

The Pliocene hominin diversity conundrum: Do more fossils mean less clarity?

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Recent discoveries of multiple middle Pliocene hominins have raised the possibility that early hominins were as speciose as later hominins. However, debates continue to arise around the validity of most of these new taxa, largely based on poor preservation of holotype specimens, small sample size, or the lack of evidence for ecological diversity. A closer look at the currently available fossil evidence from Ethiopia, Kenya, and Chad indicate that *Australopithecus afarensis* was not the only hominin species during the middle Pliocene, and that there were other species clearly distinguishable from it by their locomotor adaptation and diet. Although there is no doubt that the presence of multiple species during the middle Pliocene opens new windows into our evolutionary past, it also complicates our understanding of early hominin taxonomy and phylogenetic relationships.

hominin diversity | *Australopithecus* | *Kenyanthropus* | Pliocene | ecological diversity

If one looks back over the controversies of human evolution, they have one element in common: new discoveries, theories, methods came along which no one in the controversy anticipated. The “facts” changed, and consequently people were not right or wrong in any simple way.

S. L. Washburn and R. L. Ciochon, 1974 (1)

New fossil discoveries and analytical methods that have proliferated during the last few decades have fundamentally changed how we study and interpret hominin fossils and understand human evolution. The discovery and subsequent naming of *Australopithecus afarensis* in the late 1970s was one of the major milestones in paleoanthropology (2). Its discovery not only pushed the record of hominins to earlier than 3 million years ago (Ma) (2), but also demonstrated the antiquity of human-like bipedality (3). However, the taxonomic homogeneity of the *Au. afarensis* hypodigm has been questioned since its naming (4–7), even though the Hadar fossil sample appears to be no more variable than other living ape species (8–11). A consensus emerged during the 1980s in which *Au. afarensis*, dated to between 3.7 and 2.9 Ma, was considered to be the sole early hominin species older than 3 Ma, largely supported by the lack of fossil evidence to indicate otherwise.

When *Australopithecus bahrelghazali* was named in 1995 based on an approximately 3.5-Ma partial mandible from Chad (12), it was quickly dismissed as a geographic variant of *Au. afarensis* (13–15). The initial descriptions of *Ardipithecus ramidus* (16) and *Australopithecus anamensis* (17), followed by the naming of even earlier hominin species, such as *Orrorin tugenensis* (18), *Ardipithecus kadabba* (19, 20), and *Sahelanthropus tchadensis* (21), extended the antiquity of our lineage as far back as >6 Ma. These early hominins initially appeared to show no temporal or spatial overlap, and hence reinforced the idea that the early phases of hominin evolution were characterized by phenetic continuity and phyletic gradualism, with only one hominin species existing in a region at any given time >3 Ma (e.g., ref. 22; see discussions below).

The discovery of the Burtele partial foot from Ethiopia (23), the naming of *Kenyanthropus platyops* from Kenya (24), and more recently *Australopithecus deyiremeda* (25), all from the middle Pliocene and contemporaneous with *Au. afarensis*, challenge the concept of the single-species hypothesis. Its proponents, however, have raised a number of questions related to fossil species recognition based on small sample size (26) and lack of a clear

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demonstration of ecological diversity to support multiple related hominin taxa (27). The possibility of sympatry suggested by some of these new hominin taxa raised questions about competitive exclusion and niche partitioning, a concept long held by some paleoanthropologists (e.g., refs. 28 and 29) to justify a single-species lineage hypothesis of human evolution (30).

Hominin Fossil Record >4.5 Ma

Three hominin taxa have been recognized from sediments older than 4.5 Ma during the latest Miocene: *S. tchadensis* (21), *O. tugenensis* (18), and *Ar. kadabba* (19, 20, 31). These three taxa are among the most poorly known hominins in the fossil record. However, they push the origin of hominins to >5 Ma, yield new perspectives on the origin of the hominin clade, and shed light on the paleobiology of the earliest hominins after the split from the last chimpanzee-human common ancestor. All of these taxa share with later hominins some type of bipedal locomotion (inferred from isolated cranial and postcranial elements) and the lack of a functional canine honing complex (18,

20, 21). Their relatively larger canines compared with later hominins suggest that the last chimpanzee-human common ancestor had a functionally honing canine-third premolar complex (20, 32).

The geologically oldest *S. tchadensis* has a biochronological age of 7–6 Ma (33) and radioisotopic ($^{10}\text{Be}/^9\text{Be}$) age of 7.2–6.8 Ma (34). *Orrorin tugenensis* and *Ar. kadabba* are 6.0–5.7 Ma and 6.4–5.5 Ma, respectively (35–37). There appears to be some degree of overlap in the temporal distribution of these three taxa, indicating possible taxonomic diversity in the hominin clade from 6 Ma onwards (Fig. 1). Morphologically, however, because each taxon is known only from a handful of specimens, detailed comparative analysis is currently impossible. The differences in the few overlapping dental elements of these taxa are subtle and may not warrant generic or species-level distinction; thus, it may be premature to posit hominin taxonomic diversity in the latest Miocene (20, 32). If, however, further fossil discoveries confirm the validity of the three named species, then diversification in hominins occurred soon after the origin of the hominin clade.

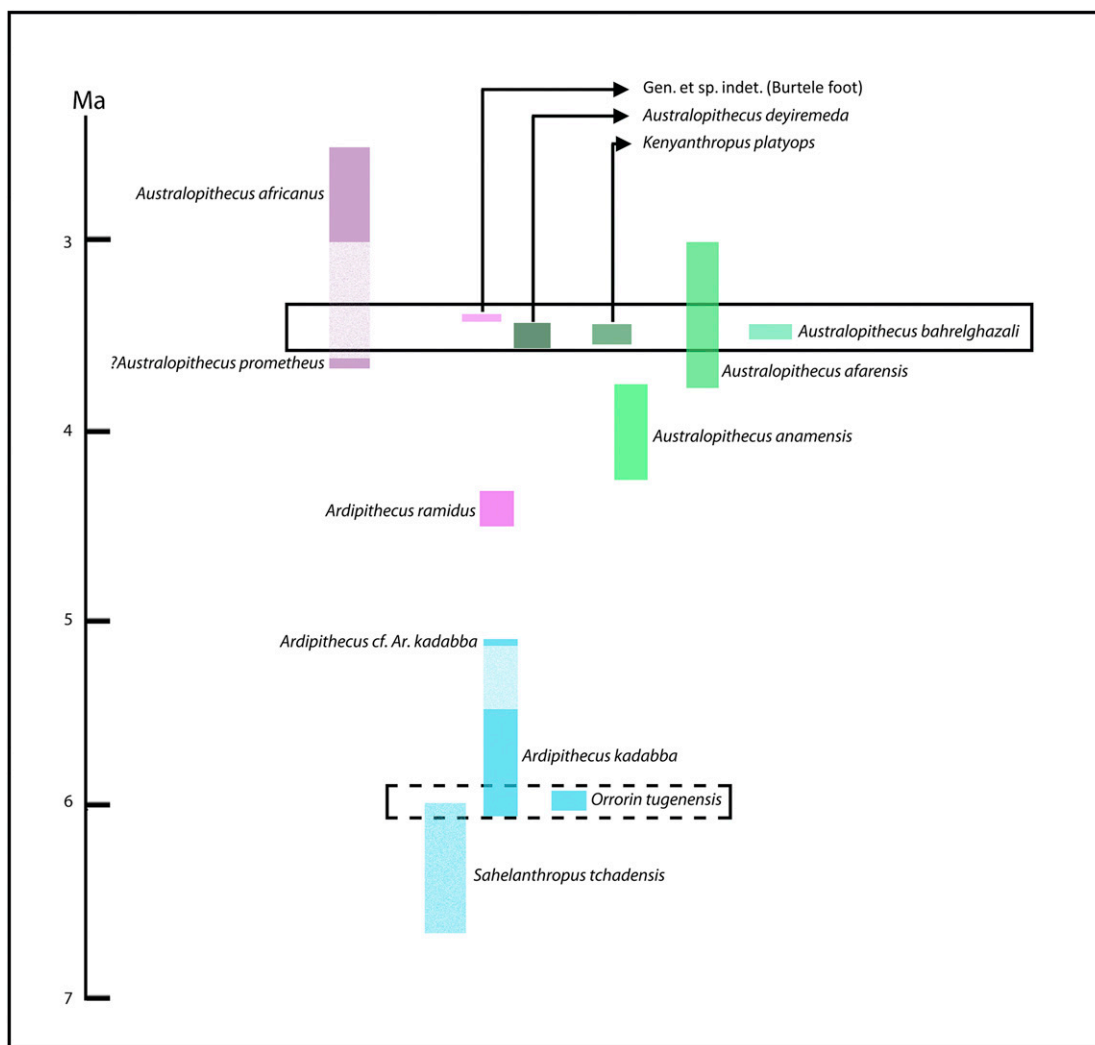


Fig. 1. Late Miocene–early Pliocene hominin species that are currently recognized in the fossil record. Columns indicate the approximate temporal distribution of each taxon. Dotted parts indicate uncertainty in the age of a taxon or the absence of fossils from that time span. The solid rectangle shows the presence of multiple contemporaneous taxa during the middle Pliocene. The dashed rectangle indicates possible hominin diversity as early as the late Miocene, if the three earliest named hominin species represent different taxa.

Hominin Fossil Record 4.5–3.9 Ma

Early Pliocene hominin evolution is shrouded in darkness largely because of the lack of fossils. Between 5.5 Ma and 4.5 Ma, only one hominin fossil has been recovered: a toe bone assigned to *Ardipithecus* cf. *Ar. kadabba* (ca. 5.2 Ma) (20, 32). At about 4.5–4.4 Ma, *Ar. ramidus* appears in the fossil record at the sites of Middle Awash and Gona in the Afar region of Ethiopia (16, 38), and is described as the probable descendant and temporal continuation of the earlier *Ar. kadabba* (20, 32, 38), also found only at these two sites (30–32). *Ardipithecus ramidus* was inferred to have been a facultative biped, retaining an opposable big toe and a mosaic of ape-like and hominin-like pelvic morphology (39, 40).

The announcement of *Ar. ramidus* was soon followed by the discovery and naming of the 4.2–3.9 Ma *Au. anamensis* from Kanapoi and Allia Bay in Kenya (17), and later from the Middle Awash of Ethiopia, where it is dated to 4.2–4.1 Ma (41). A few fossil teeth from Fejej, southern Ethiopia, dated to 4.18–4.0 Ma, are also best referred to *Au. anamensis* (42). This species might also be present at Woranso-Mille, Ethiopia, as late as approximately 3.8–3.7 Ma (43). The paleobiology of *Au. anamensis* combines primitive ape-like mandibular and dental morphology and derived traits, such as postcanine megadontia and human-like bipedal locomotor adaptation (17, 44). Morphologically, *Au. anamensis* marks the beginning of postcanine megadontia that characterizes all later *Australopithecus*, *Paranthropus*, and early *Homo* species (17, 44, 45). Phylogenetically, *Au. anamensis* possibly descended from *Ar. ramidus* (17, 41, 44), or is its “close collateral relative” (46), among other alternatives (41). There is no fossil evidence yet to indicate that *Ar. ramidus* and *Au. anamensis* overlapped temporally and spatially.

Hominin Fossil Record 3.8–3.0 Ma

Australopithecus afarensis (3.7–2.9 Ma) is one of the best-known early hominins in the fossil record; its fossil remains have been recovered largely from Tanzania (Laetoli) (47–49) and Ethiopia (Hadar, Dikika, Woranso-Mille) (2, 50–52). Until the discovery of *Ar. ramidus* and *Au. anamensis* in the 1990s, this species was considered as the earliest and most primitive hominin species that gave rise to all later hominins (e.g., ref. 2). The large number of fossil specimens assigned to this species, particularly from Ethiopia, includes partial skeletons (52–55) and a number of relatively complete cranial specimens (14) that have allowed for the better understanding of the paleobiology, locomotor adaptation, and sexual dimorphism in early hominins. Currently available fossil evidence suggests that *Au. afarensis* is a direct descendent of *Au. anamensis* and this phylogenetic relationship is considered to be the best example of phyletic gradualism in early hominin evolution (13, 15).

The discovery and naming of *Au. bahrelghazali* from Chad, central Africa (12, 56), was the first indication for the presence of more than one contemporaneous hominin species older than 3 Ma. Although the naming of this species was based on a single mandibular fragment, its discovery 2,500 km away from eastern African sites showed that early hominins had a wider geographic distribution than previously indicated by the fossil record. Alternative interpretations of its taxonomic position include suggestions that it is a geographic variant of *Au. afarensis* (13–15) or belongs to *K. platyops* (57), another middle Pliocene hominin species described below.

Kenyanthropus platyops (24, 58) is a species from Kenya that rekindled the question of middle Pliocene hominin diversity. Although its taxonomic validity was critically questioned soon

after its naming (59)—largely because of the distorted nature of the holotype specimen (KNM-WT 40000)—further detailed analysis through the use of computed tomography, which virtually corrected the distortions in the morphologically significant areas of the holotype, demonstrated that its maxillary morphology is different from that of *Au. afarensis* (58), corroborating the validity of the latter species.

BRT-VP-2/73, the 3.4- to 3.3-Ma partial foot with an opposable hallux from the Woranso-Mille (23), is the least controversial evidence for the presence of more than one hominin species during the middle Pliocene. This specimen belongs to a hominin species whose locomotor adaptation was different from what has been inferred for the contemporaneous *Au. afarensis* (2, 60), but similar to that of the 4.4-Ma *Ar. ramidus* (39, 40). However, BRT-VP-2/73 cannot be assigned to *Ar. ramidus* with confidence without the recovery of craniodental specimens that are in clear association (23), nor can it be referred to the sympatric *Au. afarensis* (52) because of the difference in locomotor adaptation. Regardless of its taxonomic affinity—whether it belongs to a late surviving *Ardipithecus* (46), *Au. deyiremeda* (see below), or to an as yet unnamed species—BRT-VP-2/73 represents the most compelling evidence for the presence of more than one hominin species during the middle Pliocene.

The most recently named species, *Au. deyiremeda*, dated to 3.5–3.3 Ma, comes from middle Pliocene sediments of the Woranso-Mille study area in the Afar region of Ethiopia (25); it is distinguished by dental and mandibular morphology from the contemporaneous *Au. afarensis*, which lived in close proximity. It is also distinguished from *K. platyops* by maxillary morphological features (Table 1). Whereas the distinctive features of *K. platyops* and *Au. bahrelghazali* have been ascribed to taphonomic distortion (59; but see ref. 58) and geographic variation, respectively, the specimens of *Au. deyiremeda* are well preserved, represented by multiple specimens, and recovered from the Afar region in sediments contemporaneous with *Au. afarensis* at Maka (45) and Dikika (51, 55). The maxilla and the two mandibles assigned to *Au. deyiremeda* likely represent three individuals and all show features that distinguish them from *Au. afarensis* (21). Furthermore, the *Au. deyiremeda* hypodigm was recovered from a region that had already provided evidence of hominin diversity (23) and the possibility that the Burtele partial foot (BRT-VP-2/73), described above, and other specimens recovered from the same locality and its vicinity (see table 1 in ref. 23) might belong to this species cannot be ruled out at this time.

Were Pliocene Hominins Diverse or Oversplit?

Understanding early hominin diversity and identifying groups that are taxonomically distinct have remained challenging tasks for paleoanthropologists. This is mainly because of the lack of consensus on how to accurately recognize a fossil species and the need to better understand inter- and intraspecific variation, all of which are muddled by generally small sample sizes, apparent geographic variation, temporal trends, sexual dimorphism, and lack of extant models, among many other factors (26, 27). Despite these caveats, however, at least four hominin species have been recognized from the middle Pliocene thus far: *Au. afarensis*, *Au. bahrelghazali*, *Au. deyiremeda*, and *K. platyops*. Among these, only *Au. afarensis* is widely accepted as a valid species, whereas the validity of the other three taxa has been questioned (see discussions above). Major criticisms pertain to our ability to distinguish taxonomic units given extremely small sample sizes (26) and lack of evidence for ecological diversity (27). Indeed,

Table 1. List of maxillary, mandibular, and dental characters and their expressions in *Au. afarensis*, *Au. bahrelghazali*, *K. platyops*, and *Au. deyiremeda*, with *Au. anamensis* as the outgroup

| Characteristic | <i>Au. anamensis</i> | <i>Au. afarensis</i> | <i>Au. bahrelghazali</i> | <i>K. platyops</i> | <i>Au. deyiremeda</i> |
|--|--------------------------------|--------------------------------|--------------------------------|--------------------|--------------------------------|
| Maxilla | | | | | |
| Subnasal prognathism* | Strong | Strong | – | Weak | Moderate |
| Nasoalveolar clivus transverse contour | Slightly convex | Convex | – | Flat | Convex |
| Anterior zygomatic origin | M ¹ | M ¹ or posterior | – | P ⁴ | P ⁴ /M ¹ |
| Mandible | | | | | |
| Symphyseal inclination | Strong | Variable [†] | Weak | – | Variable |
| Genioglossal fossa position/depth | Low/deep | Low/variable | High/shallow | – | Variable/variable |
| Mandibular corpus robusticity [‡] | Narrow | Broad | – | – | Very broad |
| Lateral corpus hollow | Absent | Present | – | – | Less defined |
| Anterior ascending ramus origin | M ₁ /M ₂ | M ₁ /M ₂ | – | – | P ₄ /M ₁ |
| Dentition | | | | | |
| Maxillary molar size | Large | Large | – | Small | Small |
| Enamel thickness | Intermediate-thin | Thick | Intermediate-thin [§] | Thick | Very thick [¶] |
| P ₃ metaconid size | Small/absent | Small | Large | – | Small |

Data compiled from refs. 12, 14, 15, 17, 24, 25, 44, 56, 58, 64.

*As measured by the subnasal angle (nasospinale-prosthion to postcanine alveolar plane).

[†]Individuals from the geologically younger sections in the Hadar Formation (e.g., A.L. 288-1, A.L. 444-2) have symphyses that are almost vertical.

[‡]Quantified by the corpus robusticity index [(corpus breadth/corpus height) × 100], taken at the M₁ level.

[§]Qualitative observations of line drawings reported in ref. 64.

[¶]M² relative enamel thickness exceeds *P. robustus* mean.

some of these taxa are only known from a single or few specimens. The obvious limitation of a small sample is that variation cannot be quantified, which removes the basis for equating paleospecies with biological species and weakens statements about differences between samples. Thus, the concern over small sample sizes is well founded, and yet it is intrinsic to vertebrate paleontology. This concern must be balanced by an appreciation of what can be hypothesized from extremely small sample sizes, particularly when a single specimen shows morphology that is functionally different from that of the existing hypodigm (e.g., BRT-VP-2/73) (23) and when the comparative sample is not especially small (i.e., comparisons with *Au. afarensis*).

Specimens assigned to *Au. bahrelghazali*, *K. platyops*, and *Au. deyiremeda* all fall outside the range of variation of *Au. afarensis* in different ways (24, 25, 56, 58). In some morphological comparisons (25, 58), variation in *Au. afarensis* is estimated from a reasonably sized sample ($n = 6$ to >15) and differences reach the level of statistical significance, despite the extremely small samples of the other species. On the other hand, the problems associated with small sample size are acute in comparisons among *Au. bahrelghazali*, *K. platyops*, *Au. deyiremeda*, and BRT-VP-2/73: either no comparisons are possible because of a lack of anatomical overlap or a single specimen of one taxon is being compared with a single specimen of a second taxon. Thus, although there are independent lines of evidence that middle Pliocene species diversity exceeded one (i.e., more than only *Au. afarensis*), the evidence that there were more than two species is much weaker until the sample size is increased for each of the named taxa.

The critique that early hominin taxonomic diversity is not supported by evidence of ecological diversity (27) is closely tied to the problems of small samples, as our understanding of the paleobiology of a hominin species necessarily depends on fossil occurrences of that species. Historically, ecological differentiation has been equated with a genus-level, rather than species-level taxonomic distinctions (29, 61). Although there are certainly theoretical expectations of a correlation between taxonomic and ecological diversity, it is arguable whether recognizing a fossil

sample as a taxonomically distinct unit should be contingent upon demonstrating ecological differentiation. Paleobiological reconstructions involve a level of inference further removed from the basic morphological comparisons that inform alpha taxonomy and not all morphological differences have an adaptive or ecologically informative underpinning. Even morphological differences that are thought to be ecologically significant do not always map onto empirical data in the manner anticipated (62, 63). Expectations around demonstrating ecological distinctness must be aligned with the limitations and resolution of paleoecological indicators and the inferential nature of research on functional morphology. Nonetheless, there is tentative evidence of ecological differences in middle Pliocene hominins. For example, isotopic composition of dental enamel (62) and enamel thickness (64) suggest dietary differences between *Au. bahrelghazali* and *Au. afarensis*, and of particular importance is the 3.4- to 3.3-Ma Burtelle foot (BRT-VP-2/73) that clearly demonstrates the existence of multiple hominin niches in the Afar region in the middle Pliocene: one that is more arboreal in addition to the more terrestrial niche of *Au. afarensis*. However, the presence of this second niche could not have been inferred from paleoenvironmental indicators alone.

Phylogenetic Relationships

The composition of the *Au. bahrelghazali*, *K. platyops*, and *Au. deyiremeda* fossil samples complicates the consideration of their phylogenetic positions. Because these species are known from few anatomical elements, proposals regarding their phylogenetic relationships are based on a small number of characters. Moreover, the sets of characters that can be considered for each species are different because of the lack of anatomical overlap among hypodigms. Perhaps most concerning is the potential that the morphology of a species may be inaccurately characterized when based on a single observation. Given these issues, hypotheses about the phylogenetic relationships of these taxa should be viewed as tentative.

The presence of some derived dentognathic features is apparent in *Au. bahrelghazali*, *K. platyops*, and *Au. deyiremeda*

(Table 1). However, none of them exhibits the full suite of synapomorphies that characterize *Paranthropus* or *Homo*. Instead, features that are traditionally considered to be integrated components of an adaptive suite in *Paranthropus*, such as small anterior dentition, large postcanine teeth, thick dental enamel, robust mandibular corpus, and facial buttressing (65), appear to be dissociated from one another in these taxa. Dentognathic morphology of *Au. afarensis* is intermediate between the more primitive species *Ar. ramidus* and *Au. anamensis* and the more derived *Paranthropus* clade. The other middle Pliocene hominin species show some *Paranthropus*-like features, but in an unexpected combination with more primitive features. Both *Au. deyiremeda* and *K. platyops* exhibit an anteriorly positioned zygomatic (commonly considered a component of facial buttressing) (24, 25, 58). Furthermore, *Au. deyiremeda* mandibles show *Paranthropus*-like relative corpus width (25) and a mandible fragment, referred to as cf. *K. platyops* (KNM-WT 8556), includes a molarized P₄ that is matched in size only by those attributed to *P. boisei* (24). However, the limited data available suggest that maxillary molar size in *Au. deyiremeda* and *K. platyops* is small compared with *Au. afarensis* and *Paranthropus* species (24, 25).

Some authors highlighted inferred *Homo*-like craniodental features of *K. platyops*, linking it to the much younger lectotype specimen of *Homo rudolfensis* (24, 66). Others argued that there is no compelling support to indicate especially close affinities between *K. platyops* and *H. rudolfensis* (67). Formal phylogenetic analyses that have included *K. platyops* (67) or both *K. platyops* and *Au. deyiremeda* (25) find that, although the specific positions of these species are unstable, they are dentognathically more derived than *Au. afarensis* in some ways and equally primitive in some others. These findings appear to reinforce the understanding that *Au. afarensis* dentognathic morphology represents the plesiomorphic condition relative to all later hominins younger than 3 Ma. However, they also challenge the long held view that *Au. afarensis* is the sole ancestor for all later hominins.

Pliocene Hominin Diversity, Sympatry, and the Question of Niche Partitioning

From the onset of the study of human origins as a scientific field, environmental and climatic changes have been posited as the driving force behind the origin, extinction, and adaptive events of the human lineage (e.g., refs. 68–72), which has had significant impact on the formulation of hypotheses regarding the evolution of hominins, particularly on the questions of taxonomic diversity and habitat preferences. The idea that two related hominin species could not have been sympatric because of overlapping resource requirements and preferences is one of the driving forces of the single species hypothesis (73). However, fossil discoveries in the 1970s and 1980s challenged this by clearly demonstrating the coexistence of *Paranthropus* and *Homo*, in some cases in close proximity, during the Pleistocene (74–76). Hominin fossil discoveries since the 1990s are now showing that hominin diversity was not limited to the Pleistocene but rather extended as far back as the middle Pliocene, if not earlier. The Pliocene hominin fossil record reviewed above, particularly from the time between 3.8 Ma and 3.0 Ma, indicates not only broad sympatry (two or more species occurring over the same region), but also direct sympatry (co-occurrence of two or more species in the same immediate area) of middle Pliocene hominins.

Taxonomic diversification and coexistence of multiple large-bodied Miocene hominoids are well documented in the Cenozoic fossil record (77). There is adequate fossil evidence to show that

multiple hominin taxa coexisted during the Pleistocene. The contemporaneous presence of multiple closely related taxa has also been documented among nonhominoid primates (78–81) and other mammalian taxa, such as bovids (82), throughout the Plio-Pleistocene. It would not be surprising, then, if hominins were as diverse at any given time in their evolutionary history, but identifying the dynamics that triggered such diversification among these relatively large-bodied hominins during the middle Pliocene and other geological times would be of paramount importance. It has been posited that the most probable explanation for diversification within any sympatric group of primates regardless of body size is niche partitioning, where each taxon develops a specific foraging strategy and exploits unique dietary resources (e.g., refs. 83 and 84). It has been shown, however, that stable coexistence among related taxa does not always require resource specialization (85), and recent studies of extant faunal communities suggest that predation pressures reduce competition in secondary consumers and promote taxonomic diversity and coexistence (86).

At Woranso-Mille, *Au. afarensis* and *Au. deyiremeda* appear to have been living in direct sympatry with each other. Thus, questions regarding how they are able to coexist and share the landscape immediately arise. Both species appeared to have broad dietary requirements (e.g., refs. 87–91), suggesting that they could have been ecological generalists (i.e., broad use of resources and high tolerance of environmental change) (92). Modern chimpanzees and gorillas are broadly sympatric across equatorial Africa and share the same habitat in many areas (93). These two closely related species have significant overlap in their dietary pattern and resource use, but differ significantly in their use of fallback foods and food-harvesting strategies. Whereas both species appear to focus on fruit as their primary, preferred food, gorillas are willing to consume herbaceous vegetation when their preferred food item is unavailable; chimpanzees, on the other hand, broaden their home range to harvest their preferred food and do not use herbaceous vegetation as their fallback food (93–96). It is possible that, analogous to modern chimpanzees and gorillas, one of the two *Australopithecus* species at Woranso-Mille had greater ecological niche breadth, or they may have specialized in different fallback foods during times of preferred food scarcity, while sharing the same resources when preferred food items are abundant.

With increasing fossil evidence, it is possible to begin to put forth hypotheses on the ecological strategies of *Australopithecus* as a clade. The association of *Au. afarensis* with different habitat types throughout its geographic and temporal range has suggested to many workers that it was a generalist with broad habitat tolerances (97–102). Although we do not have the same level of paleohabitat resolution for all of the other Pliocene hominin species, available evidence suggests that they are similarly associated with a wide range of habitat types from savanna-like grassland to an array of habitats with significant woodland components (103–106). Based on what we currently know of the paleohabitats of Pliocene *Australopithecus* species (97–106) and their dietary adaptations (62–65, 87–91, 107–109), it is not unreasonable to put forth a null hypothesis that posits *Australopithecus* was a eurytopic, or generalist, clade.

Eurytopic groups are predicted to have broad dietary breadth, wide habitat preferences, low species diversity, long species duration, and absence or rare sympatry of sister species, among other variables (110–112; see ref. 112 for complete list and discussion). Although some *Australopithecus* species are

younger than the time period reviewed here, they are all considered here for the purposes of this discussion. Species of *Australopithecus* generally have broad diets based on enamel carbon isotopic studies (63, 87, 91, 104, 107, 108), with the exception of *Au. anamensis* (62) and the much younger *Au. sediba* (109). There also does not appear to be strong habitat preference for the genus, with reconstructions of mosaic habitats for most of the *Australopithecus* sites (99, 101, 102), although it is unclear how the hominins were using the landscape. With six species currently referred to *Australopithecus*, even though this genus is considered as paraphyletic by some researchers (58, 67, 113), it would appear that it is relatively speciose. However, it is difficult to assess how long-lived each of these species might have been, or how many of them overlapped in time and space, and therefore difficult to make sound arguments about sympatry and niche partitioning among these species. However, most *Australopithecus* species appear to have been allopatric, except for *Au. afarensis*, which appears to have been sympatric with *Au. deyiremeda* at Woranso-Mille (25). Given the dietary breadth, diverse habitats, uncertainty of first and last appearance dates, and the rarity of sympatry (of at least five sites where *Au. afarensis* occur, only one site shows evidence of sympatry), the posited hypothesis cannot be rejected. If *Australopithecus* was indeed an eurytopic clade, as the currently available evidence suggests (101), then this has profound implications for how we understand its mode and rate of evolution; generalist clades, given their adaptability, have low rates of speciation and extinction (110, 112). However, only with more fossil evidence can we confidently reject or accept the hypothesis that *Australopithecus* was eurytopic. It is important to note that niche partitioning may not be the only means for multiple species within a genus to share the same habitat, as foraging strategies (93), type and quantity of resources (93), and predation pressure (86), can impact taxonomic diversity and the coexistence of sympatric species. It is necessary to better understand these factors and the interactions between them in the hominin fossil record to better understand taxonomic diversity and ecological strategies of early hominins.

Conclusion

The discovery of multiple and contemporaneous hominins older than 3 Ma since the early 1990s from various sites in Africa has raised the possibility that early hominins were as speciose as later hominins. Currently available fossil evidence indicates the possible presence of as many as four hominin species between 3.8 and 3.3 Ma: *Au. afarensis*, *Au. bahrelghazali*, *K. platyops*, and

Au. deyiremeda, in addition to the Burtele foot (BRT-VP-2/73), and whose taxonomic affinity has not been determined yet. Although debates continue on the validity of some of these named taxa, there is now clear evidence that the well-known *Au. afarensis* coexisted with at least one species, represented by the Burtele foot. The latter belonged to a species whose locomotor adaptation was different from what has been inferred for *Au. afarensis*.

Although the phylogenetic relationships of named middle Pliocene hominins remain unclear, largely because of the small sample size of each hypodigm, their contemporaneous presence raises questions regarding what adaptive strategies might have allowed for the coexistence of multiple, closely related species. Niche partitioning has commonly been cited as the strategy that allows for sympatry among related taxa. However, it is important to note that it may not be the only means for multiple species within a genus to share the same habitat, as foraging strategies, type and quantity of resources, and predation pressure, can impact taxonomic diversity and sympatry. Understanding these factors and the interactions between them have important implications for our understanding of early hominin paleobiology and paleoecology.

Although there is no doubt that these new fossil discoveries have opened new windows into our evolutionary past, they have also complicated our understanding of early hominin taxonomy and phylogenetic relationships. Nevertheless, paleoanthropologists continually seek more fossils, as it is only with bigger sample sizes from different sites and geographic areas are we able to confidently characterize species morphology, decipher phylogenetic relationships, and elucidate the complexities and intricacies of our evolutionary past.

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