

Lufengpithecus inner ear provides evidence of a common locomotor repertoire ancestral to human bipedalism

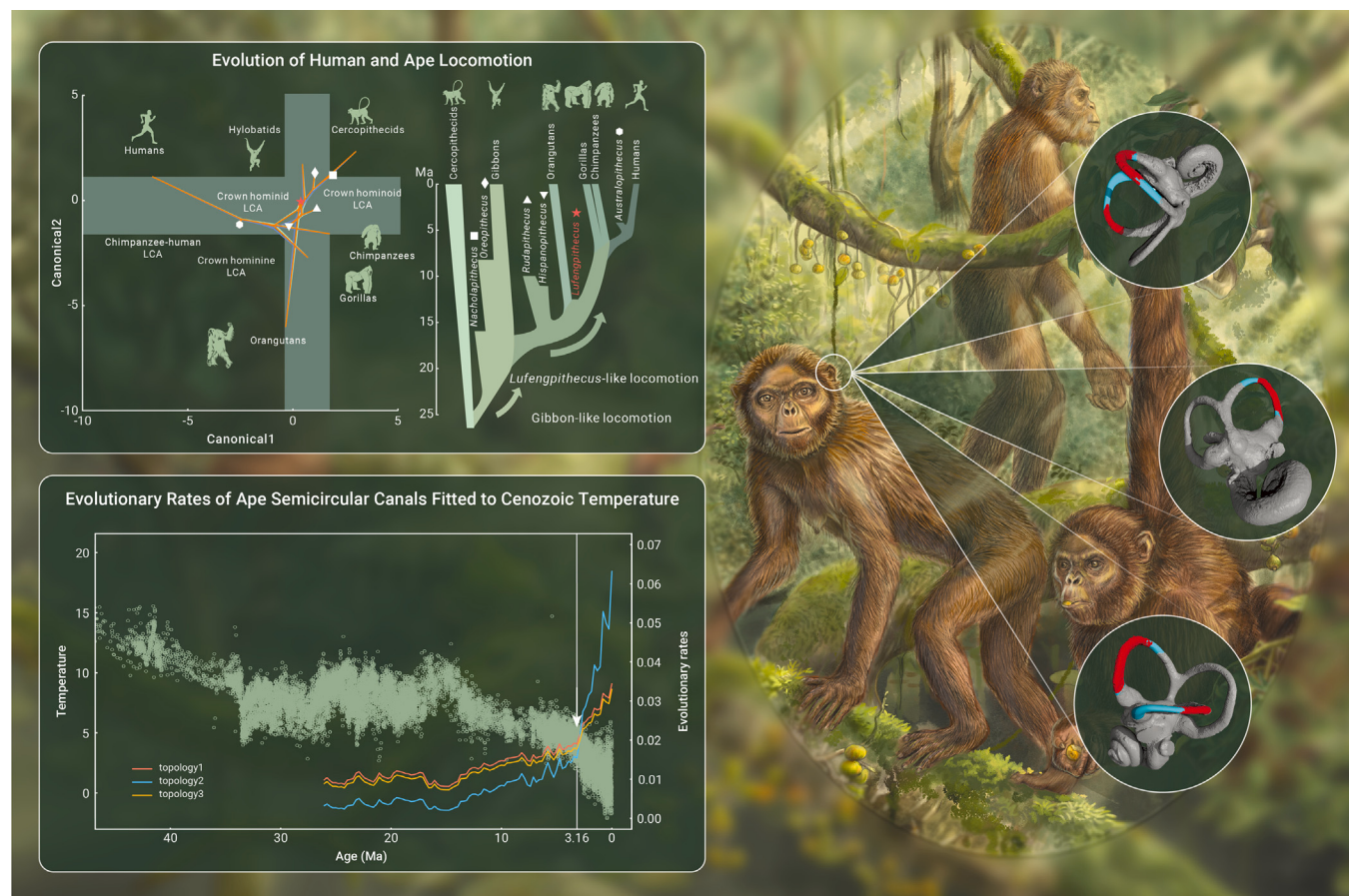
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GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Shapes of the balance organs within the inner ear shared between *Lufengpithecus* and other Miocene apes support that they shared a common pattern of locomotion.
- The ability to habitually walk and run upright on two feet in human probably evolved from this *Lufengpithecus*-like locomotion.
- Global cooling around 3.2 million years ago may have triggered an acceleration in the evolution of human bipedal locomotion.



Lufengpithecus inner ear provides evidence of a common locomotor repertoire ancestral to human bipedalism

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Various lines of evidence have been used to infer the origin of human bipedalism, but the paucity of hominoid postcranial fossils and the diversity of inferred locomotor modes have tended to confound the reconstruction of ancestral morphotypes. Examination of the bony labyrinth morphology of the inner ear of extinct and living hominoids provides independent evidence for inferring the evolution of hominoid locomotor patterns. New computed tomography data and morphometric analyses of the Late Miocene ape *Lufengpithecus* indicate that it and other stem great apes possess labyrinths similar to one another and show that hominoids initially evolved from a positional repertoire that included orthograde, below-branch forelimb suspension and progression, above-branch bipedalism, climbing, clambering, and leaping (hylobatid-like) to one that comprised above-branch quadrupedalism, below-branch forelimb suspension, vertical climbing, limited leaping, terrestrial quadrupedal running and walking, possibly with knuckle walking, and short bouts of bipedalism (chimpanzee-like). The bony labyrinth morphology of *Lufengpithecus* indicates that it probably conforms more closely to the last common ancestors of crown hominoids and hominids in its locomotor behavior than do other Miocene hominoids. Human bipedalism evolved from this common archetypal *Lufengpithecus*-like locomotor repertoire. The low evolutionary rate of semicircular canal morphology suggests that *Lufengpithecus* experienced a relative stasis in locomotor behavior, probably due to the uplift of the Tibetan Plateau, which created a stable environment in the Miocene of southwestern China.

INTRODUCTION

Determining the evolutionary pathway to human bipedalism from the quadrupedal arboreal locomotor modes of apes has been a critical question examined from a variety of perspectives and using a diversity of datasets, but it is one that is currently unresolved. It has been suggested that chimpanzee- and gorilla-like knuckle walking, orangutan-like brachiation and clambering, or hylobatid-like arboreal bipedalism may represent the ancestral locomotor pattern that gave rise to human bipedality.^{1–6} However, no definitive ancestral locomotor morphotypes have been inferred for the last common ancestors (LCAs) of hominoids, hominids, or hominins. Studies of the postcranial fossils of Miocene hominids, including the early hominins *Ardipithecus* and *Sahelanthropus*, indicate possible positional behaviors that are not found among extant apes.^{2,7–13}

The bony labyrinth of the inner ear of vertebrates houses the peripheral vestibular system comprised of three fluid-filled semicircular canals that are functionally tied to sense of balance, spatial orientation, posture, and body movements. This, in turn, is linked to modes of locomotion among living and extinct taxa.^{14–19} Comparative morphology and experimental evidence from across Vertebrata support the hypothesis that vestibular shape reflects aspects of positional behavior and that the brain and cranium are likely shaped in part by natural selection on the semicircular canals for locomotor function.¹⁵ Given the lack of consensus in the determination of ancestral locomotor repertoires derived from the fossil record and analyses of postcranial anatomy, a detailed examination of the bony labyrinth of extant and extinct apes allows for the formulation of testable hypotheses regarding the evolution of human and ape locomotor behavior. Here, we report on the bony labyrinth morphology of the Asian Miocene ape *Lufengpithecus*. Our morphometric analyses provide evidence to support a close similarity between *Lufengpithecus* and European Miocene dryopitids (i.e.,

Rudapithecus and *Hispanopithecus*) and extant African apes.^{20,21} The results shed new light on reconstructing the ancestral locomotor mode of hominids and the origin of human bipedalism.

The Late Miocene great ape *Lufengpithecus* (~7–8 Ma) from southern China was initially thought to be closely related to *Ramapithecus*, a purported early human ancestor.²² This viewpoint has since been abandoned, but the phylogenetic relationship between *Lufengpithecus* and other hominoids remains unsettled. The molars of *Lufengpithecus* have relatively thick enamel, peripheralized cusps, expansive occlusal basins, and dense and complex enamel crenulations.^{23,24} These features are considered to be similar to those of orangutans.^{25,26} Some cranial features, such as broad interorbital distance, stepped nasoalveolar clivus to the nasal passage floor, square orbits, and presence of a frontal sinus, indicate that *Lufengpithecus* may have a closer phylogenetic relationship with African apes.²⁷ Various authors have suggested that *Lufengpithecus* is a member of the *Sivapithecus*-orangutan clade, the sister taxon of extant great apes and humans, or a stem hominid.^{23,27–31} The largest collection of *Lufengpithecus* (*L. lufengensis*) specimens is from Shihuiba in Lufeng County, Yunnan Province. During the excavations of 1975–1983, four relatively complete but crushed crania of male and female specimens were recovered.³² We applied high-resolution computed tomography (CT) scanning to these crania, and this revealed that three petrosals were preserved (supplemental information).

RESULTS

The virtual models of the bony labyrinths of *Lufengpithecus* (Figures 1 and S16–S18) are stout and relatively large in internal diameter, similar to the states in *Rudapithecus* (Figures S11–S13), *Hispanopithecus* (Figure S10), and African apes (Figures S5 and S6). Measurements (Table S1) show that the canals are smaller in diameter than those of orangutans (Figure S4), *Australopithecus* (Figures S14 and S15), and humans (Figure S7) and much larger in diameter than the canals in *Nacholapithecus* (Figure S8), *Oreopithecus* (Figure S9), and hylobatids (Figure S3). The ampullae of *Lufengpithecus* are relatively slender, being similar to those of African apes, *Australopithecus*, and humans; more inflated than orangutans; and less inflated than those of *Rudapithecus*, *Hispanopithecus*, *Oreopithecus*, *Nacholapithecus*, and extant hylobatids. The relative size of the vestibule is similar to that in *Rudapithecus*, *Hispanopithecus*, and chimpanzees. The anterior semicircular canal (ASC), posterior semicircular canal (PSC), and lateral semicircular canal (LSC) of *Lufengpithecus* are compressed in the anteromedial-posterolateral, anterolateral-posteromedial, and dorsoventral planes, respectively, being similar to orangutans, gorillas, chimpanzees, *Australopithecus*, and humans. In *Rudapithecus*, *Hispanopithecus*, and *Nacholapithecus*, the ASCs, PSCs, and LSCs are compressed dorsoventrally.^{20,21} The ASC of *Lufengpithecus* is dorsolaterally projecting with an oblique long axis, a shape similar to the ASC of hylobatids (Figures S3 and S16–S18). In *Rudapithecus*, *Hispanopithecus*, and extant chimpanzees and gorillas, the ASCs also have oblique long axes and show similar dorsolateral projection. By contrast, orangutans, hylobatids, and *Oreopithecus* have more oblique and projecting ASCs. The PSC of *Lufengpithecus* is larger in diameter and more rounded than its ASC. Its posterodorsal projection is similar to that in African apes, *Hispanopithecus*, *Australopithecus*, and humans but less than that in *Rudapithecus*, *Oreopithecus*, and hylobatids. The LSC of *Lufengpithecus* is large in diameter, and its outline is a rounded triangle. The lateral extension of the LSC is similar to that in *Australopithecus*, orangutans, and *Hispanopithecus*; smaller than that in chimpanzees, gorillas,

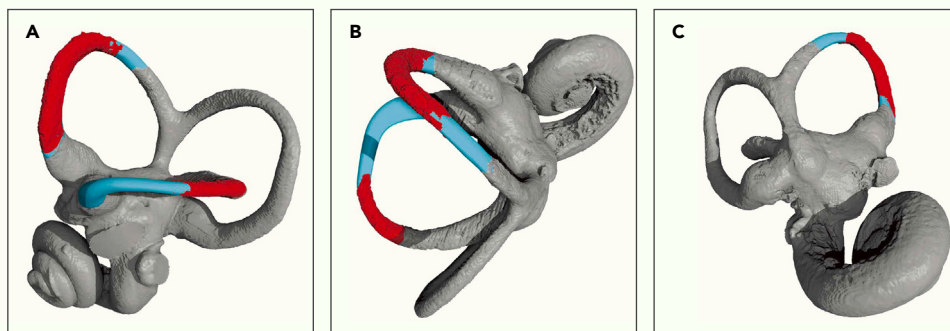


Figure 1. The virtual left bony labyrinth of *Lufengpithecus* (PA844) (A) Lateral view. (B) Superior view. (C) Medial view. Red color indicates the restored malposed parts caused by crushing of the specimen. Light blue indicates the reconstructed broken parts. The reconstruction is based on the right bony labyrinth of PA844 and PA677.

and hylobatids; and larger than that in humans, *Rudapithecus*, and *Oreopithecus*. The posterior part of the LSC of *Lufengpithecus* is straight, a state that is shared with *Rudapithecus*, *Hispanopithecus*, orangutans, and humans. The common crus of *Lufengpithecus* is moderately thick and long, being similar to *Rudapithecus*, *Hispanopithecus*, African apes, and humans. *Australopithecus* and *Oreopithecus* have a shorter and stouter common crus, whereas hylobatids and *Nacholapithecus* have a thinner and longer common crus. The round ASC of *Nacholapithecus* is similar to that of cercopithecids (Figures S1 and S2).

Previous research has revealed that the size of the bony labyrinth in vertebrates is allometrically correlated with body size. The relative, rather than absolute, size of the bony labyrinth is positively correlated with degree of agility^{17–19} and may reflect variation in locomotor patterns (but see the debates between David et al.³³ and Hanson et al.¹⁵). Relative to their estimated body mass, the size of the semicircular canal in *Lufengpithecus* falls well below the allometric regression line (Figure 2). *Australopithecus*, extant, and Miocene great apes all have smaller semicircular canals relative to their body mass than the hylobatids. Although the ASC of *Lufengpithecus* (Figure 2A) has a morphology similar to that of hylobatids, the relative size of the ASC is much smaller than that of hylobatids and is particularly close to those of *Australopithecus* and *Rudapithecus*. The LSC and PSC of *Lufengpithecus* (Figures 2B and 2C), however, are relatively larger than those of *Australopithecus* and *Rudapithecus* and roughly the same size as those of chimpanzees and other Miocene apes.

We used landmark-semilandmark-based three-dimensional geometric morphometric analyses (supplemental information) to compare the semicircular canal and vestibular morphology and to reconstruct the ancestral hominoid and hominid morphotypes. Between-group principal-component analysis on Procrustes shape coordinates shows that six extant primate groups (i.e., cercopithecids, hylobatids, orangutans, gorillas, chimpanzees/bonobos, and humans) are well separated in the first three between-group principal components (bgPCs; Figures 3A–3C, S27, and S28). The bgPC1 mainly reflects the variation of the posterolateral extension of the lateral semicircular (Figure 3D). The bgPC2 reflects the variation of the largest extension of the PSC and LSC, dorsal expansion of the ASC and vestibule, inner expansion of the ampullae of the PSC, and the anterior expansion of the ampullae of the ASC and LSC (Figure 3E). The bgPC3 reflects the variation of the largest extension of the LSC and the posterolateral expansion of the outer edge of the PSC (Figure 3F). Cercopithecids, hylobatids, and humans do not show any overlap with the African apes (Figures 3A–3C). The extant great apes (i.e., orangutans, chimpanzees/bonobos, and gorillas) slightly overlap each other (see Figures 3A–3C for African apes and 3C for orangutans and chimpanzees). The bgPC1 and bgPC2 values for *Lufengpithecus* (average of PA844 and PA677) fall within the range of hylobatids, while the bgPC3 of *Lufengpithecus* is within the ranges of variation of all great apes, except for gorillas (Figures 3A–3C). The result particularly reflects the superficial similarity shared by the ASCs of *Lufengpithecus* and hylobatids. The bgPC1 and bgPC2 values of the stem hominoid *Oreopithecus* (BAC 208) falls within the range of hylobatids, while another stem Miocene hominoid, *Nacholapithecus* (KNM-BG 42744), lies between African apes, hylobatids, and cercopithecids (Figure 3A). Their bgPC3 values fall in the overlapping region of cercopithecids, chimpanzees, and orangutans (Figures 3B and 3C). Previous linear morphometric analyses of bony labyrinths suggested that *Oreopithecus* is similar to extant apes,³⁵ consistent with our results. The bgPC1 and bgPC2 values of the dryopith *Rudapithecus* (RUD 200 and RUD 77) are close to

in the ranges of variation of cercopithecids, chimpanzees, and orangutans (Figures 3A–3C). The bgPC values of *Australopithecus* are located between African apes and modern humans (Figure 3A), a result that is consistent with previous analyses.³⁶

To further reduce the dimensionality of the morphospace, we used quadratic discriminant analysis (QDA) to classify the extant and fossil primates, including humans (Figures 4A and S29–S31). All the primates except chimpanzees and gorillas were well separated in the QDA discriminant space of the first two canonical axes (Figure 4A). Miocene and extant apes, *Australopithecus*, and humans show a cross-pattern with *Lufengpithecus* and dryopiths near the intersection in this canonical discriminant space (Figure 4A). Canonical 1 reflects the difference between bipedal humans, *Australopithecus*, and other hominoids. Canonical 2 reflects the difference within Miocene and extant apes. The stem hominoid *Nacholapithecus* falls between the ranges of cercopithecids and hylobatids, while *Oreopithecus* falls in the ellipse of hylobatids. *Rudapithecus* and *Lufengpithecus* fall between the ranges of chimpanzees and hylobatids. Humans represent an evolutionary trajectory divergent from the apes. *Australopithecus* and *Hispanopithecus* occupy the morphospace between humans and chimpanzees but are closer to the latter.

Although it has been suggested that the bony labyrinth morphology of great apes is phylogenetically informative,^{20,37} neighbor-joining cluster analyses²⁰ and our parsimony analyses (Figure S32; Table S4) based on the morphology of the bony labyrinths of extant and Miocene apes resulted in dendrograms that are not concordant with recent phylogenetic analyses of apes and humans.^{30,38,39} We therefore reconstructed the ancestral states of the bony labyrinth using three widely accepted phylogenies of hominoids (Figures 4, S19, S20–S26, and S29–S31). The results are closely similar to each other no matter which phylogenetic position of *Lufengpithecus* is assumed (Figure 4A). The LCAs of crown hominines, hominids, and hominoids all fall outside of the variation range of extant hylobatids and great apes. Previous analyses indicated that the LCAs of dryopiths, crown hominines, and crown hominids are very similar.^{20,21} Our results show that the LCAs of crown hominids and hominoids are close to each other in the QDA discriminant space but that the LCA of crown hominines is on the offshoot in the direction of bipedal humans. The LCA of chimpanzees and humans is located even further in the direction of the human locomotor pattern. The LCA of crown hominoids lies between the 95% ellipses of hylobatids and chimpanzees. Intriguingly, *Lufengpithecus* is most similar to extant chimpanzees and hylobatids and not to orangutans in the QDA discriminant space. Compared to other Miocene apes, *Lufengpithecus* is closer to the position of the reconstructed LCA of crown hominoids. The LCAs of *Lufengpithecus* and other hominoids and hominids also lie between chimpanzees and hylobatids.

We calculated the evolutionary rate of shape changes of semicircular canals based on the variation of QDA canonicals (Figures 5B–5D; see details in the supplemental materials and methods 1.4.4). Significantly accelerated evolution can be found in dryopiths and humans. Accelerated evolution of semicircular canals may reflect the rapid differentiation of novel locomotor modes that might be influenced by paleoclimatic changes. To further investigate the relationship between morphological evolution and paleoclimate, we fit Cenozoic global temperature data⁴⁰ to the evolutionary rate of semicircular canals (Figure 5A). Results suggest that evolutionary rates of semicircular canals are in negative exponential correlation with global sea surface temperature for all three possible phylogeny topologies (Figure 5A; Table S3).

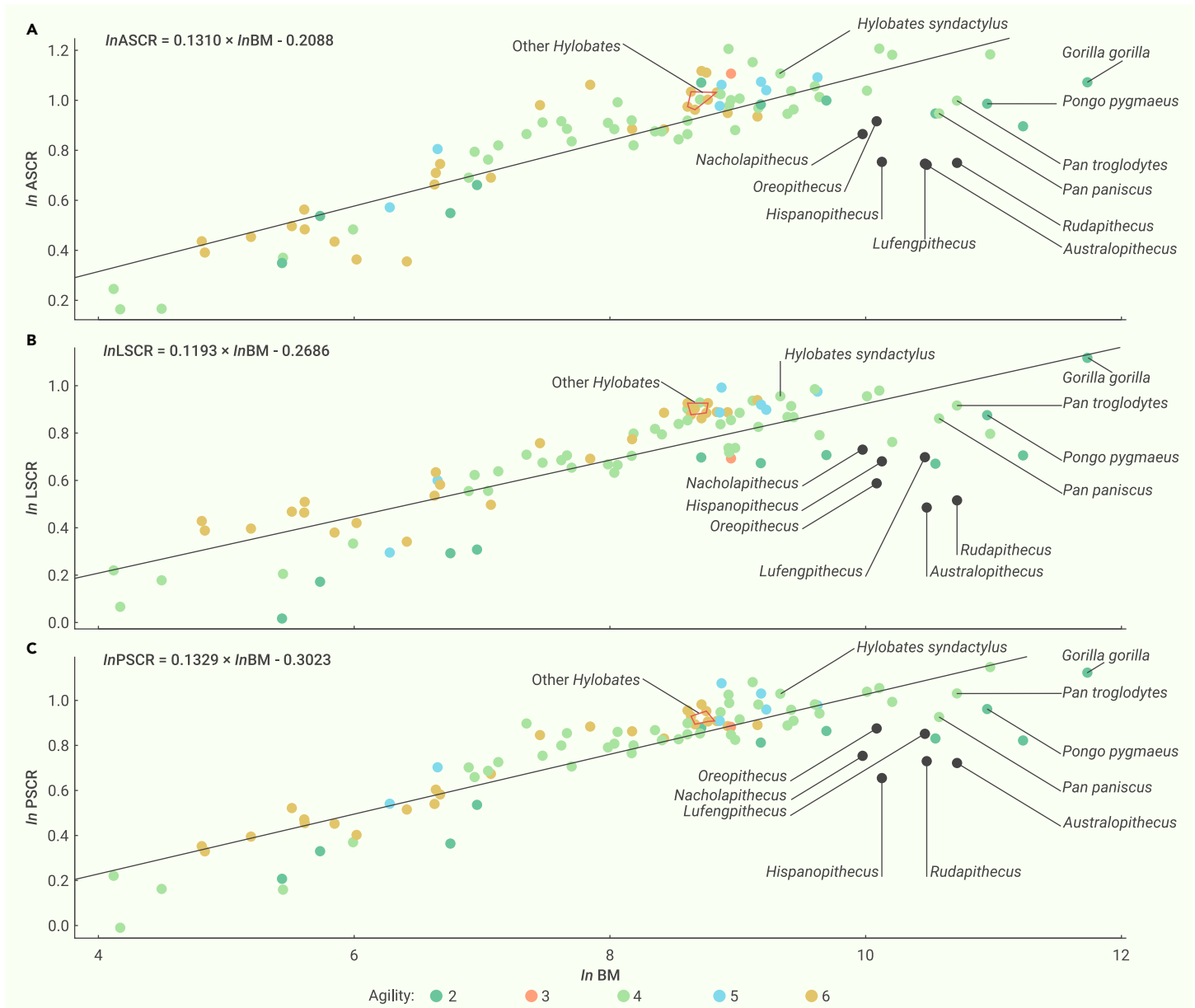


Figure 2. The relative semicircular canal sizes of *Lufengpithecus* compared to other primates (A) Anterior semicircular canals. (B) Lateral semicircular canals. (C) Posterior semicircular canals. The semicircular canal sizes are from Spoor et al.¹⁸ The body mass estimation of extant primates and fossil apes is from Spoor et al.¹⁸ and Fleagle.³⁴

DISCUSSION

The postcranial morphology of Miocene great apes shows a tendency for positional behavioral adaptations to have developed in a complex and mosaic way, initially from forelimb-dominated arboreal quadrupedalism and climbing toward the forelimb-suspension and orthograde locomotor pattern seen in extant apes.^{2,9,11,41,42} Because of the mosaic nature of this process, the positional behaviors of Miocene great apes inferred from the postcranial fossils were probably not similar to those of extant hominoids.^{7–10}

The relative semicircular canal size of primates has been suggested to be positively correlated with agility.¹⁸ The relative semicircular canal size of *Lufengpithecus* is within the range of variation of extant and Miocene great apes and is much smaller than that of hylobatids, suggesting that these great apes are less agile than the lesser apes. However, agility is not strictly correlated with locomotor pattern; for example, orangutans and gorillas have the same degree of agility, but their locomotor patterns are different. Hylobatids have the same degree of agility as tarsiers and galagos, but their locomotor patterns are very different.

Our morphological comparison and geometric morphometric analyses reveal that the bony labyrinth morphology of *Lufengpithecus* and the European Miocene dryopithecids, along with the reconstructed LCAs of hominoids

and hominoids, is in an intermediate position between the hylobatids and great apes. Given the strong correlation between the bony labyrinth morphology and locomotor mode,^{14,17–19,43} the positional bauplans of hylobatids and chimpanzees can be regarded as successive ancestral morphotypes of great apes and humans. It is important to emphasize that we do not intend to imply that ancestral conditions were identical to the specialized locomotor repertoires found in extant hominoids but rather that general aspects of their essential locomotor activity and positional behaviors can be inferred to have been shared by the LCAs. An ancestral behavioral repertoire that was hylobatid-like would include active and agile arboreality dominated by orthograde, below-branch forelimb suspension and progression, above-branch bipedalism, climbing, clambering, and leaping.^{3,44,45} A chimpanzee-like ancestral repertoire would comprise above-branch quadrupedalism, below-branch forelimb suspension, vertical climbing, limited leaping, terrestrial quadrupedal running and walking, possibly involving knuckle walking, and short bouts of bipedalism.^{3,46–51}

Our results indicate that after the phylogenetic split between hominoids and cercopithecoids, the primitive stem hominoids *Nacholapithecus* and *Oreopithecus* evolved toward a more hylobatid-like locomotor repertoire. This hypothesis is supported by the postcranial morphology of *Nacholapithecus*, which

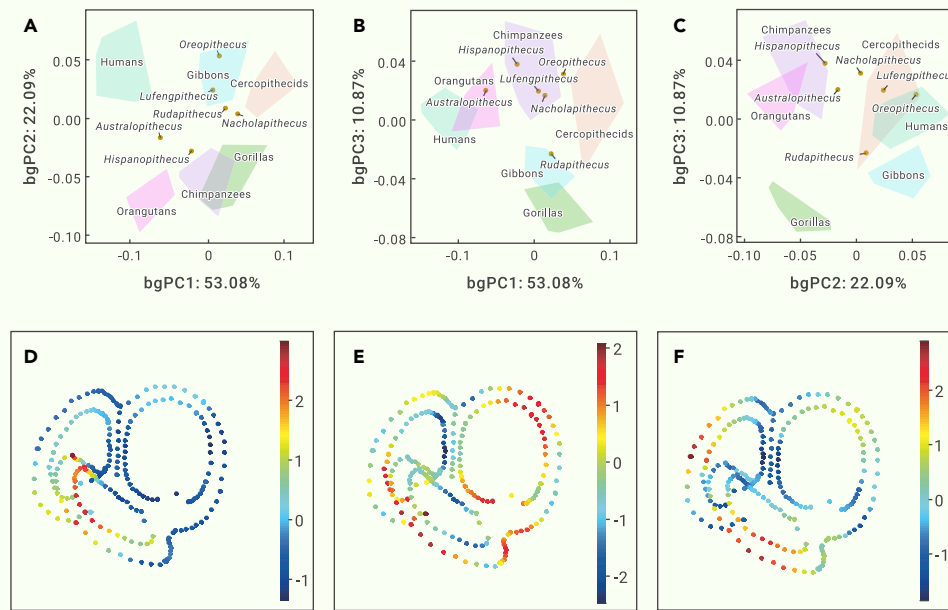


Figure 3. Between-group principal-component analysis on Procrustes shape coordinates of extant and fossil primates, including humans (A–C) Bivariable plots of the first three between-group principal components (bgPCs). (D–F) Scaled loadings of the first three bgPC renderings on the reconstructed ancestral landmarks of hominoid. Hotter color indicates greater morphological deformation.

indicates that its positional behavior consisted of forelimb-dominated and incipient antipronograde locomotor behaviors that included vertical climbing and clambering.^{52–59} *Oreopithecus* has a more derived postcranium specialized for orthograde, forelimb suspension and progression, vertical climbing, and above-branch bipedalism.^{60–65} Taking other stem hominoids into consideration (i.e., the pronograde posture of *Ekembo* and *Proconsul* and the orthograde of *Morotopithecus*), the hylobatid-like positional behavior of stem hominoids represents the transition from the generalized pronograde quadrupedal state of cercopithecids and proconsulids to the derived orthograde forelimb-dominated state of hominoids.^{60,66}

its locomotor behavior (hereafter referred to as the *Lufengpithecus*-like locomotor repertoire) than other Miocene hominoids (Figure 4A). Postcranial fossils of *Lufengpithecus* are relatively few and mostly fragmentary.^{23,32,67} Nevertheless, the scapula, clavicle, radius, and manual proximal phalanges of *Lufengpithecus* indicate that its forelimb was well adapted for suspensory behavior, being most similar in functional morphology to those of extant hylobatids and *Pongo*. The proximal femur and distal first metatarsal show that *Lufengpithecus* had a wide range of hip mobility and effective pedal grasping capabilities. Overall, the postcranial evidence points to a locomotor repertoire in *Lufengpithecus* that included forelimb suspension

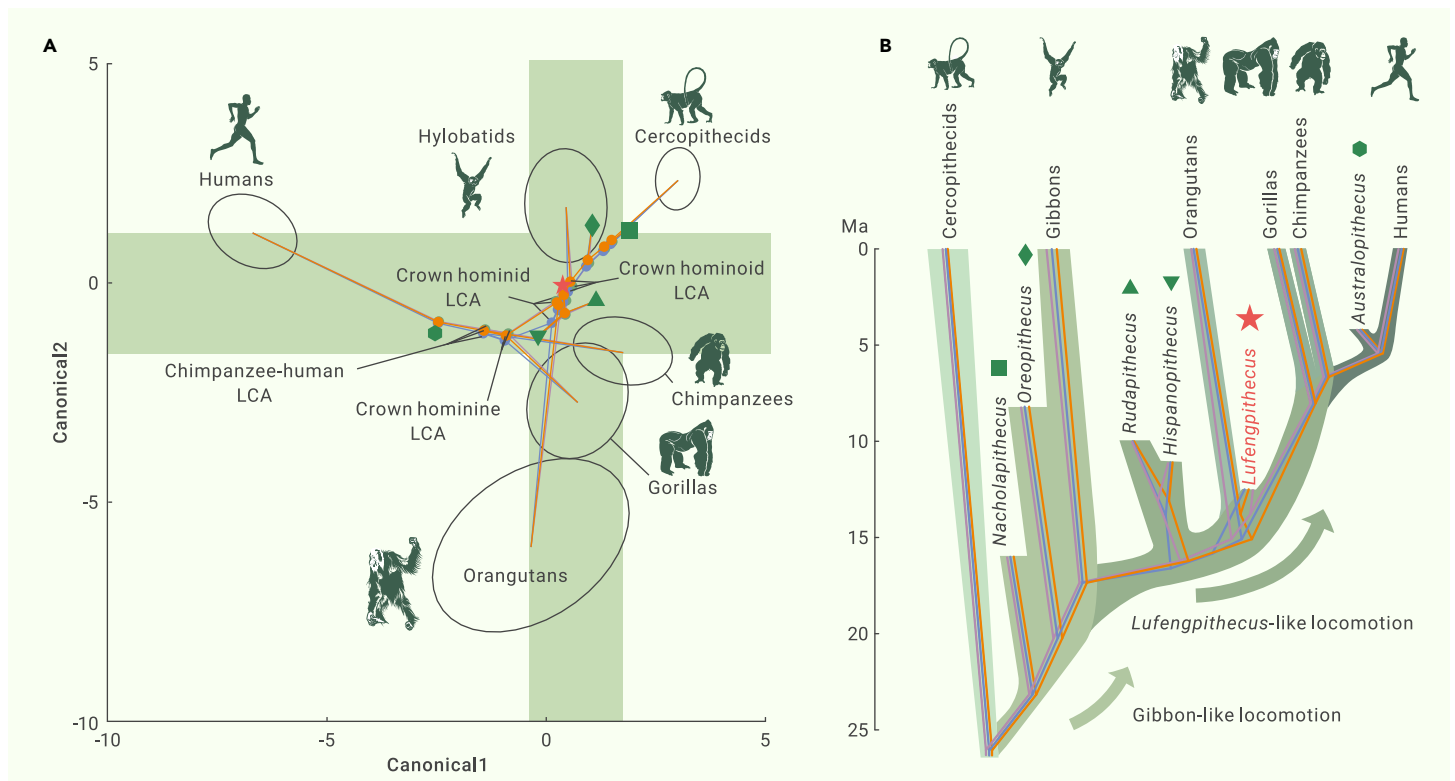


Figure 4. Polymorphospace of the bony labyrinths and conceptual graph of hominoid locomotor evolution (A) Canonical plot of quadratic discriminant analysis. Green ellipses are 95% confidence area of extant primates and humans. Symbols for fossil apes are shown in (B). (B) The hominoids developed two main generalized locomotor modes. Human bipedalism was derived from a common *Lufengpithecus*-like locomotor mode. Orange, blue, and violet lines represent three alternative phylogenetic hypotheses.



Figure 5. Evolutionary rates of semicircular canals of apes (A) Evolutionary rate fitted to Cenozoic temperature data. Green circles indicate the temperature data. Three curves correspond to three different topologies. The black arrow refers to the beginning of the accelerated evolutionary rate. (B–D) Evolutionary rate without fitting temperature data of three different topologies. (B) Topology 1: *Lufengpithecus* as a pongin, (C) topology 2: *Lufengpithecus* as a stem hominid, and (D) topology 3: *Lufengpithecus* as a stem hominine.

and progression, arboreal climbing and quadrumanous clambering, and probably above-branch bipedalism.

A recent reconstruction of the diet and locomotor behavior of the stem hominoids suggested that orthograde and forelimb suspensory positional behaviors of early hominoids evolved to enhance the locomotor flexibility for arboreal foraging in heterogeneous woodland environments.⁶⁶ The LCA of hominines and the LCA of hominins are inferred to be more similar to the *Lufengpithecus*-like locomotor repertoire than to that of terrestrial bipedal humans. It is from this generalized pattern of locomotor behavior, found widely in later Miocene hominoids and typified by *Lufengpithecus*, that humans developed their unique locomotor behavior of obligate bipedalism via a transitional phase represented by *Australopithecus*. The combination of phylogenetic, morphological, and morphometric data reveals a sequence of discrete locomotor stages within hominoid evolution starting with a hylobatid-like mode in the Early Miocene and changing to a *Lufeng-*

pithecus-like mode in the Middle Miocene of Africa before spreading across Eurasia during the later Miocene. Human bipedalism evolved from that common ancestral state that involved predominantly arboreal antipronograde quadrupedalism dominated by forelimb suspension, climbing, clambering, and above-branch bipedalism (Figure 4B).

The taxonomic diversity of later Miocene hominids in Europe diminished during the Vallesian age (11.2–8.9 Ma) due to increased aridification and cooler winter temperatures.^{68–70} Only a few relictual taxa survived in southeastern Europe into the Turolian.⁶⁹ In Asia, the uplift of the Tibetan Plateau strongly impacted the regional climate and paleoenvironment of Southwestern China, where the *Lufengpithecus* sites are located. Mesic subtropical evergreen broad-leaved forests persisted in the area throughout the Late Miocene,^{71–76} and this environment provided *Lufengpithecus* with an equable refugium, at least until the end of the Miocene.^{73,77} Evolutionary rates of shape change of the semicircular canals suggest that *Lufengpithecus* experienced relative stasis in

locomotor behavior, while significant accelerations can be observed in European and African Miocene apes and humans (Figures 5B–5D). The negative correlation between evolutionary rates and global temperature suggests that the equable environment in the Miocene of southwestern China may have provided a stable setting that promoted a relaxation of selective pressure on adaptive change in *Lufengpithecus* that resulted in a slowdown in the rate of locomotor evolution (Figure 5A). In contrast, the dramatic increase in the average evolution rate of semicircular canals starting at 3.16 Ma (Figure 5A) may reflect the rapid evolution of bipedalism in the human lineage in response to gradual global cooling. The inflection point at which the rate dramatically increases falls within the mid-Pliocene warm period of the Pliocene and marks the beginning of Pliocene continuous cooling and the onset of Northern Hemisphere glaciation.^{78,79} Against the backdrop of global cooling, the increase of grassy vegetation driven by regional-scale environmental factors⁸⁰ may be the trigger for the accelerated evolution of bipedalism in early *Homo* in Africa.

MATERIALS AND METHODS

See the supplemental information for more details about the materials and methods part.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

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