia of *Procavia* and the other extant species. The fibula was not fused to the tibia as in extant forms. The bones of the pes and manus are, except for their greater size, nearly identical to those of *Procavia*. *Thyrohyrax domorictus,* therefore, possessed feet and limbs remarkably similar to the extant hyraxes, even though the two forms are separated by at least 30 million years. It seems that the general character of the hyrax postcranium was established in early Tertiary times.

Phyletic Position of *Thyrohyrax domorictus*

Thyrohyrax domorictus is assigned to the subfamily Saghatheriinae on the basis of the morphology of the teeth and possession of the internal mandibular fenestra. Internal mandibular fenestrae are presently known only in the hyracoids of the Oligocene and Miocene of North and East Africa that are included in the Saghatheriinae. These forms all possess the full eutherian dentition, have premolars that are submolariform or distinctly molariform, have hypoconulids on M_3 and bunodont to selenolophodont molars.

Thyrohyrax differs from *Saghatherium* by the possession of an internal mandibular fenestra and inflated ramus in some forms, its less inflated cusps, its more molariform premolars with more centrally placed paraconids, the metastylids on the lower cheek teeth, mesostyles on the upper premolars, the lack of spurs on the lingual side of the ectoloph of the molars and the relatively broader and shorter upper cheek teeth. The sole species of the genus *Thyrohyrax* differs from those of *Megalohyrax* and *Pachyhyrax* by its

much smaller size, its shorter snout, its inflated ramus, its more selenodont teeth, its more molariform premolars, its metastylids and by its differently shaped upper molars.

Dentally *Thyrohyrax* is very similar to *Meroehyrax* and may be close to, although not on, the direct line of ancestry of *Meroehyrax*. The two-rooted lower canine of *Thyrohyrax,* a feature unique to the Saghatheriinae, and the overall shape and selenolophodont nature of the lower teeth are features held in common with *Meroehyrax*. The fact that *Thyrohyrax* possesses an internal mandibular fenestra, places it in the Saghatheriinae while *Meroehyrax* with a fossa is placed in the Pliohyracinae. *Thyrohyrax* may, however, be more closely related to the form that gave rise to the Pliohyracinae than any other presently known member of the Saghatheriinae.

Geological Setting

The Jebel el Qatrani formation, which is 110 to 270 m thick, north of the Birkel el Qarun, consists of terrestrial deposits of quartz sandstone, siltstones, claystones and pebble conglomerates. "The basal 100 meters [Lower Fossil Wood Zone] is characterized by a complex of large-scale trough cross-stratified channel–lag and point–bar deposits and the lack of flood plain deposits. These characteristics are indicative of a loosely sinuous, low gradient, medium velocity stream. Point-bar, levee, crevasse-splay, flood basin, and occasional transitional channel fill deposits are characteristic of the upper portion of the unit [Upper Fossil Wood Zone]." (Bowen and Vondra, in press.)

Thyrohyrax is found at Yale Quarry G which consists of 0.3 m of mottled reddish orange and light olive gray saline claystone, which represents the upper portion of a point-bar deposit. It is also found at Quarries M and I which are located in 16 m of fine– to coarse–grained grayish yellow sandstone in the lower portion of a point-bar deposit. Quarries G and I are deposited 126.2 m and 75.8 m respectively below the Widan el Faras Basalt which has been variously dated at 24.7 ± 0.4 million years and 27.3 ± 2 million years (Simons, 1968). The contact between the basalt and the Jebel el Qatrani formation is disconformable.

Acknowledgments

I am deeply indebted to Dr. Elwyn L. Simons of Peabody Museum of Natural History, Yale University, and Mr. Darwish el Faar of the Cairo Geological

Museum, Cairo, Egypt, for allowing me access to material in their collections. Helpful discussions were held with Dr. Simons and Dr. David Pilbeam of Yale University, and Dr. Carl Vondra and Mr. Bruce Bowen of Iowa State University. I am grateful for their many helpful suggestions. The photographs are by A.H. Coleman of Harvard University. The manuscript was typed by M. H. Meyer. Grants that enabled the collection of the fossils reported in this paper were Smithsonian Foreign Currency Program Grants nos. 5, 23 and 1841 and National Science Foundation Grants G-18102, GP-433 and GP–3547 made to Dr. E. L. Simons.

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