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Fossil apes and human evolution

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Single-sentence summary

Humans are one of the five surviving hominoid lineages, a decimated remainder of an ancient radiation whose fossil members are essential to understanding human origins.

Abstract

Humans diverged from apes (chimpanzees, specifically) toward the end of the Miocene ~9.3–6.5 million years ago. Understanding the origins of the human lineage (hominins) requires reconstructing the morphology, behavior, and environment of the chimpanzee–human last common ancestor. Modern hominoids (i.e., humans and apes) share multiple features (e.g., an orthograde body plan facilitating upright positional behaviors). However, the fossil record indicates that living hominoids constitute narrow representatives of an ancient radiation of more widely distributed, diverse species, none of which exhibit the entire suite of locomotor adaptations present in the extant relatives. Hence, some modern ape similarities might have evolved in parallel in response to similar selection pressures. Current evidence suggests that hominins originated in Africa from Miocene ape ancestors unlike any living species.

32

33 In 1871, Darwin (1) speculated that humans originated in Africa based on the anatomical
34 similarities with African apes (gorillas and chimpanzees) identified by Huxley (2). However,
35 Darwin urged caution until more fossils became available—the European *Dryopithecus* was the
36 only recognized fossil ape at the time (3). After 150 years of continuous discoveries, essential
37 information about human origins remains elusive due to debates surrounding the interpretation of
38 fossil apes (Figs. 1, 2).

39

40 Genomic data indicate that humans and chimpanzees are sister lineages (“hominins” and “panins,”
41 respectively; Table 1) that diverged from a “last common ancestor” (LCA) toward the end of the
42 Miocene, ~9.3–6.5 million years ago (Ma) (4, 5). All extant hominoids (apes and humans) are
43 characterized by the lack of an external tail, high joint mobility (e.g., elbow, wrist, hip), and the
44 possession of an “orthograde” (upright) body plan —as opposed to the more primitive,
45 “pronograde” body plan of other anthropoids and most other mammals (Fig. 2). These body plans
46 are associated with two different types of positional (postural and locomotor) behaviors:
47 pronograde behaviors, taking place on nearly horizontal supports with the trunk held roughly
48 horizontally; and orthograde (or “antipronograde”) behaviors, with the torso positioned vertically
49 (6, 7). Extant ape features also include enhanced joint mobility, long forelimbs relative to
50 hindlimbs, and (except gorillas) long hands with high-to-very-high finger curvature (8-10). The
51 orthograde body plan is generally interpreted as a suspensory adaptation (11, 12), or as an
52 adaptation for vertical climbing subsequently co-opted for suspension (13).

53

54 Based on similarities between chimpanzees and gorillas, a prevalent evolutionary model argues
55 that African apes represent “living fossils” and that knuckle-walking chimpanzees closely reflect
56 the morphology and behavior of the *Pan–Homo* LCA—the “starting point” of human evolution
57 (14, 15). This working paradigm also postulates that modern African apes occupy the same habitats
58 as their ancestors (16) (Fig. 1). This assumption is based on a classical scenario that situates
59 hominin origins in East Africa, due to environmental changes following the rifting of East African
60 Rift Valley during the Miocene (17). For some, a chimpanzee-like *Pan–Homo* LCA could imply
61 also that all extant ape locomotor adaptations were inherited from a modern ape-like ancestor (18).
62 However, the fossil record denotes a more complex picture: Miocene apes often display mosaic

63 morphologies, and even those interpreted as crown hominoids do not exhibit all the features
64 present in living apes (19) (Fig. 3).

65
66 The *Pan*-like LCA model builds on the “East side story” of hominin origins (17), a seriously-
67 challenged scenario. First, it is grounded in the living ape geographic distribution, which may not
68 match that at the time of the *Pan–Homo* split (Fig. 1). Second, the model relies on an outdated
69 account of the fossil record (from the 1980s), when the earliest known hominin (*Australopithecus*
70 *afarensis*) was recorded in East Africa, and no possible fossil gorillas and chimpanzees were
71 known (17). Subsequent fossil discoveries are incompatible with such a narrative:
72 *Australopithecus* remains from Chad indicate that early hominins were living ~2,500 kilometers
73 west of the Rift ~3.5 Ma (20). Furthermore, if *Sahelanthropus* is a hominin, it would push back
74 the human lineage presence in northcentral Africa to ~7 Ma (21). Moreover, continued fieldwork
75 efforts in less explored areas have shown that hominoids lived across Afro-Arabia during the
76 Miocene (22-25). In addition, remains of putative hominines have been found in East Africa (26,
77 27), perhaps even in Europe (28, 29). Finally, paleoenvironmental reconstructions for late Miocene
78 apes and hominins suggest the *Pan-Homo* LCA inhabited woodlands, not tropical rainforests (30-
79 33).

80
81 Current debates about the transition from an ape into a bipedal hominin are centered on the
82 morphological and locomotor reconstruction of the *Pan–Homo* LCA, as well as its
83 paleobiogeography. Discrepancies are caused by conflicting evolutionary signals among living
84 and fossil hominoids—indicating rampant “homoplasy” (independent evolution causing “false
85 homology”)—and further complicated by the highly incomplete and fragmentary nature of the
86 hominoid fossil record. This review argues that, in spite of the limitations, the information
87 provided by fossil apes is essential to inform evolutionary scenarios of human origins.

88
89

90 **Evidence as to humans’ place in nature**

91 *Humans’ inner primate*

92 Since Linnaeus established modern taxonomy in 1758 (34) and until the 1960s, morphological
93 similarity was the main basis for classifying organisms. Linnaeus included modern humans (*Homo*

94 *sapiens*) within the order Primates, but it was not until 1863 that Huxley provided the first
95 systematic review of differences and similarities between humans and apes (2). Imagining himself
96 as a “scientific Saturnian” Huxley stated: “The structural differences between Man and the Man-
97 like apes certainly justify our regarding him as constituting a family apart from them; though,
98 inasmuch as he differs less from them than they do from other families of the same order, there
99 can be no justification for placing him in a distinct order” (2, p. 104). Huxley’s work was motivated
100 by widespread claims (e.g., Cuvier, Owen) that humans’ “uniqueness” warranted their placement
101 in a separate order. Darwin concurred with Huxley that humans should be classified in their own
102 family within primates (1).

103

104 We now know that most “human features” are primitive traits inherited from primate (e.g.,
105 trichromatic stereoscopic vision, manual grasping) or earlier (e.g., five digits) ancestors (35). Even
106 humans’ uniquely large brains and delayed maturation are framed within a primate trend of
107 increased encephalization and slower life history compared with other mammals (35, 36). Some
108 differences in brain size may partly reflect a neocortex enlargement related to enhanced visual and
109 grasping abilities (37). Like extant great apes, humans display larger body size, larger relative
110 brain size, a slower life history profile, and more elaborated cognitive abilities than other primates
111 (hylobatids included) (36). However, modern humans are extreme outliers in terms of delayed
112 maturation, encephalization, advanced cognition and manual dexterity, ultimately leading to
113 symbolic language and technology (38).

114

115 Anatomically, only two adaptive complexes represent synapomorphies present in all hominins: the
116 loss of the canine honing complex and features related to habitual bipedalism (33, 39). Most
117 anthropoids possess large and sexually dimorphic canines coupled with body size differences
118 between males and females, reflecting levels of agonistic behavior and sociosexual structure (40).
119 The fossil record indicates that there was a reduction in canine height, leading to the loss of the
120 honing complex in early hominins (41). Habitual bipedalism is reflected in several traits across the
121 body (e.g., foramen magnum position/orientation; pelvic, lower back and lower limb morphology),
122 present (or inferred) in the earliest hominins (21, 33, 42).

123

124 Darwin linked origin of bipedalism with an adaptive complex related to freeing the hands from
125 locomotion to use and make tools (replacing large canines), leading to a reciprocal feedback loop
126 involving brain size, cognition, culture, and eventually civilization (1). Multiple variants in the
127 order of these events have been advocated, with the freeing of the hands alternatively linked to
128 tools (43), food acquisition and carrying (15), or provisioning within a monogamous social
129 structure (44), to name a few. There is general agreement that canine reduction (including social
130 structure changes), enhanced manipulative capabilities and bipedalism were interrelated during
131 human evolution. However, determining the order of events and their causality requires
132 reconstructing the ape–human last common ancestor (LCA) from which hominins originated.
133 Darwin also speculated that humans and modern African ape ancestors originated in Africa (1),
134 based on the anatomical similarities identified by Huxley, and his own observations that many
135 living mammals are closely related to extinct species of the same region. However, given the
136 limited ape fossil record then, he concluded that it was “useless to speculate on this subject” (1, p.
137 199). Using the French *Dryopithecus* to calibrate his “clock,” Darwin concluded that humans likely
138 diverged as early as the Eocene, and warned against “the error of supposing that the early
139 progenitor of the whole Simian stock, including man, was identical with, or even closely
140 resembled, any existing ape or monkey” (1, p. 199). These ideas inaugurated a century of
141 discussions about human’s place in nature.

142

143 ***Reaching the “extant” consensus***

144 Until the 1950s, the geographic origin of hominins was disputed between Africa, Asia, and Europe.
145 Following the publication of Darwin’s *On the Origin of Species* (45), Haeckel predicted that the
146 “missing link” (dubbed “*Pithecanthropus*,” the “ape-man”) would be found in Asia (46). This idea
147 led to Dubois’ 1891 discovery of *Homo erectus* in Indonesia (47). In 1925, Dart published the
148 discovery of *Australopithecus africanus*, “the man-ape from South Africa” (48). However, the
149 scientific community still focused on Europe due to the Piltdown “fossils,” until exposed as a hoax
150 (49). Asia remained a “mother continent” contender due to the “man-like ape” *Ramapithecus*,
151 discovered in the Indian Siwaliks (50).

152

153 During this time, the relationships of humans to other primates were highly contentious. Most
154 authors advocated an ancient divergence of humans from apes (51, 52), or favored a closer

155 relationship to the great apes than to the lesser apes (53, 54). A few proposed that humans were
156 more closely related to one or both of the African apes (55, 56), although these views were not
157 widely accepted (57). These alternative phylogenetic hypotheses heavily impacted reconstructions
158 of the LCA. Some (e.g., Schultz, Straus) advocated for a “generalized” ape ancestor (52), while
159 others relied on extant hominoid models. Notably, Keith developed a scenario in which a
160 “hylobatian” brachiating stage preceded an African ape-like creature: a knuckle-walking
161 “troglodytian” phase immediately preceding bipedalism (11). Focused on Keith’s “hylobatian”
162 stage, Morton proposed that the “vertically suspended posture” of a small-bodied hylobatid-like
163 ancestor caused the erect posture of human bipedalism (12). Gregory, another prominent
164 “brachiationist,” supported similar views (53). Morton argued that knuckle walking did not
165 represent an intermediate stage preceding bipedalism, but a reversion toward quadrupedalism in
166 large-bodied apes specialized for brachiation. Then, “brachiation” was used for any locomotion in
167 which the body was suspended by the hands. Currently it refers to the pendulum-like arm-swinging
168 locomotion of hylobatids (6).

169
170 By the 1960s, the Leakeys’ discoveries in Tanzania, [e.g., *Paranthropus boisei* (58), *Homo habilis*
171 (59)], reinforced the relevance of Africa in human evolution, which became established as the
172 “mother continent” with the *Australopithecus afarensis* discoveries during the 1970s (60, 61).
173 LCA models still centered on the available fossil apes (mostly represented by jaw fragments and
174 isolated teeth), found after decades of paleontological fieldwork in Africa and Eurasia. In 1965,
175 Simons and Pilbeam (62) revised and organized available Miocene apes in three genera:
176 *Dryopithecus*, *Gigantopithecus* and *Ramapithecus*. The genus *Sivapithecus* was included in
177 *Dryopithecus*, considered the ancestor of African apes, whereas *Ramapithecus* was considered
178 ancestral to humans based on its short face (and inferred small canines) (63). Leakey (64) and
179 others agreed with Simons and Pilbeam that humans belong to their own family (Hominidae, or
180 “hominids”), whereas great apes would belong to a distinct family (Pongidae, or “pongids”). He
181 also agreed that *Ramapithecus* was an Asian early human ancestor. However, Leakey proposed
182 reserving the genus *Sivapithecus* for the “Asian dryopithecines,” and claimed that the human
183 lineage could be traced back to, at least, the middle Miocene of Africa with *Kenyapithecus wickeri*
184 (~14 Ma).

185

186 Two major “revolutions” in the study of evolutionary relationships started in the 1960s. First, a
187 series of studies jumpstarted the field of molecular anthropology: Blood protein comparisons by
188 Zuckerkandl et al. (65) and Goodman (66) found that some great apes—gorillas and
189 chimpanzees—were more closely related to humans than to orangutans. Sarich and Wilson
190 developed an “immunological molecular clock” and concluded that African apes and humans share
191 a common ancestor as recent as ~5 Ma (67). These results led to decades-long debates regarding
192 the African ape–human split. For example, Washburn resurrected extant African apes as ancestral
193 models in human evolution, proposing knuckle walking as the precursor of terrestrial bipedalism
194 (68). In contrast, paleontologists argued that the molecular clock was inaccurate because of the
195 much older age of the purported human ancestors *Kenyapithecus* and *Ramapithecus* (69). Second,
196 Hennigian cladistics (“phylogenetic systematics”)—which only recognizes “synapomorphies”
197 (shared derived features) as informative for reconstructing phylogeny (70)—became slowly
198 implemented in anthropology by the mid-1970s (71).

199
200 In the 1970–1980s, the relationships among gorillas, chimpanzees and humans were still disputed.
201 Chromosomal comparisons (72), DNA hybridization (73), and hemoglobin sequencing (74)
202 supported a closer relationship between chimpanzees and humans, whereas morphology-based
203 cladistics recovered gorilla–chimpanzee as monophyletic (75). In the late 1980s, the first single-
204 locus DNA sequencing studies (76) followed in the 1990s with multiple loci analyses finally
205 resolved the “trichotomy” (77). Current genomic evidence indicates that humans are more closely
206 related to chimpanzees (5), having diverged ~9.3–6.5 Ma (4). Ever since “the molecular
207 revolution,” the perceived relevance of fossil apes in human evolution has been in jeopardy.

208

209 *African apes as time machines?*

210 Extant African apes have been considered ancestral models since Keith’s “troglodytian” stage in
211 the 1920s (11), and especially since the 1960s, with updated hypotheses inspired by the “molecular
212 revolution” (68, 78) and field discoveries on chimpanzee behavior by Goodall (79). Louis Leakey
213 played a central role in promoting Goodall’s pioneering research (subsequently fostering Fossey’s
214 in gorillas and Galdikas’s in orangutans). Currently, a prominent paradigm proposes that
215 chimpanzees represent “living fossils” closely depicting the *Pan–Homo* LCA (14, 16). This model
216 combines molecular data with the anachronistic view that *Gorilla* and *Pan* are morphologically

217 similar (75). Under these assumptions, knuckle walking—once used to defend African ape
218 monophyly (80)—is used to argue that African apes are morphologically “conservative” and only
219 display size-related differences (14). This model contends that gorillas are allometrically enlarged
220 chimps and that chimpanzees [or bonobos (78)] constitute a suitable model for the *Pan–Homo*
221 LCA, perhaps even the hominine or hominid LCAs (14). This narrative also incorporates the
222 paleobiogeographic assumption that African apes likely occupy the same habitats as their
223 ancestors: Without new selection pressures, there was no need for evolution.

224
225 If hominins originated from a chimpanzee-like LCA, human bipedalism must have evolved from
226 knuckle walking (15)—a functional compromise enabling terrestrial travel while retaining
227 climbing adaptations (80). Under this view, bipedal hominins originated from an ancestor that was
228 already terrestrial while traveling. These conclusions are logical from a “top-down” perspective,
229 based on the evidence provided by extant hominoids and early hominins. However, a fully-
230 informed theory of hominin origins must also apply a “bottom-up” approach (81, 82), from the
231 perspective of extinct apes preceding the *Pan–Homo* split. It is also essential to clarify whether
232 chimpanzees represent a good ancestral model for the *Pan–Homo* LCA. Unfortunately, the view
233 from the bottom is blurry.

234
235

236 **The tangled branches of ape evolution**

237 *The fossil ape dilemma: Homoplasy and mosaic evolution*

238 With more than 50 hominoid genera and a broad geographic distribution (Fig. 1), the Miocene has
239 been dubbed “The real planet of the apes” (83). Besides their fragmentary nature, a persistent
240 challenge is understanding the phylogenetic relationships among fossil apes exhibiting mosaics of
241 primitive and derived features with no modern analogs. The Asian Miocene ape *Sivapithecus* best
242 exemplifies this complexity. Discoveries during the 1970s and 1980s, including a facial skeleton
243 (84), clarified that *Ramapithecus* is a junior synonym of *Sivapithecus*, which is likely related to
244 orangutans (85). However, two *Sivapithecus* humeri show a primitive (pronograde-related)
245 morphology, calling into question the close phylogenetic link with *Pongo* inferred from facial
246 similarities (86).

247

248 The root of this “*Sivapithecus* dilemma” (18) is identifying where “phylogenetic signal” is best
249 captured in hominoids: the postcranium or the cranium? The former implies that a *Pongo*-like face
250 evolved independently twice; the latter that some postcranial similarities among living apes
251 evolved more than once. Both hypotheses highlight the phylogenetic noise that homoplasy
252 introduces in phylogenetic inference. Indeed, several studies have found that homoplasy similarly
253 affects both anatomical areas (87). The conclusion that *Sivapithecus* is not a pongine relies on the
254 assumption that suspensory adaptations and other orthograde-related features present in living
255 hominoids were inherited from their LCA (18). However, this is contradicted by differences among
256 living apes [e.g., forelimb and hand anatomy, degree of limb elongation, hip abduction capability
257 (8, 9, 19, 80, 88-91)]. These studies concluded that apparent similarities could represent
258 independently evolved biomechanical solutions to similar locomotor selection pressures. For
259 instance, hand length “similarities” among living apes result from different combinations of
260 metacarpal and/or phalangeal elongation in each extant genus (9).

261
262 Parallel evolution—homoplasy among closely related taxa due to shared genetic and
263 developmental pathways—could explain some postcranial similarities related to suspensory
264 behaviors among extant apes (80). Compared with convergences among distantly-related taxa,
265 parallelisms are more subtle and difficult to detect, and readily evolve when similar selection
266 pressures appear. Within extant primates, suspensory adaptations evolved independently in atelines
267 and between hylobatids and great apes (8, 80, 88, 91, 92). When the hominoid fossil record is
268 added, independent evolution of suspensory adaptations has been inferred too for orangutans,
269 chimpanzees, and some extinct lineages (9, 89, 93, 94). Knuckle walking has also been proposed
270 to have different origins in gorillas and chimpanzees (80, 93, 95). As for suspension, the pre-
271 existence of an orthograde body plan, vertical climbing, and general arboreal heritage could have
272 facilitated the independent evolution of knuckle walking to circumvent similar biomechanical
273 demands during terrestrial quadrupedalism, while preserving a powerful grasping hand suitable
274 for arboreal locomotion (9).

275
276 The possibility of parallelisms indicates that ancestral nodes in the hominoid evolutionary tree—
277 including the *Pan–Homo* LCA—cannot be readily inferred without incorporating fossils. In
278 addition, fossils from “known” evolutionary lineages are commonly used to calibrate molecular

279 clocks despite being subject to considerable uncertainty (4). Even worse, relatively complete fossil
280 apes undisputedly assigned to early members of the gorilla and chimpanzee lineages remain to be
281 found.

282

283 ***Counting crowns: The case of the European Miocene apes***

284 *Sivapithecus* and other fossil Asian great apes (e.g., *Khoratpithecus*, *Ankarapithecus*,
285 *Lufengpithecus*) are generally considered pongines (Fig. 3) based on derived craniodental traits
286 shared with *Pongo* (94, 96-98), although alternative views exist, particularly for *Lufengpithecus*
287 (99). In contrast, the phylogenetic position of apes from the African early (e.g., *Ekembo*,
288 *Morotopithecus*) and middle Miocene (*Kenyapithecus*, *Nacholapithecus*, *Equatorius*) remains
289 very controversial. Like *Sivapithecus*, they exhibit only some modern hominoid features
290 superimposed onto a primitive-looking pronograde (“monkey-like”) body plan (Fig. 2). Some
291 authors interpret this mosaicism as indicating that most Miocene apes do not belong within the
292 crown hominoid radiation and, thus, are irrelevant to reconstructions of the *Pan–Homo* LCA (14).
293 This is likely the case for early Miocene African taxa. However, the vertebrae of *Morotopithecus*
294 [~20 Ma (100) or ~17 Ma (101)] display orthograde-related features absent from other stem
295 hominoids—indicating either a closer relationship with crown hominoids or an independent
296 evolution of orthograde (102). In turn, *Kenyapithecus* and *Nacholapithecus* are commonly
297 regarded as preceding the pongine-hominine split due to the possession of some modern hominid
298 craniodental synapomorphies combined with a more primitive postcranium than in living great
299 apes (94, 103). This raises the question: Can some Miocene apes belong to the crown hominid
300 clade despite lacking many of the features shared by extant great apes?

301

302 The large-bodied apes from the middle-to-late Miocene of Europe are at the center of discussions
303 about great ape and human evolution (19, 28, 94, 104, 105). Named after *Dryopithecus* (3), they
304 are generally distinguished as a subfamily (Dryopithecinae) (94) or tribe (Dryopithecini) (28).
305 However, it is unclear if they constitute a monophyletic group or a paraphyletic assemblage of
306 stem and crown hominoids (94). Thus, we refer to them informally as “dryopiths.” These apes are
307 dentally conservative, but each genus exhibits different cranial and postcranial morphology. The
308 dryopith fossil record includes the oldest skeletons consistently exhibiting postcranial features of
309 living hominoids (orthograde body plan and/or long and more curved digits). *Dryopithecus* (~12–

310 11 Ma) is known from craniodental remains and isolated postcranials too scarce to reconstruct its
311 overall anatomy (106). In contrast, *Pierolapithecus* (~12 Ma) is represented by a cranium with
312 associated partial skeleton (19). Cranially a great ape, its rib, clavicle, lumbar, and wrist
313 morphologies are unambiguous evidence of an orthograde body plan. Yet, unlike chimpanzees and
314 orangutans (but similar to gorillas), *Pierolapithecus* lacks specialized below-branch suspensory
315 adaptations [see discussion in (10)]. The recently described *Danuvius* (~11.6 Ma, Germany), and
316 the slightly younger (~10–9 Ma) *Hispanopithecus* (Spain) (105) and *Rudapithecus* (Hungary) (28)
317 represent the oldest record of specialized below-branch suspensory adaptations (e.g., long and
318 strongly curved phalanges; Fig. 2). *Danuvius* has also been argued to show adaptations to habitual
319 bipedalism (but see below).

320
321 The different mosaic morphology exhibited by each dryopith genus is a major challenge for
322 deciphering their phylogenetic relationships (Fig. 3). Current competing phylogenetic hypotheses
323 consider dryopiths as stem hominoids (107, 108), stem hominids (94, 96, 109) or crown hominids
324 closer to either pongines (105), hominines (28), or even hominins (29, 110). However, recent
325 phylogenetic analyses of apes recovered dryopiths as stem hominids (97, 109), perhaps except
326 *Ouranopithecus* (~9–8 Ma) and *Graecopithecus* (~7 Ma) (97). *Ouranopithecus* has been
327 interpreted by some as a stem hominine, or even as a crown member more closely related to the
328 gorilla or human lineages (110). *Graecopithecus* has also been advocated as a hominin (29),
329 although the fragmentary available material hinders evaluation of this hypothesis. Such contrasting
330 views about dryopiths stem from their incomplete and fragmentary fossil record coupled with
331 pervasive homoplasy. However, as these factors are equal for all researchers, their different
332 conclusions must also relate to analytical differences (e.g., taxonomy, sampling, polymorphic and
333 continuous trait treatment). The root of the conflict is the striking differences in subjective
334 definition and scoring of complex morphologies (e.g., “incipient supraorbital torus”).

335 336 ***Paleobiogeography of the African ape and human clade***

337 150 years after Darwin speculated that modern African ape and human ancestors originated in
338 Africa, possible hominins have been found as far back as the latest Miocene of Africa (21, 33,
339 111): *Sahelanthropus* (~7 Ma), *Orrorin* (~6 Ma), and *Ardipithecus kadabba* (~5.8–5.2 Ma).
340 However, others question the feasibility of identifying the earliest hominins among the diverse

341 Miocene apes (96, 112). Puzzlingly, despite some claims based on scarce remains (113-115),
342 ancient representatives of the gorilla and chimpanzee lineages remain elusive. Some apes from the
343 African late Miocene—*Chororapithecus* (26), *Nakalipithecus* (27), and *Samburupithecus* (116)—
344 have been interpreted as hominines, but the available fragmentary remains preclude a conclusive
345 assessment. Furthermore, *Samburupithecus* is likely a late occurring stem hominoid (97, 117).

346

347 During the middle Miocene (~16.5–14 Ma), apes are first found “out of Africa.” These are the
348 genera *Kenyapithecus* (Turkey) and *Griphopithecus* (Turkey and central Europe). We informally
349 refer to them as the “kenyapiths” because there is no consensus on their relationships (28, 94, 118).
350 Kenyapiths indicate that putative stem hominids are first recorded in Eurasia and Africa before the
351 earliest record of both European dryopiths and Asian pongines at ~12.5 Ma (94).
352 Paleobiogeographical and paleontological data suggest that kenyapiths dispersed from Africa into
353 Eurasia as one of the multiple catarrhine intercontinental dispersal events occurred during the
354 Miocene (e.g., hylobatids, pliopithecoids) (83, 94). While some competing evolutionary scenarios
355 agree that kenyapiths gave rise to dryopiths in Europe, the phylogenetic and geographic origin of
356 hominines remains contentious (28, 94).

357

358 If dryopiths are stem hominids, they could either be close to the crown group or constitute an
359 evolutionary dead-end, an independent “experiment” not directly related to either pongines or
360 hominines. Alternatively, dryopiths might be crown hominids more closely related to one of these
361 groups. If dryopiths are hominines, this implies that the latter could have originated in Europe and
362 subsequently dispersed “back to Africa” during the late Miocene (28, 29, 83). This would coincide
363 with vegetation structure changes caused by a trend of increased cooling and seasonality (32) that
364 ultimately drove European apes to extinction [or back to Africa (28)]. In this scenario, hominines
365 and pongines would be vicariant groups that originally evolved in Europe and Asia, respectively,
366 from early kenyapith ancestors. Given the suspensory specializations of late Miocene dryopiths
367 (*Hispanopithecus* and *Rudapithecus*), if modern African apes originated from these forms, this
368 scenario involves that the hominine ancestor could have been more reliant on suspension than
369 living chimpanzees or gorillas. The claim that hominines originated outside of Africa may be
370 justified by cladistic analyses recovering dryopiths as stem hominines, but not based on the lack
371 of late Miocene great apes in Africa because fossils from this critical time period have been

372 discovered (~13–7 Ma) (Fig. 3). Both molecular and paleontological evidence (e.g., *Sivapithecus*)
373 situate the pongine-hominine divergence within the middle Miocene. Hence, the debate cannot be
374 settled without more conclusively resolving the phylogenetic relationships of middle Miocene
375 dryopiths.

376

377 An alternative scenario proposes a vicariant divergence for hominines and pongines from
378 kenyapith ancestors, but favors the origin of hominines in Africa (94, 119). It argues for a second
379 vicariant event between European dryopiths and Asian pongines soon after the kenyapith dispersal
380 into Eurasia. Cladistically, dryopiths would be pongines, but would share none of the currently-
381 recognized pongine autapomorphies, evolved after the second vicariant event. This scenario is
382 difficult to test, but it would be consistent with the apparent absence of clear pongine
383 synapomorphies in *Lufengpithecus* (99) and the more derived nasoalveolar morphology of
384 *Nacholapithecus* (103) compared with some dryopiths (106). However, it would imply even higher
385 levels of homoplasy—including the independent acquisition of an orthograde body plan in Africa
386 and Eurasia from pronograde kenyapith ancestors.

387

388 A third possibility is that none of the taxa discussed above are closely related to the African ape
389 and human clade (107). Under this view, bona fide extinct non-hominin hominines have yet to be
390 found in largely unexplored regions of Africa—explaining the virtual lack of a gorilla and
391 chimpanzee fossil record. According to Pilbeam, paleoanthropologists could be “like the drunk
392 looking for his keys under the lamppost where it was light rather than where he had dropped them,
393 working with what we had rather than asking whether or not that was adequate” (108, pp. 155-
394 156). Africa is a huge continent and most paleontological discoveries are concentrated in a small
395 portion of it. The greatest challenge is finding hominoid-bearing Mio-Pliocene sites outside East
396 and South Africa, even though we know they exist (20-22). Besides insufficient sampling effort,
397 this is hindered by numerous impediments to fieldwork in most of Africa, including geopolitical
398 conflicts, restricted land use development, lack of suitable outcrops (due to extensive vegetation
399 cover), and taphonomic factors [tropical forests do not favor fossil preservation (120)].

400

401 **A Miocene view of (Miocene) hominin origins**

402 *Evolution in motion*

403 The decades-long feud regarding arboreality and bipedalism in *Australopithecus afarensis*
404 exemplifies the complexity of inferring function from anatomy. “Totalist” functional
405 morphologists rely on a species’ “total morphological pattern” (121) to infer its locomotor
406 repertoire. Totalists see a bipedal early hominin with some ape-like retentions (e.g., curved fingers)
407 pointing to continued use of the trees, and that certain not-yet-human-like features (e.g., hip)
408 indicate a different type of bipedalism (122). Instead, “directionalists”—for whom functional
409 inferences are only possible for derived traits evolved for a specific function—focus exclusively
410 on bipedal adaptations (123). Totalist and directionalist interpretations of the fossil record differ
411 in the “adaptive significance” attributed to primitive features, which result in different behavioral
412 reconstructions. Two other related factors further complicate locomotor inferences in extinct
413 species: First, different positional behaviors have similar mechanical demands [e.g., bipedalism,
414 quadrupedalism and some types of climbing (39)]. Second, pre-existing morphofunctional
415 complexes originally selected to fulfill a particular function (adaptations) can be subsequently co-
416 opted for a new role (exaptations).

417

418 The mosaic nature of hominoid morphological evolution makes the functional reconstruction of
419 fossil apes especially challenging, as recently exemplified by *Danuvius* (104): It was described as
420 possessing long and curved fingers, a long and flexible vertebral column, hip and knee joints
421 indicative of extended postures, and an ankle configuration aligning the foot perpendicular to the
422 long axis of the tibia. Such a combination of features was functionally interpreted as indicating
423 below-branch suspension combined with above-branch bipedalism. However, a critique to the
424 original study concluded that the morphological affinities of *Danuvius* with modern great apes
425 support a positional repertoire including orthogrady and suspension, but not bipedalism (124). Part
426 of the “problem” with the original interpretation is that it infers a derived locomotor behavior—
427 bipedalism—from primitive features that are also functionally related to quadrupedalism. For
428 instance, the inferred “long-back” morphology of *Danuvius* is characteristic of most quadrupedal
429 monkeys and other Miocene apes (125), denoting the lack of trunk specialization seen in extant
430 great apes. The *Danuvius* femoral head joint, being (primitively) posterosuperiorly expanded
431 (126), is consistent with flexed quadrupedal hip postures that are not used during human-like

432 bipedalism. In addition, the distal tibia configuration of *Danuvius* is shared with *Ekembo* and
433 cercopithecoids (104), thus being likely plesiomorphic and not unique to bipeds. When the
434 primitive and derived features of *Danuvius* are considered, a totalist would argue that it combined
435 high degrees of plesiomorphic quadrupedal locomotion with novel (suspensory) behaviors,
436 whereas a directionalist would downplay the primitive features in favor of the newly derived
437 adaptive traits (i.e., suspension).

438

439 The late Miocene *Oreopithecus* (~7 Ma, Italy) is another example of conflicting phylogenetic and
440 functional signals. Phylogenetic interpretations of *Oreopithecus* include cercopithecoid, stem
441 hominoid and hominid (even hominin) status (127). However, current phylogenetic analyses
442 suggest that *Oreopithecus* could represent a late occurring stem hominoid (97, 128), with
443 postcranial adaptations to alternative types of orthograde, such as forelimb-dominated behaviors
444 (129) and terrestrial bipedalism (130). Even if not directly related to hominins (or modern
445 hominoids), the locomotor adaptations of *Oreopithecus*—and other Miocene apes—are worthy of
446 further research to understand the selection pressures that led to the (independent) emergence of
447 modern hominoid positional behaviors.

448

449 To distinguish true locomotor adaptations from exaptations, current research efforts focus on
450 plastic “ecophenotypic” traits—potentially denoting how fossil hominoids were actually moving.
451 Bone is a living tissue, and growth is expected to occur in predictable ways that reflect loading
452 patterns throughout life (131). Thus, cross-sectional and trabecular bone properties and their links
453 to behavior are widely investigated (132, 133). Yet, experimental studies indicate that internal
454 bone morphology does not necessarily match stereotypical loading patterns (134). Ample evidence
455 suggests that irregular loading, including low-magnitude, can be more osteogenically potent than
456 stereotypical loading (135). This may bias interpretations of individual fossils with a species-
457 atypical loading pattern during life (e.g., due to an injury). Bone (re)modeling also does not
458 consistently occur in response to changes in loading pattern: It can occur in ways that detract
459 from—rather than enhance—function (136), and may manifest differentially across the skeleton
460 (137). Incongruence also exists between actual bone performance and expectations based on
461 aspects of internal morphology (138). Finally, there is a strong genetic component to the
462 responsiveness of bone (re)modeling to loading (136), which is largely unknown for most species.

463 The confidence with which internal bone structures can be used to retrodict behavior in fossil
464 species remains a work in progress.

465

466 ***Before bipedalism***

467 Competing hypotheses about the locomotor behavior immediately preceding hominin bipedalism
468 include terrestrial knuckle walking (15), palmigrade quadrupedalism (93), and different types of
469 arboreal (orthograde) behaviors such as climbing and suspension (7), vertical climbing (139), or
470 arboreal bipedalism and suspension (104, 140). Miocene great apes can enlighten this question by
471 helping to identify the polarity of evolutionary change preceding the *Pan–Homo* divergence (81,
472 82). For instance, if *Pierolapithecus* is interpreted as an orthograde ape without specific suspensory
473 adaptations but retaining quadrupedal adaptations [see alternatives in (10)], the orthograde body
474 plan and ulnocarpal contact loss could be interpreted as an adaptation to vertical climbing,
475 subsequently co-opted for suspension (19). Similarly, habitual bipedalism might have directly
476 evolved from other orthograde behaviors without an intermediate stage of advanced suspension or
477 specialized knuckle walking. Hence, *Pierolapithecus* complements previous hypotheses that
478 biomechanical aspects of the lower limb during quadrupedalism and vertical climbing could be
479 functionally “pre-adaptive” for bipedalism (39, 139).

480

481 A holistic view indicates that the *Pan–Homo* LCA was a Miocene ape with extant great ape-like
482 cognitive abilities, likely possessing a complex social structure and tool traditions (36, 38, 141).
483 This ape would exhibit some degree of body size and canine sexual dimorphism (with large honing
484 male canines) (15), indicating a polygynous sociosexual system (40). Based on Miocene apes and
485 earliest hominins, it is also likely that the *Pan–Homo* LCA was orthograde and proficient at vertical
486 climbing [see alternative interpretation based on *Ardipithecus* (33, 93)], but not necessarily at
487 specialized below-branch suspension or knuckle walking (9, 33). Chimpanzees seem to retain the
488 *Pan–Homo* LCA plesiomorphic condition in some regards [e.g., brain and body size (38), vertebral
489 counts (125), foot morphology (142)]. However, in others [e.g., interlimb (93), hand (9), pelvis
490 (143) length proportions; femur morphology (89)] early hominins are more similar to generalized
491 Miocene apes. These results further reinforce the idea that functional aspects of other locomotor
492 types were co-opted for bipedalism during hominin origins.

493

494 The “East Side Story” scenario links the divergence of chimpanzees and humans to the rifting of
495 East Africa, which would have triggered a vicariant speciation event from the ancestral *Pan–Homo*
496 LCA (17). Chimpanzees would have remained “frozen in time” in their ancestral tropical forest
497 environment, while humans would be the descendants of the group “left behind” on the east side
498 of the Rift. Major climate and landscape changes would have then forced earliest hominins to adapt
499 to more open (grassland savanna) environments by acquiring bipedalism—and the rest is history.
500 Several decades after the proposal of this scenario, where do we stand?

501
502 The landscape of East Africa has dramatically changed during the last 10 million years due to
503 tectonic events leading to specific climatic conditions and associated changes in vegetation
504 structure—from mixed tropical forest to more heterogeneous and arid environments than
505 elsewhere in tropical Africa (144, 145). The trend of progressive aridification did not culminate in
506 the predominance of savanna environments until ~2.0 Ma—roughly coinciding with hominin brain
507 size increase and the appearance of *Homo erectus*—and was punctuated by alternating episodes of
508 extreme humidity and aridity, resulting in a fluctuating extension of forests through time (144,
509 145). Despite ongoing discussions about early hominin paleoenvironments (woodland with forest
510 patches vs. wooded savanna) (146), evidence from Miocene apes (30, 31) supports that the *Pan–*
511 *Homo* LCA inhabited some kind of woodland. Therefore, it has been suggested that the *Pan–Homo*
512 LCA was probably more omnivorous than chimpanzees (ripe fruit specialists) and likely fed both
513 in trees and on the ground (33)—in agreement with isotopic analyses for *Ardipithecus ramidus*
514 (41).

515
516 Bipedalism would have emerged due to the selection pressures created by the progressive
517 fragmentation of forested habitats and the need for terrestrial travel from one feeding patch to the
518 next. Data on extant ape positional behaviors (Fig. 4) suggest that hominin terrestrial bipedalism
519 originated as a posture rather than a means of travel on the ground (147) or in trees (140). Rose
520 (39) proposed a long process of increasing commitment to bipedality in the transition to more
521 complex open habitats throughout the Plio-Pleistocene, and Potts (148) argued that key stages in
522 hominin evolution may relate to adaptive responses to cope with highly-variable environments.
523 The fossil and archeological records provide a new twist to the order of evolutionary events in
524 early hominin evolution. The remains of *Orrorin* and *Ardipithecus ramidus* indicate that habitual

525 terrestrial bipedalism, enhanced precision grasping, and loss of canine honing evolved at the dawn
526 of the human lineage well before brain enlargement (9, 33, 89, 93). It was not until later in time
527 (maybe starting with *Australopithecus* (149), and continuing with *Homo*), that some pre-existing
528 hand attributes were co-opted for purposive and systematic stone tool making in more
529 encephalized hominins with more advanced cognitive abilities (38, 150).

530

531 ***The specialization trap***

532 That hominins continuously evolved since the *Pan–Homo* LCA is universally accepted, but the
533 possibility that all living hominoids (including chimpanzees) experienced their own evolutionary
534 histories is sometimes disregarded. Potts (151) suggested that the greater cognitive abilities of
535 great apes originated to continue exploiting fruit supplies from densely forested environments in
536 front of strong environmental variability. Coupled with locomotor adaptations (e.g., vertical
537 climbing, suspension) enabling an efficient navigation through the canopy, this “cognitive trap”
538 would consist of an adaptive feedback loop between diet, locomotion, cognition and life-history.
539 Although hominids originated approximately during the “Mid-Miocene Climatic Optimum” (~17–
540 15 Ma), their subsequent radiation from ~14 Ma onward paralleled a trend of climatic
541 “deterioration” during the rest of the Miocene (152). Great apes might have initially thrived by
542 evolving particular adaptations to more efficient exploit their habitats, thereby occupying new
543 adaptive peaks without abandoning the same area of the adaptive landscape broadly occupied by
544 earlier stem hominoids. Nevertheless, this evolutionary strategy would become unsustainable once
545 a particular paleoenvironmental threshold was surpassed. This could explain the fate of European
546 dryopiths, which survived for some time under suboptimal conditions (despite the progressive
547 trend of cooling and increased seasonality) until they vanished (94).

548

549 The dietary, locomotor and cognitive specializations of late Miocene great apes would have
550 hindered their shift into new adaptive peaks suitable for the more open environments toward the
551 latest Miocene (153). The Miocene planet of the apes became the time of the more generalist Old
552 World monkeys, enabling their survival in a wider variety of seasonal habitats (30, 92, 154). The
553 same specialization trap can explain the delayed retreat of pongines (and hylobatids) to
554 southeastern Asia throughout the Plio-Pleistocene. The highly specialized orangutans remain
555 extant, but not for long as their habitat continues to shrink. African apes could partially overcome

556 the specialization trap by evolving (perhaps in parallel) semiterrestrial adaptations—knuckle
557 walking. Gorillas also expanded their dietary range (more folivorous) and enlarged their body size.
558 Contrary to the view that gorillas are “enlarged” chimpanzees, morphometric analyses indicate
559 that gorillas underwent their own evolutionary history, resulting in different ontogenetic
560 trajectories (155, 156) and postcranial differences that cannot be explained by size-scaling effects
561 (9, 143). Why, when, and how many times knuckle walking evolved is more difficult to explain
562 than the origin of hominin bipedalism. Habitat fragmentation coupled with a higher reliance on
563 arboreal feeding might be invoked (i.e., knuckle walking serves both terrestrial and arboreal
564 locomotion). This idea is difficult to reconcile with the premise that continuous-canopy forests
565 covered the tropical belt of central and western Africa since the Miocene—unless gorillas and
566 chimpanzees evolved in less densely-forested habitats (30, 31, 114), and retreated to tropical
567 forests when outcompeted by hominins and/or cercopithecoids. Ironically, the same specializations
568 that allowed great apes to survive despite major environmental challenges since the late Miocene
569 might ultimately doom them to extinction.

570
571 Hominins might have escaped the great ape specialization trap by evolving novel and more radical
572 adaptations: bipedalism (another specialized orthograde locomotion), concomitant freeing of the
573 hands, and subsequent enhanced manual dexterity, brain configuration, sociosexual behavior, and
574 culturally-mediated technology. Human evolution also reflects the progressive adaptation
575 (biological first, cultural later) to ever-changing environments (39, 148). Some essential changes
576 (upright posture, enhanced cognition) are just the continuation of a trend started in Miocene
577 hominoids (19, 36, 151). While escaping from the great ape specialization trap humans might have
578 fallen in another evolutionary cul-de-sac—with current human activities and overpopulation
579 leading the biosphere to a point beyond return (157). Will humans escape their own specialization
580 trap?

581
582

583 **Conclusions and perspectives**

584 Fossils uniquely inform deep-time evolutionary studies, which is essential to plan for the future
585 (158). However, we must be aware of the many existing limitations, and the gaps in our knowledge.
586 For example, we need more fossils because we are likely missing vastly more than what we have.

587 More fieldwork is necessary to find fossil apes close to the gorilla or chimpanzee lineages, and it
588 is essential to extend such efforts to unexplored or undersampled areas (Fig. 1). It is also essential
589 to continue developing tools of phylogenetic inference. Bayesian approaches are promising, but
590 uncertainty remains about their applicability to morphological data (159). Improvements in the
591 treatment of continuous characters and recent methodological advances for analyzing 3D
592 geometric morphometric data within a cladistic framework (in combination with traditional
593 characters) are promising for reconstructing fossil hominoid phylogeny (160). The oldest (recently
594 retrieved) ancient DNA is ~1 Ma (161). Paleoproteomics could be a complementary solution since
595 it has enabled sampling further back in time up to ~2 Ma, recently confirming the pongine status
596 of *Gigantopithecus* (162). Future technological advances in paleoproteomics could potentially
597 help to answer key questions by retrieving paleoproteomes from Miocene apes.

598
599 Locomotor reconstructions of the *Pan–Homo* LCA and other fossil hominoids are seriously
600 hampered by the lack of current analogs. Washburn spotted the fundamental limitation: “it is not
601 possible to bring the past into the laboratory. No one can see a walking *Australopithecus*” (163, p.
602 67). Such inferences rely on morphofunctional assumptions of bone, joint, or muscle function, but
603 experimentally-derived biomechanical data are required to test these assumptions and provide
604 reliable inferences from fossils. Technological advances now facilitate non-invasive kinematic
605 data collection from animals in their natural environments (164). In turn, experimental and
606 morphological information should be integrated to better predict the locomotion of fossil
607 hominoids. Forward dynamic simulations offer a powerful pathway for predicting de novo
608 movements in fossil species while iterating possible effects of morphology and soft tissue (165).

609
610 Humans are storytellers: Theories of human evolution often resemble “anthropogenic narratives”
611 that borrow the structure of a hero’s journey to explain essential aspects such as the origins of erect
612 posture, the freeing of the hands, or brain enlargement (166). Intriguingly, such narratives have
613 not drastically changed since Darwin (166). We must be aware of confirmation biases and ad hoc
614 interpretations by researchers aiming to confer their new fossil the starring role within a pre-
615 existing narrative. Evolutionary scenarios are appealing because they provide plausible
616 explanations based on current knowledge, but unless grounded in testable hypotheses, they are no
617 more than “just-so stories” (167).

618

619 Many uncertainties persist about fossil apes, and the day in which the paleobiology of extinct
620 species can be undisputedly reconstructed is still far. However, current disagreements regarding
621 ape and human evolution would be much more informed if—together with early hominins and
622 living apes—Miocene apes were also included in the equation. This approach will allow us to
623 better discern primitive and derived traits, the common from the specific, or the unique. This is the
624 role of fossil apes in human evolution.

625

626

627 **Table**

628 **Table 1. Simplified taxonomy of extant primates.**

629 Order Primates

630 Suborder Strepsirrhini (non-tarsier “prosimians:” lemurs, galagos and lorises)

631 Suborder Haplorrhini (tarsiers and simians)

632 Infraorder Tarsiiformes (tarsiers)

633 Infraorder Simiiformes [=Anthropoidea] (simians or anthropoids: monkeys, apes and
634 humans)

635 Parvorder Platyrrhini (New World monkeys)

636 Parvorder Catarrhini (Old World simians)

637 Superfamily Cercopithecoidea (Old World monkeys)

638 Superfamily Hominoidea (apes and humans)

639 Family Hylobatidae (“lesser apes:” gibbons and siamangs)

640 Family Hominidae (“great apes” and humans)

641 Subfamily Ponginae (the orangutan lineage)

642 Genus *Pongo* (orangutans)

643 Subfamily Homininae (the African ape and human lineage)

644 Tribe Gorillini (the gorilla lineage)

645 Genus *Gorilla* (gorillas)

646 Tribe Panini (the chimpanzee lineage)

647 Genus *Pan* (common chimpanzees and bonobos)

648 Tribe Hominini (the humans lineage)

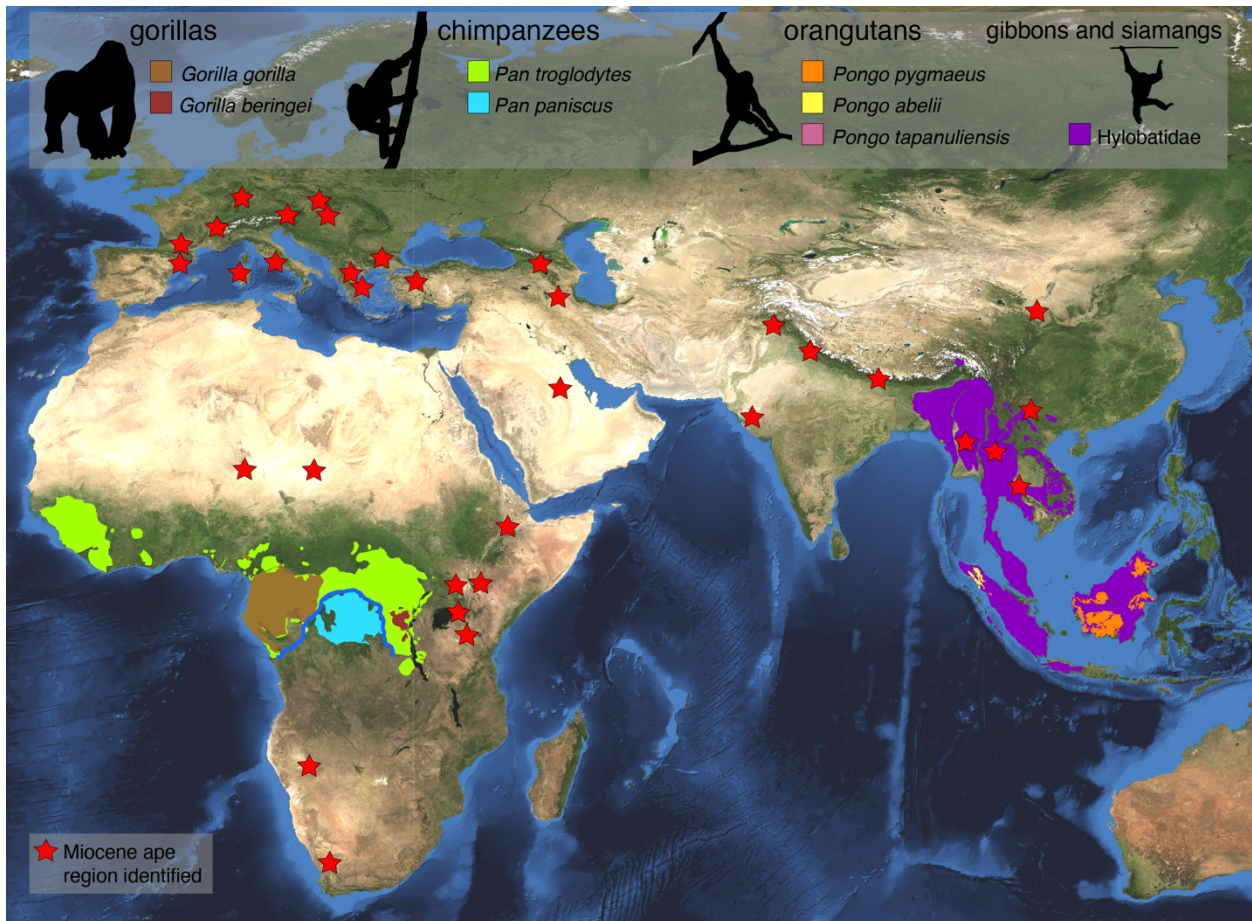
Genus *Homo* (humans)

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The adjectives “lesser” and “great” refer to the smaller size of the former relative to great apes and human group, not to old evolutionary notions based on the Scala Naturae. Given that some apes are more closely related to humans than to other apes, the word “ape” is a gradistic term used here informally to refer to all non-hominin hominoids. Finally, the taxonomic convention used (the most common), does not reflect that panins and hominins are monophyletic [although some do; e.g., (168)].

658 **Figure captions**

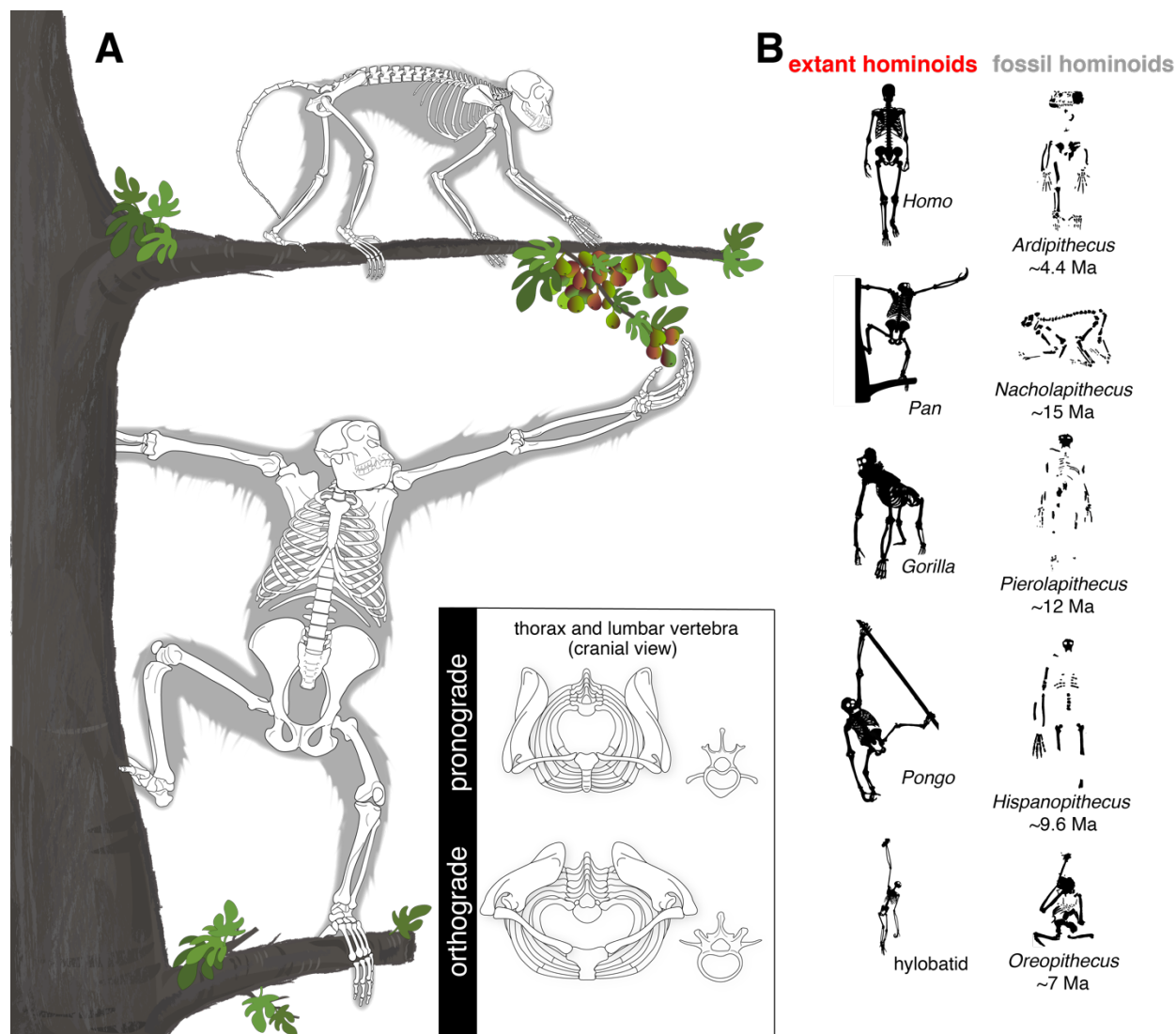
659



660

661 **Fig. 1. Extant and fossil ape distribution.** Extant apes live in (or nearby) densely-forested areas
662 around the equator in Africa and Southeast Asia. Except for the recently-recognized tapanuli
663 orangutan (which may represents a subspecies of the Sumatran orangutan), each of the three extant
664 great ape genera presently has two geographically separated species. The Congo River
665 (highlighted) acts as the current barrier between common chimpanzees (*Pan troglodytes*) and
666 bonobos (*P. paniscus*). Red stars indicate regions with Miocene sediments (spanning ~23–5.3
667 million years ago) where fossil apes have been uncovered (some regions may contain more than
668 one site; contiguous regions are indicated with different stars if they extend over more than a
669 political region). It is possible that modern great ape habitats do not represent the ancestral
670 environments where the great ape and human clade evolved. Paleontologically, the vast majority
671 of Africa, west of the Rift Valley, remains highly unexplored. Extant ape ranges were taken from
672 the International Union for Conservation of Nature (IUCN Red List).

673



674

675 **Fig. 2. Pronograde vs. orthograde body plan.** (A) Macaque (above) and chimpanzee (below) in

676 typical postures, showing general differences between pronograde and orthograde body plan

677 characteristics. In comparison to a pronograde monkey, the modern hominoid orthograde body

678 plan is characterized by the lack of an external tail (the coccyx being its vestigial remnant), a

679 ribcage that is mediolaterally broad and dorsoventrally shallow, dorsally-placed scapulae that are

680 cranially elevated and oriented, a shorter lower back and long iliac blades. Modern hominoids have

681 higher ranges of joint mobility, such as the full elbow extension shown here, facilitated by a short

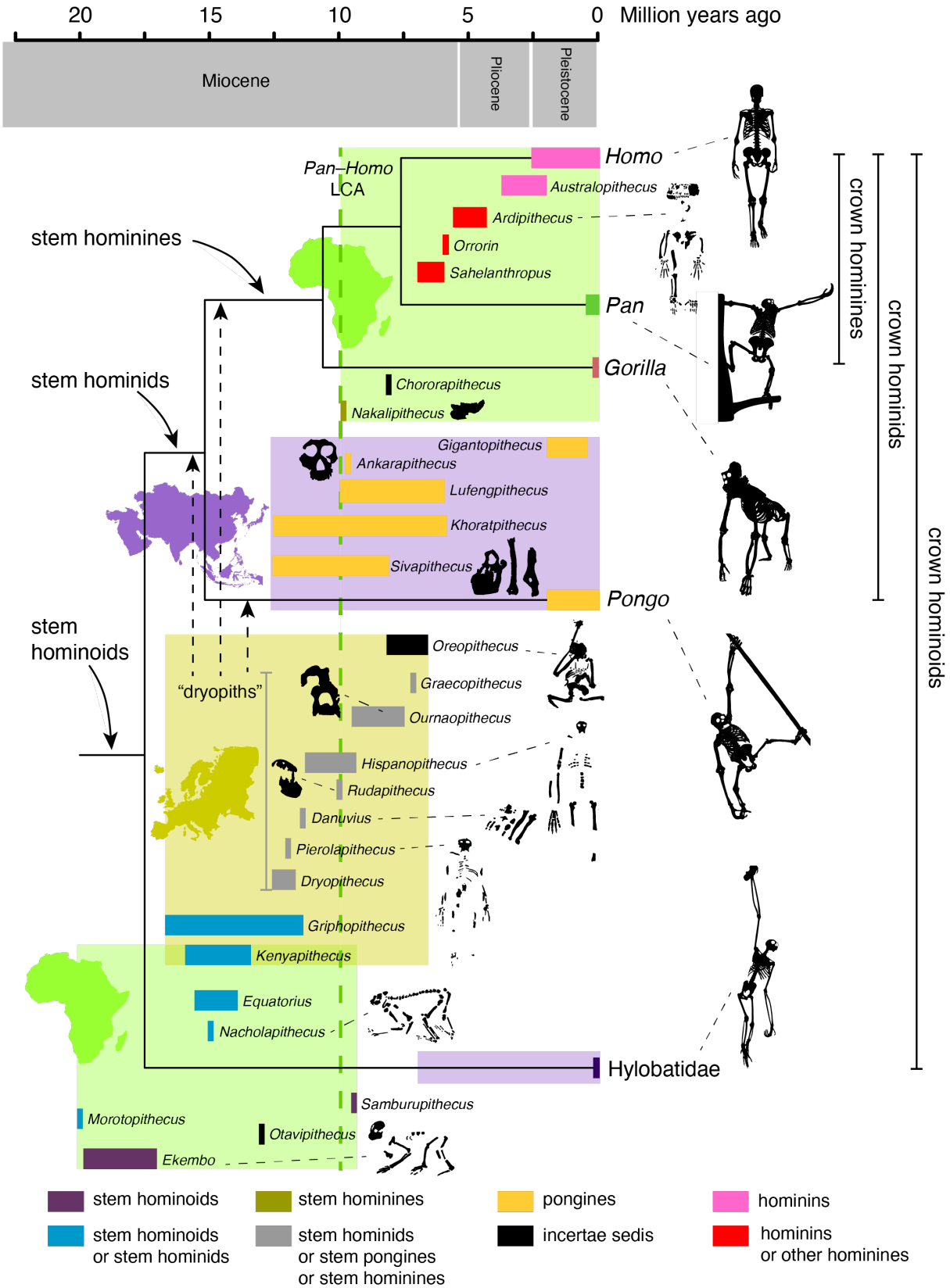
682 ulnar olecranon process. The inset further shows differences in lumbar vertebral anatomy,

683 including more dorsally situated and oriented transverse processes in orthograde hominoids. (B)

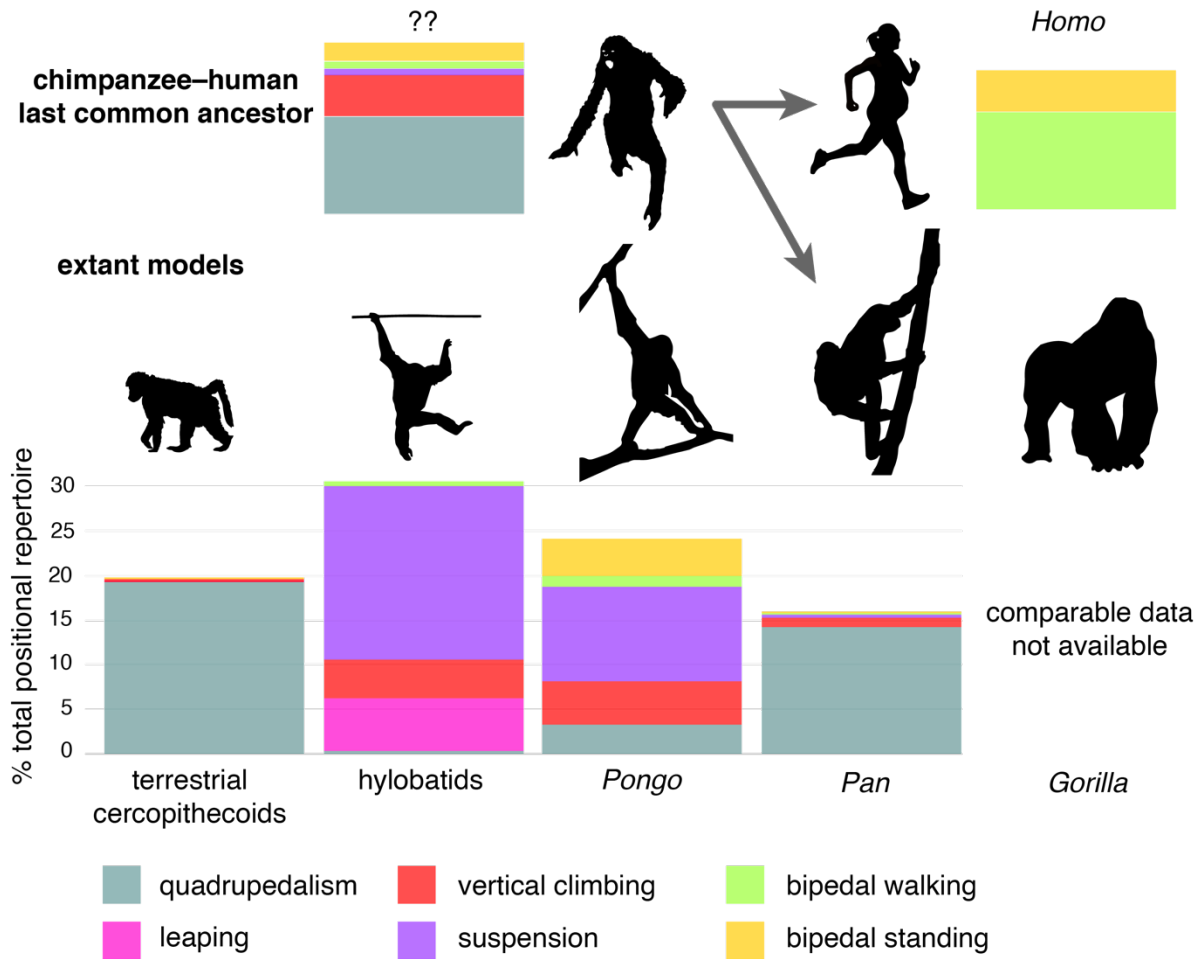
684 Representatives of each extant hominoid lineage (left column) show different postural variations

685 associated with an orthograde body plan. The orthograde body plan facilitates bipedal walking in

686 modern humans, and different combinations of arboreal climbing and below-branch suspension.
687 Knuckle walking in highly terrestrial African apes is seen as a compromise positional behavior
688 superimposed onto an orthograde ape with long forelimbs relative to the hindlimbs. Associated
689 skeletons of fossil hominoids (right column) show that an orthograde body can be disassociated
690 from specific adaptations for suspension (e.g., *Pierolapithecus* exhibits shorter and less curved digits
691 than *Hispanopithecus*). Other fossil apes exhibit primitive “monkey-like” pronograde body plans
692 with somewhat more modern ape-like forelimbs (e.g., *Nacholapithecus*). Approximate age in
693 millions of years ago (Ma) is given to representative fossils of each extinct genus: *Ardipithecus*
694 (ARA-VP-6/500), *Nacholapithecus* (KNM-BG35250), *Pierolapithecus* (IPS21350),
695 *Hispanopithecus* (IPS18800), and *Oreopithecus* (IGF 11778). Silhouettes of extant and fossil
696 skeletons are shown at about the same scale.
697



699 **Fig. 3. Phylogenetic relationships among living hominoids and chronostratigraphic ranges**
700 **of fossil hominoids.** A time-calibrated phylogenetic tree of living hominoids is depicted next to
701 the spatiotemporal ranges of the fossil hominoids mentioned in the text. Fossil taxa are color-coded
702 based on possible phylogenetic hypotheses. The vertical dotted line indicates that there is a
703 continuity in the African fossil ape record. However, currently, it is sparse between ~14–10 million
704 years ago. Robust and lasting phylogenetic inferences of apes are difficult, in part, due to the
705 fragmentary nature of the fossil record and probable high levels of homoplasy. Many Miocene ape
706 taxa are represented only by fragmentary dentognathic fossils, and the utility of mandibles and
707 molars for inferring phylogeny in apes has been questioned. Another area of uncertainty relates to
708 the position of many early and middle Miocene African apes relative to the crown hominoid node.
709 The discovery or recognition of more complete early Miocene fossil hylobatids would help resolve
710 their position, and thus, what really defines the great ape and human family. Splitting times are
711 based on the molecular clock estimates of Springer et al. (169) (hominoids and hominids) and
712 Moorjani et al. (4), which are more updated for hominines and *Pan–Homo*. Silhouettes are not to
713 scale.
714



715
 716 **Fig. 4. The positional repertoire preceding human bipedalism.** Although one particular
 717 behavior can dominate the locomotor repertoire of a given species, the full positional repertoire
 718 (postural and locomotor behaviors) of living primates is diverse, complex and not fully understood.
 719 For example, some locomotor behaviors are not totally comparable (e.g., monkey quadrupedalism
 720 vs. African ape knuckle walking). Furthermore, comprehensive data are not yet available for some
 721 extant hominoids (e.g., *Gorilla*). Bipedalism did not appear de novo in hominins, it existed as a
 722 posture or locomotion within a broader Miocene ape positional repertoire. The combined evidence
 723 of Miocene apes and early hominins indicate that the locomotor repertoire of the *Pan*–*Homo*
 724 last common ancestor likely included a combination of positional behaviors not represented among
 725 living primates. Over time, bipedal behaviors became the predominant activity within the
 726 repertoire of early hominins (and knuckle walking in the chimpanzee lineage). Locomotor
 727 behaviors (plus bipedal standing) in each taxon represent percentages of total positional behavior
 728 repertoire (full repertoire not shown, hence these do not add to 100%). Data were taken from (Hunt

729 2016). Quadrupedalism includes Hunt's categories "quadrupedal walk" and "quadrupedal run",
730 suspension includes "suspensory," "brachiate," "clamber," and "transfer." The locomotor
731 repertoire compositions of the LCA and modern humans (*Homo*) are conjectural, for illustrative
732 purposes.

733

734

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