LETTER

Eocene primates of South America and the African origins of New World monkeys

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The platyrrhine primates, or New World monkeys, are immigrant mammals whose fossil record comes from Tertiary and Quaternary sediments of South America and the Caribbean Greater Antilles[1,2]. The time and place of platyrrhine origins are some of the most controversial issues in primate palaeontology, although an African Palaeogene ancestry has been presumed by most primatologists[3,4]. Until now, the oldest fossil records of New World monkeys have come from Salla, Bolivia[5,6], and date to approximately 26 million years ago[7], or the Late Oligocene epoch. Here we report the discovery of new primates from the ?Late Eocene epoch of Amazonian Peru, which extends the fossil record of primates in South America back approximately 10 million years. The new specimens are important for understanding the origin and early evolution of modern platyrrhine primates because they bear little resemblance to any extinct or living South American primate, but they do bear striking resemblances to Eocene African anthropoids, and our phylogenetic analysis suggests a relationship with African taxa. The discovery of these new primates brings the first appearance datum of caviomorph rodents and primates in South America back into close correspondence, but raises new questions about the timing and means of arrival of these two mammalian groups.

The primate material reported on here comprises one complete and two incomplete upper molars and one complete lower molar from the Santa Rosa local fauna of eastern Peru[8] (Extended Data Fig. 1), all of which have a generalized crown morphology. The upper molars have vague resemblances to small callitrichines (living marmosets and tamarins), but with primitive morphologies closer to Palaeogene African anthropoids. The lower molar also exhibits an undoubted primitive pattern resembling some Palaeogene African anthropoids. Thus, not only do the Santa Rosa specimens represent the oldest New World monkeys known and hint strongly towards an African ancestry, they also alter prior perceptions and interpretations of early New World monkey morphotypes.

Order Primates Linnaeus, 1758
Suborder Anthropoidea Mivart, 1864
Parvorder ?Platyrrhini E. Geoffroy, 1812
Family *incertae sedis*
Perupithecus gen. nov.

Generic diagnosis. *Perupithecus* differs from all platyrrhines, except the extinct *Branisella*, *Szalatavus*, *Lagonimico*, and *Micodon* and the extant Callitrichinae by having an upper first molar ($M^{?1}$) with subtriangular outline with a narrow lingual side. The $M^{?1}$ differs from those of all known platyrrhines in having paracone, metacone, and protocone connected by more trenchant crests surrounding a moderately deep trigon basin. Trigon reduction in *Perupithecus* $M^{?1}$ is compensated by a more expanded side lingual to protocone, thus differing from all platyrrhines, which have a more enlarged trigon and less developed lingual shelf. An entoprotocrista (absent from first upper molars in all

known platyrrhines) descends from tip of protocone to reach the lingual cingulum, isolating a precingulum that extends mesiolingually to the anterior face of the protocone. The crestiform hypocone of *Perupithecus* $M^{?1}$ resembles that of some Callitrichinae, but differs from those in Pitheciidae, Atelidae, and Cebinae, where the upper molars are more quadrangular with developed hypocones. The $M^{?1}$ has a deep mesial fovea formed by a preprotocrista that divides buccally into a preparaconular crista that reaches the parastyle and a hypoparacrista that contacts the paracone (mesial fovea less developed and shallower in *Branisella*, reduced or absent in Callitrichinae, and occasionally present, but shallower, in other platyrrhines).

Type species. *Perupithecus ucayaliensis*.

Etymology. *Peru*, from Peru, the country of origin, and *pithecus*, the Greek word for monkey.

Perupithecus ucayaliensis sp. nov.

Figures 1–3a and Extended Data Fig. 2.

Holotype. Complete upper left molar ($M^{?1}$), Instituto Geológico, Minero y Metalúrgico (INGEMMET), Lima, Colleción Paleontológica del INGEMMET (CPI) 6486. Natural History Museum of Los Angeles County (LACM) 6289/155085; plastotype.

Etymology. *ucayaliensis*, after the department in which the Santa Rosa locality occurs.

Type locality and age. Santa Rosa, Atalaya Province, Ucayali Department, Peru. Left bank of Yurúa River, at 9° 29′ 39′ S, 72° 45′ 48′ W. Yahuarango Formation. LACM locality 6289 (ref. 9). ?Late Eocene (see discussion of locality and age in Supplementary Discussion 1).

Species diagnosis. Same as for genus.

Measurements. Labiolingual, 3.5 mm; mesiodistal, 2.6 mm.

Description. *Perupithecus ucayaliensis* was a small primate, comparable in size to the tamarins *Callimico* and some species of *Saguinus*, among
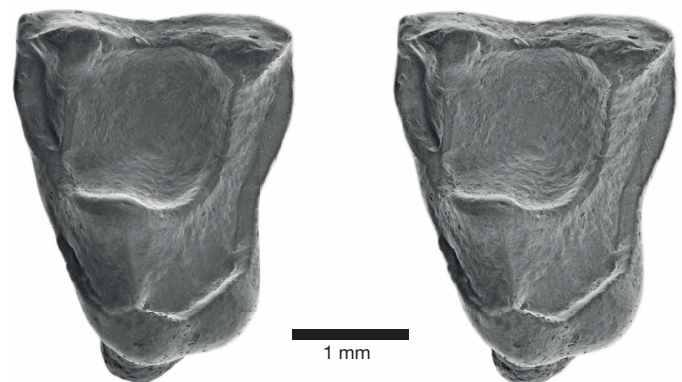

Figure 1 | Stereo-pair scanning electron microscope (SEM) images of *Perupithecus ucayaliensis*, holotype. Left $M^{?1}$, CPI-6486 (LACM 6289/155085), in occlusal view. Scale bar, 1 mm.

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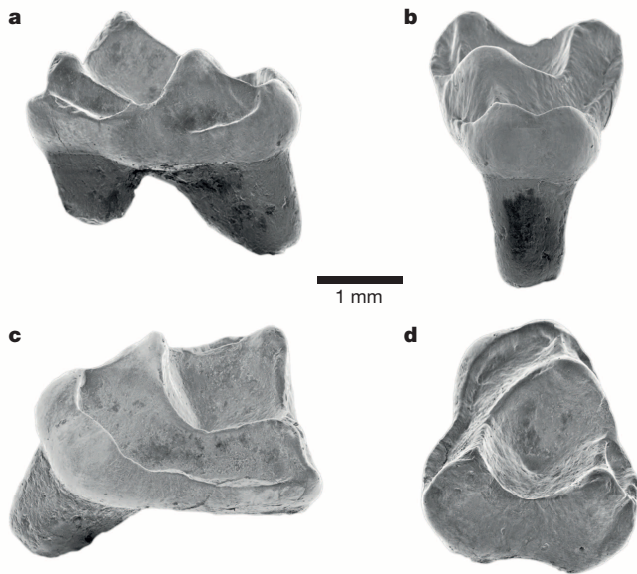
Figure 2 | SEM images of *Perupithecus ucayaliensis*, holotype. CPI-6486 (LACM 6289/155085) (left M$^{?1}$), in (**a**) mesiolingual, (**b**) lingual, (**c**) distolingual, and (**d**) occlusobuccal views. Note the deep mesial fovea and entoprotocrista in **a**, the crestiform hypocone in **b**, the proportions between the trigon basin and lingual side in **c**, and the flat buccal side in **d**, as discussed in the text. Scale bar, 1 mm.

the callitrichines. Although the upper molar of *Perupithecus* is distinct from that of all known platyrrhines, it does resemble some extinct Eocene African anthropoids, such as *Talahpithecus*[10] (Fig. 3b) and *Proteopithecus*[11], by having M$^{?1}$ with subtriangular outline with a narrow lingual side hosting an entoprotocrista. The M$^{?1}$ further resembles that of *Talahpithecus* by having a crestiform hypocone, an expanded side lingual to protocone, and protocone connected to paracone and metacone by trenchant crests surrounding the trigon.

The holotype, INGEMMET CPI-6486 (LACM 6289/155085; plastotype), has been interpreted as a left M$^{?1}$ primarily because the paracone and metacone are aligned buccally (Fig. 1). The metacone is placed more lingually in first upper molars of *Branisella* and callitrichines. The subtriangular crown of *Perupithecus* has three main cusps of comparable size connected by trenchant crests completely enclosing a moderately deep trigon. The cusps have little apical wear, with the metacone worn the most. Buccally, the paracone and metacone are connected by descending postparacrista and premetacrista, forming a 'V' shape in lateral view. Parastyle and metastyle are present, as in *Branisella*, *Szalatavus*, and unworn upper molars of some callitrichines, as well as in *Talahpithecus*, although the metastyle is poorly developed in the latter, as in *Perupithecus*. There is no mesostyle.

The protocone, paracone, and metacone are well-developed, but not basally enlarged as seen in *Branisella* and *Szalatavus*, with the protocone slightly higher and tilted buccally. The cusps and entire crown are lower than observed in *Branisella* and *Szalatavus*. The preprotocrista and postprotocrista meet the preparacrista and hypometacrista, respectively, in the middle part of the trigon. The preprotocrista ends in a deep mesial fovea in an area with a small bulge similar to a vestigial paraconular area. *Talahpithecus* also has a well-developed, but less deep, mesial fovea.

There is a small swelling (vestigial entostyle or pericone?) where the entoprotocrista contacts the lingual cingulum. The lingual cingulum connects distally to a crestiform hypocone with a slightly enlarged base, as seen in *Callimico*. Posterior to the hypocone, the postcingulum is complete, reaching the metastylar area. There is no talon enlargement, which gives a subtriangular outline similar to that of *Branisella*, *Szalatavus*, and callitrichines, as well as some African taxa such as *Talahpithecus* and *Proteopithecus*. The molar has one well-developed lingual root and two buccal roots. The molar crown morphology of *Perupithecus* is consistent with an insectivorous-frugivorous diet.

Gen. et sp. *incertae sedis* A

Two additional primate upper molars, a left and right M^1 or M^2 (CPI-7000 and CPI-7001, respectively; LACM 6289/157193 and 6289/157063, casts) are recorded from Santa Rosa. Both specimens (Fig. 3c, d) lack their buccal sides, and CPI-7001 also has the area encompassing the mesial fovea broken and the preprotocrista worn. The remaining morphology and smaller size (~70% of the size of *Perupithecus*) of these specimens indicate that they belong to a genus distinct from *Perupithecus*. We refrain from formally naming these specimens because their incomplete nature prevents determination of the state of several diagnostic characters.

These molars differ from *Perupithecus* in having a poorly developed mesiolingual cingulum that is interrupted lingual to the protocone before continuing towards the hypocone; a better developed hypocone placed on a distolingual expansion of the cingulum, and by lacking an entoprotocrista and its swelling on the lingual cingulum. The paracone and metacone development cannot be seen because of the broken buccal sides. A mesial fovea is present, shallower than in *Perupithecus*; and the hypoparacrista descends more vertically from the paracone to meet the postparaconule crista, whereas *Perupithecus* has a longer, less inclined hypoparacrista. The paraconule area is more developed than in *Perupithecus*. The distal part of the CPI-7000, although broken, exhibits a postcingulum that curves back behind the metacone area, giving a 'waisted' appearance, as in callitrichines, *Branisella*, *Szalatavus*, and *Perupithecus*, as well as *Talahpithecus* and other African anthropoids. The cusps are basally broader than in *Perupithecus*, and the trigon crests are less trenchant. In overall shape, the mesiolingual side with a weak cingulum, the distolingual expansion with the small hypocone, the waisted distal part, and the less developed mesial fovea are callitrichine-like characters, usually more common in first upper molars. These features, however, are also seen in first upper molars of *Branisella* and *Proteopithecus*, thus indicating a primitive pattern.

Gen. et sp. *incertae sedis* B

The Santa Rosa local fauna has also produced an isolated right M$_3$ (CPI-6487; LACM 6289/156981, cast) (Fig. 4) whose primate status is indicated by the overall cusp positions and general morphology. The specimen has an unusually high protoconid and metaconid, which prevents its attribution to either of the genera represented by the Santa
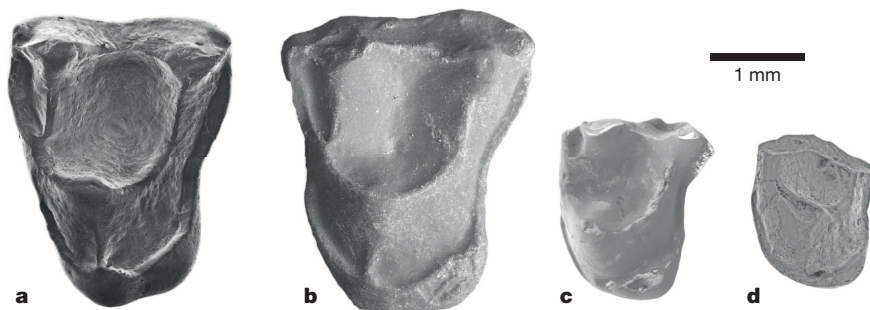

Figure 3 | Comparison SEM images. **a**, Holotype of *Perupithecus ucayaliensis* (CPI-6486 (LACM 6289/155085)); **b**, cast of holotype of *Talahpithecus parvus* (DT1-31); **c**, unassigned left upper molar (M^1 or M^2) (CPI-7000; LACM 6289/157193); and **d**, unassigned right (reversed) upper molar (M^1 or M^2) (CPI-7001; LACM 6289/157063), in occlusal views. Scale bar, 1 mm.
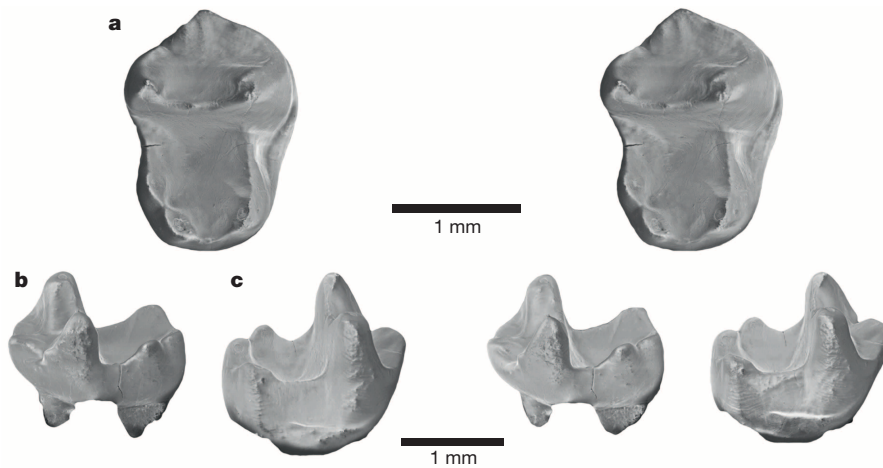
Figure 4 | **Stereo-pair SEM image of unassigned primate right M$_3$.** CPI-6487; LACM 6289/156981 in (**a**) occlusal, (**b**) lingual, and (**c**) buccal views. Note the twinned entoconid-hypoconulid, as well as the low paraconid, in **b**, and the reduced buccal cingulid and height of the protoconid and metaconid in **c**. Scale bar, 1 mm.

Rosa upper molars, where the trigon basins are not particularly deep and the cusps are lower and less differentiated.

This molar has five cusps, with a pointed protoconid and a lower metaconid transversely aligned with medial and lateral protocristids; the latter are connected to each other, closing the trigonid distally and separating it from the talonid. The cusps are relatively broad at the base and have an occlusal relief with moderate shearing crests (not pointed cusps and sharp crests as expected in primitive bats or insectivores). Distinctive features include a reduced paraconid in a restricted trigonid; a trigonid slightly higher relative to the talonid; a remnant buccal cingulum and no distal cingulum; a hypoconid not pointed nor buccally displaced; and a relatively developed and moderately deep talonid basin with narrow buccolingual margins with respect to the trigonid, as typical in lower third molars. A low paraconid connects to the protoconid through a paracristid descending almost vertically from the tip of the protoconid. A small sulcus separates the paraconid from the premetacristid that descends from the metaconid. The talonid has a moderate cristid obliqua that connects distally with the protoconid. The hypoconid is well-developed with a moderate posthypocristid. The twinned hypoconulid and entoconid are separated by a shallow sulcus. The entocristid is short, meeting the descending and also short postmetacristid. The trigonid is wider than the talonid and proportionally large (more than one-third the total length of the molar), and the talonid is relatively narrow, suggesting that CPI-6487 is a third lower molar.

A developed hypoconulid twinned to the entoconid is a primitive character seen in several Palaeogene anthropoids from Africa, such as *Proteopithecus*, *Talahpithecus*, and the Oligopithecidae. The paraconid placed almost mesially, which gives a triangular occlusal shape to the trigonid, also illustrates the primitiveness of this lower molar. In general, platyrrhines tend to shorten the trigonid mesiodistally, losing the paraconid, except for some individuals where the paraconid is insignificant and does not affect the buccolingually rectangular shape of the reduced trigonid. Only callitrichines and *Soriacebus* have trigonids larger mesiodistally, but in most cases the paraconid is lost. Compared with callitrichines, CPI-6487 has a better developed talonid with moderate cusps. Callitrichines not only trend towards reducing the talonid in M$_{1-2}$, they have extremely reduced entoconids and hypoconids in some taxa. They also lose third molars (except for *Callimico*). There are no known platyrrhines, living or extinct, with a comparable lower molar structure, and even for other anthropoids, the structure of this M$_3$ is notably primitive.

The evidence presented above documents a surprising diversity of primates for such an early site in South America. Previously, the lack of a fossil record for New World monkeys pre-dating the Salla primates led to significantly differing hypotheses on platyrrhine evolutionary history[2,12–15], most of which *Perupithecus* and the other Santa Rosa primates falsify.

The most striking aspect of *Perupithecus* is its strong resemblance to the Eocene African anthropoid *Talahpithecus* (Fig. 3b) from the late Middle Eocene (~38–39 million years (Myr)) of Dur At-Talah, Libya[10], although this locality has been suggested to be Late Eocene in age (~35–36 Myr)[16]. *Perupithecus*, like *Talahpithecus*, exhibits such anthropoid features as an M[?1] with a well-developed lingual cingulum and the presence of a hypocone, absence of paraconule, reduced stylar shelf with almost no buccal cingulum, reduced parastyle and metastyle, as well as shorter preparacrista and postmetacrista. *Talahpithecus* is similar to *Perupithecus* in size and overall morphology, and differs only in some minor details, such as having the buccal side basal to the metacone slightly developed.

Our phylogenetic analyses (see Supplementary Discussion 2 and Extended Data Figs 3 and 4) placed *Perupithecus* and *Talahpithecus* as sister taxa, a stem clade assigned with doubts to the Platyrrhini. We recognize that the characterization of *Perupithecus* and *Talahpithecus* as sister taxa in our phylogenetic analysis might be a result of morphological convergence, although we regard it as unlikely. *Talahpithecus* was originally attributed to the Oligopithecidae[10], which another study[17] included in the Catarrhini. However, the oligopithecid status of *Talahpithecus* is uncertain because it is based on three isolated teeth, two of which are broken. In addition, an undescribed anthropoid from the BQ-2 levels of Fayum represented by upper and lower dentitions has been mentioned, and close similarities with *Talahpithecus* were discussed[16]. This undescribed anthropoid had three upper and lower premolars, as in platyrrhines and in contrast to oligopithecids, and it might also represent a close relative of platyrrhines.

On the basis of the position of *Talahpithecus* and *Perupithecus* as sister taxa, closely linking the Peruvian and North African primates, the following preliminary hypotheses arise: (1) the Santa Rosa primates are members of a pre-platyrrhine anthropoid stock that differentiated in Africa from anthropoid ancestors; (2) they are Eocene platyrrhines of immediate African ancestry; or (3) platyrrhines originated in Africa, where they subsequently became extinct, and *Talahpithecus* is an early representative of their radiation, which possibly included *Proteopithecus* as part of a basal stock. *Perupithecus* fits well in any scenario depicting an African origin for platyrrhines, but more specimens are needed to determine whether the Santa Rosa primates are best explained by any of these hypotheses.

The advanced Late Eocene anthropoids of northern Africa were possibly preceded by the dispersal of stem anthropoids, the eosimiiforms (Eosimiidae + Afrotarsidae *sensu* ref. 18), from Asia to Africa by the Middle Eocene[18,19]. A possible morphological intermediate between African eosimiiforms and simiiforms is *Amamria*[19]. Although *Amamria* might be a basal anthropoid, some differences with respect to *Perupithecus* and expected early platyrrhine representatives are noted (that is, developed stylar shelf internalizing the paracone and metacone, better

developed lingual cingulum, absence of entoprotocrista). Similarly, the platyrrhine primates also might have originated via an east–west migration (that is, Africa to South America) of middle to Late Eocene anthropoids of still uncertain relationships, although crown anthropoids such as *Talahpithecus* were certainly involved.

South America and Africa have been separated since the early Late Cretaceous, so vicariance of primates does not appear reasonable as an explanation for their appearance in the Eocene on two continents separated by the Atlantic. Numerous studies have focused on the possibility of primates crossing the Atlantic to reach South America from Africa (for example, refs 20, 21), with rafting across the Atlantic usually considered a feasible way for how primates arrived in South America, presuming they originated in Africa[4]. It has also been proposed that perhaps more than one rafting event carried more than one primate taxon successfully across the Atlantic in the Palaeogene[22,23], suggesting a possible early African diversification before arrival in South America. This might favour the arrival of different higher clades in South America, thus allowing the diversification of more than one lineage. A similar means of arrival in South America has often been proposed for the hystricognath rodents[24], the dispersal of amphisbaenian and gekkotan lizards[25], and the Opisthocomiformes, a Neotropical group of birds (hoatzins) with weak flight capabilities and alleged African origin[26]. And, with the discovery of the Santa Rosa primates, the re-established, relatively contemporaneous first appearance datum of primates and rodents in South America leads to consideration of possible similarities of intercontinental dispersal mechanisms for the two mammalian groups. However, the derived status of Santa Rosa rodents relative to contemporaneous African rodents hints that rodents and primates might not have had simultaneous crossing episodes. Or, alternatively, the two groups had differing rates of diversification after arrival in South America.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Author Contributions All co-authors participated in the development of the manuscript. M.B., M.F.T., and K.E.C. wrote the manuscript and discussed all the different topics addressed in the paper. L.C. and N.N. performed the phylogenetic analysis. L.C. and F.J.G. performed the early analysis distinguishing the primate specimens from metatherians. K.E.C. and L.C. secured and edited the figures.

METHODS

No statistical methods were used to predetermine sample size.

The specimens were collected by wet screen-washing at the outcrop, followed by subsequent laboratory wet screening and separation into different size fractions (that is, >2 mm, <2 mm >1 mm, etc.). Treatment with 10% formic acid reduced the subsequent volume of matrix by ~85%. Further concentration of matrix using heavy liquid techniques and lithium metatungstate was attempted, but large quantities of manganese and iron compounds limited volume reduction. This problem was partly resolved by separating the heavier minerals before attempting to separate the fossils from the lighter minerals. *In situ* fracturing of fossil teeth[9] resulted in numerous partial specimens after processing.

The Santa Rosa primates are very small and rare. Whereas rodents and metatherians occur by the hundreds in the Santa Rosa local fauna, so far only four primates have been found. Discovery of the primates was delayed long after the initial description of the palaeofauna[8] because they only occur in the small size fraction of the matrix, the processing of which was not possible because of time constraints and the volume of matrix before discovery of the formic acid treatment. However, with the discovery of the first primate specimen in 2013, efforts to process the smaller-sized matrix were energized. Application of new techniques and funding made processing of smaller-sized material possible, and it is from this material that the primates have come.

The specimens described herein are permanently housed in the collections of the Área de Paleontología, Dirección de Geología Regional, INGEMMET, Lima, Peru. Casts are maintained in the Vertebrate Paleontology Department at the Natural History Museum of Los Angeles County.
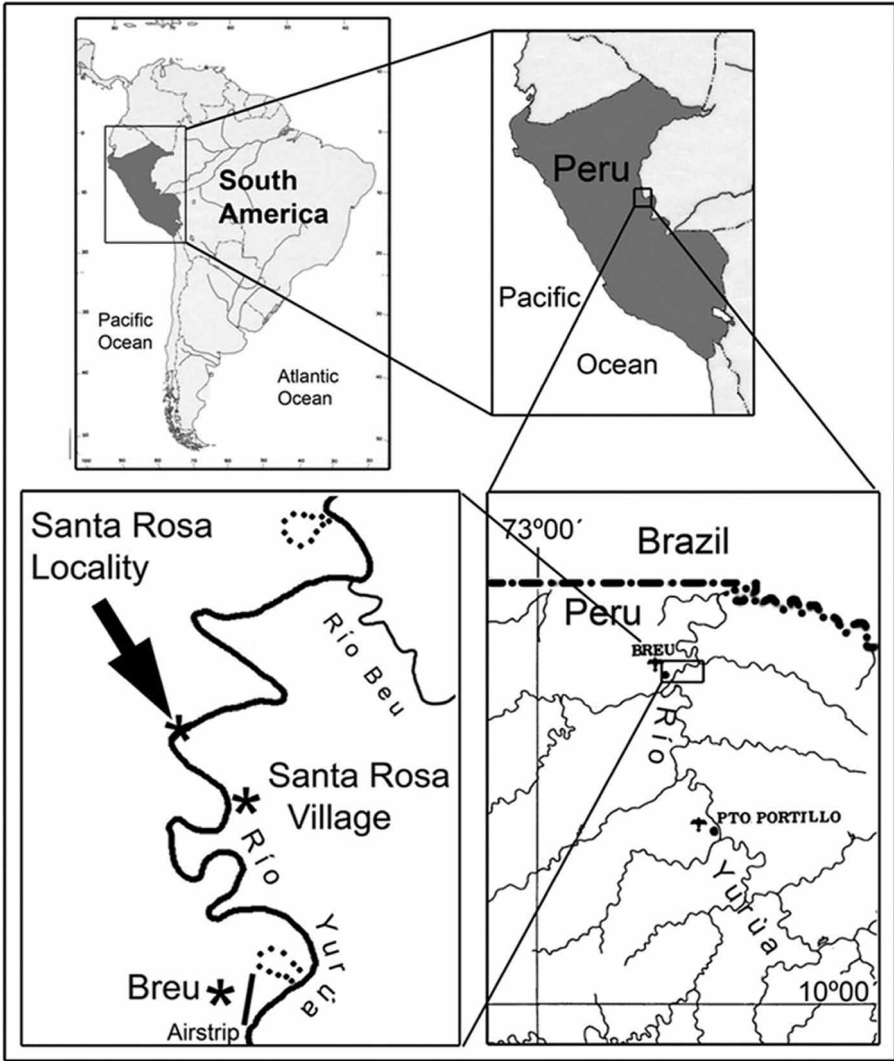
Extended Data Figure 1 | Location of the Santa Rosa locality, adapted from ref. 9.
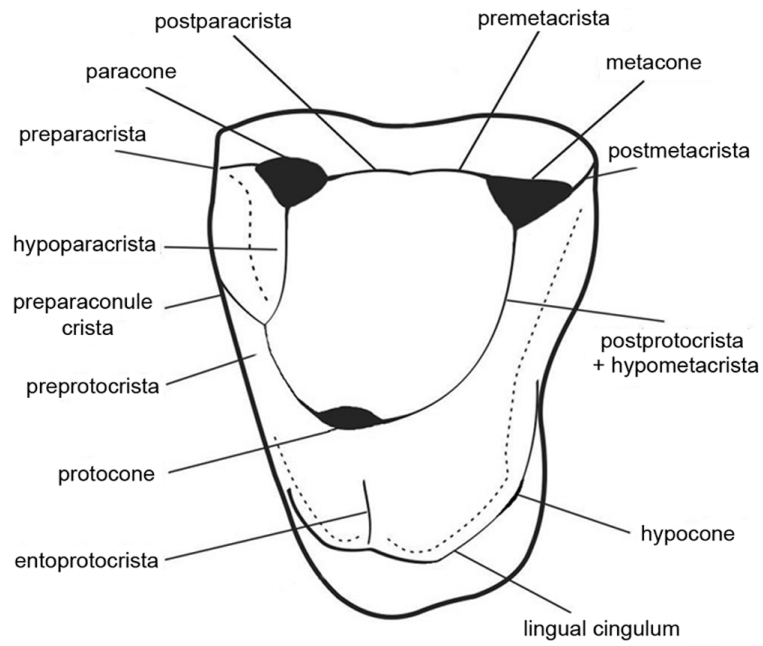
Extended Data Figure 2 | Outline drawing of the holotype of *Perupithecus*, with parts labelled. For outline drawings of African anthropoids, see refs 16, 19.
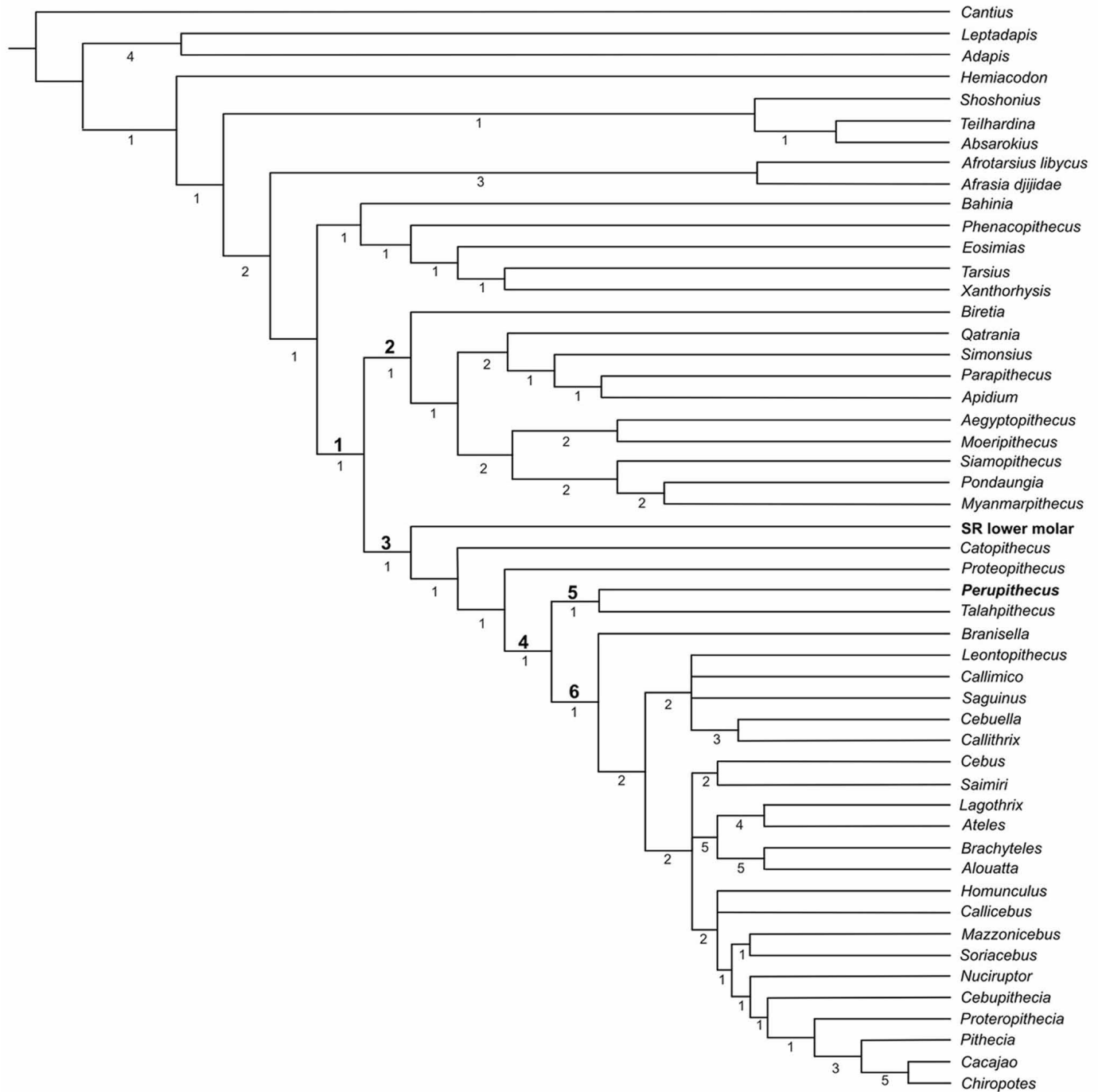
Extended Data Figure 3 | Phylogenetic positions of *Perupithecus* and the lower molar CPI-6487 with *Cantius* as outgroup and using Bremer support for the clades. It is the result of the six most parsimonious trees of 955 steps, with a consistency index of 0.274 and a retention index of 0.574.
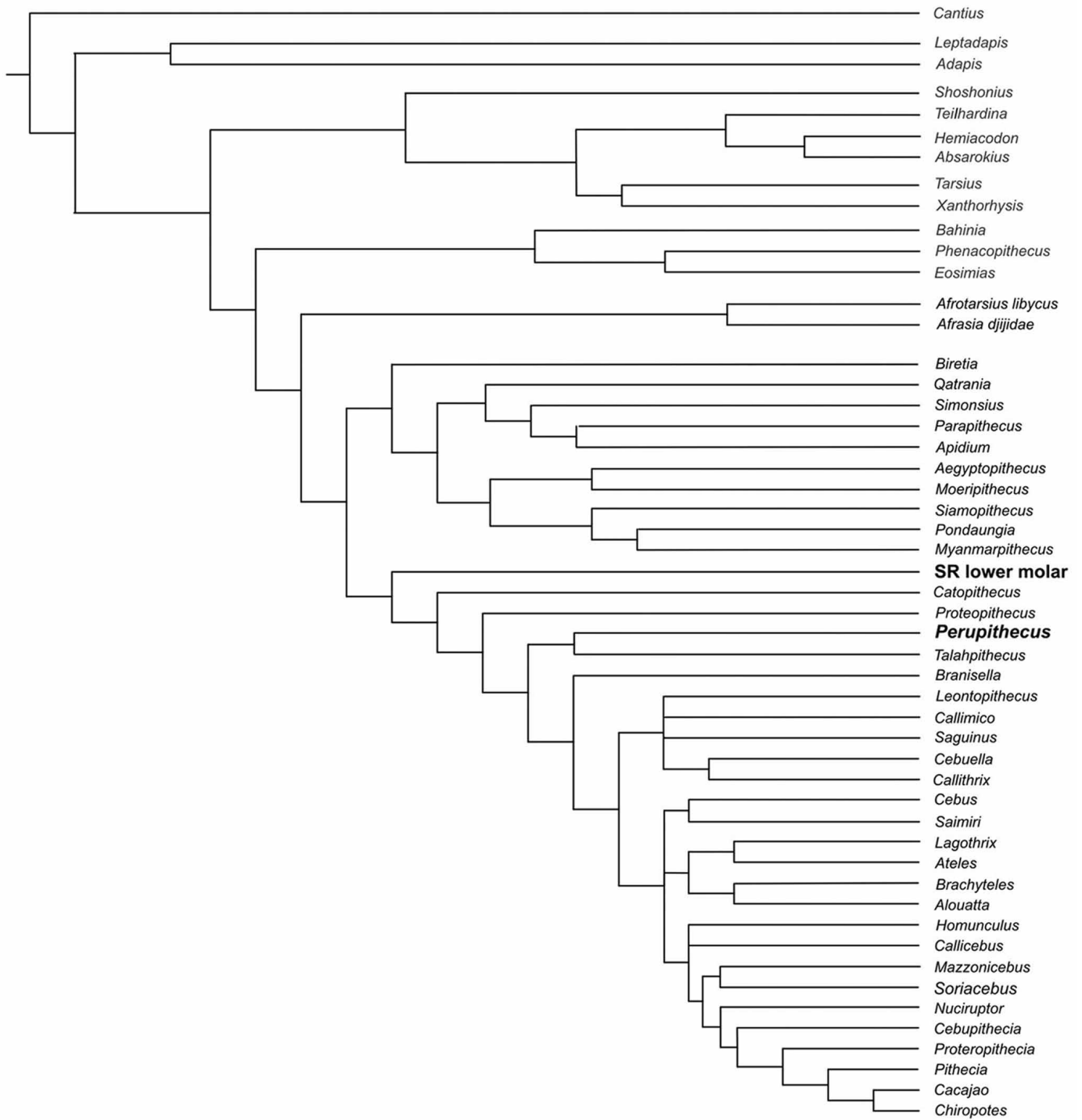
Extended Data Figure 4 | Phylogenetic positions of *Perupithecus* and the lower molar CPI-6487 with *Cantius* as outgroup, 'Omomyidae + Tarsiidae' of ref. 18 constrained, and using Bremer support for the clades. It is the result of the six most parsimonious trees of 958 steps, with a consistency index of 0.273 and a retention index of 0.572.