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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 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 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.

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.

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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 hystricognath evolution and biogeography.

2. RESULTS

Systematic palaeontology

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

Plesion Cachiyacuy, New Genus.

Type species. Cachiyacuy contamanensis, New Species. Etymology. Contraction of Cachiyacuy (Local River) and cuq, 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 Eobranisamys, Branisamys, Essallamys, Sallamys, Eoepina 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 mesoloph.

Eocene rodents from Amazonia

b}n2. RESULTS

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Eobransamys, Brantsamys and Canaanimys in the absence of taeniodont pattern on upper teeth owing to the presence of a strong lingual protoloph. Differs from Eoinamys 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.

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

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(s) are more salient than in C. contamanensis.

Plesion Canaanimys, New Genus.

Type species. Canaanimys maquiensis, 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.

Canaanimys maquiensis, 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(s), 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, Protophiomys, Waslansmys, Phiomys, Hosdaubia, Bagitimus and Ottomanta). 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 rivieri 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. romeropittmanae in being about half the size, and from E. rivieri in being 20 per cent smaller and in showing sharper crests and more salient cusps (plesiomorphic traits). The 2 diminutive M’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 Tinguiurica [5], Santa Rosa [21], La Cantera [13] and younger localities [4]), with a 30–120 g estimated adult body mass range: C. maquiensis (figure 2t–z), C. kummeli (figure 2i–l) and cf. Eoespina sp. (figure 2e’–f’) were meadow vole-sized, while C. contamanensis (figure 2a–k) and Eobransamys sp. (figure 2a’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, Canaanimys and cf. Eoespina share a similar dental bauplan with the earliest Afro-Asian hystricognaths (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 Canaanimys, Cachiyacuy and their Old World counterparts, such as Protophiomys and Baluchimys (for Canaanimys) 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 Cachiyacuy 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, M1 (1.67 × 1.71); (p) MUSM 1885, r M1 (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) Canaanimus naguissis new gen. and sp.: (t) MUSM 1889, r M1 (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 P4 (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).
Gaudeamus coeval African phiomyid dental pattern, noticeably reminiscent of that of the *Eoincamys* and subsequent Palaeogene cavioid caviomorphs (such as *Archetypomys erlianensis*). The phylogeographic world map at 40 Ma and privileged phylogeographic sketch of Palaeogene hystricognath rodents, as inferred by both the consensus tree shown in (a) and the geographical range of concerned taxa (coloured circles; same colour codes as in (a)).

Subsequent Palaeogene cavioid caviomorphs (such as *Eoincamys* and *Incarnys*) exhibit a highly specialized dental pattern, noticeably reminiscent of that of the coeval African phiomyid *Gaudeamus*. 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.

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. 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.
(CPS; 45.4 ± 4.1 Ma; figure 3a), as estimated by molecular analyses [9,15]. Based on the present work and recent discoveries of stem hystriocnathid in the Late Eocene of Asia [8] and Africa [11,14], the initial radiations of Old World phiomorphs and New World caviomorphs were apparently synchronous and rapid in both land masses (figure 3a). The inferred calibrated phylogeny of Palaeogene hystriocnathid highlights a significant Middle Eocene gap in the Old World hystriocnath record (figure 3a). Based on our phylogenetic analysis, Africa is the homeland for the last common ancestor of caviomorphs (figure 3b). The latest reconstructions of South Atlantic geometry, palaeowinds and palaeocurrents during the Middle Eocene [7] are consistent with trans-Atlantic sweeps dispersal of hystriocnathids from Africa to South America [2,10].

An Asian origin for stem Hystriocnathid and stem anthropoid primates has gained strong support in recent years [8,11,38,39]. Based on our phylogeny (figure 3a,b), stem hystriocnathid rodent probably invaded Africa from Asia around the Early–Middle Eocene transition. However, at that time and/or by the time of the estimated CPS [9,15], only zygodontid anomalurids are known from Africa, which are phylogenetically remote from the clade Hystriocnathi [40]. The latter are not recorded in Africa before the latest Middle Eocene [8,11,41]. Similar timing and dispersal scenarios are proposed for stem anthropoid primates [38,39]. By contrast, the present discovery further extends the temporal gap between South America’s first appearance datum of rodents (now greater than or equal to 41 Ma) and that of primates (Late Oligocene of Bolivia, approx. 26 Ma [16]), thus suggesting the possibility of distinct dispersal events from Africa for both groups, as hypothesized by molecular data [9].

Morphological and molecular evidence [17,18] presently provide no definitive answer as to whether platyrrhines underwent a radiation before Late Oligocene times, but the platyrrhine/catahriine divergence is estimated to have occurred around the Middle–Late Eocene transition on molecular grounds [9]. This period records both the earliest African caviomorphs/stem anthropoids (of Asian origin [39]) and the earliest South American caviomorphs (figure 3a). Africa may have played the role of a stopover for pioneer platyrrhines, within a ‘land-mass-hopping’ process between Asia and South America, as for caviomorphs several million years earlier (figure 3). Once again, it is not clear whether platyrrhines and caviomorphs diverged in Asia or in Africa [39]. However, in the Old World, most Middle Eocene–Early Oligocene localities with hystriocnathids also yield primates [8,11,14,39,41], a situation that strongly contrasts with the coeval South American fossil record. Moreover, based on palynological data [33,37] and current palaeoenvironmental reconstructions [42], low-latitude areas of South America were seemingly highly favourable to the survival and expansion of platyrrhine primates throughout Palaeogene times. The Palaeogene platyrrhine record in South America is so far restricted to the Late Oligocene deposits of the Salla-Luribay area in Bolivia [16,17], but it can be expected that other regions of South America hosted primates much before.

According to South America’s fossil record, and given 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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REFERENCES


