Fossil and molecular evidence constrain scenarios for the early evolutionary and biogeographic history of hystricognathous rodents

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The early evolutionary and paleobiogeographic history of the diverse rodent clade Hystricognathi, which contains Hystricidae (Old World porcupines), Caviomorpha (the endemic South American rodents), and African Phiomorpha (cane rats, dassie rats, and blesmols) is of great interest to students of mammalian evolution, but remains poorly understood because of a poor early fossil record. Here we describe the oldest well-dated hystricognathous rodents from an earliest late Eocene (≈ 37 Ma) fossil locality in the Fayum Depression of northern Egypt. These taxa exhibit a combination of primitive and derived features, the former shared with Asian “baluchimyine” rodents, and the latter shared with Oligocene phiomorphs and caviomorphs. Phylogenetic analysis incorporating morphological, temporal, geographic, and molecular information places the new taxa as successive sister groups of crown Hystricognathi, and supports an Asian origin for stem Hystricognathi and an Afro-Arabian origin for crown Hystricognathi, stem Hystricidae, and stem Caviomorpha. Molecular dating of early divergences within Hystricognathi, using a Bayesian “relaxed clock” approach and multiple fossil calibrations, suggests that the split between Hystricidae and the phiomorph-caviomorph clade occurred ≈ 39 Ma, and that phiomorphs and caviomorphs diverged ≈ 36 Ma. These results are remarkably congruent with our phylogenetic results and the fossil record of hystricognathous rodent evolution in Afro-Arabia and South America.

Caviomorpha | Eocene | Hystricidae | Oligocene | Phiomorpha

The fossiliferous sedimentary deposits exposed north of Birket Qarun in the Fayum Depression, northeast Egypt, have produced a remarkable collection of fossil mammals from localities that range in age from earliest late Eocene (≈ 37 Ma, early Priabonian) to latest early Oligocene (≈ 29 Ma, late Rupelian) (1–3). Among the more common mammals represented in these deposits are primitive members of the hystricognathous rodent clade Phiomorpha, now represented by the living cane rats (Thryonomyidae), dassie rats (Petruridae), and blesmols (Bathergidae). Early Oligocene (i.e., ≈ 33.9 – 28.5 Ma) phiomorphs from Egypt have played a central role in debates surrounding the origin of Hystricognathi (4, 5), a large radiation currently represented by 230 extant species; in addition to Phiomorpha, the group also includes the New World Caviomorpha and Old World porcupines of the family Hystricidae (6). Members of Hystricognathi are distinguished from other rodents by a number of derived anatomical features, most notably the placement of the angular process on the mandible, which is situated lateral to the long axis of the lower incisor, rather than in the same plane as the lower incisor (as in taxa with “sciurognathous” mandibles) (7).

The distribution of early fossil phiomorphs and caviomorphs on isolated southern landmasses during the Paleogene is a longstanding paleobiogeographic problem in mammalian evolution (8, 9). The discovery of hystricognathous tsaganomyid (10) and “baluchimyine” (11–13) rodents in Paleogene deposits of Asia has been interpreted as supporting an Asian origin for the stem lineage of Hystricognathi (10, 13, 14), but because early phiomorphs and caviomorphs have strictly

Afro-Arabian and South American distributions, respectively, the early biogeographic history of crown Hystricognathi remains a matter of persistent debate. Some have argued that phiomorphs and caviomorphs are likely to have shared a common Afro-Arabian ancestor (15–17), while others have suggested that the phiomorph-caviomorph split might have occurred in Asia, and that caviomorphs dispersed to South America either through Afro-Arabia or via a southern Gondwanan route (13, 18). One critical issue that has hindered understanding of the group’s historical biogeography is the phylogenetic position of the family Hystricidae, which has been placed as either the sister group of a phiomorph-caviomorph clade or as the sister group of Caviomorpha, in recent molecular phylogenetic analyses (9, 19–21). Temporal and tectonic constraints on competing biogeographic hypotheses have also been limited by radically different molecular estimates of the phiomorph-caviomorph split, which range in age from ≈ 85 Ma to ≈ 36 Ma (9, 18, 19, 22, 23).

Here we present two lines of evidence that help to constrain competing scenarios for the early evolutionary and biogeographic history of Hystricognathi. First, we describe the oldest well-dated hystricognathous rodents, based on a number of recently recovered mandibular and maxillary remains and isolated teeth of two recently discovered species from a ≈ 37 Ma locality in the Fayum Depression. Second, we present independent estimates for the time of origin of crown Hystricognathi, and for the divergence between Caviomorpha and Phiomorpha, employing a Bayesian “relaxed clock” analysis of a recently published molecular dataset that provided strong support for the placement of Hystricidae as a sister group of a Phiomorpha-Caviomorpha clade (24). The fossil and molecular evidence are remarkably congruent in suggesting an Afro-Arabian origin of crown Hystricognathi in the late-middle Eocene, and a late Eocene divergence of Caviomorpha and Phiomorpha.

Cusp and crest nomenclature follows Wood and Wilson (25) and Marivaux et al. (14) [see [supporting information \(SI\) Fig. S1](#)].

Results

Systematic Paleontology. Placentalia Owen, 1837; Order Rodentia Bowdich, 1821; Infraorder Hystricognathi Tullberg, 1899; Genus *Protophiomys* Jaeger et al., 1985.

Type Species. *Protophiomys algeriensis* Jaeger et al., 1985.

Distribution. Late Eocene of eastern Algeria and northern Egypt and possibly Namibia (26).

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Fig. 1. Isolated teeth of *Protophiomys aegyptensis*, sp. nov. (A) DPC 21220G, right DP⁴; (B) DPC 21385J, right DP⁴; (C) DPC 21360G, left P⁴; (D) DPC 21452H, right P⁴; (E) DPC 21371M, right M¹; (F) DPC 21293Q, right M¹; (G) DPC 21500N, left M¹; (H) DPC 21294H, right M²; (I) CGM 83695, holotype right M²; (J) DPC 21538G, left M²; (K) DPC 21221I, left M²; (L) DPC 21747K, left M²; (M) DPC 21452I, left M³; (N) DPC 21374I, right M³; (O) DPC 21358K, left DP₄; (P) DPC 21488I, right M₁; (Q) DPC 21747L, right M₁; (R) DPC 21538H, left M₁; (S) DPC 21374J, left M₁; (T) DPC 21296I, right M₂; (U) DPC 21221G, right M₂; (V) DPC 21360I, right M₂; (W) DPC 21294I, right M₃; (X) DPC 21365F, right M₃; (Y) DPC 21220I, right M₃.

Emended Diagnosis. Cheek teeth with low cusps and lophs; metaloph joins the metaconule and never connects to the posteroloph; mesolophule is weakly-developed or nonexistent on the upper cheek teeth; endoloph present on M²⁻³; metalophulid II is short on lower cheek teeth; anterior cingulid is either very weak or absent altogether on lower molars.

***Protophiomys aegyptensis*, New Species.**

Etymology. Specific epithet is from *aegyptos*, Greek for Egypt.

Holotype. CGM 83695, an upper right M² (Fig. 1I).

Type Locality. Birket Qarun Locality 2 (BQ-2), Fayum, Egypt.

Formation and Age. Umm Rigl Member of Birket Qarun Formation, earliest Priabonian in age (≈ 37 Ma).

Diagnosis. *P. aegyptensis* differs from the type species *P. algeriensis* in exhibiting the following combination of features: DP⁴ (Fig. 1*A* and *B*) lacks a complete endoloph and does not bear an x-shaped pattern of crests around the metaconule; cheek teeth all larger in size (see [Table S1](#)); central basin of upper cheek teeth (Fig. 1*E–N*) is open labially via a narrow notch; mesolophule is weak and variably reaches the labial wall, connecting with the mesostyle of M²; lower cheek teeth have a relatively short metalophulid II that never reaches the midline of the tooth and is oriented toward either the lingual wall or the metaconid; DP₄ is relatively long and narrow, with a longer anterior basin, a metaconid that is placed transverse to the protoconid, a complete posterior arm of the protoconid, and a well-developed anterior arm of the protoconid with an anteroconid; M₁ differs in having a strong metalophulid I that connects the metaconid with the protoconid, and in having a very weak anterocingulid; a notch is present between a long posterior arm of the metaconid and the entoconid on the lingual wall; ectostylid is present; posterior basin is long and has a relatively low posterolophid that weakly connects with the entoconid on M₃.

Description. DP⁴ (see Fig. 1*A* and *B*) is a small molariform tooth with crown length greater than width; the lingual margin is narrower than the labial margin. The primary cusps are almost equal in height, but the protocone and hypocone are larger in occlusal view, with crests that are more obliquely oriented than those on the paracone and metacone. There is no mesolophule. The anteroloph is low and weak and fuses with a small parastyle near the base of the paracone. The metaloph courses lingually from the metacone parallel to the protoloph; it is connected to the metaconule via a short and weakly developed crest. A well-developed metaconule is connected to the hypocone via the latter cusp's anterior arm. The posteroloph runs labially from the hypocone, coursing around the posterior margin of the tooth, but does not connect to the metacone, leaving a small notch.

Isolated P⁴s attributable to *P. aegyptensis* demonstrate that the species replaced its DP⁴ during life, unlike the derived phiomorphs that appear in the same area later in the Paleogene. P⁴ is roughly triangular in outline (Fig. 1 C and D) and smaller than DP⁴. The paracone and metacone are equal in size and separated by a deep notch. The anteroloph is the weakest and lowest of the 4 transverse lophs. The metaloph and the posteroloph connect the metacone to a very small hypocone. The protocone is connected to the small hypocone by an endoloph.

M¹ (see Fig. 1 *E–G*) is roughly square in shape and bears 4 primary cusps, as well as a small, centrally placed metaconule. The hypocone is directly distal to the protocone and connects to the metaconule via a long anterior arm. The labial wall bears a deep notch between the posterior arm of the paracone and the anterior arm of the metacone; a small mesostyle is variably present. The anteroloph runs parallel to the protoloph to connect to the mesial base of the paracone; a small parastyle is present. The M¹ lacks an endoloph, and the lingual sinus is continuous with the central basin. The curved metaloph runs lingually and then mesially to connect to the metaconule and is never oriented distally toward the posteroloph. The mesolophule and mure are either very weak or absent altogether.

M² (see Fig. 1*H-L*) is the largest upper cheek tooth. Overall it is very similar to M¹, but differs in having a relatively reduced and more labially situated hypocone, a taller and more curved anteroloph, an endoloph that reaches the anterior arm of the hypocone (closing the lingual side

Fig. 2. Mandibles, maxillae, and isolated teeth of *Waslamys attiai*, gen. et sp. nov. (A) DPC 21360H, right DP⁴; (B) 21365E, right DP⁴; (C) 21296K, right P⁴; (D) DPC 21294G, left M¹; (E) DPC 21452K, left M¹; (F) 21221H, right M²; (G) DPC 21296B, left M²; (H) DPC 23305H, left M²; (I) DPC 21374G, left maxillary fragment with DP⁴; (J) DPC 23305G, right maxillary fragment with P⁴; (K) DPC 21358I, left maxilla with M²⁻³; (L) CGM 83690, right maxilla with P⁴-M³; (M) DPC 21293P, left DP⁴; (N) DPC 21371N, left P⁴; (O) DPC 21365D, left P⁴; (P) DPC 22442L, right M¹; (Q) DPC 21839H, right M¹; (R) DPC 21371L, right M²; (S) DPC 21296C, left mandible with M²⁻³; (T) DPC 21296J, right M³; (U) DPC 21220H, left M³; (V) DPC 21488H, left mandible with M¹⁻²; (W) DPC 21452J, left mandible with P⁴-M²; (X) DPC 21488H, left mandible with M¹⁻²; (Y) DPC 21220I, right M³.

of the central basin), greater development of the mure (although that crest never reaches the protoloph), a weak and interrupted mesolophule that variably reaches the mesostyle on the labial wall, a more narrow labial notch, and a relatively short and low posteroloph that is connected to the base of the metacone.

M³ (see Fig. 1 *M* and *N*) is heart-shaped and is the smallest upper molar. It differs from M¹⁻² in having a reduced metacone and hypocone, the latter of which is labially positioned. A weak mure reaches the midline of the protoloph. An obliquely oriented meta-
loph courses from the lingual side of the metacone and connects to the metaconule. There is no mesolophule, and the endoloph is low.

The P⁴ of *P. aegyptensis* is not yet known. The DP⁴ (Fig. 1*O*) has a broad talonid and a narrow trigonid. The “anterolophid” runs from the anterior side of the protoconid toward the mesial side of the metaconid and terminates mesiolabially to the metaconid, leaving a wide notch in the anterior wall of the anterior basin. The metaconid is placed transverse to the protoconid, and a similarly transversely oriented posterior arm of the protoconid joins these cusps. A well-developed anterior arm of the hypoconid attaches to the hypolophid near that crest’s junction with the ectolophid. A short mesolophid protrudes from a weak mesoconid. The posterior arm of the metaconid occupies most of the area between the metaconid and entoconid, and there is a wide notch in the lingual wall. A well-developed hypoconulid is present. The posterior basin is open lingually. The labial sinus is wide and deep and bears a worn ectostylid.

The M¹ (Fig. 1 *P–S*) is rectangular in outline and has 5 major cusps. The mesial part of the tooth is narrower than the distal part. A very weak and low anterocingulid runs parallel to the metalophid I, which is medially interrupted in some individuals. The metalophid II is short and never reaches the midline of the tooth. The posterior arm of the metaconid forms most of the lingual wall and is interrupted by a narrow notch at the base, where a very short anterior arm of the entoconid is present. A mesostylid is variably present. The posterolophid does not

connect to the entoconid, and the transverse hypolophid runs labially from the entoconid to the confluence of the ectolophid and anterior arm of the hypoconid. In the labial sinusid there is a well-developed ectostylid. The hypoconulid is distinct, and a low, poorly developed postcingulid runs labially from that cusp.

The M² (Fig. 1 *T–V*) is generally similar to M¹, but differs in having trigonids and talonids of almost equal width, and a well-developed mesostylid at the end of the posterior arm of the metaconid. An incipient anterocingulid is present on the M² of one individual (Fig. 2*T*). The M³ (Fig. 1 *W–Y*) is the longest lower molar. The metaconid is tall and mesially situated and the distal part of the crown is relatively long and narrow. The hypoconulid is submerged into the posterolophid and the ectostylid is relatively small.

***Waslamys*, New Genus.**

Type Species. *Waslamys attiai*, New Species.

Etymology. Combination of *wasla*, Arabic for “joint, junction, or connection,” in reference to the combination of dental features seen in later African phiomorphs and Asian baluchimyines, and *mys*, Greek for mouse.

Generic Diagnosis. As for the type species.

Waslamys attiai, New Species.

Etymology. In honor of the late Yousry Attia, for his important contributions to the study of vertebrate paleontology in Egypt.

Holotype. CGM 83690, a right maxilla with P⁴-M³.

Type Locality. Birket Qarun Locality 2 (BQ-2), Fayum, Egypt.

Formation and Age. Umm Rigl Member of Birket Qarun Formation, earliest Priabonian in age (≈ 37 Ma).

Phylogenetic Analysis. We added 20 additional stem and crown hystricognathous rodents (including *P. aegyptensis* and *Waslamys*), and 7 additional morphological characters to Marivaux et al.'s (14) matrix, and analyzed the interrelationships of stem and crown Hystricognathi using various approaches, including addition of a chronobiogeographic character. Parsimony analysis of morphological features alone in PAUP* 4.0b10 (Fig. S2) recovers a topology that is inconsistent with recent molecular results by nesting Hystricidae within Caviomorpha; this result is also highly unparsimonious biogeographically in implying a South American origin for the clade containing both Hystricidae and the late Eocene African genus *Gaudeamus*. All of the later Paleogene African rodents are placed as stem hystricognaths, rather than as phiomorphs, as is traditionally thought (4). Parsimony analysis following implementation of a backbone constraint (constraining the South American caviomorphs and the extant phiomorph *Thryonomys* to be the sister group of Hystricidae) again places all of the Paleogene African rodents as stem hystricognaths. These peculiar results are likely due to the highly autapomorphic molar teeth of extant *Thryonomys*, which has converged on similarly specialized hystricids and caviomorphs. Both of these analyses most parsimoniously reconstruct an Afro-Arabian origin for crown Hystricognathi.

The topology recovered from our chronobiogeographic analysis (Fig. 3), in which we constrained Oligocene African phiomorphs such as *Phiomys*, *Paraphiomys*, and *Metaphiomys* to be placed closer to the Phiomorpha-Caviomorpha clade than to Hystricidae, is more consistent with previous interpretations in placing *Phiomys* and *Metaphiomys* as stem phiomorphs; *Thryonomys* is nested deep within a phiomorph clade whose earliest members date to ≈ 34 Ma. *Gaudeamus* is again placed as a sister taxon of Hystricidae; to our knowledge this is a unique result that has not been previously considered. *Protophiomys* and *Waslamys* are placed as consecutive sister taxa of crown Hystricognathi, while all of the Asian baluchimyines fall outside of that clade. Baluchimyines (i.e., *Baluchimys*, *Bugtimys*, *Hodsahibia*, *Lindsaya*, and *Lophibaluchia*) are clearly paraphyletic with respect to crown Hystricognathi, and the complex stem lineage of Hystricognathi is expanded to include other enigmatic Paleogene taxa, such as *Sacaresia* from the Oligocene of Mallorca (27) and *Confiniummys* and *Ottomania* from near the Eocene-Oligocene boundary in Turkey (28).

Molecular Dating. We used a Bayesian relaxed molecular clock method to date the origin of crown Hystricognathi and the split between Phiomorpha and Caviomorpha. The method was implemented by the *mcmctree* program of PAML v. 4.2 (29), using Blanga-Kanfi et al.'s (24) recently published DNA sequence dataset, comprised of 6 nuclear genes from 49 taxa. The mean estimates for the nodes of interest (Table S2, Fig. S3, Fig. 4) are about 15% younger than those presented in a recent analysis (19), but are remarkably congruent with the fossil record. The divergence of Caviomorpha and Phiomorpha is estimated to have occurred at 36.1 Ma (95% credibility interval 33.4–39.0 Ma), very close to Opazo's (22) previously published estimate of 36.6 ± 2.5 Ma. Based on the results of our chronobiogeographic analysis, there are no stem phiomorphs present at the ≈ 37 Ma Locality BQ-2, and the oldest stem phiomorph fossils are found at a ≈ 34 Ma site [Quarry L-41 (3)]. The oldest caviomorph fossils are at least 31.5 Ma (30), perhaps even older (31), leaving a ≈ 4 million year-long window for the caviomorph dispersal to South America in either the latest Eocene or earliest Oligocene. The origin of crown Hystricognathi is estimated to be 39.0 Ma (95% credibility interval 36.1–41.9 Ma): that is, ≈ 2 Ma older than *P. aegyptensis* and *Waslamys*. The taxon identified as the oldest stem hystricid in our analysis is ≈ 34 Ma *Gaudeamus*, which already has a highly derived dental pattern at the time of its first appearance in the fossil record (4), suggesting a substantial previous phase of evolution in Afro-Arabia. Again, this result would be consistent with an early (≈ 39 Ma) origin of stem Hystricidae in Africa, but these results contradict a previous analysis

Fig. 4. Molecular clock estimates for divergence dates within Ctenohystera. Date estimates in Ma appear in white at each node. These estimates are the mean of the posterior distribution. The 95% credibility intervals are represented by thick horizontal bars at each node. Within this part of the tree, there is 1 calibration at >50 Ma, which is shown at the most basal node. See the *SI Text* for the complete tree, including all node estimates and their 95% credibility intervals.

that aligned *Gaudeamus* with extant *Thryonomys* to the exclusion of highly derived Oligocene and Miocene phiomorphs (32), because our molecular dating results estimate that *Thryonomys* diverged from *Petromys* in the early Miocene, around 18 Ma.

Discussion

Previously, the oldest known hystricognathous rodent was late Eocene *Protophiomys algeriensis* from Bir el-Ater in Algeria (33). We consider it likely that *P. aegyptensis* and *Waslamys attiai* are at least slightly older than the relatively poorly-dated *P. algeriensis*, because BQ-2 and nearby contemporaneous localities lack any evidence for the presence of the immigrant artiodactyl family Anthracotheriidae, a group that otherwise makes its first appearance in Afro-Arabia at Bir el-Ater. Furthermore, Jaeger et al. noted that “several species of [undescribed] phiomysids...are recorded in this locality [Bir el-Ater], and they can be related to some of the Oligocene Fayum phiomysids” (ref. 33, p. 575). There are no derived phiomysid taxa at BQ-2, again supporting an earlier age for this level.

Jaeger et al. placed *P. algeriensis* in the family Phiomysidae, but cautioned that it was “premature to consider these species as closely related phylogenetically. *Protophiomys algeriensis* can be considered as an upper Eocene primitive morphotype in the evolution of African phiomysids.” (ref. 33, p. 575). The genus was subsequently reevaluated by Flynn et al. as being a “chapattimyid of baluchimyine affinity” (ref. 11, p. 51). Marivaux et al.'s (13) phylogenetic analysis of dental characters found the phiomorph-caviomorph clade to be more closely related to two Oligocene Asian baluchimyine lineages (*Bugtimys-Hodsahibia* and *Lophibaluchia*) than to *Protophiomys*. Their topology implies two independent dispersals of hystricognathous rodents into Afro-Arabia: one from within a paraphyletic “Baluchimyinae” that gave rise to *Protophiomys*, and another that gave rise to either phiomorphs alone or to a phiomorph-caviomorph clade.

The topology derived from our chronobiogeographic analysis implies that *Protophiomys* and *Waslamys* are advanced stem members of Hystricognathi, and that a dispersal from Asia to Afro-Arabia occurred along a deeper portion of the stem lineage of

Hystricognathi. The very slight morphological differences separating Asian baluchimyines and the earliest Afro-Arabian taxa, such as *Protophiomys* and *Waslamys*, strongly suggests that these taxa record what are, perhaps, the very earliest stages of hystricognathous rodent evolution in Afro-Arabia. This hypothesis is further supported by the lack of morphological diversity observable among the hystricognathous rodents represented at BQ-2. This scenario is clearly not consistent with molecular estimates for the time of origin of crown Hystricognathi that range in age from ≈ 85 to ≈ 43 Ma (9, 18, 19, 23, 34).

The temporal and phylogenetic evidence provided by these fossil discoveries, combined with younger molecular estimates for basal divergences within crown Hystricognathi, suggests that the key events determining the distribution of Oligocene-to-Recent hystricognathous rodents occurred between ≈ 40 and ≈ 34 million years ago. Afro-Arabia and South America were fully isolated during this interval, so vicariance (31) can clearly be ruled out as a mechanism underlying the divergence between Phiomorpha and Caviomorpha. As appears to have been the case for platyrrhine anthropoids (35), the caviomorph colonization of South America evidently occurred via a chance dispersal from Afro-Arabia across the vast South Atlantic. Future paleontological research in the late middle Eocene of Afro-Arabia and Asia should help to further clarify the later stages of evolution along the stem lineage of Hystricognathi, while recovery of fossils between ≈ 37 and ≈ 34 Ma in Afro-Arabia should help to illuminate the nature of the caviomorph-phiomorph split.

Materials and Methods

Phylogenetic analysis was based on a modified version of Marivaux et al.'s (14) morphological character matrix. The chronobiogeographic character takes into account temporal succession of fossil taxa [as in stratocladistics (36)] and also adds a step to tree length for every implied transoceanic dispersal (given reconstructed paleogeography) (37). (See *SI Materials and Methods*).

Molecular dating was implemented by the *mcmcree* program of PAML v. 4.2 (29), using Blanga-Kanfi et al.'s (24) DNA sequence dataset, comprised of 6 nuclear genes from 49 taxa (rodents as well as lagomorph and euarchontan outgroups; see *SI Materials and Methods*). This molecular clock analysis was calibrated with 10 "soft bounds" (38, 39) from the fossil record. Seven of these calibrations were within Rodentia but outside of crown Hystricognathi, which allowed date estimates that were independent of the controversial early fossil record of hystricognathous rodents. Importantly, we considered it likely that, based on the reasonably good early fossil record of stem and crown rodent evolution, crown Rodentia likely did not originate before the K-T boundary. Cretaceous zambdalestids previously identified as members of Glires (40), and often used as "upper bound" calibrations for the time of origin of Glires in molecular dating analyses (19), are here considered to be stem placentals (41).

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