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Evolution

Ptolemaiida, a new order of Mammalia—with description of the cranium of *Ptolemaia grangeri*

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ABSTRACT **All records of the exotic mammalian family Ptolemaiidae are known from 182 m of section in the lower to middle parts of the upper Eocene and lower Oligocene Jebel Qatrani Formation, Fayum Depression, Egypt. Previous tentative assignments of ptolemaiid affinity have suggested that these animals are allied with the primitive suborder Pantolesta (currently placed in the order Cimolesta). Though perhaps ultimately derived from an unknown member of that group, the likelihood that ptolemaiids constitute a distinct group is considered, and analysis of all known materials of *Ptolemaia, Qarunavus,* and *Cleopatrodon* demonstrates that these genera belong in their own order, the Ptolemaiida, described here. The morphologically unique dentition and only known ptolemaiid cranium, that of *Ptolemaia grangeri*, is described. Although *Qarunavus* and *Cleopatrodon* show some similarities in primitive characters to European merialine Paroxyclaenidae (suborder Pantolesta), their affinities clearly lie with *Ptolemaia* and the Ptolemaiida.**

Paleontological expeditions to the lower Tertiary badlands of the Fayum Depression of Egypt under the direction of the senior author have greatly expanded knowledge of Paleogene North African mammals. At present, 19 families are recognized. These families fall into two groups—one of which had its origin outside Africa, and the other, a smaller and perhaps more intriguing set, had an apparent African endemic origin. Among the latter groups are at least some of the various families of early primates, the macroscelidid and tenrecoid insectivores, the proboscideans, the arsinoitheres, and, possibly, members of the aquatic order Sirenia. With these also belongs the group that forms the subject of this contribution, the new order Ptolemaiida.

The Ptolemaiida is one of the most restricted of mammalian orders known in terms of both its temporal and its geographic distribution. It is confined to an occurrence in or near three fossil vertebrate quarries between the 62- and 244-m levels (1) of the Jebel Qatrani Formation, and fossils of Ptolemaiida have been found only in a small area of about 3.0 × 1.5 km in the Fayum Depression of Egypt. No postcranial bones have been positively identified to date, and all known specimens total only eight mandibles, two maxillary fragments, a skull fragment bearing the frontal bones, one skull, and 36 isolated teeth.

The oldest known members of this order come from in or near quarry A in the lower sequence of the Jebel Qatrani Formation, a site actively worked by the American Museum of Natural History expedition of 1907. There, the first ptolemaiid specimen, the type of *Ptolemaia lyonsi*, was collected, and it was later described by Osborn (2). Early collectors also secured from quarry A right and left juvenile mandibles of a somewhat larger ptolemaiid. These specimens became part of the collections of the British Museum of Natural History and the Stuttgart Natural History Museum. Simons and Gingerich (3) assigned these specimens to a new genus and species, *Qarunavus meyeri*. A specimen located on the desert surface north of quarry A in 1961 also belongs to Osborn's type species, *P. lyonsi*.

In 1978, after heavy rain eroded deeply into Fayum badland channels, fossil bones were exposed at what became vertebrate fossil quarry V, at the 166-m level of the Jebel Qatrani Formation. Since then, collecting at quarry V has yielded all other specimens of ptolemaiids (the new species *Ptolemaia grangeri* and the new genus and species *Cleopatrodon ayeshae*), except for a single mandible and two isolated teeth from quarry I (244-m level). The quarry I specimens were placed in the new species *Cleopatrodon robusta* (4). The very restricted distribution, even for Fayum sites and faunas, hints that ptolemaiids must have had a lifestyle that significantly constrained their paleoenvironmental distribution, an inference bolstered by their highly aberrant dental morphology. The Ptolemaiida are presently known from 48 specimens that record three genera and five species. No certain record of the group exists elsewhere.

SYSTEMATIC PALEONTOLOGY

Ptolemaiida, New Order.

Holotype. ***Ptolemaia lyonsi* Osborn, 1908.** *Diagnosis.* Among all mammals, the Ptolemaiida most closely resemble the Merialinae (Cimolesta, Pantolesta, Paroxyclaenidae) of the Eocene of England and France. From merialines (and therefore from Pantolesta and Order Cimolesta and all other orders of mammals), the Ptolemaiida differ in the unique combination of the following characters: (*i*) dental formula = I3/?3, C1/1, P2–4/2–4, M3/3 where I, C, P, and M refer to numbered upper incisor, canine, premolar, and molar teeth (i, c, p, and m = lower); (*ii*) incisors small and slightly procumbent; (*iii*) upper canine tall, straight, and piercing, with striated enamel; (*iv*) lower canine short and broadly curved; (*v*) premolars bunodont, high-crowned, and increasing in size posteriorly, greatly hypertrophied in *Ptolemaia*; (*vi*) P2/2–P3/3 elongate; (*vii*) P4/4 semimolariform or molariform with at least hypoconid and either metaconid or lingually expanded protoconid (p4 of *P. grangeri* possesses all principal trigonid and talonid cusps); (*viii*) molars bunodont, somewhat high-crowned to greatly hypertrophied and decreasing in size from M1/1 to M3/3 (excepting M3/3 of *Cleopatrodon*; M3/3 is unknown in *Qarunavus*); (*ix*) lower molar trigonids greatly compressed anteroposteriorly with large lingual paraconids closely appressed to metaconids; (*x*) lower molar talonids with entoconids weak or absent and talonid notch open; (*xi*) premolars and molars lacking stylar shelves and lacking lingual and labial cingulae; and (*xii*) lower molars vespiform in occlusal view, with pronounced internal constriction at the hypoflexid and talonid notch.

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Abbreviations: CGM, Cairo Geological Museum; DPC, Duke University Primate Center; I/C/P/M and i/c/p/m, numbered incisor/canine/premolar/molar upper and lower teeth respectively.

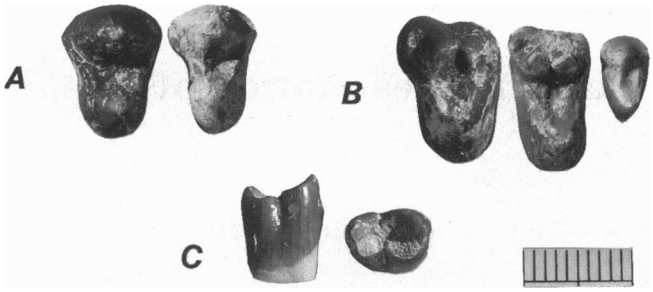

FIG. 1. Upper teeth of Ptolemaiida. (*A*) Right P3 (DPC 6281) and right P4 (DPC 6500) of *C. ayeshae*. (*B*) Composite M1–3 of *P. grangeri*, shown as a left dentition; right M1 = DPC 10408 (reversed), left M2 = DPC 3229, and left M3 = DPC 10298. (*C*) Right m3 (reversed) of *P. grangeri* in labial (*Left*) and occlusal (*Right*) views. (Bar = 10 mm.)

Included taxa. The type genus; *Qarunavus* Simons and Gingerich, 1974; *Cleopatrodon* Bown and Simons, 1987.

Distribution. Fayum Depression, Egypt; 62- to 244-m levels of Jebel Qatrani Formation (upper Eocene–lower Oligocene).

***P. grangeri* Bown and Simons, 1987.** *Holotype.* CGM (Cairo Geological Museum, Egypt) 42843, left m3 [see Fig. 2; also see figure 1*E* of Bown and Simons (4)].

Hypodigm. The type specimen and DPC (Duke Primate Center) 695, left m1 (see Fig. 2); DPC 2062, frontal bones of skull; DPC 2320, left p4; DPC 2666, left p2; DPC 3229, left M2 (Fig. 1*B*); DPC 3994, right M2 [see Fig. 4*C* of Bown and Simons (4)—formerly assigned to *C. ayeshae*]; DPC 5434, left edentulous ramus with alveoli for c and p2–m3 [see Fig. 1*C* of Bown and Simons (4)]; DPC 5458, right p3 (Fig. 2—formerly believed to be p4); DPC 7293, M3 of indeterminate side; DPC 10262, left p4; DPC 10296, left p2 (Fig. 2); DPC 10298, left? M3 (Fig. 1*B*); DPC 10309, left m3 (Fig. 1*C*); DPC 10354, right p4 (Fig. 2); DPC 10408, right M1 (Fig. 1*B*); DPC 10684, skull with left C, P4, M2 and right C, I2, P4 and alveoli for all other teeth (Figs. 3 and 4); DPC 10816, right p4; CGM field number 87-54, right p4.

Description of previously unreported dental elements. Recently found teeth of *P. grangeri* include several isolated teeth as well as teeth preserved in the skull (DPC 10684, described below). These specimens greatly supplement what was previously known of the dentition and provide information, in composite, about the morphology of I2, C1/1, P4–M3, and p2–m3. The new skull (DPC 10684, Figs. 3 and 4), the composite dentition, and an edentulous lower jaw (DPC 5434) show that P2–4 and p2–4 increase in size posteriorly, whereas P4–M3 and p4–m3 decrease in size posteriorly. P4, p4, and M1–3/1–3 have greatly hypertrophied crowns, equal to or exceeding that in the type of the genus, *P. lyonsi*. The dental formula of *P. grangeri* is I3/?, C1/1, P3/3, M3/3.

I2 is a tiny, pointed tooth with a broad crest arising from the base of the enamel on the internal side to a point just posterior to the tip of the crown. The tooth exhibits minor posterointernal wear from the tip of the crown to just above the crown base. The alveoli of left I1–3 and right I1 and I3 show that the incisors were slightly procumbent. I1 is slightly the largest incisor, and I2 and I3 are of about equal size. I3 is separated from the immense canines by a narrow but deep fossa for housing the lower canines.

The upper canines (C1/1) possess vertically striated enamel, and a cross-section of the tooth at the base of the enamel is elliptical but with a strong crest at (at least) the posterior axis of the ellipse. The canines are very tall, vertically implanted, and uncurved (straight and piercing). Minor wear on the canine tips has just penetrated the enamel; however, on the anterior face of the crown, strong wear produced by the lower canine has obliterated the enamel and penetrated deeply into the dentine. This wear is even and flat, extends from the tip of the crown dorsad to at least 7 mm above the enamel line in the right canine, and reaches to near the tip of the left canine and at least 3.6 mm above the base of the enamel in that tooth.

Alveoli show that P2 had two about equisized roots that were aligned anteroposteriorly. The anterior alveolus is displaced somewhat by labial crushing on the right side. P2 was probably a trenchant tooth. In contrast, the two alveoli for P3 show that whereas the anterior alveolus is only slightly larger than the posterior alveolus for P2, the posterior P3 alveolus is very much larger and housed two partially conjoined roots, the lingual being the larger. This morphology, combined with the configuration of the crown of P4, suggests that P3 is probably a sectorial tooth and, like P4, with a very large parastyle.

Both left and right P4 are preserved in the palate of the skull, DPC 10684 (Fig. 4*A*). Though deeply worn, it is clear that P4 is a tall, roughly triangular, three-rooted tooth with very thick enamel and a conspicuous parastyle. Wear on the crown has eradicated all other cusps; however, inflections of the enamel

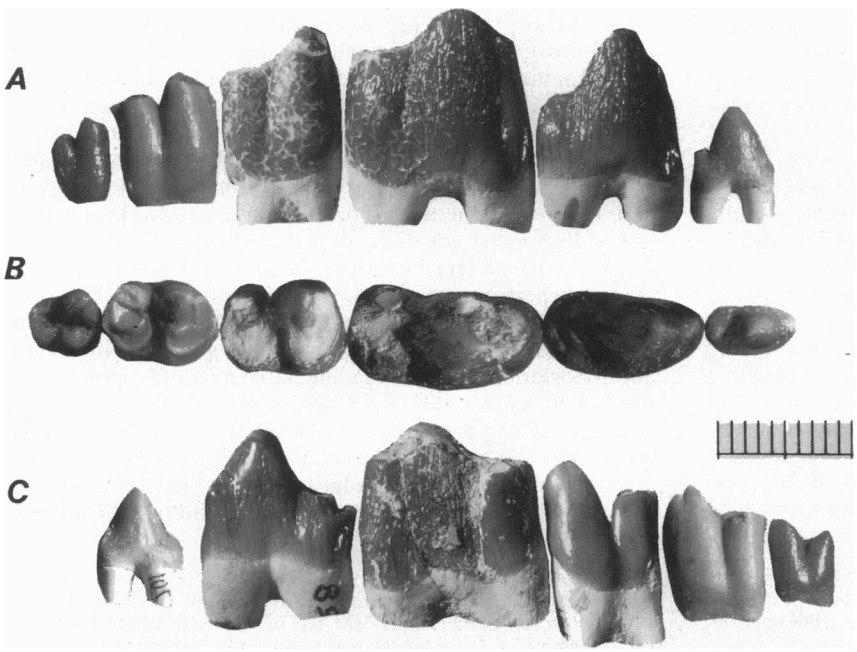

FIG. 2. Composite lower cheek teeth of *P. grangeri* in labial (*A*), occlusal (*B*), and lingual (*C*) views. In *A* and *B*, right is anterior; in *C*, left is anterior. p2 = DPC 10296 (reversed), p3 = DPC 5458, p4 = DPC 10354, m1 = DPC 12441, m2 = DPC 695 (reversed photograph of cast), and m3 = CGM 42843 (type of species, reversed photograph of cast). (Bar = 10 mm.)

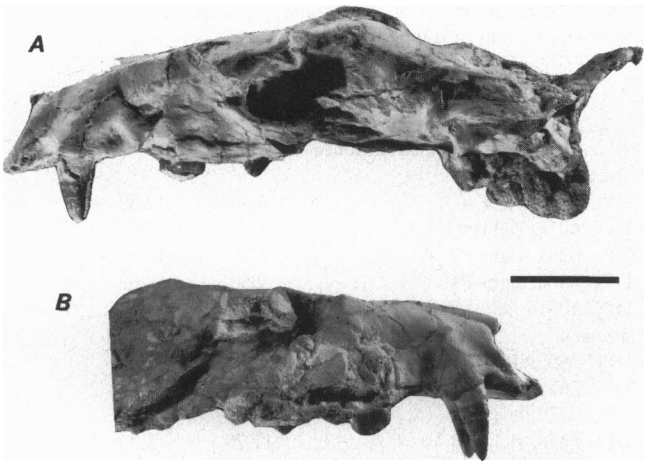

FIG. 3. Cranium of *P. grangeri* in left lateral (*A*) and right lateral (*B*) aspects (front part of skull only in *B*). (Bar = 15 mm.)

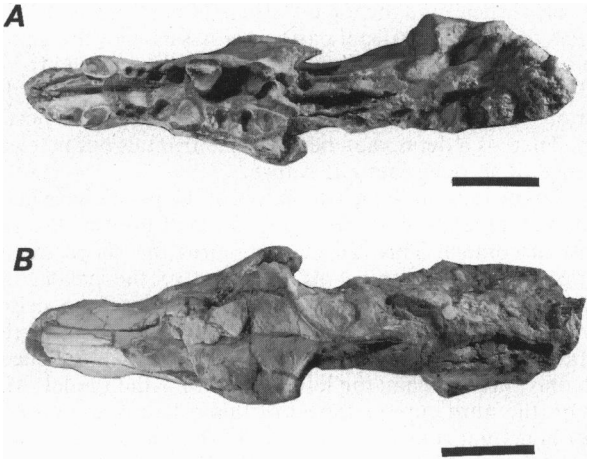

FIG. 4. Cranium of *P. grangeri* in ventral (*A*) and dorsal (*B*) aspects. (Bars = 15 mm.)

on the labial side of the right P4 indicate the former presence of closely set paracone and metacone cusps. Wear on P4/4–M3/3, seen in isolated teeth, was invariably apical, tending to flatten the topography of the crown.

The molar morphology of *P. grangeri* is known from both teeth and alveoli in the skull and mandible. M1/1 is much larger than M2/2, and M2/2 is much larger than M3/3, based on relative alveolar size and the composite upper and lower dentitions. M1 and M2 possess one lingual and two labial roots, the labial moieties being conjoined or closely appressed, and the lingual root is much shallower and mesiodistally broad. M3 has a shallow single (though conjoined) root. The lingual moiety of this root is mesiodistally broad, whereas the labial moiety is long anteroposteriorly (as seen in DPC 7293 and DPC 10298). The roots of all the upper molars are exceptionally shallow relative to crown height, and tooth stability in the maxilla was probably augmented by the unique shelf of bone that buttresses P4–M3 on the labial side of the maxillae (Figs. 3 and 4*A*). In contrast to the more transverse M1, the buccal length of P4 is nearly equal to tooth width.

M1 (Fig. 1*B*) is a triangular, bunodont tooth that lacks stylar shelves and cingulae, and, though much broader with respect to length than the less transverse P4, it otherwise closely resembles that tooth. There is a small parastyle well below the level of the paracone. The paracone is large and is appressed by a tiny, almost connate, metacone. The pre- and postprotocristae are strong and enclose a small but deep trigon basin. Conules, hypocone, and hypocone shelf are absent. The protocone is about the same size as the paracone. It is situated far internally, in about the middle of the tooth (as seen in occlusal view), and is supported by a massive, lingually descending base.

The morphology of M2 in *P. grangeri* has been clarified by the presence of that tooth in the new skull (Fig. 4*A*), which shows that DPC 3994, formerly referred to *C. ayeshae* [see Figure 4*C* in Bown and Simons (4)], actually belongs in *P. grangeri*. Additionally, another isolated M2, DPC 3229 (Fig. 1*B*), is also known. DPC 3229 is relatively unworn and shows P2 to be a very transverse, bunodont, tribosphenic tooth with a subequal paracone and metacone, a much larger protocone, and a small parastyle. The M2 entirely lacks cingulae.

M3 (Fig. 1*B*), known from two specimens, is a high-crowned, short, broad, simple tooth with two cusps—a large, tall protocone and a smaller and shorter labial cusp that is flanked by tiny para- and metastyles. Although minute with respect to M2, M3 is likewise very high-crowned.

The lower second premolar (Fig. 2) is a long, narrow, two-rooted sectorial tooth with vertically striated enamel. It has a tall, central protoconid, a smaller posterobasal cusp, and a minute anterobasal cusp. The lower third premolar of *P. grangeri* was originally described as a p4 [see figure 4*C* of Bown and Simons (4)]. It is a high-crowned tooth, nearly as large as p4, and possesses vertically striated enamel. The lower fourth premolar (Fig. 2) is also very high-crowned with vertically striated enamel. In contrast to p3, it is molariform and has a well-differentiated trigonid and talonid. The paraconid and metaconid are of about equal size and the metaconid is exactly opposite the protoconid. The hypoconid and entoconid are also about the same size, and the hypoconulid, though slightly smaller, is very large. The talonid is open between the entoconid and the metaconid.

The lower first molar (Fig. 2) is very high-crowned with a trigonid and talonid of equal length, though the trigonid is broader than the talonid. The paraconid is large, lingually situated, and closely appressed to the metaconid. The metaconid and protoconid are about equal in size, the postvallid is transverse, and the cristid obliqua joins it in the middle. The hypoconid is larger than the entoconid, and the hypoconulid is shelflike. A deep, vertical fissure divides the tooth at the cristid obliqua on the labial side and the opposing entoconid notch on the lingual side and descends to near the base of the enameled portion of the hypertrophied crown, dividing the molar into two pillar-like moieties. m2, though smaller, is identical to m1. m3 is represented by the type of the species and by DPC 10309 (Fig. 1*C*; a somewhat differently worn tooth than the type specimen) and has been adequately described (4).

Measurements of recently found teeth of *P. grangeri* are in Table 1.

Description of the cranium of *P. grangeri*. The cranium, DPC 10684 (Figs. 3 and 4), was collected by the senior author in 1990 at quarry V. It is crushed from side-to-side, causing near apposition of the two sides of the palate. The anterior half of the skull—from the region of the pterygoids and orbits forward—is more completely preserved than is the posterior portion. The braincase is crushed and shattered posteriorly on the right side, whereas the left side is somewhat better preserved.

Rostrum and palate. Despite postmortem lateral compression, this cranium is very long and narrow. The nasal aperture is oval in outline, and the premaxillae, holding three incisors each, jut far forward from it. The premaxillae have a large ascending wing but their posterior suture with the maxilla appears to be fused and cannot be traced. On the left side particularly, there is a depressed area or embrasure to receive the tip of the lower canine. Posterior to this is a swollen area or canine pillar behind which occurs a distinct depression, or canine fossa. About 1.5 cm behind this fossa is an opening for a large (infraorbital?) foramen. The sides of the rostrum are

relatively vertical, and the top is flattened where the nasals and frontals cojoin. In the distal part of the nasals, they are gently rounded dorsally, and their distal ends project distinctly beyond the premaxillae. At a point almost directly above the anterior rim of the orbits, the nasals are also broader posteriorly. There is a depression between the frontals but no clear evidence of an open metopic suture.

As already indicated, the two halves of the palate have been crushed together so that the lingual sides of the two P4s are almost in contact. This crushing obscures the shape of the anterior palatine foramina. At the front of the palate, the premaxillae project far forward and each contains three incisor alveoli, the central being the largest. For the right side the central incisor is preserved, as are both canines. Of the cheek teeth only three remain, the left and right P4 and the left M2. Perhaps the most curious aspect of this palate is an elevated rim of bone that runs from the back of the canine all the way to the end of the dentition behind M3. This ridge can be seen most clearly on the right side of DPC 10684. At the back of the palate, the openings of the posterior nares extend anteriorly slightly past the level of the back of the third molars. A deeply incised sinus canal occurs just medial to the root sockets of right M2 and M3.

Orbit. At the anterior margin of the left orbital opening, there is a slightly depressed area that may be a lacrimal foramen located outside the orbit. This area is missing on the right side of the skull. Below this lacrimal area, a very shallow extension of the anterior wing of the jugal runs forward. Considering the size of the entire skull, the orbital opening is relatively small. The orbital fossa appears to be confluent with the temporal fossa and, judging from the remaining portion of the jugal (and a projection above it downward from the side of the frontal), it appears that the orbit was open posteriorly and lacked a postorbital bar. The anterior rim of the orbit is situated directly above the anterior edge of M2, and the posterior part of the orbit lies some distance behind the hard palate and dentition.

Dorsacranium. As indicated, the flattened dorsum of the frontals has no clearly demarked metopic suture but, at its position in the midline, there is a groove that may actually reflect this structure. From each side of the frontals, the temporal lines or ridges converge posteriorly and join at the frontal-parietal suture, forming the anterior end of a pronounced sagittal crest. This crest, although damaged, runs posteriorly to join the similarly damaged nuchal crests. At the posterior end, the sagittal and nuchal crests combine to form a very large and long posterodorsal process.

Basicranium. The wings of the pterygoids are reasonably well preserved, especially on the left side, and are quite long. On both sides of the basicranium, the articular surface of the glenoid fossa is preserved. It is anteroposteriorly short but moderately deep and is marked by a distinct postglenoid process. The auditory region is poorly preserved, but there appears to be no evidence of an expanded bulla or an ossified ectotympanic. The left occipital condyle is relatively complete, but both it and the foramen magnum seem to be extraordinarily small for a skull of this absolute size. The brain case is so distorted that no clear impression of the size or degree of expansion of the brain can be determined. Compared with a modern mammal such as the coyote (*Canis latrans*) with a cranium of about the same size, brain volume would have been very much less in *P. grangeri*.

Measurements of the cranium of *P. grangeri* are in Table 1.

***C. ayeshae* Bown and Simons, 1987.** *Holotype.* CGM 40242 (type), left ramus with canine, p1–m3 [see figures 2*C* and 3 of Bown and Simons (4)].

Hypodigm. The type specimen and DPC 73, left P4; DPC 3265, left p2–3; DPC 3991, left C; DPC 4330, right m1; DPC 4545, left ramus with c and p1–m3; DPC 5667, left p2; DPC 6015, left c; DPC 6058, right m1; DPC 6281, right P3 (Fig. 1*A*); DPC 6500, right P4 (Fig. 1*A*); DPC 8220, left p3; DPC 8222, left p4; DPC 9468, left P3; DPC 10311, right dP3–4; DPC 10815, left M1; DPC 12435, left ramus with c and p1–m3; CGM field number 84-347, left m1.

Table 1. Measurements of new ptolemaiid material from the Fayum Depression of Egypt

	Measurements, mm		
	Length	Width	Other
Isolated dental elements			
C. ayeshae			
DPC 73, left P4	9.00	12.60	
DPC 6058, right m1	X	X	
DPC 6281, right P3	8.40	11.80	
DPC 6500, right P4	9.50	12.60	
DPC 10815, left M1	8.00	11.50	
P. grangeri			
DPC 695, left m2	9.40	6.50	
DPC 2666, left p2	X	X	
DPC 3229, left M2	7.55	13.10	
DPC 5458, right p3	11.70	5.90	
DPC 7293, M3	X	X	
DPC 10262, left p4	12.30	7.00	
DPC 10296, left p2	7.80	4.35	
DPC 10298, left M3	5.00	7.85	
DPC 10309, left m3	7.30	4.70	
DPC 10354, right p4	14.30	7.35	
DPC 10408, right M1	9.05	14.50	
DPC 10816, right p4	12.60	7.15	
DPC 12441, right m1	9.60	6.45	
CGM field 87-54, right p4	13.20	6.55	
Skull and dentition			
P. grangeri, DPC 10684			
Right I2	4.30	3.10	
Right C	9.20	6.10	
Left C	9.00	5.85	
Right C, height*			20.60
Left C, height*			23.18
Right P4	12.10	12.30	
Left P4	12.15	11.70	
Left M2	X	11.85	
I1–M3 alveoli, right	84.60		
I1–M3 alveoli, left	88.71		
Palatal length	86.70		
Back of palate to back of occipital condyles			90.45
Breadth of nasal aperture			14.20
Base of nasals to top of premaxilla			17.00
Tip of nasals to base of saggital crest			93.00
Breadth of frontals across orbits			44.05
Skull length			178.20

The lower tooth width was measured across the talonid. X, Broken specimen.
*Tip of crown to contact of root with maxillary bone.

Description of new dental elements. DPC 73, DPC 6281, and DPC 6500 are the only new specimens of ptolemaiids preserving teeth (P3 and P4) that were unknown to us in 1987. DPC 12435 is a new and magnificent lower jaw but yields no additional information beyond that provided by the type specimen and DPC 4545. DPC 3994, a right M2, formerly identified by us (4) as *C. ayeshae*, is transferred to *P. grangeri*.

P3 and P4 of *C. ayeshae* (Fig. 1*A*) are very similar to each other. Both are bunodont with a small protocone and a much larger paracone, have a moderately sized protoconule and smaller metaconule, possess small parastyles, and lack cingula. P4 is slightly larger than P3 but is not molariform nor does it

possess the large parastyle seen in *P. grangeri*. Measurements of P3 and P4 of *C. ayeshae* are in Table 1.

DISCUSSION AND CONCLUSIONS

The history of study of the possible relationships of ptolemaiid mammals was reviewed most recently by Bown and Simons (4). Osborn (2) suggested that the dental peculiarities of *P. lyonsi* perhaps warranted its placement in a new order. However, most recent workers have consistently linked the ptolemaiids to and compared them with various members of what now stands as McKenna's (5) cimolestan suborder Pantolesta (3, 4, 6–14). Bown and Simons (4) believed *Qarunavus* to be the most generalized ptolemaiid and that there was a major but poorly understood radiation of these mammals in the early Tertiary of Africa, with monotypic *Qarunavus* and the two species of *Cleopatrodon* constituting a conservative line, and *P. lyonsi* and *P. grangeri* belonging to another, dentally more advanced lineage. The new specimens of *C. ayeshae* and especially of *P. grangeri* described above, together with information about new specimens of paroxyclaenid pantolestans from the Eocene of Europe, materially alter only our conclusions about the ordinal affinities of the Ptolemaiidae. *Ptolemaia, Qarunavus*, and *Cleopatrodon*, though perhaps ultimately of pantolestan derivation, possess sufficient gnathic and cranial specializations to warrant their recognition as a new order of mammals, here named the Ptolemaiida.

Russell and Godinot (14) described in 1988 two new genera of paroxyclaenid pantolestans (*Euhookeria* and *Merialus*) from upper Eocene rocks of England and lower Eocene rocks of France, respectively, and placed them in a new subfamily of the pantolestan Paroxyclaenidae, the Merialinae. With regard to *Ptolemaia*, Russell and Godinot (p. 328 of ref. 14) noted that "..perhaps a particular relationship to the merialine paroxyclaenids is discernable." Merialines differ from paroxyclaenines in (*i*) having lingually situated molar paraconids that are close to the metaconids, (*ii*) possessing simple premolariform premolars, and (*iii*) lacking a metaconid on p4. It is in these three merialine characters (of which at least the second and third are surely plesiomorphic) that the merialines vaguely resemble *Cleopatrodon* and *Qarunavus*; however, we record several qualifications. First, the permanent p4 is unknown in *Qarunavus*; second, the p4 in *Cleopatrodon* is semimolariform and possesses two talonid cusps and has either a metaconid or a greatly expanded protoconid; and last, the p4 in *P. grangeri* (and possibly *P. lyonsi* as well) is fully molariform and has not only distinct but also large, paraconid, metaconid, hypoconulid, entoconid, and hypoconid cusps.

No other mammalian order shares the combination of dental characters seen in ptolemaiids. Whereas it may ultimately be proven that the Ptolemaiida were derived from the Order Cimolesta, and even from the merialine paroxyclaenids, no meaningful diagnosis of either group is broad enough to include *Ptolemaia* and its bizarre dental specializations. *Ptolemaia, Qarunavus*, and *Cleopatrodon* are morphologically very distant from *Merialus* and *Euhookeria*, their closest mammalian counterparts, and they are, correspondingly, equally distant from the order and suborder containing the Merialinae. A hallmark of the Pantolesta (and the order Cimolesta in general) is the lack of pronounced dental specializations—a circumstance that has caused members of that group (under various taxonomic appellations) to have been referred together with many other relatively generalized (and unrelated) mammals in the "Insectivora" or "Proteutheria" for half a century. Both *Merialus* and *Euhookeria* are very poorly known, and additional material (especially of *Euhookeria*) may show that both are perhaps best regarded to be members of early, very generalized branches of the Order Ptolemaiida.

The ordinal status of the Ptolemaiida is rendered more interesting, but none the less secure, by the descriptions of *Qarunavus* and *Cleopatrodon* and the recognition of their relationship to *Ptolemaia*. Those two genera are clearly the most generalized members of the Ptolemaiida and, quixotically, appear to have survived the latest (*Cleopatrodon robusta* from quarry I, 244-m level of Jebel Qatrani Formation). What the Fayum ptolemaiids clearly constitute is a small sample of specimens taken from a largely unknown but significant radiation of a unique group—all collected from rocks recording a brief interval of time, and all taken from a tiny area in the Fayum Depression of Egypt.

When assuming that an animal dentally similar to *Cleopatrodon* or *Qarunavus* formed part of the ancestry of *Ptolemaia*, trends in the evolution of the ptolemaiid dentition included: (*i*) increase in proportionate size and height of P3/3–M1/1; (*ii*) decrease in proportionate size and height of P2/2 and M2/2–M3/3; (*iii*) hypertrophy of P3/3–M3/3; (*iv*) decrease in size or loss of P1/1–P2/2; and (*v*) loss of transverse shear capacity in all teeth. Wear on ptolemaiid teeth is usually extensive and on P3/3–M2/2, even in the early stages, generally records no shear (i.e., it is rapidly flattening the topography of both the upper and lower cheek teeth). In Fig. 2, it is seen that p2–m3 of *P. grangeri* form a convex-upward arcuate pattern, the most hypsodont (and most worn) teeth occurring at the apex of the arc. In contrast, the upper cheek teeth (Fig. 1*B*), with the exception of the massive P4 and M1, are diminutive and exceptionally shallow-rooted, apparently having acted as a pestle against which worked the center of the massive lower dental battery.

A combination of morphology and the wear on teeth of *P. grangeri* suggests that the function of such a dental array was largely vertical crushing with virtually no shear capacity. The extreme hypsodonty and wear on p3–m2 supports this hypothesis and indicates that the food utilized consisted principally of a resilient, abrasive material. Dorr (11) fancifully conjectured that the pantolestine pantolestan *Palaeosinopa simpsoni*, which possesses a pattern of similar flat, apical molar wear, but lacks the hypertrophy of the central cheek teeth seen in *Ptolemaia*, might have incorporated insects and mollusks as the major portion of its food. Whereas a similar mode of life is possible for the ptolemaiids, there is as yet insufficient evidence to determine what might have been the principal food preferences of Ptolemaiida.

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