

First North American fossil monkey and early Miocene tropical biotic interchange

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Supplementary Methods**Methods: Comparative Morphology**

Comparisons were done within the morphological framework outlined and discussed in Kay et al. (2008)³¹ and Kay (2015)¹ with reference to the literature for fossil taxa as follows (see also Kay, 2015¹, Table 1 and references therein): *Perupithecus*, ?Late Eocene, Peru¹⁶; *Branisella*, Late Oligocene, Bolivia^{32,33}; *Chilecebus*, early Miocene, Chili³⁴; *Tremacebus*, early Miocene, Argentina^{35,36}; *Dolichocebus*, early Miocene, Argentina³¹; *Mazzonicebus*, early Miocene, Argentina³⁷; *Soriacebus*, early Miocene, Argentina³⁸; *Carlocebus*, early Miocene, Argentina³⁹; *Homunculus*, late early Miocene, Argentina⁴⁰⁻⁴²; *Proteropithecina*, middle Miocene, Argentina⁴³; *Nuciraptor*, middle Miocene, Colombia⁴⁴; *Mohanamico*, middle Miocene, Colombia⁴⁵; *Cebupithecina*, middle Miocene, Colombia⁴⁶; *Stirtonia*, middle Miocene, Colombia⁴⁷; *Neosaimiri*, middle Miocene, Colombia⁴⁸; *Patasola*, middle Miocene, Colombia⁴⁹; *Lagonimico*, middle Miocene, Colombia⁵⁰; *Micodon*, Middle Miocene, Colombia^{49,51}; *Miocallicebus*, middle Miocene, Colombia⁵²; *Acrecebus*, late Miocene, Brazil⁵³; *Paralouatta*, ?early Miocene and Quaternary, Cuba⁵⁴⁻⁵⁶; *Xenothrix*, Quaternary, Jamaica^{57,58}; *Insulacebus*, Quaternary, Haiti²³; *Antillothrix*, Quaternary, Dominican Republic⁵⁹⁻⁶². Additional comparisons were made to specimens and casts of fossil and extant platyrrhines. Three-dimensional images of relevant fossil platyrrhines were reconstructed from micro CT scans (see Methods 3-D Data Acquisition).

Methods: Phylogenetic Analysis of Morphological Data

Three phylogenetic analyses were conducted to investigate the phylogenetic position of *Panamacebus*. All phylogenetic and divergence analyses were conducted using the resources of the High Performance Computing Center at the University of Florida.

Panamacebus was added to an existing morphological character matrix which was analyzed using the same parameters as the original analysis¹ with 177 ordered characters and all characters given a weight other than one (Supplementary Data 1). A second analysis employed a different constraint tree (Supplementary Data 2) derived from a recent molecular supermatrix^{21,22}. This supermatrix contained 372 extant primate species and 61,199 nucleotides (including gaps), which we re-analyzed before using this topology as our new constraint (see description below). The second constraint tree differs from the constraint used in the original analysis¹ in two respects. First, *Aotus* is more closely related to *Saguinus* than it is to *Saimiri* and *Cebus*, and, second, *Cebuella* is absent from the molecular dataset, which is a result of *Cebuella* being synonymous with *Callithrix pygmaea*^{63,64}. The third analysis was conducted using the character ordering and weighting scheme of Kay (2015)¹ but without any constraint.

Three additional iterations of the second phylogenetic analysis with *Panamacebus*, described above, were conducted to assess the impact of the character ordering and weighting scheme imposed by Kay (2015)¹ on the topology: 1) characters ordered but unweighted, 2) characters unordered but weighted, and 3) characters unordered and unweighted (Supplementary Data 1). These analyses were conducted using the first constraint tree¹.

Each maximum parsimony analysis was conducted in PAUP v 4.0 beta⁶⁵ using a heuristic search with 1,000 random addition sequence replicates and tree-bisection-reconnection (TBR) branch swapping. Multi-state characters were treated as polymorphic. Bootstrapping was also performed with 1,000 bootstrap replicates analyzed with a heuristic search algorithm with three random-addition sequence replicates and TBR branch swapping. Trees resulting from all analyses (Supplementary Figs. 4-10) were rooted *a posteriori* with *Aegyptopithecus*, *Apidium*, *Catopithecus*, *Proteopithecus*, *Simonsius*, *Hylobates*, *Miopithecus*, and *Presbytis* and the out-group was set monophyletic to the in-group following Kay (2015)¹.

Methods: Phylogenetic Analysis of Molecular Data and Constraint Tree

A recent phylogenetic analysis of a molecular supermatrix compiled by Perelman et al. (2011)²¹ and updated by Springer et al. (2012)²⁰ was used for the second constraint tree

and for the molecular dating analysis. The molecular sequence alignment was re-analyzed using maximum likelihood in RAxML version 7.3.2⁶⁶. A rapid bootstrap analysis was conducted followed by a search for the most likely tree (-f a) under the general time reversible (GTR) plus gamma model of nucleotide evolution. The dataset was partitioned by gene segment, enabling RAxML to estimate the GTR model, empirical base frequencies, and the shape parameter (α) of the gamma distribution for each of the 79 partitions. Two iterations of this analysis were performed, each with 500 maximum likelihood inference replicates made from 500 distinct maximum parsimony starting trees. Each analysis resulted in a single “best” tree with the lowest maximum likelihood score obtained in the analysis. Both trees were rooted with Lagomorpha and compared by eye; these topologies from our replicate analyses were identical. The tree was modified appropriately for use as a constraint tree (Supplementary Data 2) for our phylogenetic analysis; any taxa that were not present in Kay’s (2015)¹ analysis were removed from the tree and species-level clades were collapsed to the genus level.

Methods: Divergence Dating Recalibration Analyses

We modified the sequence alignment from Springer et al. (2012)²⁰ in Geneious v6.1.6 (Biomatters Ltd.) to decrease computational time required for this analysis and this reduced sequence alignment contained 190 taxa and 46,851 sites (Supplementary Data 3). We conducted two separate Bayesian Markov chain Monte Carlo (MCMC) analyses in BEAST v1.8⁶⁷, the first using the Yule model⁶⁸, a pure birth process, and the second using the birth-death model⁶⁹ of speciation. The BEAGLE library v2.1⁷⁰ was used in conjunction with BEAST to decrease computational time; each analysis took approximately 20 days to complete.

Input files for BEAST were generated in BEAUti v1.8⁶⁷. Analyses were conducted under a lognormal relaxed molecular clock in which the rates along branches are uncorrelated. We used a GTR + gamma nucleotide substitution model with 4 rate categories and estimated base frequencies. A single data partition was employed and 15 calibration points were set (Supplementary Table 2; Supplementary Data 4); 14 nodes were calibrated following Springer et al. (2012)²⁰ and a 15th node was calibrated to the date corresponding to the age of *Panamacebus* (20.93 +/- 0.17 Ma). This node joins the

following platyrrhine genera: *Aotus*, *Callimico*, *Callithrix*, *Leontopithecus*, *Saguinus*, *Cebus* and *Saimiri*. The position of this calibration at this node was determined by the position of *Panamacebus* in our phylogenetic analysis. Based on the variation in the phylogenetic placement of *Panamacebus*, we took a conservative approach and calibrated the divergence of Cebinae and Callitrichinae as opposed to calibrating a node within Cebinae as suggested by the placement of *Panamacebus* in the phylogeny using the first molecular constraint (Fig.3a). All 15 priors were specified using a lognormal distribution (Supplementary Table 2). The root of the tree was specified with a uniform prior distribution with a mean value and an initial value of 83 (standard deviation = 1). The mean of the root was based on the estimated divergence of Euarchonta and Glires⁷¹. We used a gamma distribution for the “ucl.d.mean” prior with an initial value of 1, shape = 0.001, scale = 1,000. Other parameters were set to default priors. A random starting tree was used and analyses were conducted with an MCMC chain length of 200,000,000 states sampled every 10,000 states. We determined the number of states to remove prior to convergence of the MCMC chains after examining the summary statistics in Tracer v1.6 (Supplementary Table 5). Two independent replicate analyses were conducted for the Yule model and the birth-death model and similar results were obtained from these analyses. We combined the results of the replicate analyses for each model in Log Combiner v1.8 to increase the number of states available for analysis after excluding the burn-in. Maximum clade credibility trees were generated in TreeAnnotator v1.8⁶⁷ to summarize the trees (Supplementary Figs. 4-10).

Methods: Paleogeographic Reconstruction (Fig. 4; Extended Data Figure 8)

Boundaries of the tectonic blocks used in the reconstruction (inset in Extended Data Figure 8) are mapped structures in regional and local maps. For the area of interest near the Canal Basin, major boundaries include the deformed belts north and south of Panama⁷²⁻⁷⁵, the Canal Basin faults^{30,76,77}, eastern Panama and the Uramita fault^{78,79}, and Northern Andes tectonic blocks⁸⁰⁻⁸².

Early Miocene paleogeographic reconstruction was modified from published paleogeographic, paleomagnetic, and stratigraphic data. Boundaries of the tectonic blocks used in this reconstruction are mapped structures in regional and local maps. For the area

of interest near the Canal Basin, major boundaries include the deformed belts north and south of Panama⁷³, the Canal Basin faults⁷⁷, eastern Panama and the Uramita fault⁷⁸, and Northern Andes tectonic blocks⁸³.

The regional tectonic configuration of the late Oligocene-early Miocene⁸⁴ was modified for Panama with the palinspastic reconstruction of Panamá-northwestern Colombia³⁰, Maracaibo⁸⁵; Farallon⁸⁶; Central America⁸⁷; and Leeward Antilles⁸⁸.

Paleomagnetic data suggests a paleolatitudinal shift from south to north through the Cenozoic for the Caribbean plate⁸⁹, thus the reconstruction suggests a slightly more meridional position for the Isthmus than today. Data in two sites of the Azuero Peninsula indicate that the accreted seamount province⁹⁰ was located near equatorial paleolatitudes at the end of the Cretaceous⁹¹ implying about 8° to 10° northward translation during the Cenozoic. Paleomagnetic data from ODP sites 999 and 1001 record a 5° to 15° northward translation of the Hess escarpment during Cenozoic times⁸⁹. Published paleomagnetic data³⁰ from the volcanoclastic basement of central Panama, with a total of 12 sites with $\alpha_{95} \leq 11^\circ$, preliminarily suggest that the basement of the isthmus formed in southern paleolatitudes. Statistical reliability tests for near equatorial sites, however, require the number of sites to be greater than 30 with $\alpha_{95} \leq 10^\circ$ ⁹².

A regional strain marker was derived from the Campanian to Eocene magmatic arc of Panama⁷³ that is offset by a left-lateral strike-slip fault, and later overprinted by an Oligocene-Miocene arc. Piercing points were derived from integrated provenance analyses that constrain the postcollisional subduction character of the margin along northwestern Colombia⁹³. Another piercing point for this reconstruction is the Eocene and younger interaction between the lesser Antilles and northern South America, well established by paleomagnetic and provenance analyses of conglomerates in Bonaire⁸⁸.

Sedimentary environments were extrapolated from published stratigraphic sections, that were placed over the palinspastic reconstruction in the following locations:

- 1) Pacific sections that include conglomerate and sandy strata⁹⁴; 2) upper Magdalena Basin⁹⁵; 3) Amaga Formation coal-bearing and sandy-conglomeratic⁹⁶; 4) Choco⁹⁷; 5) easternmost Panama⁹⁸; 6) western Panama⁹⁹; 7) Panama¹⁰⁰; 8) Canal basin¹⁰¹; 9) northwestern Colombia^{102,103}; 10) Sierra Nevada Santa Marta, unnamed sandy and conglomeratic strata¹⁰⁴; 11) Guajira Peninsula¹⁰⁵; 12) Falcon¹⁰⁶; 13) Falcon/Lara¹⁰⁷; 14)

middle Magdalena Basin¹⁰⁸; 15) Floresta Massif¹⁰⁹; 16) axial Cordillera Oriental¹¹⁰; 17) foothills¹¹¹; 18) southern middle Magdalena Basin¹¹².

Methods: Paleobotanical Analysis of Miocene Forests

We compiled pollen and spore occurrence data from nine different formations of Oligocene to middle Miocene age (Supplementary Table 3). The samples come from Florida¹¹³, Puerto Rico¹¹⁴, southern Mexico¹¹⁵⁻¹¹⁹, Costa Rica¹²⁰, and Panama²⁷; the number of samples per formation ranges from 2 to 52 (Supplementary Table 7). We assigned the plant families and genera to coarse biogeographic categories based on modern species distributions and fossil evidence following Gentry (1982)¹²¹ and Jaramillo et al. (2014)²⁷. The categories are Gondwana-Amazonian, Gondwana-northern Andean, Gondwana-southern Andean, Laurasian, or unassigned. Next, we calculated the percent contribution of the biogeographic regions to the species (morphotype) richness in each fossil flora. Taxa that were not assigned to a biogeographic region were excluded from calculations of biogeographic affinity following Jaramillo et al. (2014)²⁷.

Methods: Biochronology

The mammalian biochronology is summarized from the literature^{6-9,14,122-134} and includes mid- to high latitude areas of North America but not the inferred temporal range extensions based on the Panama occurrences (Supplementary Table 6).

Supplementary Results

Results: Stratigraphic Context of Lirio Norte Local Fauna

The late Oligocene to early Miocene Bas Obispo and Las Cascadas formations represent the oldest subaerial sequences cropping out along the Panama Canal area⁷⁷. They are characterized by massive accumulations of volcanoclastic sediments ranging from welded tuffaceous agglomerates and black vitric lavas to pyroclastic fall deposits and discrete intervals of more clastic fluvial sediments^{11,135}. The basal part of the Las Cascadas Formation, mostly consisting of non-fossiliferous crudely layered volcanic breccias and tuffs, unconformably overlies the welded and massive volcanic agglomerates of the

middle to late Oligocene Bas Obispo Formation³⁰. The upper part of the Las Cascadas Formation is characterized by fossiliferous volcanoclastic sequences^{6,7} deposited in alluvial systems³⁰. At the Lirio Norte locality (Extended Data Fig. 1), the fossiliferous sequence includes ~ 15 m of normally graded sequences composed predominately by lapilli tuffs locally conglomeratic, followed by green sandstones, conglomerates, volcanic breccias and agglomerates. Fossils are concentrated in fine-grained layers (lapilli tuffs and sandstones) but isolated remains are also present in coarser lithologies at the Lirio Norte locality (Fig. 1).

Results: Geochronology of Lirio Norte Local Fauna

An ash layer that forms the upper-most part of a several meter thick, welded andesitic tuff within the Las Cascadas Formation was collected for radioisotopic dating. The tuff is exposed within the conformable section of the Las Cascadas Formation approximately 0.25 m below the principal mammalian fossil-bearing unit (Extended Data Fig. 2). A weighted mean of the $^{206}\text{Pb}/^{238}\text{U}$ ages gives 20.93 ± 0.17 Ma (2 σ) (Fig. 1), which we interpret to be the eruption age of the andesitic tuff and a close approximation of the absolute age of the Las Cascadas principal mammal fossil horizon, including the primate specimens. These data are likewise consistent with a $^{206}\text{Pb}/^{238}\text{U}$ age of 19.3 ± 0.4 Ma for a welded tuff unit within the overlying Culebra Formation³⁰.

Results: Biochronology: Lirio Norte Local Fauna

The overall biochronological signal of the mammals from the Las Cascadas Formation, Lirio Norte Local Fauna (L.F.), is taken from the individual biochrons of the taxa that have been studied or identified so far from the fossiliferous horizon. The faunal list (Extended Data Table 1) is evolving as we continue to make new discoveries, but nevertheless we interpret an unambiguous biochronological signal that relates to what is known from North American Land Mammal Ages (NALMAs) from high-latitude North America, where these biochrons (generic level) are characterized (e.g., Tedford et al. 2004¹⁴; Albright et al. 2008¹³). Seventeen mammal species classified in sixteen genera, are currently recognized from the Lirio Norte L.F. (Supplementary Table 6). When comparing these taxa to their occurrences in high-latitude North America, 10 genera have

meaningful biochronological significance, whereas six remain unstudied and are not yet informative regarding biochronology. Five of the genera are known to co-occur in Arikareean (Ar) faunal zone 3, seven or eight of the genera co-occur within Ar4, ten in Hemingfordian (He) faunal zone 1, four in He2, and three thereafter during the Barstovian NALMA (Extended Data Fig. 3). Two of the occurrences, those of the immigrant taxa *Cynelos* and the blastomerycine, are of particular importance because their First Appearance Datums (FADs) define the beginning of Ar4, *sensu* Tedford et al. (2004¹⁴). Furthermore, a number of taxa (e.g., *Texomys*, *Cynelos*, *Arretotherium*, *Aguscalientia*) do not persist in the known fossil record beyond He1, and *Petauristodon* and aff. *Bassaricyonoides* are otherwise known from He1 and younger localities at higher latitudes. Thus, the age of the Lirio Norte L.F. is no older than Ar4 and no younger than He1. The radiometric date reported here of 20.93 ± 0.17 Ma helps to refine this estimate, demonstrating a correlation to Ar4 (22.8 and 18.5 Ma¹³). The Arikareean occurrences of *Petauristodon* and *Bassaricyonoides* are thus interpreted as temporal and geographic range extensions in Panama.

Results: Detailed Description of *Panamacebus transitus*

Seven isolated teeth (Fig 2; Extended Data Figs. 4–7) are here referred to *P. transitus* based on their proximity, similarity in size, and morphologies consistent with identification as those of a single taxon of New World monkey.

Upper molars—The holotype (UF 280128) of *P. transitus* is an isolated complete crown of an unworn left M¹ with no roots. The enamel is moderately crenulated and the crown is rectangular in occlusal view with dimensions (M¹ mesiodistal length [ML] = 4.42 mm; buccolingual width [BW] = 5.94 mm) consistent with those of a medium sized New World Monkey (est. 2.7 kg¹³⁶) in the range of the White-Headed Capuchin (*Cebus capucinus*) that lives in Panama today. The crown is only slightly narrower lingually (~8%) than buccally and is comprised of four distinct cusps with the paracone the tallest, the metacone and protocone somewhat shorter and similar in height to each other, and a smaller, yet distinct, hypocone located slightly lingual to the protocone. The three major cusps are bulbous and massive, somewhat set apart with a relatively broad, shallow trigon

basin. A strong prehypocrista extends from the hypocone buccolingually to the postprotocrista and encloses the talon lingually. A sharp, distinct hypoparacrasta extends lingually from the paracone to the buccal margin of the preprotocrista, forming the distal border of a small rectangular mesial basin (=mesial fovea¹⁶). Likewise, a distinct hypometacrasta extends from the metacone to join the postprotocrista at the intersection with the prehypocrista. The distolingual cingulum of M^1 is well developed, forming a narrow shelf that extends from a moderately sized and distinct hypocone, wraps around the lingual aspect of the protocone, and terminates at the level of the protocone on the mesial margin of the crown. The M^1 lacks a mesostyle, metaconule, and paraconule.

An isolated left M^2 (UF 281001) possesses a partial lingual root, exhibits minor abrasion on the crenulated enamel of the occlusal surface, and is smaller than that of the M^1 (M^2 ML = 3.62 mm; BW = 4.84 mm). The crown of M^2 is somewhat narrower lingually (16%) than buccally giving it a slight triangular profile. In comparison to the M^1 , the paracone and protocone of the M^2 are more similar in height with a slightly smaller metacone and, although the hypocone is somewhat broken, it would have been a distinct cusp similar to that of M^1 . The M^2 has a well-developed lingual cingulum, but the cingulum is relatively shorter than that of the M^1 , terminating lingual to the protocone at a poorly-developed entoprotocrista. The position, orientation, and development of other cristae are similar to that of M^1 with the exception of the hypometacrasta terminating buccally to the intersection of the postprotocrista and prehypocrista. As for M^1 , the M^2 lacks a mesostyle, metaconule, and paraconule.

Lower incisors—A partial left I_1 (UF 280130) preserves about two-thirds of an apparently moderately tall and vertical crown that was likely spatulate, with distal widening evident towards the broken tip. In cross-section, the crown of I_1 is oval (ML/BW] = 0.68] with well-developed enamel and lingual swelling at the base. Distal and mesial lingual crests are present but do not meet on the lingual heel to form a lingual cingulid. A right I_2 preserves part of the root and a complete crown, somewhat larger than that of I_1 (ratio of cross sectional areas, $I_1/I_2 = 0.83$). The crown of a right I_2 (UF 267048) is similar to that of I_1 in being moderately high, vertical, spatulate, oval in cross section (ML/BW = 0.66), and having well-developed enamel with strong lingual swelling

at the base and well-developed, yet separate, distal and mesial crests. In lateral view, the lower incisor crowns are gently curved. The presence of an anterior interstitial facet on I_2 indicates a lack of spacing between the incisors and wear on the edges of the I_2 crown indicate that the lower incisors would have formed an arcuate battery.

Lower canine—A right C_1 (UF 280131) preserves a nearly complete root and crown (with some missing enamel). The crown is considerably taller and larger in cross-sectional area than that of the incisors, with a rounded lingual crest and a raised and unbroken lingual cingulum that runs from a large distal heel to the mesial terminus of the paracristid.

Lower premolars—Two isolated lower premolars (UF 280127, left P_2 ; UF 280129, left P_4), with complete crowns and most of their roots, were recovered in direct association with each other and with similar wear patterns suggesting the possibility that they belong to a single individual. Both lower premolars are single rooted. Both premolars are moderately high crowned and inflated, with sloping cusp margins. The trigonid of P_2 is unicuspid with a protoconid but no metaconid, and the talonid is small and lacks a hypoconid and entoconid. The crown of P_4 has a lingually expanded protoconid that is connected to a closely set and relatively smaller metaconid by a short transversely-oriented protocristid. The talonid of the P_4 is relatively broad and bordered by a weakly-developed hypoconid and entoconid.

Results: Comparative Morphology of *Panamacebus transitus*

Comparisons were done within the morphological framework outlined and discussed in Kay et al. (2008)³¹ and Kay (2015)¹ with reference to the literature for fossil taxa (see Methods).

Discovery of a fossil monkey in the early Miocene of Panama, recovered from a basin that was connected with North American continental terrains, together with a diversity of other mammals with exclusively North American and Eurasian affinities, might suggest a comparison to Old World Monkeys (catarrhines) that likely similarly dispersed from Africa into Asia by the early Miocene¹³⁷. In fact, the upper molars of *Panamacebus* compare fairly well with those of early Miocene pliopithecids from

China¹³⁸ in having a somewhat rectangular outline in occlusal view, relatively low and rounded cusps, a distinct hypocone, a well-developed prehypocrista, a broad and well developed lingual cingulum, and lack of distinct conules. However, the lower premolars of *Panamacebus* contrast strongly with those of catarrhines in retaining a P₂ (lost in Old World Monkeys) and in having a single-root on P₄ (it is double rooted in Old World Monkeys). Thus, *Panamacebus* is clearly part of the platyrrhine radiation despite its geographic location outside of South America.

Upper molars—The M¹ of *Panamacebus* is notably larger in occlusal area than that of M², a condition within Cebidae that is more similar to that of extant callitrichines than that of extant or fossils cebines, including *Neosaimiri* from the Middle Miocene of Colombia (Extended Data Fig. 4) and extant *Cebus* (Extended Data Fig. 5), which have a relatively larger M² (although still smaller than M¹). We note that this condition appears to have evolved several times in platyrrhine evolution (e.g. middle Miocene pitheciid *Cebupithecia* (Supplementary Fig. 2) and Quaternary *Xenothrix* from Jamaica have similar proportions). The M¹⁻² of *Panamacebus* is similar to that of most platyrrhines in lacking inflation of the protocone. This contrasts with the presence of an inflated protocone found on the upper molars of *Acrecebus* + *Cebus* (Extended Data Fig 5), pitheciids (except *Callicebus*), and *Xenothrix*. The M¹⁻² of *Panamacebus*, however, exhibit a buccally expanded paracone, similar to that of other cebines (except *Aotus*), some atelids, all pitheciids, and some stem platyrrhines. Notably, the most basal stem platyrrhines including *Perupithecus*, *Branisella*, *Soriacebus*, *Mazzonicebus*, and *Homunculus* lack this condition indicating that the buccal expansion likely evolved several times in platyrrhine evolution.

Among crown platyrrhines, the M¹ of *Panamacebus* is similar to that of cebines, atellids, and pitheciids in having a large hypocone, in contrast to that of callitrichines in which it is either absent or reduced. A large hypocone on M¹ is also characteristic of many stem platyrrhines, although the more reduced condition of the hypocone in *Tremacebus*, *Soriacebus*, *Branisella*, and *Perupithecus* may be the plesiomorphic condition for the clade. The hypocone on M² of *Panamacebus* is also relatively large, similar to that of most crown platyrrhines (except callitrichines in which it is lacking, and

certain pitheciines, including *Chiropotes* and *Cebupithecia* [Supplementary Fig. 3], in which it is more reduced) and many stem platyrrhines (except *Xenothrix*, *Tremacebus*, *Soriacebus*, and *Branisella* in which it is more reduced).

As for nearly all crown platyrrhines (with the exception of *Callimico*), the crowns of M^{1-2} of *Panamacebus* lack a paraconule. Among stem platyrrhines, this characteristic is probably plesiomorphic, with *Perupithecus*, *Branisella*, *Mazzonicebus*, and *Soriacebus* also lacking a paraconule, although it is present in others, including *Dolichocebus*, *Chilecebus*, *Tremacebus*, *Carlocebus*, and *Homunculus*. Lack of a metaconule on M^{1-2} of *Panamacebus* is a shared characteristic with other platyrrhines with the exception of the cebine clade *Acrecebus* + *Cebus* (Extended Data Fig 5) and the callitrichine *Callimico*. We should note that a metaconule is variably present in a number of platyrrhines, including *Branisella*. Lack of a mesostyle on M^{1-2} of *Panamacebus* is similar to that of other cebines and many other platyrrhines (including *Perupithecus*), although it is present in most callitrichines, some atelids (e.g., *Brachyteles*, *Alouatta*, *Stirtonia*), and the stem platyrrhines *Paralouatta* and *Dolichocebus*. *Panamacebus* is similar to most other platyrrhines, with the exception of *Leontopithecus*, *Saimiri*, *Antillothrix*, *Paralouatta*, and *Tremacebus*, in lacking a pericone on its upper molars. The variable appearance of a paraconule, metaconule, mesostyle, and pericone among stem and crown platyrrhines suggests independent evolution of cusps in these positions.

The M^{1-2} postprotocrista of *Panamacebus* is similar to that of other cebids (except *Acrecebus* + *Cebus*; Extended Data Fig 5) in that it is continuous with a hypometacrista that reaches to the base of the metacone. This contrasts with the condition in atelids (except *Stirtonia*), pitheciids (except *Cebupithecia* [Supplementary Fig. 3]), and most stem platyrrhines (except *Xenothrix*, *Soriacebus*, and *Branisella*) in which this crest does not reach the base of the metacone. As for all platyrrhines except *Mazzonicebus* and *Soriacebus*, the M^{1-2} of *Panamacebus* lacks a postprotocrista spur (Kay, 2015¹). While otherwise highly variable within platyrrhines, the M^{1-2} of *Panamacebus* is similar to other cebids (except *Cebuella* and *Acrecebus* + *Cebus*; Extended Data Fig 5) in having a sharp hypometacrista. *Panamacebus* is similar to almost all other platyrrhines in having an M^{1-2} prehypocrista that is oriented buccolingually towards the postprotocrista. In contrast, *Cebus* and *Acrecebus* have a more buccally oriented prehypocrista⁵³. On the other hand,

among cebids *Panamacebus* is most similar to *Aotus* and *Acrecebus* + *Cebus* (Extended Data Fig. 5) in having a strong M^{1-2} prehypocrista rather than the weak-to-absent condition of *Saimiri* and *Neosaimiri* (Extended Data Fig. 4). We note that while this characteristic is somewhat variable within clades, a strong hypocrista may be plesiomorphic for crown platyrrhines (it is also strong in *Xenothrix*, but otherwise reduced or absent in other stem platyrrhines). As for all extant and fossil platyrrhines (with the exception of *Homunculus* and *Dolichocebus*) the crowns of M^{1-2} of *Panamacebus* lack a preprotoconule crista.

The M^{1-2} of *Panamacebus* is similar to that of other cebids in having a strong and complete lingual cingulum (except *Saguinus* and *Aotus* in which it is weak). While a weak or absent lingual cingulum is also present in atelids, some pitheciids and the stem platyrrhines *Xenothrix* and *Carlocebus*, it is likely that the strong condition exhibited by *Panamacebus* is plesiomorphic for Platyrrhini (it is well developed in both *Perupithecus* and *Branisella*). The M^{1-2} of *Panamacebus* is similar to that of many other platyrrhines (including *Perupithecus*) in lacking a buccal cingulum, in contrast to that of callitrichines, some atelids, and the stem platyrrhines *Paralouatta*, *Carlocebus*, *Homunculus*, and *Branisella* that have a buccal cingulum (although it is variably expressed in several of these taxa). Among cebids the M^{1-2} of *Panamacebus* is similar to *Saimiri*, *Neosaimiri* (Extended Data Fig. 4), and most callitrichines (except *Saguinus*) in having an anterior cingulum, as opposed to the weak or absent condition of *Aotus* and *Acrecebus* + *Cebus* (Extended Data Fig 5). More broadly, presence of an anterior cingulum is found throughout Platyrrhini, with several likely losses in pitheciines (e.g., *Callicebus*) and stem platyrrhines (e.g., *Antillothrix*, *Paralouatta*, *Dolichocebus*, *Chilecebus*).

Lower incisors (Extended Data Fig. 6)—Both *Panamacebus* and *Aotus* have an I_1 crown that is almost as large as that of I_2 , which differs from that of other cebines. In this way, they are more similar to most callitrichines (except *Saguinus*) and contrast with the rest of Platyrrhini (except *Paralouatta*) which all have a relatively smaller I_1 . The rounded cross-sectional shape of I_2 is similar to that of many platyrrhines including most cebids (except *Cebuella* and *Callithrix*) and atelids. This contrasts with the mesiodistally compressed cross-sectional area of the I_2 of pitheciids (except *Callicebus* and *Pithecia*) and the stem

platyrrhines *Mazzonicebus* and *Soriacebus*. *Panamacebus* has moderately high crowned incisors (higher than that of other cebines) similar to those of some callitrichines (e.g., *Saguinus*, *Lagonamico*), *Callicebus*, and *Homunculus*. The spatulate shape and gently curved buccal outlines of the incisor crowns of *Panamacebus* are similar to those of all other platyrrhines except those of *Cebuella* and *Callithrix* which have more acutely curved buccal outlines with a more lanceolate shape. *Panamacebus* has a strong lingual swelling (“heel”) on the base of the crown of I₂, similar to that of other cebids (except *Cebuella* and *Callithrix*) and atelids. In contrast, the I₂ of pitheciids (except *Callicebus*), *Paralouatta*, *Mazzonicebus*, and *Soriacebus* lack lingual swelling. *Panamacebus* has a strong lingual cingulum on its lower incisor similar to of other cebids (except *Lagonamico* and *Mohanamico* which lack a cingulum) but differs from most cebids (except *Cebuella*) in that the cingulum is not complete. Atelids also have a lingual cingulum (incomplete in all but *Brachyteles* and *Lagothrix*) and both *Dolichocebus* and *Branisella* have a complete lingual cingulum.

Lower canine—The rounded cross-sectional shape of the C₁ of *Panamacebus* is similar to that of all other platyrrhines except that of *Cebuella* and *Callithrix* in which it is mesiodistally compressed. Likewise, the C₁ of *Panamacebus* is similar to most other platyrrhines in having a rounded lingual crest. In contrast, the lingual crest of *Aotus*, *Mohanamico*, and some pitheciids (e.g., *Pithecia*, *Cacajao*, *Chiropotes*, *Cebupithecia* [Supplementary Fig. 2]) is sharper. The C₁ is similar to that of other platyrrhines (except *Paralouatta*) in having a tall crown that would have extended at or above the tooth row, with an obliquely oriented paracristid.

Lower premolars—The lower premolars of *Panamacebus* are relatively inflated, with sloping cusp margins, similar to the condition among cebines which otherwise have less inflated crowns with more marginally positioned cusps (e.g., *Saimiri*, *Neosaimiri* [Fig. 2], *Aotus*). In this way *Panamacebus* lower premolars are also similar to those of all stem platyrrhines (except *Branisella* which lacks inflation) as well as certain callitrichines (e.g., *Cebuella*, *Callithrix*, *Leontopithecus*), certain pitheciids (e.g., *Cebupithecia*, *Nuciraptor*, *Proteropithecia*), and *Ateles*.

The P₂ of *Panamacebus* lacks a buccal cingulum, which is true for all other platyrrhines except *Carlocebus*. The P₂ metaconid of *Panamacebus* is only defined by swelling, without a clear cusp present. In this way it is similar to that of most other platyrrhines with the notable exceptions among cebids and the pitheciid *Chiropotes* for which it is larger and better defined.

The P₄ of *Panamacebus*, while somewhat worn in this region, is similar to all other platyrrhines in having a very reduced paraconid (if it was present at all). As for many other platyrrhines, the cristid obliqua on the P₄ is weak in *Panamacebus*; in contrast, it is stronger in some pitheciids (e.g. *Pithecia*, *Cacajao*, *Chiropotes*). The metaconid on the P₄ of *Panamacebus* is similar to that of most other platyrrhines in being widely spaced from the protoconid, as opposed to the more closely spaced condition in some callitrichines (e.g., *Cebuella*, *Callithrix*, *Saguinus*, *Lagonamico*) and *Paralouatta*. As for nearly all crown platyrrhines, the lingual wall of the P₄ trigonid is closed by the premetacristid to form a basin in *Panamacebus*. In contrast the atelids *Brachyteles* and *Stirtonia* (Supplementary Fig. 2), the pitheciid *Nuciraptor*, and the stem platyrrhines *Dolichocebus* and *Homunculus* lack a lingual basin. There is a distinct oval wear patch in the position of entoconid on the P₄ of *Panamacebus*, indicating that this cusp was present as in other cebines, but unlike that of callitrichines which all lack a distinct entoconid. While presence of a distinct entoconid is found in many platyrrhines, it is lacking in *Ateles*, *Chiropotes*, *Cebupithecia* (Supplementary Fig. 2), *Paralouatta*, *Mazzonicebus*, and *Branisella* indicating that its loss happened many times in the evolution of the group. The lateral and medial protocristid is continuous between the metaconid and protoconid on the P₄ of *Panamacebus*, similar to that of all other platyrrhines except *Brachyteles* (which lacks a lateral protocristid altogether) and *Mazzonicebus* in which it is not continuous. As for all crown platyrrhines and the stem platyrrhines *Homunculus* and *Branisella*, the P₄ lateral protocristid of *Panamacebus* is transversely oriented, as opposed to the rest of stem platyrrhines in which it is distolingually oriented. The P₄ hypoconid of *Panamacebus* is similar among cebines to that of *Saimiri* and *Neosaimiri* in being positioned distal to the metaconid. In contrast, it is distal to the protoconid in *Cebus* (Extended Data Fig. 7) and *Aotus*, similar to that of most callitrichines, pitheciids, and stem platyrrhines (except *Xenothrix* and *Paralouatta*). In *Panamacebus* the P₄

hypocrista is similar to other platyrrhines in lacking the strong shearing development found in the pitheciids *Pithecia*, *Cacajao*, and *Chiropotes*. While the length of the talonid relative to that of the trigonid of P₄ is highly variable among platyrrhines, they are of similar length in *Panamacebus* (midline of the trigonid/midline of the talonid= 1.51/1.62) most similar among cebines to that of *Cebus* (Extended Data Fig. 7). In contrast, the relative length of the talonid is shorter in *Saimiri*, *Neosaimiri* (Extended Data Fig. 6), and *Aotus*.

Results: Phylogenetic Analysis of *Panamacebus*

We successfully replicated the results of the phylogenetic analysis conducted by Kay (2015)¹ before adding *Panamacebus* to this data set (results not shown). Our first analysis contained *Panamacebus* and used the same parameters set by Kay (2015)¹, including ordering 177 characters and weighting 399 characters. This analysis resulted in two well resolved most parsimonious (MP) trees that are 126,733 steps in length (Fig. 3a, Supplementary Fig. 4). These two MP trees differ only in the presence of sister group relationship between *Cebupithecia* and *Nuciruptor* in one tree, whereas in the other tree this sister group relationship is not recovered, though *Cebupithecia* is adjacent to *Nuciruptor*. In the strict consensus of these trees *Panamacebus* falls within crown Platyrrhini, specifically within Cebidae (Supplementary Fig. 5).

To explore the effect of weighting and ordering on the placement of *Panamacebus* and the stability of the overall tree topology, we conducted three additional analyses using Kay's (2015)¹ constraint tree with different combinations of ordered and weighted characters. Our analysis with characters ordered and equally weighted yielded 11 MP trees with 2,083 steps. In the strict consensus of these trees (Supplementary Fig. 6), the majority of taxa form a polytomy, though there is some resolution at the tips of the tree within the Callitrichinae, Atelidae and within the outgroup taxa *Aegyptopithecus*, *Hylobates*, *Miopithecus*, and *Presbytis*. When all characters were weighted but none were ordered we obtained one MP tree 119,479 steps in length (Supplementary Fig. 7). Callitrichinae and Cebidae are well resolved in this tree and the position of *Panamacebus* is maintained within Cebinae, as in the analysis with characters ordered and weighted. When characters are equally weighted and un-ordered we obtained 66 MP trees 1,935

steps in length. The strict consensus of these trees is highly unresolved, with the majority of taxa forming a polytomy (Supplementary Fig. 8). The relationships within Callitrichinae are well resolved but *Panamacebus* is more closely related to Callitrichinae than to Cebinae. Relationships within Cebinae are completely unresolved in this tree and Atelidae and Pitheciidae are non-monophyletic.

The results of the analysis using the constraint tree derived from Springer et al. (2012)²⁰ and the unconstrained analysis demonstrate the influence of the constraint tree on the tree topology. Conducting the analysis with characters ordered and weighted following Kay (2015)¹ with a different constraint tree derived from Springer et al. (2012)²⁰ yielded 4 MP trees with a length of 127,183 steps. Overall the topology of the strict consensus of these trees (Supplementary Fig. 9) is similar to the analysis using Kay's constraint tree, but there is less resolution within Cebidae with sister taxa *Cebus* and *Acrecebus*, *Saimiri* and *Neosaimiri* forming a polytomy with *Aotus* and *Panamacebus*. The relationships within Callitrichinae, however, are well resolved and the remainder of the tree topology is identical to the result from the analysis using Kay's constraint tree.

We obtained five MP trees from the unconstrained analysis with all characters ordered and weighted following Kay (2015)¹ with a length of 124,010 steps. The strict consensus of these trees (Supplementary Fig. 10) is poorly resolved; Cebinae, Callitrichinae, and Atelidae are all non-monophyletic. *Panamacebus* falls out in a polytomy with taxa from the Greater Antilles, *Paralouatta*, *Xenothrix*, and *Antillothrix*. The results of our phylogenetic analyses are influenced heavily by the constraint tree used, as illustrated by the comparisons with our unconstrained analysis (Fig. 3c) in which the new taxon forms a polytomy with fossil taxa from the Greater Antilles. The low bootstrap support for the position of *Panamacebus* (<50) is a reflection of the large amount of missing data for this taxon in the character matrix. Ordering and weighting characters following Kay (2015)¹ also influences the topology of the tree; altering or removing these *a priori* assumptions results in a poorly resolved tree topology with low bootstrap support (<50) at many nodes.

Overall, these results demonstrate the high sensitivity of this analysis to character weighting and, to a lesser extent, ordering. The placement of *Panamacebus* in these trees

varies depending on the whether characters are ordered and/or weighted and whether the analysis is constrained or unconstrained. In part this is because of the relative lack of morphological data for this new taxon; once more material is recovered it should be re-analyzed in a new morphological character taxon matrix to better understand the relationship of *Panamacebus* to other Platyrrhini.

Results: Divergence Dating Analysis

The divergence estimates resulting from our analysis (Extended Data Figs. 9-10) of the reduced sequence alignment derived from Springer et al. (2012)²⁰ are congruent with results from the previous analysis²⁰. The analyses conducted under both birth-death and Yule models yielded highly similar, well-supported results with respect to both the divergence estimates and the tree topology (Supplementary Table 5, Extended Data Figs. 9-10). For clarity, here we refer only to specific dates from the maximum clade credibility tree from the birth-death analysis (Extended Data Fig. 9).

For each calibrated node, our 95% credibility intervals overlap with those of Springer et al. (2012)²⁰. Our estimate of the split between Haplorhini and Strepsirrhini has a wider range than previously reported²⁰ falling between 61.56-81.42 Ma (posterior probability [PP]: 0.83), in contrast to Springer et al.'s (2015)²⁰ date of 60.99-76.72 Ma. The estimate for the divergence of Platyrrhini and Catarrhini (most recent common ancestor [MRCA] of Simiiformes) falls between 30.82-44.41 Ma (PP:1.0). These dates overlap with, but are slightly younger than, those reported by Springer et al. (33.55-49.48 Ma) and by Kiesling et al. (2015)¹⁸ (36.04-42.07 Ma).

We estimate that the divergence of pitheciids from atelids and cebids occurred 22.93-27.14 Ma (PP:0.99) which aligns with Springer et al.'s estimate (19.26-27.49 Ma), and is also congruent with Kiesling et al.'s (2015)¹⁸ date of 25.14-26.36 Ma. Importantly, our new divergence estimate for the split between Callitrichinae and Cebinae, based on the phylogenetic position of *Panamacebus* and calibrated with the radioisotopic date (20.77-21.90 Ma, PP: 1.0), overlaps with the range estimated by Springer et al. (2012)²⁰ (16.07-23.5 Ma) and narrows the estimated range from 7.43 Ma to just 1.13 Ma. This range also overlaps with the dates obtained by Perelman et al. (2011)²¹ (15.66-24.03 Ma). Our inferred divergence of Cebidae from Atelidae (21.84-24.93 Ma, PP:0.99) also

reduces the interval estimated for this split from 7.97 Ma (Springer et al., 2012)²⁰ to 3.09 Ma. Springer et al. (2012)²⁰ estimated that the divergence between Cebids and Atelids was 18.14–26.11 Ma.

Our estimate for the split between *Cebus* and *Saimiri* is 13.83–19.77 Ma (PP:1.0), a range that is slightly narrower than the estimate obtained by Springer et al. (2012)²⁰ (13.76–20.79 Ma). This difference is subtle but relevant because it likely results from our new fossil calibration. Furthermore, multiple other divergence estimates within Platyrrhini are also narrower than the estimates obtained by Springer et al. (2012)²⁰ including MRCA estimates for *Pithecia*, *Chiropotes*, *Callicebus*, *Brachyteles*, *Lagothrix*, *Ateles*, Cebidae, *Cebus*, and *Callithrix*. The divergence of *Aotus* from other cebids (*Saguinus* + *Leontopithecus* + *Callithrix*) falls between 19.33–21.55 Ma (PP:1.0).

The MRCA of Catarrhini is estimated at 20.67–27.68 Ma (PP:1.0), which is congruent with both Springer et al. (2012)²⁰ (19.67–32.83 Ma) and Perelman et al. (2011)²¹ (25.66–37.88 Ma).

Results: Paleobotanical Analysis of Miocene Forests and Platyrrhine Distributions

The floras in Southern Mexico, and Florida have a significantly larger Laurasian component than the flora of Costa Rica and Panama during the early Miocene (Supplementary Table 7). Despite the presence of the Central American Seaway during the early Miocene, the floras of southern Central America (southern Costa Rica and Panama) are composed of almost exclusively South American (Gondwanan) taxa^{27,121}. Our data indicate that there was a gradient in tropical forest composition from primarily Gondwanan taxa in Costa Rica and Panama to more Laurasian taxa in Southern Mexico and Florida (Supplementary Table 3).

This dichotomy could be explained by the relative antiquity of the landscapes and species-area effects. Most of Mexico and the Gulf Coast have had terrestrial landscapes at least since the Eocene. These habitats were fully connected to the North American continent and were consequently occupied by Laurasian forests. By contrast, terrestrial landscapes of Panama and Costa Rica are much younger, and only were developed extensively until the early Miocene. These areas were essentially a new terrestrial landscape that emerged from the oceans during the lower part of the early Miocene.

Fossil evidence indicates that these territories were first colonized by Gondwanan-derived South American taxa rather than by Laurasian forests, even though there was a physical connection with Mexico/Gulf Coast while a seaway separated Panama from South America. Why that would be the case is still an unsolved question. A possible explanation is the combination of strong niche conservatism and biome area.

Gondwanan-South American tropical forests of the Miocene covered extensive areas of South America, an area almost as large as North America. By contrast, Laurasian Mexican tropical forests of the Miocene occupied a much smaller area. Once the new tropical landscape of Costa Rica and Panama emerged, Gondwanan-South American tropical forests, derived from a much larger species pool, were able to move into these new territories where they outcompeted Laurasian forests.

This gradient of forest type in Central America could have limited the northern range of platyrrhines in the Neotropics during the early Miocene if platyrrhine distribution is governed by the availability of suitable forest habitat rather than climate. Whereas important elements of the Gondwanan flora for platyrrhines include Moraceae, Fabaceae, Chrysobalanaceae, Sapotaceae, Arecaceae, and Anacardiaceae, the most important elements of the tropical Laurasian flora include Juglandaceae (*Engelhardia*, *Carya*), Fagaceae (*Quercus*), Pinaceae and Ulmaceae.

The forests of Amazonia and tropical Africa share many plant families and genera. Historically, this pattern has been explained by the continents' shared gondwanan history¹³⁹⁻¹⁴¹; however, floristic exchange between tropical Africa and tropical south America has continued since the Late Cretaceous and throughout the entire Cenozoic by long-distance dispersal events facilitated by ocean circulation patterns¹⁴²⁻¹⁵¹. During the early Miocene, the Gondwanic broadleaf forests of southern South America (Patagonia) were likewise more similar to Gondwanic tropical South America (Amazonia) than to Laurasian forests at equivalent latitude in North America¹⁵². Important elements of Patagonian broadleaf forests that have been identified in early Miocene pollen records include Arecaceae, *Bombax*, *Coupania*, Lauraceae, Malpighiaceae, and Rubiaceae^{153,154}. Because closely related plants tend to be ecologically similar¹⁵⁰, we suggest that the ecological requirements of platyrrhine monkeys were met in the Gondwanan forests of Patagonia, but not by the Laurasian forests of Southern Mexico and further north. By the

middle Miocene, however, the expansion of arid climates and open vegetation at high southern latitudes^{153,154} likely contributed to the restriction of New World Monkeys to tropical forests.

Supplementary References (not included in Text, Methods, or Extended Data)

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