Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography

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The long-term isolation of South America during most of the Cenozoic produced a highly peculiar terrestrial vertebrate biota, with a wide array of mammal groups, among which caviomorph rodents and platyrrhine primates are Mid-Cenozoic immigrants. In the absence of indisputable pre-Oligocene South American rodents or primates, the mode, timing and biogeography of these extraordinary dispersals remained debated. Here, we describe South America’s oldest known rodents, based on a new diverse caviomorph assemblage from the late Middle Eocene (approx. 41 Ma) of Peru, including five small rodents with three stem caviomorphs. Instead of being tied to the Eocene/Oligocene global cooling and drying episode (approx. 34 Ma), as previously considered, the arrival of caviomorphs and their initial radiation in South America probably occurred under much warmer and wetter conditions, around the Mid-Eocene Climatic Optimum. Our phylogenetic results reaffirm the African origin of South American rodents and support a trans-Atlantic dispersal of these mammals during Middle Eocene times. This discovery further extends the gap (approx. 15 Myr) between first appearances of rodents and primates in South America.

Keywords: South America; Hystricognathi; Mid-Eocene climatic optimum; phylogeny; Platyrhini

1. INTRODUCTION

The origin and biogeographic history of South American caviomorph rodents (e.g. guinea pigs, chinchillas, capybara) and platyrrhine primates (e.g. marmosets, capuchins, spider monkeys) are hotly debated issues in mammal evolution [1–14]. Fossil-constrained molecular analyses for both groups suggest either a Cretaceous vicariance event related to the break-up of Gondwana or an Eocene dispersal to South America, probably from Africa [9,15]. In the absence of indisputable pre-Oligocene South American rodent or primate fossils [16–18], the mode, timing and biogeography of these dispersals have so far remained poorly constrained [5,13,19,20]. Until now, the earliest South American hystricognathous rodents described, from low-latitude Santa Rosa [21], Peru (latest Eocene–Oligocene [13,20]) and higher-latitude Tinguiririca [5,19], Chile (earliest Oligocene, approx. 32 Ma), primarily included crown-group caviomorphs, thereby suggesting a much earlier in situ initial radiation of the group.

Here, we report the discovery of the oldest known South American caviomorphs, deriving from a 30-cm-thick lens of light-grey clay with irregular limestone concretions at the top of the Yahuarango Formation [22], designated CTA-27 (figure 1). A Middle Eocene age for CTA-27 (earlier than 40.94 Ma) is based on 40Ar/39Ar step heating of single
Figure 1. Stratigraphical range of CTA-27 locality (inferred by radioisotopy, vertebrate biochronology and palynostratigraphy) and Mid-Cenozoic global climate. The age of CTA-27 is bracketed between 41.6 Ma (base of the Gran Barranca Member [23,24]) and 40.94 Ma (youngest age provided by 40Ar/39Ar datings at CTA-29; electronic supplementary material, figure S6). Age of both key Palaeogene vertebrate localities and biotic events of South America are based on data from Flynn et al. [19], Goin et al. [25,26], Goin & Candela [27], Shockey et al. [28], López [29] and Vucetich et al. [13]. Global climate is inferred by the δ18O temperature scale of Zachos et al. [30] (red curve to the right), showing the Mid-Eocene Climatic Optimum by the time of deposition of CTA-27. Barran., Barrancan; Barton., Bartonian; FAD, first appearance datum; Mus., Mustersan; Priabon., Priabonian; SALMA, South American Land Mammal Age; Tingui., Tinguirirican.

The specimens described here are permanently stored in the Museum of Natural History in Lima, Peru (MUSM). These new rodents allow us to document the pattern and the timing of major events in early hystriognath evolution and biogeography.

2. RESULTS

Systematic palaeontology

Placentalia Owen, 1837; Order Rodentia Bowdich, 1821; Infraorder Hystriognathi Tullberg, 1899; Parvorder Caviomorpha Wood, 1955.

Plesion Cachiyaucy, New Genus.

Type species. Cachiyaucy contamantensis, New Species.

Etymology. Contraction of Cachiyaucy (Local River) and cuz, Quechua for guinea pig.

Generic Diagnosis. Rodents characterized by brachydont and bunolophodont teeth. Upper molars are pentalophodont with strong mesolophule and distinct and long metaloph. Differs from Eobransamys, Bransamys, Esollamys, Salamys, Eoespina and Draconomys in showing a long metaloph not backwardly directed and connected to the posteroloph, but transverse and without lingual connection. Accessory, thin and short enamel crests may connect the metaloph to the posteroloph and/or to the mesolophule. Differs from

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Eobransamys, Bransamys and Cananaimys in the absence of a taeniodont pattern on upper teeth owing to the presence of a strong lingual protoloph. Differs from Eobransamys and Incamys in having brachydont instead of hypsodont teeth, pentalophodont instead of tetralophodont upper molars, thinner and transverse instead of strong and oblique crests, and in the absence of a taeniodont pattern on both upper and lower teeth (i.e. lingual protoloph and anterior arm of hypoconid lacking).

Other species. Cachiyacuy kummeli, New Species.

Formation and age. Top of the Yahuarango Formation [22], latest Lutetian in age (≈41 Ma).

Cachiyacuy contamanensis, New Species.

Etymology. Refers to the geographical provenance of the specimens, close to the city of Contamana.

Holotype. MUSM 1871, a right M² (figure 2b).

Type locality. CTA-27 Locality, Loreto, Peru.

Diagnosis. Cachiyacuy contamanensis (body mass estimated at 80–120 g) is approximately 30 per cent larger than C. kummeli. Differs from C. kummeli in having upper molars with generally buccal cusps and styles more marked, and lower molars sometimes developing accessory enamel crests.

Cachiyacuy kummeli, New Species.

Etymology. Dedicated to Bernhard Kummel, the geologist who first extensively described the Cachiyacu section in the 1940s [22].

Holotype. MUSM 1882, a left M¹ (figure 2m).

Type locality. CTA-27 Locality, Loreto, Peru.

Formation and age. Top of the Yahuarango Formation, latest Lutetian in age (approx. 41 Ma).

Diagnosis. Cachiyacuy kummeli (body mass estimated at 30–40 g) is approximately 30 per cent smaller than C. contamanensis. The molars have slightly thinner transverse crests and the cusp(ids) are more salient than in C. contamanensis.

Plesion Cananaimys, New Genus.

Type species. Cananaimys maquienis, New Species.

Etymology. Combination of Canaan, name of a local Shipibo native community, and mys, Greek for mouse.

Generic diagnosis. As for the type species.

Cananaimys maquienis, New Species.

Etymology. Specific epithet is for Maquía, the locality where the fossils were found.

Holotype. MUSM 1890, a right M² (figure 2a).

Type locality. CTA-27 Locality, Loreto, Peru.

Formation and age. Top of the Yahuarango Formation [22], latest Lutetian in age (approx. 41 Ma).

Diagnosis. Tiny rodent (body mass estimated at approx. 40 g) characterized by brachydont and bunolophodont teeth. It differs from all other caviomorphs in having teeth with moderately low and sharp transverse crest(ids), lower molars having generally incomplete metalophulid II, and pentalophodont upper molars with a well-developed metaloph that turns anteriorly (not posteriorly) and connects either to the mesolophule lingually or to the mesial extremity of the anterior arm of the hypocone—a primitive condition that is reminiscent of that found in stem Hystricognathi (e.g. Baluchimys, Protohippomys, Wasamys, Phiomys, Hodsuhibia, Bugtimmys and Ottomants). The lingual protoloph is either slightly developed or lacking (i.e. taeniodont pattern).

In addition, four teeth are referred to the cavioid Eobransamys sp. (figure 2a–d) and 2 diminutive teeth to the octodontoid cf. Eoespina sp. (figure 2e–f). The teeth referred to Eobransamys sp., notably the only upper molar (figure 2b'), display features reminiscent of upper molars of Eobransamys romeropittmanae and of Eobransamys riverae from Santa Rosa, Peru [21]. This is particularly evident in the development of a taeniodont (absence of lingual protoloph, i.e. hypoflexus and paraflexus are merged) and pentalophodont pattern, characterized by the presence of a strong and transverse mesolophule, and a strong and distinct metaloph, which is transverse and connected to the posteroloph. However, Eobransamys sp. differs substantially from E. riverae in being about half the size, and from E. riverae in being 20 per cent smaller and in showing sharper crests and more salient cusps (plesiomorphic traits). The 2 diminutive M³'s referred to cf. Eoespina sp. (figure 2e–f) resemble those of Eoespina woodi from Santa Rosa [21], in showing a tetralophodont pattern with strong and long mesolophule, antero-, proto- and posteroloph (no metaloph), and having a rounded crown outline in occlusal view. The specimens from CTA-27 differ in having less inflated cusps, and in showing a mesiodistally narrower and lingually constricted internal sinus (hypoflexus).

3. DISCUSSION

All five rodent taxa currently known from Contamana CTA-27 are remarkably small compared with subsequent caviomorphs (including those from Tinguirirca [5], Santa Rosa [21], La Cantera [13] and younger localities [4]), with a 30–120 g estimated adult body mass range: C. maquienis (figure 2t–z), C. kummeli (figure 2l–s) and cf. Eoespina sp. (figure 2e–f) were meadow vole-sized, while C. contamanensis (figure 2a–k) and Eobransamys sp. (figure 2d–d') were small rat-sized (see the electronic supplementary material). Interestingly, this very small size distribution for the oldest known South American caviomorphs is comparable to that observed in Africa [11] for the earliest known radiation of the sister group: the phiomorphs [2,3,5,8,11]. In addition, the moderate morphological disparity among CTA-27 rodents suggests a short interval of caviomorph evolutionary history in South America prior to the Contamana record (figure 3a). Cachiyacuy, Cananaimys and cf. Eoespina share a similar dental bauplan with the earliest Afro-Asian hystriocognaths (phiomyids [11] and baluchimyines [8]; latest Middle Eocene–Early Oligocene in age; figure 3a), including brachydonty, bunolophodonty, upper molar pentalophodonty [8], low crest obliquity and multi-serial subtype one to two incisor enamel microstructure [34]. This is exemplified by the striking dental resemblances between Cananaimys, Cachiyacuy and their Old World counterparts, such as Protophionys and Baluchimys (for Cananaimys) and Phiomys and Metaphiomys (for Cachiyacuy; figure 3a). CTA-27 thus probably documents the earliest stages of caviomorph evolution (i.e. their first adaptive radiation in South America). However, the dental pattern of Cananaimys is somewhat paradoxical as it appears quite primitive in showing a metaloph configuration that is unique among caviomorphs (otherwise found only in basal phiomyids and baluchimyines), but also quite specialized in having taeniodont upper molars, as in advanced cavioid caviomorphs (figure 2t–v). Some
Figure 2. Scanning electron microscope images (in occlusal view) and dimensions (length × width, in millimetres) of fossil caviomorph teeth from CTA-27. (a–k) Cachiyacuy contamanensis new gen. and sp.: (a) MUSM 1870, right (r) M3 (2.34 × 2.44); (b) MUSM 1871, r M2 (holotype; 2.22 × 2.69); (c) MUSM 1872, left (l) M4 (reversed; 2.07 × 2.22); (d) MUSM 1873, r P4 (1.82 × 2.38); (e) MUSM 1874, l DP4 (reversed; 2.03 × 1.98); (f) MUSM 1875, DP3 (0.77 × 0.82); (g) MUSM 1876, r M3 (2.46 × 2.24); (h) MUSM 1877, r M2 (2.44 × 2.36); (i) MUSM 1878, r M1 (2.15 × 1.99); (j) MUSM 1879, r P4 (1.99 × 2.0); (k) MUSM 1880, r DP4 (2.31 × 1.53). (l–s) Cachiyacuy kummeli new gen. and sp.: (l) MUSM 1881, broken r P4 (reversed; 1.16 × –); (m) MUSM 1882, l M1 (holotype; 1.45 × 1.63); (n) MUSM 1883, l M2 (1.69 × 1.87); (o) MUSM 1884, l M1 (1.67 × 1.71); (p) MUSM 1885, r M3 (1.6 × 1.47); (q) MUSM 1886, r M2 (1.83 × 1.67); (r) MUSM 1887, r M1 (1.59 × 1.54); (s) MUSM 1888, l DP4 (reversed; 1.53 × 1.2). (t–z) Canaanumys magueniensis new gen. and sp.: (t) MUSM 1889, r M3 (1.5 × 1.87); (u) MUSM 1890, r M2 (holotype; 1.63 × 1.95); (v) MUSM 1891, l M1 (reversed; 1.46 × 1.82); (w) MUSM 1892, l M3 (1.71 × 1.36); (x) MUSM 1893, l M2 (reversed; 1.8 × 1.79); (y) MUSM 1894, l M1 (reversed; 1.54 × 1.57); (z) MUSM 1895, broken r DP4 (– × 1.07). (a’–d’) Eobranisamys sp.: (a’) MUSM 1896, l P1 (1.86 × 2.33); (b’) MUSM 1897, l M1 (2.39 × 2.49); (c’) MUSM 1898, broken r M3 (– × 2.23); (d’) MUSM 1899, l M3 (2.47 × 2.06). (e’,f’) cf. Eoespina sp.: (e’) MUSM 1912, r M2 (1.48 × 1.85); (f’) MUSM 1913, l M2 (1.51 × 1.77).
subsequent Palaeogene cavioid caviomorphs (such as *Eoincamys* and *Incamys*) exhibit a highly specialized dental pattern, noticeably reminiscent of that of the coeval African phiomysid *Gaudeamus* [3,12,14]. The phylogenetic position of the latter as a derived caviomorph in the current analysis (figure 3a) is supported by dental characters such as hypsodonty or crest obliquity. These comparable dental patterns, highly specialized for Palaeogene rodents, are likely to reflect adaptive convergence rather than close phylogenetic affinities [14].

The dramatic global cooling and drying episode recorded around the Eocene–Oligocene transition (approx. 34 Ma; opening of Drake Passage and development of Antarctic ice sheet [30,35]) are usually regarded as having shaped major faunal changes in South America, including the arrival of caviomorphs [19,36]. The presence of caviomorph rodents in approximately 41-Ma-old sediments of Peruvian Amazonia shows that both their dispersal and initial radiation occurred instead during a much warmer and wetter period, around the Mid-Eocene Climatic Optimum [30,37] (figures 1 and 3a), which is consistent with the associated palynoflora (see electronic supplementary material, table S3). Such a view strongly supports the Middle Eocene caviomorph/phiomorph split
that middle- and high-latitude areas were extensively investigated in the last centuries [1,36] (i.e. much more than low-latitude regions, including western Amazonia [20]), the earliest caviomorphs seemingly expanded southward during the late Middle Eocene–Early Oligocene period, from low (Peruvian Amazonia; approx. 41 Ma or earlier) to middle (central Chile; approx. 32 Ma [5,19]) and then to high latitudes (Patagonian Argentina; approx. 30 Ma [13]). Such a southward shift, fully contradictory to the apparent northward expansion as deduced from the fossil record available 20 years ago, highlights the critical dependence of deep time dispersal scenarios on the fossil record, and shows how severely under-sampled the tropics are.

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