Early tertiary elephant-shrews from Egypt and the origin of the Macroscelidea

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ABSTRACT Recent expeditions to the Fayum Depression, Egypt, have made possible the discovery of mandibles and a maxilla of a new genus and species of late Eocene elephant-shrew as well as initial evidence of the upper dentition of the early Oligocene taxon *Metoldobotes*. These fossils demonstrate that macroscelideans underwent a significant radiation in the Early Tertiary of Africa. Two new subfamilies are recognized and described. These Tertiary macroscelideans are the most primitive elephant-shrews known and indicate that previous hypotheses of a close phylogenetic relationship between macroscelideans and either lagomorphs, erinaceotans, or tree-shrews are unlikely. Rather, the dental anatomy of the Fayum macroscelideans provides evidence for a derivation of the order from within the Condylarthra.

The Order Macroscelidea comprises the living elephant-shrews and a diverse series of Eocene through Pleistocene fossil forms. Early workers placed macroscelidids with erinaceids, tupaiids, and leptictids in the Insectivora, ranking them with tree-shrews in the suborder Menotyphla (1–5). Other authors (6–10), however, realized that tree-shrews and elephant-shrews were not closely related, and the order Macroscelidea was created for these animals in recognition of their unique morphology (4). Most recent workers have considered macroscelideans a sister group of lagomorphs and rodents (11–17) or as a branch of the Anagalida (which are distributed in the Asian Paleocene and early Eocene), which are probably also related to rodents and lagomorphs (18). Alternatively, some molecular studies have indicated dermopteran affinities for elephant-shrews (19) or show that the order has long been separated from all other eutherian mammals (20). No recent studies have attempted to compare in detail the morphology of fossil macroscelideans—that are known almost exclusively from dental remains—with that of other early mammals, although a dental similarity to the late Paleocene to early Eocene subfamily Louisininae (Hyopsodontidae, Condylartha) has been noted (21).

Analysis of recently collected macroscelidean fossils from upper Eocene and lower Oligocene deposits of the Jebel Qatrani Formation, Egypt, has led to the recognition of considerable early diversity in this group and to a substantially different interpretation of the origin and interordinal relationships of the Macroscelidea than those previously proposed. A brief report on this material has been presented (50th annual meeting of the Society of Vertebrate Paleontology, October 10–13, 1990, in Lawrence, KS).

SYSTEMATICS

Order Macroscelidea Butler 1956; Subfamily Herodotinae, New Subfamily

Subfamilial diagnosis. Herodotines differ from all other macroscelideans in having a weak cristid obliqua on P_4–M_2

that does not ascend the posterior trigonid wall; brachydont molars; a low, labiolingually oriented paracristid; M_1 paraconid located at the midline and abutting the bases of the metaconid and protoconid; a strong P_3 entocristid and large P_3 hypoconid; retained cingula on upper and lower molars; three- or four-cusped M_3; P_4 metaconid directly lingual of protoconid; and hypocone smaller than protocone on P^4–M^2.

Type genus. Herodotius. Included genus: *Chambius.*
Distribution. Late Eocene of North Africa.

Herodotius, New Genus

Generic diagnosis. Herodotius is morphologically closest to *Chambius* but differs from it in having M_{1-2} hypoconulid lacking; slightly narrower P_3 talonid with poorer separation between entoconid and hypoconid; more lingually placed P_3 hypoconid; smaller M_1 paraconid; smaller M_3 talonid; more weakly developed crests; well-developed distal and mesial cingulids on M_{1-2}; distinct conules on P^4–M^2 lacking; fully developed P^4 hypocone bearing distinct pre- and posthypocristae; P^4 postprotocrista unconnected to hypocone; and relatively larger M^3.

Type species. Herodotius pattersoni, new species.
Distribution. Late Eocene of Egypt.
Etymology. For Herodotus, 5th Century B.C. Greek historian and traveler, who visited the Fayum area and wrote an entertaining account of its antiquities.

H. pattersoni, New Species

Holotype. Cairo Geological Museum 42177, a right dentary with P_4–M_3 and alveoli of C–P_3 (Fig. 1).
Type locality. Locality 41, at the 47-m level in the lower sequence of the Jebel Qatrani Formation, Fayum Depression, Egypt.
Hypodigm. Type: DPC 10167, a left dentary containing roots of I_{1-2}, I_3–P_1 alveoli, P_2–M_3 (Figs. 1 and 2), both found by one of the authors (E.L.S.); and DPC 10717, a right maxillary fragment with P^4–M^3, the broken base of P^3, and associated crushed cranial fragment, found by Mr. Callum Ross.
Species diagnosis. Only known species; as for genus.
Etymology. For Bryan Patterson, formerly professor at Harvard and student of the Macroscelidea.
Description. Measurements (in mm) of type are P_4 length, 3.7; P_4 width, 2.0; M_1 length, 3.5; M_1 trigonid width, 2.9; M_1 talonid width, 2.9; M_2 length, 3.4; M_2 trigonid width, 3.0; M_2 talonid width, 2.8; M_3 length, 2.1; M_3 maximum width, 2.2. Measurements of DPC 10167 are P_3 length, 3.0; P_3 width, 1.5; P_4 length, 3.6; P_4 width, 2.1; M_1 length, 3.5; M_1 width, not measurable due to damage; M_2 length, 3.3; M_2 trigonid width, 2.8; M_2 talonid width, 2.5; M_3 length, 2.4; M_3 maximum width, 1.9. Measurements of DPC 10717 are P^4 length, 3.1; P^4 width, 3.3; M^1 length and posterior width, not measurable

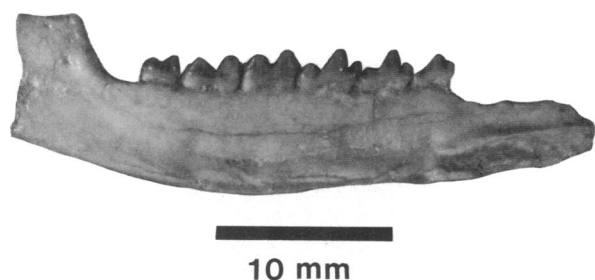Abbreviation: DPC, Duke Primate Center.

FIG. 1. Lingual view of Duke Primate Center (DPC) 10167, left mandible of *H. pattersoni* containing P^2–M^3.

due to damage; M^1 anterior width, 3.5; M^2 length, 3.1; M^2 anterior width, 3.6; M^2 anterior width, 3.0; M^3 length, 1.7; M^3 maximum width, 2.0.

Description. The mandibular dentition is known from two specimens, a left mandible containing P_2–M_3 and preserving the alveoli of all other teeth and a right mandible with P_4–M_3. These specimens do not differ in size and differ only slightly in amount of wear. Because both specimens were found in the same portion of the quarry at Locality 41 (but were found several days apart) it is possible that they belong to the same individual; however, the absence of a more direct association precludes definite identification as one individual.

The mandibular ramus is long and slender and shallows only slightly anteriorly. Two labial mandibular foramina are present, one beneath the canine and another beneath P_1. The symphyseal rugosity is long and thin and extends posteriorly to P_2. The ascending ramus is lacking, but the base of this structure is present and indicates that it had a vertical anterior border. The masseteric crest and fossa are well-developed.

The three incisor alveoli are approximately equal in size. Those for I_{1-2} are anteriorly inclined and that of I_3 is more upright. The canine alveolus is large and oval. A short diastema separates the alveoli for the canine and P_1. The lower first premolar had two roots and was apparently equal in length to P_2. The lower second premolar also has two roots and is dominated by a large labiolingually compressed protoconid. The paraconid is about half the height of the protoconid and situated directly mesial to it. There is an incipient talonid. The lower third premolar is similar to P_2 but has a larger paraconid and a centrally placed hypoconid with a small, cristaform entoconid mesiolingual to it. The hypoconid and entoconid are separated by a small fissure.

The lower fourth premolar is fully molariform and is slightly longer and narrower than M_1. The metaconid and protoconid are subequal in size and are transversely aligned. The paraconid is large and centrally placed, and it is somewhat lower than the other trigonid cusps. The position of the paraconid imparts a prow-like shape to the trigonid. The paracristid is low (not elevated) and is notched between the paraconid and protoconid. A minor cingulid is present between the protoconid and paraconid. The posterior trigonid wall forms a steep, unbroken wall. The talonid consists of

transversely aligned, equal-sized entoconid and hypoconid. There is no hypoconulid. The cristid obliqua is very weak and ends at the base of the posterior trigonid wall. There is no talonid basin, but only a steeply angled transverse valley.

The molars are square, bunodont, slightly exodaenodont, and lack hypoconulids. M_2 is the largest of the molars, and M_3 is very reduced in size. On M_1 and M_2 the protoconid and metaconid are large, subequal in size, and transversely aligned. A weak protolophid connects the two cusps. The paracristid is low and transverse. A paraconid is present only on M_1, where it is small and abuts the base of the protoconid and metaconid at the midline of the tooth. The trigonid is wider than the talonid. The talonid cusps are also subequal in size, transversely aligned, and joined by a weak lophid. The cristid obliqua is very short and weakly developed. A minor labial cingulid traverses the hypoflexid, and there are well-developed pre- and postcingulids. The bunodonty and shortness of the entire tooth cause the trigonid and talonid cusps to be appressed and reduce the talonid basin to a steep-walled transverse valley.

The upper dentition is known only from DPC 10717 (Fig. 3). The upper fourth premolar is molariform and bears a well-developed, anteriorly projecting parastyle. The paracone is taller and larger than the metacone. The hypocone is smaller than the protocone, located more labially and separated from it by a valley. A posterior cingulum is present and continuous with the posthypocrista and the labial cingulum.

The first and second upper molars are quadritubercular and have poorly developed crests. Both have a minor ectoflexus. Both lack conules. There is a well-developed parastyle formed on the labial cingulum and connected to the paracone by a weak preparacrista. The preprotocrista is very short and directed anterolabially. A postprotocrista is lacking. The hypocone is a distinct cusp and placed more labially than the protocone. The prehypocrista is directed labially, joining to the base of the metacone and forming a low loph. On M^1 the metacone is missing due to breakage; on M^2 the paracone and metacone are subequal in size, and the paracone is greater in height. The metacone is more lingually placed than the paracone; combined with the posterolabial position of the hypocone relative to the protocone this makes the posterior half of the tooth much narrower than the anterior half. M^3 is much reduced in size and lacks a hypocone entirely. The preprotocrista extends to the labial edge of the tooth in the form of an anterior cingulum.

The maxilla and the associated cranial fragment of DPC 10717 are much distorted by crushing. This crushing, combined with the very delicate nature of the fossil bone, makes preparation of the cranial remains a slow process. A full description and discussion of the cranial remains will be made
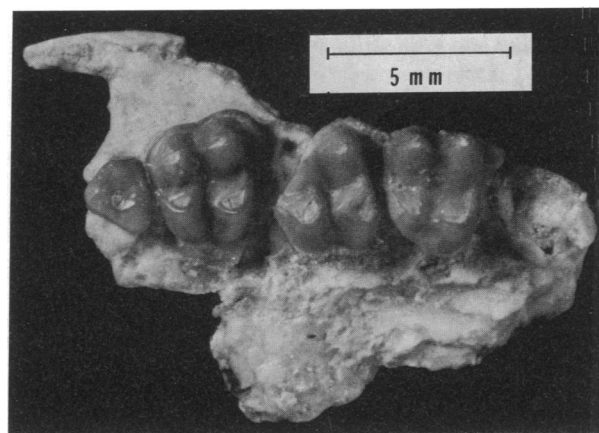

FIG. 2. Occlusal views of DPC 10167 (*Lower*) and CGM 42177 (*Upper*), type specimen of *H. pattersoni*.

FIG. 3. Occlusal view of DPC 10717, right P^4–M^3 of *H. pattersoni*.

when the specimen is more fully prepared. The preliminary preparations, however, have revealed several aspects of the maxillary anatomy that differ from those of other elephant-shrews.

The lateral surface of the maxilla is preserved relatively undistorted (Fig. 4). The zygomatic arch arises just posterior to M^2, in contrast to more recent macroscelideans, in which this structure arises more anteriorly, above the first molar. The most distinctive feature of the maxilla of *Herodotius*, however, is the presence of a large, rather anteriorly placed infraorbital foramen opening into a fossa above P^3. The distolabial root of P^3 projects into this fossa. In living forms, the infraorbital foramen opens directly beneath the orbit and above M^1, and no fossa is present. The more anterior position of the infraorbital foramen is probably primitive, as many Paleogene condylarthrans, "insectivores," and anagalids have an infraorbital foramen opening above the premolars.

Subfamily Metoldobotinae, New

Subfamilial diagnosis. Differs from all other macroscelideans in its large size and in having single rooted P_1–P_2, enlarged procumbent I_3 with lingual groove, and M_3 lost, coupled with profound reduction of M_2. Differs from Herodotinae (and resembles Miocene to Recent macroscelideans) in the following characters: absence of upper molar paraconule and cingula; presence of an upper molar anteroloph; P_4 metaconid positioned distolingual to protoconid; M^{1-2} hypocone equal to protocone in size. Differs from Myohyracinae, Mylomygalinae, Rhynchocyoninae, and Macroscelidinae in retaining an upper molar metaconule and in lacking hypsodont molars with reentrant folds, an upper molar hypoloph, and prismatic cheek teeth.

Type. *Metoldobotes stromeri* Schlosser.

Distribution. Early Oligocene of the Jebel Qatrani Formation, Fayum Depression, Egypt.

Metoldobotes cf. *M. stromeri* Schlosser, 1910

New material. DPC 4154, a left M^2 (Fig. 5), provides evidence of the upper dentition of *Metoldobotes*. It is a bulbous, five-cusped tooth with a minor ectoflexus and a posterior half that is much reduced in width. The anteroloph is directed from the protocone to the labial edge of the tooth and is not directly connected to the paracone. There is no paraconule. A small bulbous metaconule is present at the center of the tooth and is connected to the hypocone by means of a short, distolingually oriented crista. The hypocone and metacone are small and closely appressed to one

FIG. 5.   DPC 4154, left M^2 of *Metoldobotes* cf. *M. stromeri* from Quarry M.

another. Measurements (in mm) for DPC 4154 are length, 3.2; anterior width, 4.7; posterior width, 3.3.

DISCUSSION

Analysis of the recently collected Egyptian elephant-shrew material clarifies phyletic relationships within the order Macroscelidea and provides an opportunity to address the question of the origin of the order. Although *Chambius* and *Herodotius* show considerable phenetic similarity to members of the Louisininae in having bunodont molars, reduced third molars, and P_4s with a well-developed talonid, greater cladistic similarity can be found between these early macroscelidean genera and the early Eocene North American "hyopsodontid" condylarth *Haplomylus*. In particular, *Haplomylus* shares a suite of dental characters with both African genera to the exclusion of other hyopsodontid condylarths: (*i*) molariform P_4 with enlarged paraconid on the midline and talonid composed of two cusps, (*ii*) P_{2-3} with well-developed paraconid, (*iii*) P^4–M^2 postprotocrista (when present) directed toward the hypocone rather than the metaconule, (*iv*) M_{1-2} trigonids wider than talonids, (*v*) reduction of M_{1-2} hypoconulids, (*vi*) reduction of $M^3/_3$, and (*vii*) enlarged P^4 parastyles and transversely widened P^4. All of these characters may be considered to be derived with respect to the most generalized representatives of the Condylarthra. In characters *i*, *ii*, and *vii*, *Haplomylus* is also more similar to phenacodontid than hyopsodontid condylarths. These dental features therefore suggest phyletic ties between Macroscelidea and certain of the Condylarthra.

Although *Metoldobotes* is one of the most-derived macroscelideans, its combination of primitive and advanced traits serve as morphological links between the condylarthran-grade herodotine macroscelideans and the more-derived post-Oligocene forms. *Metoldobotes* is similar to Miocene to Recent macroscelideans in having paraconule loss, possession of a tall P_4 paracristid, a P_4 metaconid distolingual to the protoconid, a P_4 cristid obliqua that invades the posterior trigonid wall and ascends to the tip of the metaconid, a relatively higher crowned tooth than herodotines, and a well-developed anteroloph on the upper molars. Nonetheless, *Metoldobotes* resembles other Paleogene macroscelideans and is more primitive than all younger forms in the combination of its overall bunodonty and in having molars equal in length and width, a large centrally placed metaconule, a well-developed masseteric crest, a labiolingually oriented molar paracristid, and a long mandibular symphysis.
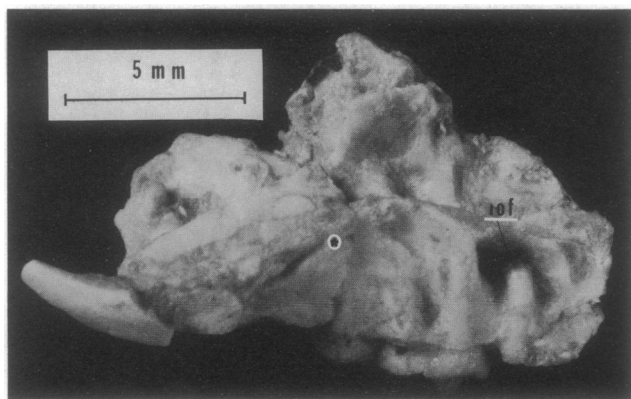

FIG. 4.   Lateral view of DPC 10717 showing the position of the zygomatic arch (base marked by a white circle) and infraorbital foramen and fossa (iof).

CONCLUSIONS

The dental morphologies of *Herodotius, Chambius,* and *Metoldobotes* clearly link living and Neogene macroscelideans with condylarthrans, a group commonly accepted as having given rise to diverse groups of hoofed mammals as well as hyracoids, proboscideans, and sirenians. This affinity is considered by us to be greater than that shared by macroscelideans and any members of the Erinaceota, Scandentia, Lipotyphla, Anagalida, or Lagomorpha.

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