PALEONTOLOGY

A parapithecid stem anthropoid of African origin in the Paleogene of South America

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Phylogenetic evidence suggests that platyrrhine (or New World) monkeys and caviomorph rodents of the Western Hemisphere derive from source groups from the Eocene of Afro-Arabia, a landmass that was ~1500 to 2000 kilometers east of South America during the late Paleogene. Here, we report evidence for a third mammalian lineage of African origin in the Paleogene of South America—a newly discovered genus and species of parapithecid anthropoid primate from Santa Rosa in Amazonian Perú. Bayesian clock–based phylogenetic analysis nests this genus (*Ucayalipithecus*) deep within the otherwise Afro-Arabian clade Parapithecoidea and indicates that transatlantic rafting of the lineage leading to *Ucayalipithecus* likely took place between ~35 and ~32 million years ago, a dispersal window that includes the major worldwide drop in sea level that occurred near the Eocene-Oligocene boundary.

The geographic and phylogenetic origins of South America's platyrrhine monkeys and caviomorph rodents have long been among the most intriguing topics in the study of mammalian evolution (*1–5*). Both clades are thought to have originated in the Eocene of Afro-Arabia (*6–8*), thereby requiring one or more transatlantic rafting events to place these lineages in South America (*1–4*). Here, we describe a derived parapithecid anthropoid of African origin in the upper Paleogene of Amazonian Perú that (i) provides the most compelling phylogenetic link available of a South American fossil mammal to an Afro-Arabian clade; (ii) substantially constrains the timing of the transatlantic dispersal that gave rise to this South American parapithecid lineage and possibly other South American primate lineages; and (iii) suggests that eustatic sea level fall that was coincident with the onset of Antarctic glaciation might have played a role in facilitating transatlantic dispersal.

The Santa Rosa locality comprises an ~100-m-long fluvial deposit exposed along the left bank of the Río Yurúa, ~7.5 km south of the border between Perú and Brazil, in the Departamento de Ucayali, Perú (*9*). The locality has previously yielded a single upper molar of a possible stem platyrrhine (*Perupithecus*) (*6*); fragmentary teeth of an unnamed second anthropoid taxon (*6*); numerous isolated teeth and maxillary and mandibular fragments of caviomorph rodents (*10, 11*) and marsupials (*12*); and rare remains of bats, notoungulates, and enigmatic mammals of unclear affinities (*9*).

Systematics. Order Primates Linnaeus 1758. Suborder Anthropoidea Mivart 1864. Family Parapithecidae Schlosser 1911. *Ucayalipithecus* gen. nov. **Generic diagnosis:** The holotypic M₂ (lower second molar) of *Ucayalipithecus* differs from that of *Qatrania* (*13*) from the lower Oligocene of Egypt (Fig. 1I) in having less basal flare of the buccal margin and no accessory cusp in the distolingual fovea, and it differs from *Qatrania* and *Abuqatrania* (latest Eocene of Egypt, Fig. 1K) (*14*) in having a relatively small hypoconulid and no development of a distobuccal cingulid on the distal surface of the hypoconid. The M₂ of *Ucayalipithecus* further differs from that of *Abuqatrania* in having a relatively broad trigonid and in lacking a distinct paraconid. **Type species:** *Ucayalipithecus perdita.* **Etymology:** *Ucayali*, for the Peruvian department in which the Santa Rosa locality occurs, and the Greek *pithekos*, meaning monkey or trickster.

Ucayalipithecus perdita. Figure 1, A and J. **Holotype:** M₂ crown, missing enamel from base of protoconid; Instituto Geológico, Minero, y Metalúrgico (INGEMMET), Lima, Colección Paleontológica del INGEMMET (CPI) 7936. **Etymology:** *perdita*, Latin for lost. **Type locality and age:** Santa Rosa, Yahuarango Formation(?), LACM (Natural History Museum of Los Angeles County) Locality 6289, upper Eocene or lower Oligocene. **Species diagnosis:** As for genus. **Hypodigm:** The holotype; CPI-7937 [LACM 6289/155061], a partial right upper molar identified as an M¹; CPI-7938 [LACM 6289/157063], a partial left upper

molar identified as an M²; and CPI-7928, a lower left M₃. **Description:** See supplementary materials for detailed description.

The four teeth in the *Ucayalipithecus perdita* hypodigm differ very little from those of primitive Fayum parapithecids. The M₃ referred to *U. perdita* differs from those of the parapithecids *Qatrania wingi* and *Abuqatrania basiodontos* in having a relatively large entoconid cusp. The M¹ referred to *U. perdita* differs from the M¹? attributed to *Q. wingi* (*15*) (Fig. 1C) in having a more rounded lingual margin of M¹; a large accessory cusp in the region of the pericone on M¹; a less distinct mesial cingulum; a relatively large paraconule; M¹ conules that are more lingually placed relative to the base of the protocone; and a metaconule that is closely appressed to the protocone and roughly transverse to the hypoconule rather than being placed mesiobuccal to the hypoconule.

The known teeth of *Ucayalipithecus* are radically different from those of platyrrhines, and several features, in combination, confirm this taxon's parapithecid identity. For instance, the upper molars referred to *U. perdita* differ from those of early platyrrhines (Fig. 1, D to G) in having bulbous and basally inflated primary cusps, very restricted trigon basins, well-developed conules (although no metaconule is present on M²), large and bulbous pericones and adjacent accessory cusps (particularly on M¹), and a hypoconule on M¹, and these upper molars also differ in lacking several crests (preprotocrista, postprotocrista, hypoparacrista, hypometacrista, and prehypocrista). Unlike the single known upper molar (M¹?) of *Perupithecus* (Fig. 1D) from Santa Rosa, which potentially closely approximates the ancestral condition for basal stem platyrrhines and/or crown Anthropoidea generally, the M¹ of *Ucayalipithecus* has a paraconule, a metaconule, a hypoconule, and an accessory cusp in the region of the pericone rather than well-developed crests that connect the crestiform primary cusps and delimit a large trigon basin. The hypocone cusps of *Ucayalipithecus* approach the protocones in size, rather than being a crestiform expansion of the distolingual cingulum as in *Perupithecus*. Although most platyrrhines have more basally inflated cusps than those of *Perupithecus* and well-developed hypocones, they differ from *Ucayalipithecus* in typically having primary cusps that are more peripherally placed on the crown and distinct crests that connect these cusps and delimit capacious trigon basins. The lower molars of early platyrrhines typically have trenchant crests (paracristids, protocristids, pre- and postmetacristids, oblique cristids, and hypocristids), poorly developed or absent hypoconulid cusps, expansive and gently concave talonid basins, and differentiated trigonid basins, all features that are lacking

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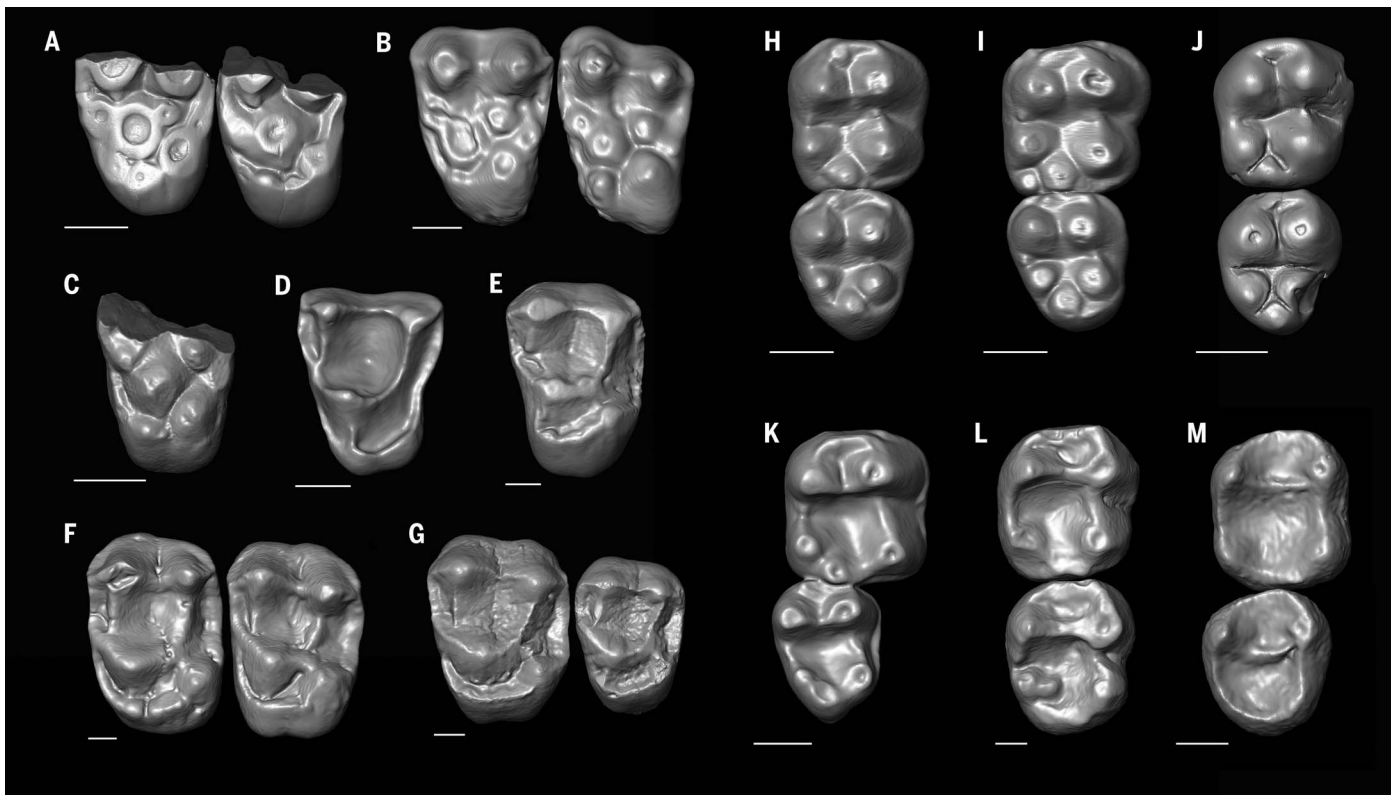
Fig. 1. Upper and lower molars of *Ucayalipithecus perdita* compared with those of parapithecids and platyrrhines. (**A**) CPI-7937, a partial right upper molar (reversed for comparison) identified as an M¹, and CPI-7938, a partial left upper molar identified as an M², of *Ucayalipithecus perdita* (Santa Rosa Locality, Perú). (**B**) Left M¹⁻² of the early Oligocene parapithecid *Apidium bowni* [DPC (Duke Lemur Center Division of Fossil Primates) 5264, Quarry V, Jebel Qatrani Formation, Egypt]. (**C**) Right M¹? (reversed for comparison) of the early Oligocene parapithecid *Qatrania wingi* [YPM (Yale Peabody Museum of Natural History) 18008, Quarry E, Jebel Qatrani Formation, Egypt]. (**D**) Right M¹? of *Perupithecus ucayaliensis* (CPI-6486, Santa Rosa Locality, Perú). (**E**) Left M² of the late Oligocene platyrrhine *Canaanimico amazonensis* [MUSM-2499, Locality CTA (Contamana)–61, Perú (*29*)]. (**F**) Left M¹⁻² of the early Miocene platyrrhine *Carlocebus carmenensis* [MACN Pv (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Colección de Paleovertebrados) SC254, M¹, Portezuelo Sumich Sur, Pinturas Formation, Argentina; MACN Pv SC317, M², Loma de las Ranas, Pinturas Formation, Argentina]. (**G**) Left M¹⁻² of the early Miocene platyrrhine *Panamacebus transitus* [UF (Florida Museum of Natural History) 280128 and 281001, Locality YPA-024, Las Cascadas Formation, Panama (*30*)]. (**H**) Right M₂₋₃ of the late Eocene parapithecid *Abuqatrania basiodontos* (DPC 14236, Locality 41, Jebel Qatrani Formation, Egypt). (**I**) Right M₂₋₃ of the early Oligocene parapithecid *Qatrania wingi* (DPC 6125, Quarry E, Jebel Qatrani Formation, Egypt). (**J**) Right M₂ (CPI-7936) and left M₃ (CPI-7928, reversed for comparison) of *Ucayalipithecus perdita* (Santa Rosa Locality, Perú). (**K**) Left M₂₋₃ (reversed for comparison) of the late Eocene proteopithecid *Proteopithecus sylviae* (DPC 20406, Locality 41, Jebel Qatrani Formation, Egypt). (**L**) Right M₂₋₃ of the early Miocene platyrrhine *Carlocebus carmenensis* (MACN Pv SC63, M₂, Portezuelo Sumich Norte, Pinturas Formation, Argentina; MACN Pv SC248, M₃, Portezuelo Sumich Norte, Pinturas Formation, Argentina). (**M**) Right M₂₋₃ of the extant platyrrhine *Aotus trivirgatus* [AMNH (American Museum of Natural History) 93077, Parintins, Amazonas, Brazil]. Scale bars, 1 mm.

in *Ucayalipithecus*. Body mass estimates for *U. perdita* based on M₂ area range from 319 g [all-primate equation of Egi *et al.* (*16*)] to 366 g (anthropoid equation), which are similar in size to small members of the platyrrhine genus *Callithrix* and the ancestors of Platyrrhini, the latter of which were probably no larger than ~400 g (*17*).

Bayesian clock (tip-dating) analysis of a combined molecular-morphological matrix (*18*) in MrBayes (*19*) placed *Ucayalipithecus* deep within the otherwise African clades Parapithecoidea and Parapithecidae with perfect support [i.e., a posterior probability (PP) of 1.0 for a parapithecid clade that includes *Ucayalipithecus*] (Fig. 2 and materials and methods in the supplementary materials). The sister taxon of *Ucayalipithecus* is identified as *Q. wingi*, a parapithecid from the lower Oligo-

cene Quarry E in the lower sequence of the Jebel Qatrani Formation (Fayum Depression of northern Egypt) (*13*, *15*, *20*) (PP = 0.75). A crown anthropoid (Platyrrhini and Catarrhini) clade that excludes Parapithecoidea was strongly supported (PP = 0.98), indicating that parapithecoids are stem anthropoids that have no relevance to either the phylogenetic or biogeographic origin of Platyrrhini (*14*, *21*). We tested an alternative hypothesis (which might be considered plausible based solely on biogeographic considerations) that *Ucayalipithecus* is not a parapithecid but rather a parapithecid-like stem platyrrhine by constraining *Ucayalipithecus* to form a clade with platyrrhines (including the bunodont late Oligocene stem platyrrhine *Branisella*) to the exclusion of parapithecids and estimating the ln marginal likelihoods of the primary and alternative hy-

potheses using stepping stone analyses of the morphological matrix in MrBayes. Comparison of estimated ln marginal likelihoods (constrained: −21,555.23; unconstrained: −21,524.55) yields a 2 × logₑBF (BF, Bayes factor) test statistic of 61.36 and thus, based on the recommendations of (*22*), "very strong" evidence in favor of rejecting the alternative hypothesis that *Ucayalipithecus* is a stem platyrrhine. Bayesian ancestral reconstruction of continental geography onto the "allcompat" tree derived from the clock analysis unambiguously reconstructs an Afro-Arabian origin for the clade containing Parapithecoidea and crown Anthropoidea (PP = 0.97), as well as Parapithecoidea (PP = 0.99) and Parapithecidae (PP = 1.0), and therefore strongly supports independent dispersals of stem Platyrrhini and the *Ucayalipithecus* lineage from Afro-Arabia to South America.
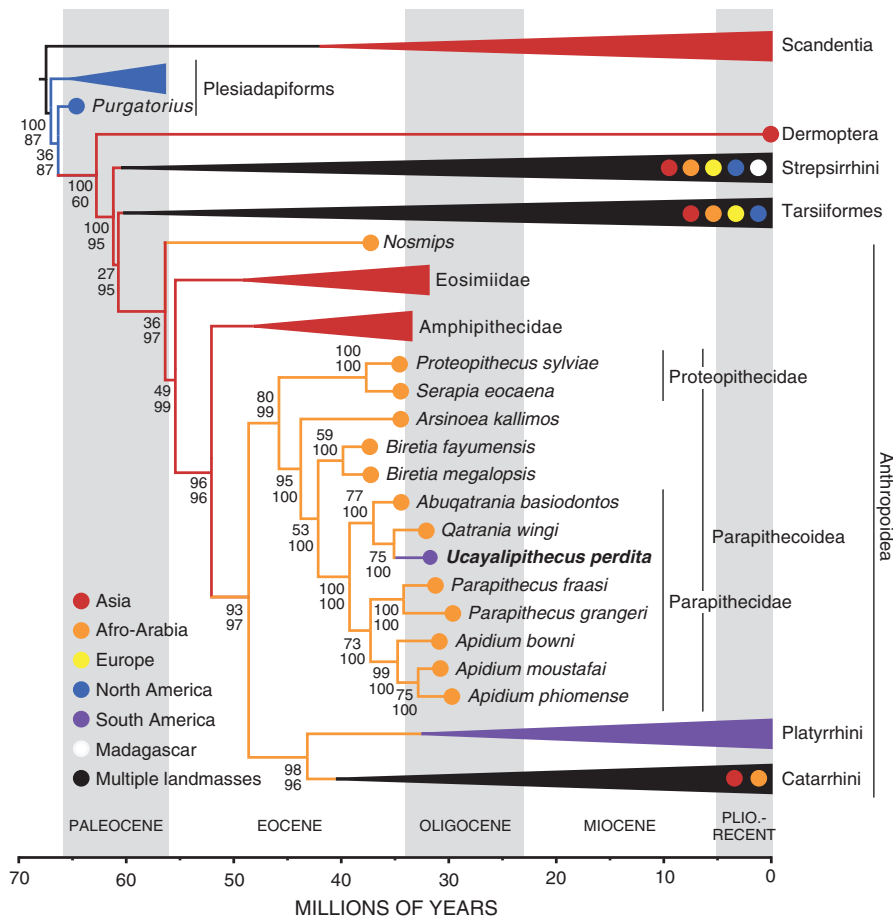
Fig. 2. Phylogenetic position and geographic origin of *Ucayalipithecus perdita*. "Allcompat" consensus tree derived from a Bayesian clock (or tip-dating) analysis of a combined molecular and morphological matrix in MrBayes 3.2.5, with major nonparapithecoid clades collapsed. Top number at each node is the posterior probability (×100) for each node on the basis of Bayesian clock analysis of the character matrix. Bottom number is the posterior probability of ancestral reconstructions of geography onto the allcompat tree (calculated in MrBayes). Multiple colored circles for a collapsed clade indicate that multiple geographic locations are present within that clade. Plio., Pliocene.

We also tested the proposed upper Eocene age of the Santa Rosa locality in the clock analysis by placing a broad uniform prior on the tip age of *Ucayalipithecus*, from the beginning of the late Eocene to the end of the early Oligocene [37.8 to 28.1 million years ago (Ma)]. The resulting mean tip age for *Ucayalipithecus* was 31.7 Ma, about midway through the early Oligocene. A secondary clock analysis in which the single known tooth of *Perupithecus* was included, assigned the same broad age prior, and constrained to be a stem platyrrhine returned a mean tip age of 28.8 Ma for that taxon. Available evidence from the admittedly very limited sample of Santa Rosa anthropoids therefore supports a lower Oligocene, rather than an upper Eocene (*10*), age for the site. The divergence of *Ucayalipithecus* from its African sister taxon *Qatrania* is estimated to have occurred at 35.1 Ma (latest Eocene), suggesting that the transatlantic dispersal event that gave rise to the *Ucayalipithecus* lineage occurred between 35.1 and 31.7 Ma. Importantly,

this interval includes the major eustatic drop in sea level that occurred in the earliest Oligocene (*23*), and our results leave open the possibility that dispersals of parapithecids and ancestral Platyrrhini to South America were broadly coincident with, and might have been facilitated by, this drop in sea level.

The discovery of a parapithecid stem anthropoid in the late Paleogene of Peruvian Amazonia is entirely unexpected and provides a notable example of how important paleontological information is for understanding the ephemeral forces that shaped modern biodiversity. Without these four tiny teeth recovered from an isolated outcrop deep in a remote part of the Amazon basin, it could not have been predicted that early stem platyrrhines of South America were living alongside, and competing for resources with, a phylogenetically independent anthropoid lineage. The fact that the Santa Rosa locality is more than 4000 km from the easternmost point of South America and far from any coastal area that could have served

as the initial docking point for the ancestors of *Ucayalipithecus* after their transatlantic dispersal further suggests that parapithecids may have already been broadly distributed across equatorial South America by the time the fossils described here were deposited in Amazonian Perú. There is no reason to assume that platyrrhine competition with parapithecids in South America would have been trivial, as the arboreal (*24*) and largely frugivorous (*25, 26*) parapithecoid relatives of *Ucayalipithecus* persisted in Africa alongside several other primate lineages for at least ~11.5 million years [from their first-appearance datum of ~37 Ma (*27*) to their last-appearance datum of 25.5 Ma (*28*)].

The recognition that both parapithecids and stem platyrrhines survived a transatlantic rafting event further reveals that these early anthropoid lineages were not only able to persist despite presumed water and food scarcity—thereby suggesting the existence of physiological adaptations that allowed them to successfully cope with a situation that mimicked strong seasonality (*3*)—but were able to immediately adjust their foraging behavior to the unfamiliar resources and phenological patterns that they encountered upon arrival in South America. This combined evidence from South American parapithecids and stem platyrrhines strongly suggests that early anthropoids must have been highly resilient to unpredictable environments and implies a degree of behavioral flexibility that would have been an evolutionary advantage for Anthropoidea during the major environmental perturbations of the later Paleogene, including the global cooling event at the Eocene-Oligocene boundary.

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A South American anthropoid
Although there are many primate lineages in the Old World, it is thought that the New World is home to just one group, the platyrrhine monkeys, which appear to have colonized the region during the Eocene. Seiffert *et al.* describe a new primate species on the basis of fossil molars found in the Peruvian Amazon that appears to belong to the Parapithecidae, a group of stem anthropoid primates best known from northern Africa (see the Perspective by Godinot). The fossils appear to be from a well-differentiated lineage, suggesting that this species had been evolving within South America for some time. It is likely that the ancestors of this new species arrived via a transatlantic rafting event when sea levels dropped at the Eocene –Oligocene transition ~32 to 35 million years ago.
Science, this issue p. 194; see also p. 136

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