Corrections

ANTHROPOLOGY; EARTH, ATMOSPHERIC, AND PLANETARY SCIENCES

Correction for "Stable isotope-based diet reconstructions of Turkana Basin hominins," by Thure E. Cerling, Fredrick Kyalo Manthi, Emma N. Mbua, Louise N. Leakey, Meave G. Leakey, Richard E. Leakey, Francis H. Brown, Frederick E. Grine, John A. Hart, Prince Kaleme, Hélène Roche, Kevin T. Uno, and Bernard A. Wood, which appeared in issue 26, June 25, 2013, of *Proc Natl Acad Sci USA* (110:10501–10506; first published June 3, 2013; 10.1073/pnas.1222568110).

The authors note that on page 10501, left column, line 13 of the abstract, "*ca*. 35/65 ratio" should instead appear as "*ca*. 65/35 ratio." Both the online article and the print article have been corrected.

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COMMENTARY

Correction for "Stable carbon isotopes and human evolution," by Richard G. Klein, which appeared in issue 26, June 25, 2013, of *Proc Natl Acad Sci USA* (110:10470–10472; first published June 6, 2013; 10.1073/pnas.1307308110).

The author notes that on page 10470, middle column, first paragraph, lines 13 and 16, "∂13C ‰" should instead appear as "δ13C ‰."

Also, on page 10471, middle column, first paragraph, line 3 "65%" should instead appear as "35%."

Both the online article and the print article have been corrected.

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Stable carbon isotopes and human evolution

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Paleoanthropologists have long relied on skull and tooth morphology to infer fossil hominin diets, but from the early 1980s, they have also looked to microscopic wear traces in dental enamel, and since the early 1990s, they have looked increasingly to the stable isotope composition of skeletal tissues. The most commonly used stable isotopes are varieties of the light elements nitrogen and carbon. Nitrogen isotope ratios can provide information about the degree of carnivory vs. herbivory (1), but nitrogen can be extracted only from fossil bones that retain protein, which means specimens mostly younger than 100,000 y in temperate latitudes and usually much younger than 25,000 y closer to the Equator. In contrast, antemortem carbon isotope ratios persist indefinitely in dental enamel (2), and the main limitation is that they reflect ancient diets mostly in tropical or subtropical settings where the plants divide subequally between ones that follow a C_4 photosynthetic pathway and others that follow a C_3 pathway. This is not a problem for paleoanthropology, because early hominins (humans broadly understood) evolved in tropical and subtropical Africa, and their teeth are preserved in numerous African sites. Four articles in PNAS show how stable carbon isotopes have illuminated the diets of hominins that lived in Africa between roughly 4.1 and 1.3 Ma.

Link Between Carbon Isotopes and Ancient Diets

In tropical and subtropical environments, the tissues of plants that follow a C_4 photosynthetic pathway, mainly grasses and some sedges, tend to be enriched in ^{13}C relative to ^{12}C. In contrast, the tissues of plants that follow a C_3 pathway, mainly trees, shrubs, bushes, and forbs, tend to be much poorer in ^{13}C. The tissues of plants that follow the Crassulacean acid metabolism (CAM) photosynthetic pathway, mainly succulents, resemble C_4 plants in ^{13}C enrichment, but they were probably rarely important to early hominins, because they occur mostly in deserts. Dietary reconstruction depends on the observation that the $^{13}C/^{12}C$ ratios in herbivores reflect the ratios in the plants they eat, and the ratios in carnivores reflect the ratios in their prey.

The $^{13}C/^{12}C$ ratio is recorded in various tissues, but from a fossil perspective, dental enamel is by far the most important. This is because its density promotes survival, and it resists postdepositional chemical alteration (diagenesis). It thus retains the antemortem $^{13}C/^{12}C$ signal. Enamel that is especially enriched in ^{13}C normally implies a diet composed largely of grasses or animals, including insects, that eat grasses. Enamel that is significantly depleted in ^{13}C implies a diet that included mostly nuts, fruits, leaves, or other parts of nongrassy plants or of animals that eat such plants. Values are usually expressed as a departure in ^{13}C per mil ($=\partial^{13}C$ ‰) from an accepted standard, and they have been determined for a variety of African savanna ungulates (3). $\partial^{13}C$ ‰ in the enamel of species that feed on C_4 grasses commonly ranges between 1.7 and 3.9. In the enamel of species that feed on nongrassy plants, it typically ranges between −14.9 and −10.2.

Stable Carbon Isotopes in Dental Enamel and Early Hominin Environments

In general, stable carbon isotopes reveal only what a species selected from the surrounding vegetation and not the overall vegetational community. However, if the $^{13}C/^{12}C$ ratio shifts over long intervals in the teeth of species that were almost certainly grazers, a reasonable inference is that there was a shift in the nature of the available grass. Thus, an increase in ^{13}C enrichment in grazer enamel across multiple lineages implies that C_4 grasses spread at the expense of C_3 plants in tropical and subtropical latitudes between 8 and 3 Ma (4, 5). This is paleoanthropologically significant, because it supports the "savanna hypothesis," according to which hominin bipedalism represents an adaptive response to the increasingly patchy distribution of trees or tree stands vs. grasses in tropical and subtropical Africa beginning roughly 8 Ma.

By 2 Ma or so, African savannas closely resembled historic ones and fossil ungulates mainly anticipated living ones such as equids (zebras), alcelaphine (wildebeest/hartebeest) antelopes, reduncine (waterbuck/reedbuck) antelopes, and hippotragine (roan/sable) antelopes that feed primarily on C_4 grasses (grazers) and others such as giraffids and tragelaphine (kudu/bushbuck) antelopes that feed primarily on the leaves of C_3 bushes, shrubs, and trees (browsers). Enamel $^{13}C/^{12}C$ ratios show that fossil species after 2 Ma divide between grazers and browsers exactly as their anatomical resemblances to living species would predict (6), which confirms that the grazer/browser ratio in a fossil site can be used to estimate the relative abundance of grass vs. bush nearby, or more conservatively, that differences in grazer/browser ratios between sites can be used to gauge differences in the abundance of grass vs. bush nearby.

Stable Carbon Isotopes in Dental Enamel and the Diet of Early Hominins

Fig. 1 presents the time spans and putative evolutionary relationships of the hominin species mentioned below.

In paleoanthropology, the first application of stable carbon isotope analysis was to South African *Australopithecus africanus* (∼2.8–2.1 Ma), *Paranthropus robustus* (∼2–1.2 Ma), and early *Homo* (∼2 Ma). The results indicated that the dental enamel of each species was relatively enriched in ^{13}C and to about the same extent (7, 8). This has been interpreted to mean that, on average, each species obtained 25–30% of its carbon from grassy (C_4) foods even if it obtained the bulk from berries, nuts, fruits. leaves, or other C_3 items. In contrast, it was recently shown that the enamel of the east African australopith, *Paranthropus boisei* (2.3–1.2 Ma), is much richer in ^{13}C, and as stressed below, the degree of enrichment implies that it obtained 75–80% of its diet from C_4 sources (9). Carbon isotopes cannot pinpoint the specific grass-based foods that the various species consumed, but significant differences in jaw and tooth morphology and in microwear (7) suggest that the different species exploited different sources. For *A. africanus* and *P. robustus*, the principal ones may have been grass seeds, grass roots, the underground storage organs (USOs) of sedges, and termites, whereas for early *Homo*, the flesh or marrow of grazing ungulates may also have been important. For *P. boisei*, the principal source may have been especially large quantities of sedge USOs. The great difference in ^{13}C enrichment between *P. boisei* and *P. robustus* was unexpected, because the species are remarkably similar in skull and tooth

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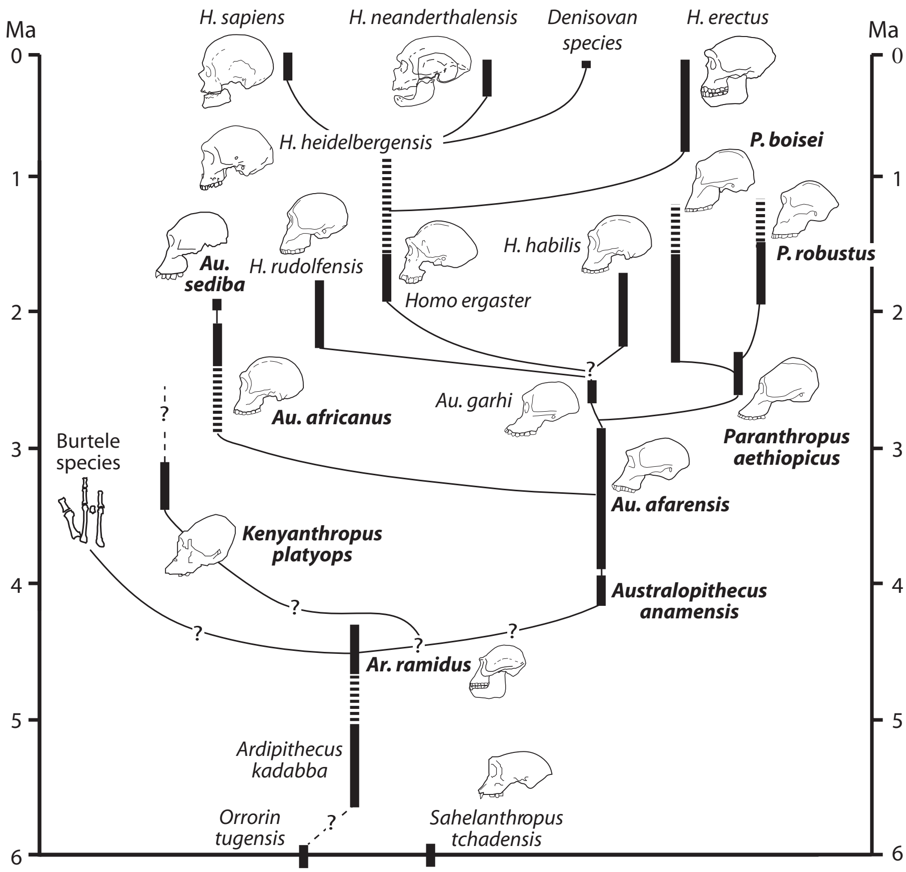

Fig. 1. Hypothetical phylogeny of the Hominini. Boldface marks species for which stable carbon isotope observations are available. Observations for early *Homo* have thus far been presented without reference to species. Broken bars indicate probable as opposed to directly established time spans.

morphology. However, they also differ in their enamel microwear (9), and the implication may be that they did not share an especially close common ancestor but evolved their craniodental similarities in parallel.

In *PNAS*, Cerling et al. (10) report on stable carbon isotopes in the teeth of hominins that lived between 4.1 and 1.4 Ma in the Lake Turkana basin of northern Kenya. The results indicate that the oldest species, *Australopithecus anamensis* (4.2–4.0 Ma), rarely consumed C_4 foods, even though these were probably readily available nearby. In its strong C_3 preference, *A. anamensis* recalls its putative ancestor, *Ardipithecus ramidus* (11), and also the common chimpanzee, which favors C_3 foods almost exclusively even in relatively open savanna settings where potential C_4 foods abound (12). In contrast to the results for *A. anamensis*, those for *Kenyanthropus platyops* (3.6–3.0 Ma), which was coeval and possibly conspecific with Ethiopian *Australopithecus afarensis* (13), sometimes indicate significant consumption of C_4 foods. The results for *Paranthropus aethiopicus* (2.6–2.3 Ma) and for sympatric *P. boisei* and early *Homo* (2–1.5 Ma), reveal a persistent interest in C_4 foods, but as noted previously, the degree in *P. boisei* was exceptional. Cerling et al. estimate that it consumed 75% C_4 items compared with 65% in early *Homo*, although *Homo* increased its C_4 consumption toward 1.5 Ma, perhaps because it fed increasingly on the flesh of grazing ungulates.

Wynn et al. (14) report on stable carbon isotopes in the teeth of later *Australopithecus afarensis* (3.4–2.9 Ma) from localities in the Hadar region of north-central Ethiopia. *A. afarensis* is generally thought to have descended from *A. anamensis* about 3.8 Ma, and it is a likely common ancestor for all hominins that postdate 2.6 Ma, including *A. africanus, Paranthropus* spp., and *Homo.* Carbon isotope ratios show that later *A. afarensis* consumed C_4 foods to about the same extent as most subsequent hominins, and *A. afarensis* is thus the oldest species to document the conspicuous dietary divide between hominins and chimpanzees. Among later species, only *Australopithecus sediba*, dated to about 2 Ma at Malapa Cave, South Africa, may have resembled chimpanzees in a strong preference for C_3 foods (15). This may mean it was as peculiar in its diet as it was in its anatomy, but secure dietary inference requires an enlarged sample of analyzed teeth.

Sponheimer et al. (8) review the principles that allow dietary inferences from stable carbon isotopes. They summarize all of the available observations, involving 175 teeth from multiple early hominin species between 4.4 and 1.3 Ma, and they explore the likely relationship between inferred diets and the form of early hominin jaws and teeth. They suggest that the increased interest in C_4 foods by australopiths after 4 Ma could largely explain a broadly simultaneous expansion in the chewing surfaces of the postcanine (premolar and molar) teeth and in the thickness of the mandibular body. They also stress that the trend toward increasing C_4 consumption after 4 Ma is nearly unique to the hominins. Coeval mammal species remain consistently oriented toward C_4, C_3, or mixed C_3/C_4 diets. The trend in hominins is thus likely to reflect fundamental evolutionary change.

Finally, Cerling et al. (16) report on carbon isotope ratios in enamel of the extinct gelada baboons *Theropithecus brumpti* (4-2.5 Ma) and *Theropithecus oswaldi* (2.0–0.9 Ma). Fossils of both species frequently accompany those of hominins in eastern Africa, especially in Kenya from which Cerling et al. obtained their samples. *T. oswaldi* is thought to have descended from *Theropithecus darti*, a broad contemporary of *T. brumpti* in southern Africa, and to have replaced *T. brumpti* in eastern Africa after 2.5–2 Ma. Isotope ratios for all three fossil *Theropithecus* species imply they favored grassy C_4 foods, but this was especially true for *T. oswaldi*, for which the ratios suggest 80% C_4 consumption. The difference from *T. brumpti* may reflect a difference in surroundings, because associated mammals suggest that *T. oswaldi* occupied more open savanna settings. In the degree to which extinct geladas favored grassy foods, they anticipate their smaller, surviving relative, *Theropithecus gelada*, which feeds almost exclusively on grass stems and seeds in the central Ethiopian highlands. Among other known primates, living or extinct, only *P. boisei* approximated the geladas in its C_4 emphasis. Geladas evolved unusually high-crowned postcanine teeth to masticate large quantities of grassy items. *P. boisei* may have evolved unusually large postcanine tooth surfaces for the same purpose.

Conclusion

Twenty years ago, we might have guessed, based mainly on the savanna settings in which early hominins evolved, that they depended increasingly on grassy foods or on creatures that ate grasses. The craniodental morphology of *P. boisei* might also have led to us to speculate that it relied on grassy foods to a particularly great extent, rivaling only gelada baboons among known primates. Now, thanks to stable-isotope analyses, we no longer have to guess, and the broad pattern of early hominin dietary evolution is established. Continuing isotope research will tell us what early *A. afarensis* (3.8–3.4 Ma) is likely to have eaten, whether the diet of *A. sediba* was truly chimpanzee-like, and perhaps most interesting, whether different diets distinguished the three species of early *Homo* that are now thought to have coexisted between 2 and 1.5 Ma (17).

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