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; Platyrrhini

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 $^{40}Ar/^{39}Ar$ step heating of single
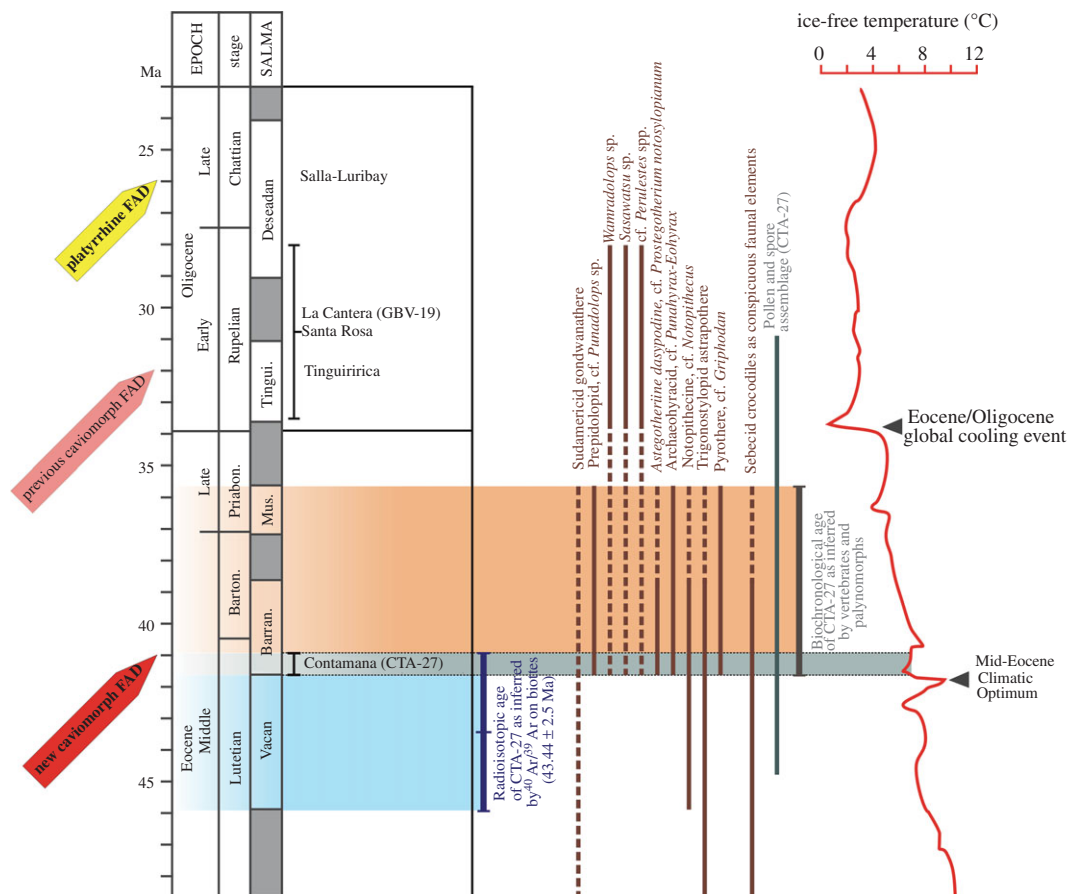
Figure 1. Stratigraphical range of CTA-27 locality (inferred by radioisotopy, vertebrate biochronology and palynostratigraphy) and Mid-Cenozoic global climate. The age of CTA-27 is bracketed between 41.6 Ma (base of the Gran Barranca Member [23,24]) and 40.94 Ma (youngest age provided by ^{40}Ar/^{39}Ar 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 δ^{18}O 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., Tinguiririran.

biotite grains separated from a tuffaceous silt located 47 m above the fossiliferous level in the same section, and dated to 43.44 ± 2.5 Ma (see the electronic supplementary material). As summarized in figure 1, a late Middle Eocene age for CTA-27 (41.6–40.94 Ma) is further refined by mammalian biochronology: in CTA-27, the rodents were found in association with typical Middle to Late Eocene marsupials and endemic ungulates, such as the polydolopimorph *Punadolops* (Barrancan–Mustersan South American Land Mammal Age, SALMA [25]), an astegotheriine dasypodid armadillo close to *Prostegotherium notostylopianum* (Vacan–Barrancan SALMA [31]), a small archaeohyracid notoungulate related to *Eohyrax* (Barrancan) and *Punahyrax* (Barrancan–Mustersan [32]), a small pyrothere closely allied to *Griphodon* (Vacan–Mustersan), and an unidentified trigonostylopid astrapothere (Vacan–Mustersan), which consistently constrain a Barrancan–Mustersan biochronological range (41.6–35.8 Ma; figure 1; electronic supplementary material) for the locality. CTA-27 also has yielded a diversified, strictly continental palynoflora characteristic of the Middle Eocene to Early Oligocene (44.8–30.9 Ma; palynological zones T6-T10 [33]; figure 1 and electronic supplementary material). The flora indicates a tropical rainforest habitat, with no evidence of savannah vegetation.

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 Hystricognathi Tullberg, 1899; Parvorder Caviomorpha Wood, 1955.

Plesion *Cachiyacuy*, New Genus.

Type species. *Cachiyacuy contamanensis*, New Species.

Etymology. Contraction of *Cachiyacu* (Local River) and *cuy*, 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*, *Eosallamys*, *Sallamys*, *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

Eobranisamys, *Branisamys* and *Canaanimys* in the absence of taeniodont pattern on upper teeth owing to the presence of a strong lingual protoloph. Differs from *Eoincamys* 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 ($\approx$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 M^2 (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 M^1 (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(id)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 M^2 (figure 2u).

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(id)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*, *Waslamys*, *Phiomys*, *Hodsahibia*, *Bugtimys* and *Ottomania*). The lingual protoloph is either slightly developed or lacking (i.e. taeniodont pattern).

In addition, four teeth are referred to the cavioid *Eobranisamys* sp. (figure 2a'–d') and 2 diminutive teeth to the octodontoid cf. *Eoespina* sp. (figure 2e'–f'). The teeth referred to *Eobranisamys* sp., notably the only upper molar (figure 2b'), display features reminiscent of upper molars of *Eobranisamys romeropittmanae* and of *Eobranisamys riverai* 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, *Eobranisamys* sp. differs substantially from *E. romeropittmanae* in being about half the size, and from *E. riverai* in being 20 per cent smaller and in showing sharper crests and more salient cusps (plesiomorphic traits). The 2 diminutive M^2s 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 Tinguiririca [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 2l–s) and cf. *Eospina* sp. (figure 2e'–f') were meadow vole-sized, while *C. contamanensis* (figure 2a–k) and *Eobranisamys* 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. *Eospina* 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 *Canaanimys* 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
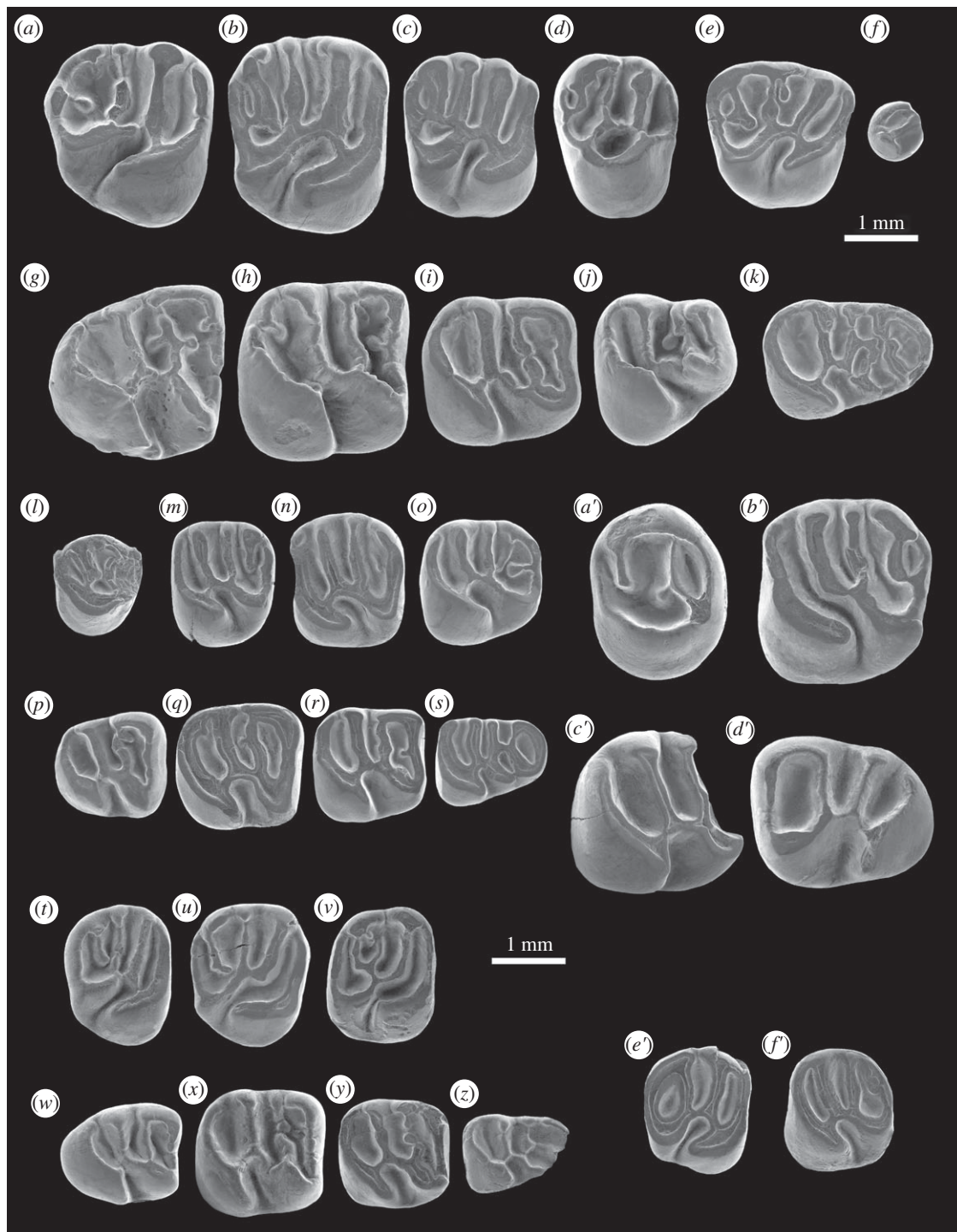
Figure 2. Scanning electron microscope images (in occlusal view) and dimensions (length × width, in millimetres) of fossil caviomorph teeth from CTA-27. (*a–k*) *Cachiyacuy contamanensis* new gen. and sp.: (*a*) MUSM 1870, right (r) M^3 (2.34 × 2.44); (*b*) MUSM 1871, r M^2 (holotype; 2.22 × 2.69); (*c*) MUSM 1872, left (l) M^1 (reversed; 2.07 × 2.22); (*d*) MUSM 1873, r P^4 (1.82 × 2.38); (*e*) MUSM 1874, l DP^4 (reversed; 2.03 × 1.98); (*f*) MUSM 1875, DP^3 (0.77 × 0.82); (*g*) MUSM 1876, r M_3 (2.46 × 2.24); (*h*) MUSM 1877, r M_2 (2.44 × 2.36); (*i*) MUSM 1878, r M_1 (2.15 × 1.99); (*j*) MUSM 1879, r P_4 (1.99 × 2.0); (*k*) MUSM 1880, r DP_4 (2.31 × 1.53). (*l–s*) *Cachiyacuy kummeli* new gen. and sp.: (*l*) MUSM 1881, broken r P^4 (reversed; 1.16 × –); (*m*) MUSM 1882, l M^1 (holotype; 1.45 × 1.63); (*n*) MUSM 1883, l M^2 (1.69 × 1.87); (*o*) MUSM 1884, l M^3 (1.67 × 1.71); (*p*) MUSM 1885, r M_3 (1.6 × 1.47); (*q*) MUSM 1886, r M_2 (1.83 × 1.67); (*r*) MUSM 1887, r M_1 (1.59 × 1.54); (*s*) MUSM 1888, l DP_4 (reversed; 1.53 × 1.2). (*t–z*) *Canaanimys maquiensis* new gen. and sp.: (*t*) MUSM 1889, r M^3 (1.5 × 1.87); (*u*) MUSM 1890, r M^2 (holotype; 1.63 × 1.95); (*v*) MUSM 1891, l M^1 (reversed; 1.46 × 1.82); (*w*) MUSM 1892, l M_3 (1.71 × 1.36); (*x*) MUSM 1893, l M_2 (reversed; 1.8 × 1.79); (*y*) MUSM 1894, l M_1 (reversed; 1.54 × 1.57); (*z*) MUSM 1895, broken r DP_4 (– × 1.07). (*a′–d′*) *Eobranisamys* sp.: (*a′*) MUSM 1896, l P^4 (1.86 × 2.33); (*b′*) MUSM 1897, l M^1 (2.39 × 2.49); (*c′*) MUSM 1898, broken r M_2 (– × 2.23); (*d′*) MUSM 1899, l M_3 (2.47 × 2.06). (*e′,f′*) cf. *Eoespina* sp.: (*e′*) MUSM 1912, r M^2 (1.48 × 1.85); (*f′*) MUSM 1913, l M^2 (1.51 × 1.77).
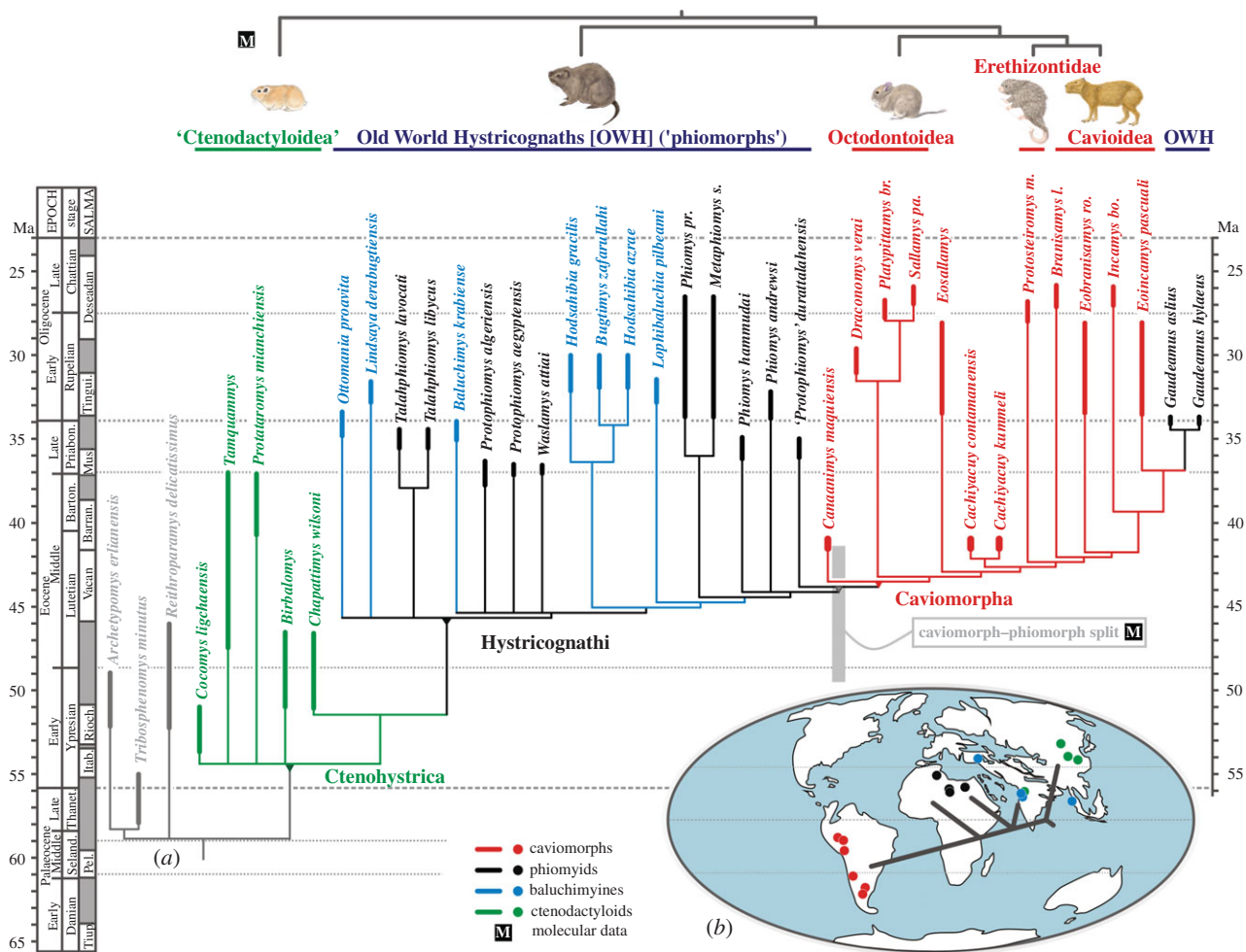
Figure 3. Phylogeny and dispersal scenario of Palaeogene caviomorph rodents and related taxa. (*a*) Phylogeny of Contamana rodents among Palaeogene ctenohystricans (Ctenohystrica), hystricognaths (Hystricognathi) and caviomorphs (Caviomorpha). Strict consensus cladogram obtained with a maximum-parsimony PAUP (phylogenetic analysis using parsimony) heuristic search (see the electronic supplementary material). The consistency (CI), retention (RI) and homoplasy (HI) indices of the 13 shortest trees (859 steps) are 0.33, 0.63 and 0.68, respectively. Branch support of the concerned nodes (Bremer indices) appears in the electronic supplementary material, figure S2*a*. Contamana rodents included in this analysis (bold type) are stem caviomorphs (i.e. not referable to Octodontoidea, Erethizontidae or Cavioidea). cf. *Eoespina* sp. (not included, two teeth) is interpreted as a stem octodontoid. *Eobranisamys* sp. (four teeth) might be connected to the *Eobranisamys romeropittmanae* branch (Cavioidea), which suggests a late Middle Eocene age for the common ancestor of cavioids. Sister-group relationships between *Gaudeamus* (advanced phiomorph; Old World Hystricognath, OWH) and *Eoincamys* (caviomorph) probably document a striking convergent dental evolution [11,14], rather than independent dispersal from South America to Africa. Light-grey shaded bar illustrates molecular estimate ranges for the caviomorph–phiomorph split (CPS; 45.4 ± 4.1 Ma [9]), thus located behind the morphologically supported CPS node (grey triangle). On top, dark-grey tree sketches phylogenetic relationships among living ctenohystricans as supported by molecular data [9]. Barran., Barrancan; Barton., Bartonian; Itab., Itaboraian; Mus., Mustersan; Pel., Peligran; Priabon., Priabonian; Rioch., Riochican; SALMA, South American Land Mammal Age; Seland., Selandian; Thanet., Thanetian; Tingui., Tinguiririan; Species name abbreviations: *bo.*, *bolivianus*; *br.*, *brachyodon*; *l.*, *luribayensis*; *m.*, *medianus*; *pa.*, *pascuali*; *pr.*, *paraphiomyoides*; *ro.*, *romeropittmanae*; *s.*, *schaubi*. Rodent drawings by M. J. Orliac. See the electronic supplementary material for further details. (*b*) Palaeogeographic 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 *Incamys*) exhibit a highly specialized dental pattern, noticeably reminiscent of that of the coeval African phiomyid *Gaudeamus* [3,12,14]. The phylogenetic position of the latter as a derived caviomorph in the current analysis (figure 3*a*) 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 3*a*), 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 3*a*), as estimated by molecular analyses [9,15]. Based on the present work and recent discoveries of stem hystricognaths 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 3*a*). The inferred calibrated phylogeny of Palaeogene hystricognaths highlights a significant Middle Eocene gap in the Old World hystricognath record (figure 3*a*). Based on our phylogenetic analysis, Africa is the homeland for the last common ancestor of caviomorphs (figure 3*b*). The latest reconstructions of South Atlantic geometry, palaeowinds and palaeocurrents during the Middle Eocene [7] are consistent with trans-Atlantic sweepstakes dispersal of hystricognaths from Africa to South America [2,10].

An Asian origin for stem Hystricognathi and stem anthropoid primates has gained strong support in recent years [8,11,38,39]. Based on our phylogeny (figure 3*a,b*), stem hystricognathous rodents 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 zegdoumyid anomaluroids are known from Africa, which are phylogenetically remote from the clade Hystricognathi [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/catarrhine divergence is estimated to have occurred around the Middle–Late Eocene transition on molecular grounds [9]. This period records both the earliest African catarrhines/stem anthropoids (of Asian origin [39]) and the earliest South American caviomorphs (figure 3*a*). 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 catarrhines diverged in Asia or in Africa [39]. However, in the Old World, most Middle Eocene–Early Oligocene localities with hystricognaths 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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