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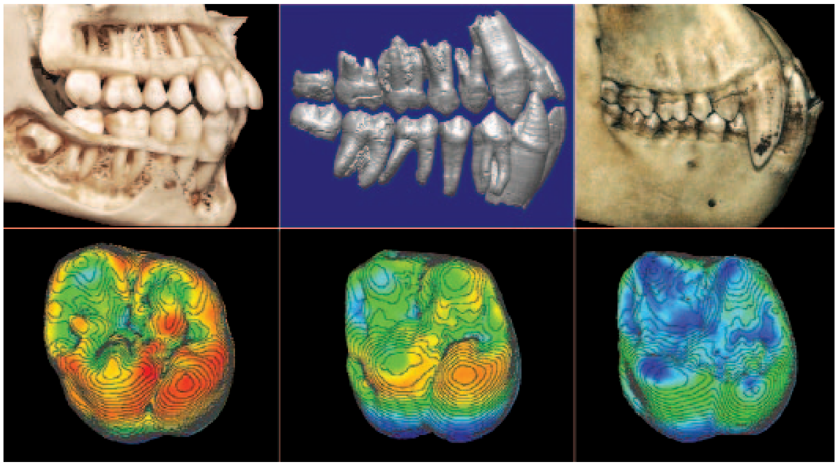
Paleobiological Implications of the *Ardipithecus ramidus* Dentition

Gen Suwa, Reiko T. Kono, Scott W. Simpson, Berhane Asfaw, C. Owen Lovejoy, Tim D. White

Teeth are highly resilient to degradation and therefore are the most abundant specimens in the primate fossil record. The size, shape, enamel thickness, and isotopic composition of teeth provide a wealth of information about phylogeny, diet, and social behavior. *Ardipithecus ramidus* was originally defined in 1994 primarily on the basis of recovered teeth, but the sample size was small, limiting comparison to other primate fossils. We now have over 145 teeth, including canines from up to 21 individuals. The expanded sample now provides new information regarding *Ar. ramidus* and, using comparisons with teeth of other hominids, extant apes, and monkeys, new perspectives on early hominid evolution as well.

In apes and monkeys, the male's upper canine tooth usually bears a projecting, daggerlike crown that is continuously sharpened (honed) by wear against a specialized lower premolar tooth (together these form the C/P_3 complex). The canine tooth is used as a slicing weapon in intra- and intergroup social conflicts. Modern humans have small, stublike canines which function more like incisors.



Dentitions from human (left), *Ar. ramidus* (middle), and chimpanzee (right), all males. Below are corresponding samples of the maxillary first molar in each. Red, thicker enamel (~2 mm); blue, thinner enamel (~0.5 mm). Contour lines map the topography of the crown and chewing surfaces.

All known modern and fossil apes have (or had) a honing C/P_3 complex. In most species, this is more developed in males than females (in a few species, females have male-like large canines, either for territorial defense or for specialized feeding). The relatively large number of *Ar. ramidus* teeth, in combination with Ethiopian *Ar. kadabba*, Kenyan *Orrorin*, and Chadian *Sahelanthropus* [currently the earliest known hominids at about 6 million years ago (Ma)], provide insight into the ancestral ape C/P_3 complex and its evolution in early hominids.

In basal dimensions, the canines of *Ar. ramidus* are roughly as large as those of female chimpanzees and male bonobos, but their crown heights are shorter (see figure). The *Ar. ramidus* sample is now large enough to assure us that males are represented. This means that male and female canines were not only similar in size, but that the male canine had been dramatically "feminized" in shape. The crown of the upper canine in *Ar. ramidus* was altered from the pointed shape seen in apes to a less-threatening diamond shape in both males and females. There is no evidence of honing. The lower canines of *Ar. ramidus* are less modified from the inferred female ape condition than the uppers. The hominid canines from about 6 Ma are similar in size to those of *Ar. ramidus*, but (especially) the older upper canines appear slightly more primitive. This suggests that male canine size and prominence were dramatically reduced by ~6 to 4.4 Ma from an ancestral ape with a honing C/P_3 complex and a moderate degree of male and female canine size difference.

In modern monkeys and apes, the upper canine is important in male agonistic behavior, so its subdued shape in early hominids and *Ar. ramidus* suggests that sexual selection played a primary role in canine reduction. Thus, fundamental reproductive and social behavioral changes probably occurred in hominids long before they had enlarged brains and began to use stone tools.

Thick enamel suggests that an animal's food intake was abrasive; for example, from terrestrial feeding. Thin enamel is consistent with a diet of softer and less abrasive foods, such as arboreal ripe fruits. We measured the enamel properties of more than 30 *Ar. ramidus* teeth. Its molar enamel is intermediate in thickness between that of chimpanzees and *Australopithecus* or *Homo*. Chimpanzees have thin enamel at the chewing surface of their molars, whereas a broad concave basin flanked by spiky cusps facilitates crushing fruits and shredding leaves. *Ar. ramidus* does not share this pattern, implying a diet different from that of chimpanzees. Lack of thick enamel indicates that *Ar. ramidus* was not as adapted to heavy chewing and/or eating abrasive foods as were later *Australopithecus* or even *Homo*. The combined evidence from the isotopic content of the enamel, dental wear, and molar structure indicates that the earliest hominid diet was one of generalized omnivory and frugivory and therefore differed from that of *Australopithecus* and living African apes.

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The Middle Awash *Ardipithecus ramidus* sample comprises over 145 teeth, including associated maxillary and mandibular sets. These help reveal the earliest stages of human evolution. *Ar. ramidus* lacks the postcanine megadontia of *Australopithecus*. Its molars have thinner enamel and are functionally less durable than those of *Australopithecus* but lack the derived *Pan* pattern of thin occlusal enamel associated with ripe-fruit frugivory. The *Ar. ramidus* dental morphology and wear pattern are consistent with a partially terrestrial, omnivorous/frugivorous niche. Analyses show that the *ARA-VP-6/500* skeleton is female and that *Ar. ramidus* was nearly monomorphic in canine size and shape. The canine/lower third premolar complex indicates a reduction of canine size and honing capacity early in hominid evolution, possibly driven by selection targeted on the male upper canine.

Fossilized teeth typically represent the most abundant and best preserved remains of hominids and other primates. They provide crucial evidence on variation, phylogenetic relationships, development, and dietary adaptations. Furthermore, because canines function as weapons in interindividual aggression in most anthropoid species, they additionally inform aspects of social structure and behavior.

We have now recovered and analyzed a sample of 145 non-antimeric tooth crowns comprising 62 cataloged dentition-bearing specimens of *Ardipithecus ramidus* from the Lower Aramis Member of the Sagantole Formation, about five times more than previously reported (*1*, *2*) (Fig. 1 and table S1). All permanent tooth positions are represented, with a minimum of 14 individuals for both the upper canine and upper second molar (M^2) positions. Excluding antimeres, 101 teeth have measurable crown diameters. In addition, seven *Ar. ramidus* specimens with teeth have been described from Gona (*3*). These are broadly comparable to their Aramis counterparts in size, proportions, and morphology but slightly extend the smaller end of the species range in some mandibular crown diameters.

The major morphological characteristics of the *Ar. ramidus* dentition have been outlined in previous studies of Aramis and Gona fossils (*1*, *3*, *4*). Comparisons of *Ar. ramidus* with Late Miocene hominids (*Ar. kadabba*, *Orrorin tugenensis*, and *Sahelanthropus tchadensis*) have identified slight but distinct differences, particularly in the canine (*4*–*6*). Other subtle features of incisors and postcanine teeth have been noted as phylogenetic or taxonomic distinctions (*5*–*10*). However, the most recent and comprehensive evaluation of the available Late Miocene materials concluded that these differences are minor compared with extant ape (and later hominid) genus-level variation and that both *Ar. ramidus* and *Ar. kadabba* dentitions exhibit phenetic similarities with early *Australopithecus* (*4*).

The expanded *Ar. ramidus* sample of the present study allows a more definitive phylogenetic placement of *Ar. ramidus* relative to the more primitive *Ar. kadabba* and the more derived *Au. anamensis* and *Au. afarensis* (*11*). Here, we focus on the paleobiological aspects of the *Ar. ramidus* dentition, including variation, size, and scaling, probable dietary niche, and canine/lower third premolar (C/P_3) complex evolution and its behavioral implications. We also address the alleged phylogenetic importance (*7*) of enamel thickness in *Ar. ramidus* (*1*). This is now made possible by the more comprehensive dental collection that includes key associated dental sets.

Crown size, proportions, and variation. The *Ar. ramidus* dentition is approximately chimpanzee-sized (fig. S1 and tables S2 to S4). Mean canine size is comparable to that of female *Pan troglodytes*, although the incisors are smaller. Upper and lower first molars (M1s) are *P. troglodytes*–sized but tend to be buccolingually broader (figs. S1 to S3). The second and third molars (M2s and M3s) are both absolutely and relatively larger (figs. S1 and S4 to S6). Postcanine size and proportions of *Ar. ramidus* are similar to those of *Ar. kadabba* and other ~6.0-million-year-old forms (*O. tugenensis* and *S. tchadensis*) (*4*–*10*), as well as to many Miocene hominoids (although Miocene ape lower molars tend to be buccolingually narrower) (fig. S3).

Variation within the Aramis dental sample is low. In modern anthropoids, the coefficient of variation (CV) is lowest in M1 and M2, with single-sex and mixed-sex values usually ranging from about 3.5 to 6.5 (*12*–*14*). At Aramis, *Ar. ramidus* upper and lower M1s and M2s are less variable (CVs ranging from 2.5 to 5.6) than those of *Australopithecus afarensis* and *Au. anamensis* (table S2). However, these *Australopithecus* samples represent multiple sites and span a much greater time than the Aramis fossils (*11*). The low variation seen in Aramis *Ar. ramidus* probably reflects spatially and temporally restricted sampling and low postcanine sexual dimorphism as in *Pan* (*15*) (table S5).

The Aramis postcanine dentition is also morphologically more homogenous than known *Australopithecus* species samples. For example, the six relatively well-preserved M^1s (Fig. 1) differ little in features otherwise known to vary widely within hominid and modern hominoid species (*16*, *17*), including Carabelli's expression, occlusal crest development, and hypocone lingual bulge. This suggests that the Aramis *Ar. ramidus* collection samples regional demes or local populations with persistent idiosyncratic tendencies. The ubiquitous occurrence of single rooted lower fourth premolars (P_4) (now seen in eight non-antimeric Aramis P_4s) suggests increased frequency of otherwise rare variants from genetic drift, absent substantial selection for larger and/or more complicated root systems (*18*). Because this anatomy is shared with Gona *Ar. ramidus* (*3*), it appears characteristic of this regional population.

Morphology and evolution of the C/P_3 complex. The C/P_3 complex of anthropoids has behavioral and evolutionary importance because canine size and function are directly linked to male reproductive success (*19*). Therefore, clarifying the tempo and mode of the evolution of the C/P_3 complex, from hominid emergence through its early evolution, is important.

Not counting antimeres, 23 upper and lower canines from 21 *Ar. ramidus* individuals are now known from Aramis. Three more have been described from Gona (*3*), and seven from the ~6.0-million-year-old *Ar. kadabba*, *O. tugenensis*, and *S. tchadensis* (*4*–*10*). There are no examples of a distinctly large male morphotype in any of these collections (Fig. 1 and figs. S7 and S8), suggesting that canine sexual dimorphism was minimal in Mio-Pliocene hominids. In basal crown dimensions, *Ar. ramidus* canine/postcanine size ratios overlap extensively with those of modern and Miocene female apes (fig. S9). Absolute and relative canine heights are also comparable to those of modern female apes, although canine height appears exaggerated in *P. troglodytes* [Fig. 1; figs. S8, S10, and S11; and supporting online material (SOM) text S1].

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Canine shape of *Ar. ramidus* is either comparable to female apes or more derived toward *Australopithecus* (*11*) (Fig. 1 and figs. S12 and S13). The upper canine (UC) is clearly derived in *Ar. ramidus*, because it has a diamond-shaped lateral crown profile with elevated and/or flaring crown shoulders (*n* = 5 from Aramis and *n* = 1 from Gona) [this study and (*3*, *4*, *6*)]. However, the lower canine (LC) retained much more of the morphology of the female ape condition (*4*, *5*) (Fig. 1, figs. S11 to S13, and SOM text S1). A hominid-like incisiform LC morphology (high mesial shoulder, developed distal crest terminating at a distinct distal tubercle) is seen in some female apes (e.g., *Ouranopithecus* and *P. paniscus*), whereas the LCs of *Ar. kadabba* and *Ar. ramidus* tend to be conservative, exhibiting a strong distolingual ridge and faint distal crest, typical of the interlocking ape C/P_3 complex (*4*) (Fig. 1 and SOM text S1).

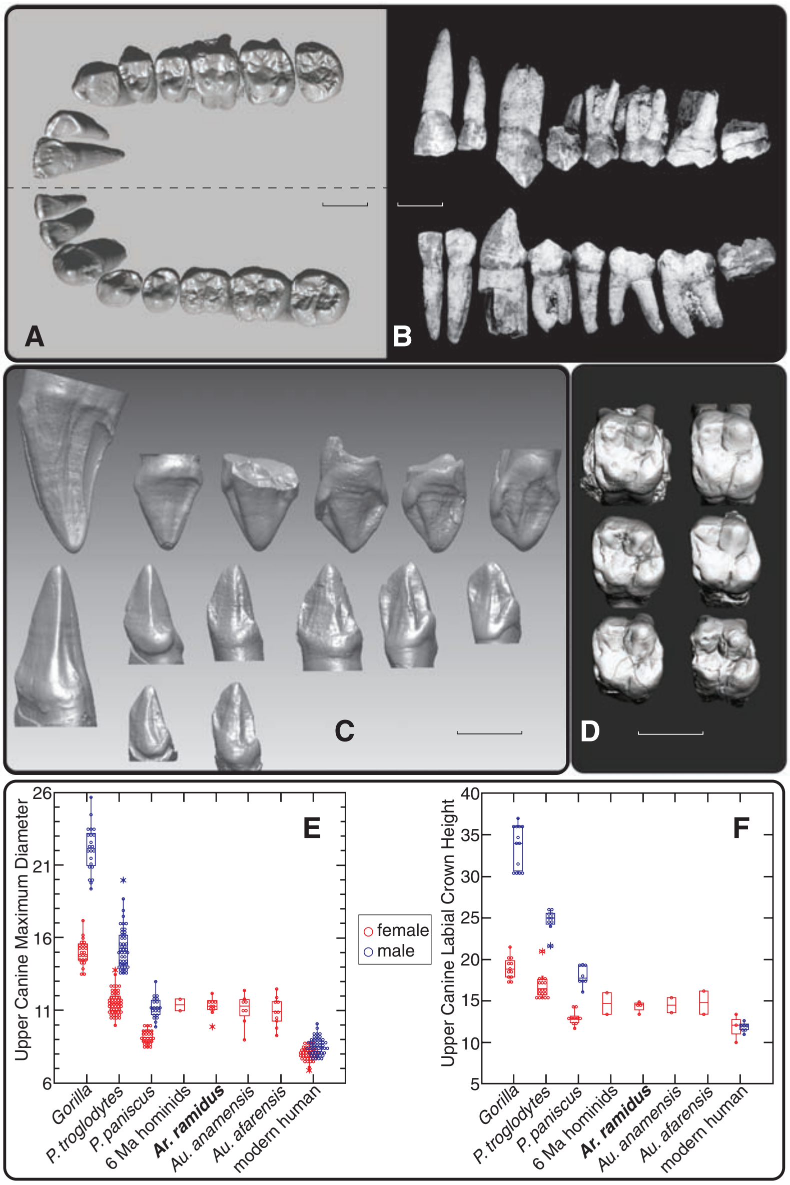

Fig. 1. Representative examples of the Aramis *Ardipithecus ramidus* dentition. (**A**) Occlusal view micro-CT–based alignment of *ARA-VP-1/300*: top, maxillary dentition; bottom, mandibular dentition. The better-preserved side was scanned and mirror-imaged to form these composites. (**B**) *ARA-VP-1/300* in buccal view: top, right maxillary dentition (mirrored); bottom, left mandibular dentition. (**C**) Comparison of canine morphology (micro-CT–based renderings). Top row, lingual view of upper canines, from left to right: male *P. troglodytes* (cast), female *P. troglodytes* (cast), *Ar. kadabba ASK-VP-3/400*, *Ar. ramidus ARA-VP-6/1*, *Au. afarensis L.H. 6* (cast), *Au. afarensis A.L. 333x-3* (cast, mirrored). Lower rows, distolingual view of lower canines, main row from left to right: male *P. troglodytes* (cast), female *P. troglodytes* (cast), *Ar. kadabba* (*STD-VP-2/61*), *Ar. ramidus ARA-VP-1/300*, *Au. africanus Sts 50* (mirrored), *Au. africanus Sts 51*. Lowest two specimens are ape lower canines with hominid-like features: left, *P. paniscus* (cast); right, *Ouranopithecus macedoniensis RLP-55* (cast). The *Ar. ramidus* upper canine is highly derived, with a diamond-shaped crown with elevated crown shoulders. The lower canine tends to retain aspects of primitive ape features. Further details are given in the SOM figures and SOM text S1. (**D**) M^1 morphology (micro-CT–based renderings) showing relatively little morphological variation among the Aramis individuals. Top row left, *ARA-VP-1/300* (mirrored); right, *ARA-VP-1/1818*. Middle row left, *ARA-VP-1/3288*; right, *ARA-VP-6/500*. Bottom row left, *ARA-VP-6/502* (mirrored); right, *KUS-VP-2/154*. (**E** and **F**) Box plot of upper canine maximum diameter and labial height (in mm). *Ar. ramidus* includes Aramis and published Gona materials (*2*). The ~6-million-year-old hominids are represented by *Ar. kadabba* (*ASK-VP-3/400*) and *O. tugenensis* (*BAR 1425'00*) (*7*). Symbols give central 50% range (box), range (vertical line) and outliers. See SOM figures and text S1 for additional plots and details.

The *Ar. ramidus* P_3 is represented by seven observable crowns, ranging from obliquely elongate to transversely broad (*1*) (fig. S14). The *Ar. ramidus* P_3 is relatively smaller than that of *Pan* and typically not as asymmetric or elongate in occlusal view (figs. S15 and S16). In these respects, the *Ar. ramidus* P_3 is comparable to those of *Au. anamensis* and *Au. afarensis*. However, *Ar. ramidus* is more primitive than *Australopithecus* in retaining a proportionately higher P_3 crown (fig. S16). It appears that there was a decrease of P_3 size from the ancestral ape to *Ar. ramidus* conditions, but this reduction was greater in basal crown dimensions than in crown height (SOM text S1).

In *Ar. ramidus*, the combined effect of (i) reduced canine size and projection and (ii) reduced size and mesiobuccal extension of the P_3 results in the absence of upper canine honing (defined as distolingual wear of the UC against the mesiobuccal P_3 face, cutting into the lingual UC crown face and resulting in a sharpened distolabial enamel edge). Instead, apical wear in *Ar. ramidus* commences early and thereafter expands as wear progresses. None of the known UCs or P_3s exhibits evidence of honing (fig. S14). However, both upper and lower canines project beyond the postcanine occlusal plane before heavy wear, resulting in steep and beveled wear slopes, as also seen in examples of *Au. afarensis* and *Au. anamensis* (*1*, *4*, *20*).

Two *Ar. ramidus* specimens provide associated maxillary and mandibular dentitions with minimal canine wear. One is almost certainly female (*ARA-VP-6/500*), and the other is a probable male (*ARA-VP-1/300*) (see below). Both individuals possess a UC with a shorter crown height than the associated LC (>10% difference in *ARA-VP-1/300*) (*21*). In contrast in most anthropoid species, the UC is greater in height than the LC (fig. S17), a condition exaggerated in males of dimorphic species (over 50% in some papionins). Although less extreme in extant great apes (*22*), the UC still exceeds LC crown height by up to ~20% (fig. S18). In modest samples of modern great ape canines with little to no wear, we found no instances of LC height exceeding that of the UC (25 males and 27 females). This pattern of relative UC and LC height in *Ar. ramidus* appears unique among anthropoids and indicates differential reduction of the UC in hominids. The UC < LC height relation is retained in modern humans.

Morphological changes in the series *Ar. kadabba*–*Ar. ramidus*–early *Australopithecus* support the hypothesis of selection-induced UC reduction. As detailed above, the UC is clearly derived in *Ar. ramidus*, whereas the LC tends to retain the primitive female apelike condition. *Au. anamensis*, geologically younger than *Ar. ramidus* but older than *Au. afarensis*, exhibits a polymorphic condition represented by both primitive and advanced LC morphologies (*4*, *20*) (SOM text S1). The more incisiform morphology becomes universal in *Au. afarensis* and later hominids. Furthermore, compared with both male and female apes, *Ar. ramidus* exhibits a small UC crown (both basal diameter and height) relative to apico-cervical root length, more so than the LC (figs. S19 and S20). This observation provides further support to the interpretation that the UC crown was differentially reduced (SOM text S1).

A broader comparison of *Ar. ramidus* with extant and Miocene apes illuminates aspects of C/P_3 complex evolution. Compared with cercopithecoids, hominoids tend to have smaller P_3s with less extensive honing (fig. S15). Compared with other modern and Miocene apes, both species of *Pan* appear to show P_3 reduction. The P_3 of *Ar. ramidus* is even smaller, suggesting further reduction of the C/P_3 complex from an ancestral ape condition. At first sight, the comparatively small P_3 size in *Pan* appears paradoxical, because among the modern great apes both male and female *P. troglodytes* have relatively large and tall canines (figs. S9 and S10 and SOM text S1). However, this apparent paradox is removed by a broader perspective on tooth and body size proportions. Both *Pan* species share with atelines and *Presbytis* (sensu stricto) small postcanine size relative to body size (Fig. 2, figs. S21 and S22, and SOM text S2), low postcanine dimorphism, and low to moderate canine size dimorphism (figs. S23 to S25). Conversely, papionins exhibit the opposite condition: large postcanines, large canines, and extreme dimorphism. We therefore hypothesize that the basal *Pan* condition was characterized by a somewhat reduced C/P_3 complex as part of a generally small dentition relative to body size and that the canines were secondarily enhanced leading to modern *P. troglodytes*.

The *ARA-VP-6/500* skeleton and sexual dimorphism. Of the 21 individuals with canines, *ARA-VP-6/500* has UC and LC that are strikingly small; its UC ranks either 12th or 13th (of 13), and its LC ranks seventh (of eight) in size (table S6). However, postcranially, *ARA-VP-6/500* is a large individual with an estimated body weight of ~50 kg (*23*). Was *ARA-VP-6/500* a small-canined male or a large-bodied female?

We began our evaluation of *ARA-VP-6/500* (*24*) by estimating the degree of dimorphism in the *Ar. ramidus* canine (SOM text S3). Even in modern humans, the canine is metrically the most dimorphic tooth. Mean basal crown diameter of human male canines is about 4 to 9% larger than that in females (table S5). Our analysis indicates that *Ar. ramidus* was probably only marginally more dimorphic than modern humans (tables S6 to S9 and SOM text S3), with a probable range of 10 to 15% dimorphism (in canine mean crown diameter). This is substantially less dimorphic than modern great apes, whose male canines (mean crown diameter) are larger than those of females by 19 to 47%.

On the basis of the above dimorphism estimate, the probability of a male having canines as small as those of *ARA-VP-6/500* can be evaluated by bootstrapping (*2*). Assuming 12% dimorphism in mean canine size (table S8), the probability that *ARA-VP-6/500* is a male is <0.03 (if the UC is ranked 12th of 13) or <0.005 (if ranked 13th) (table S9 and SOM text S4). We conclude that *ARA-VP-6/500* is a large-bodied female, a conclusion also corroborated by cranial anatomy (*25*). This shows that skeletal size dimorphism in *Ar. ramidus* must have been slight (*11*), as is the case in both species of *Pan* (*26*, *27*).

The *ARA-VP-6/500* skeleton and dimorphism estimates allow us to place the *Ar. ramidus* dentition within a broader comparative framework. Scaling analyses (*2*) show that the UC of *Ar. ramidus* was relatively small in both sexes (fig. S22 and SOM text S2). In particular, male UC height of *Ar. ramidus* is estimated to be close to that of female *P. paniscus* and *Brachyteles* and to be much lower than that of male *P. paniscus* (which has the least projecting male canine among extant catarrhines) (Fig. 2).

Canine development and function. In cercopithecoids with highly dimorphic canines, canine eruption is typically delayed in males, beginning after the age of eruption in females (*28*) and apparently corresponding with species-specific patterns of body size growth spurts (*29*–*31*). Once male canine eruption is initiated, it then proceeds at a higher rate than in females, but it can still last for several years depending on species (*31*). As a consequence, males attain full canine eruption as they approach or achieve adult body size, both of which are necessary for reproductive success (*19*).

Sexually distinct patterns of canine eruption in relation to body size growth have yet to be well documented in modern great apes but appear to broadly share the cercopithecoid pattern described above (*28*, *32*–*34*). Initiation of canine eruption in *P. troglodytes* differs by about 1.5 to 2 years between the sexes (*35*). In males of both *P. troglodytes* and *P. paniscus*, full canine eruption appears to coincide broadly with M3 eruption (observations of skeletal materials), with polymorphism in the eruption sequence of the two teeth. By contrast in females of both species, full canine eruption is attained before M3 eruption.

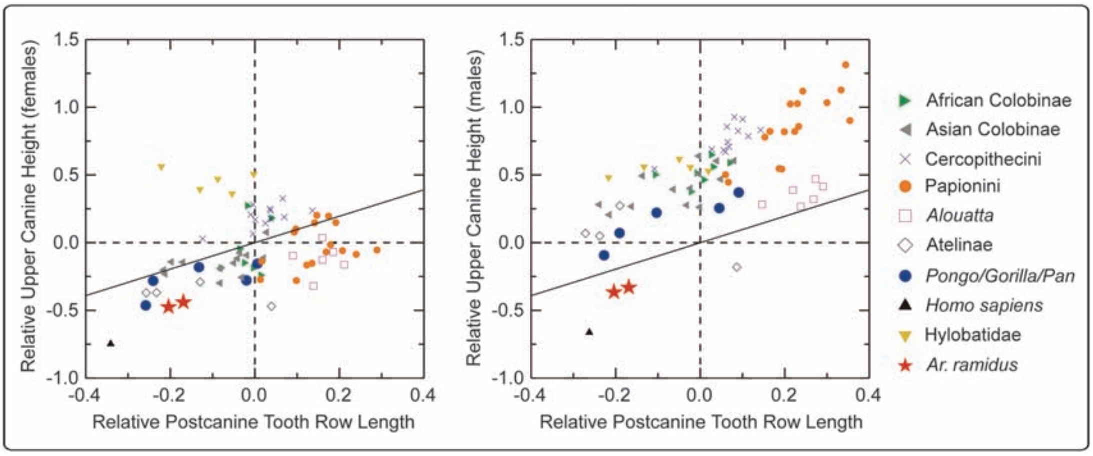

Fig. 2. Size and scaling of the *Ardipithecus ramidus* dentition. Natural log-log scatter diagram of relative upper canine height (*y* axis) against relative postcanine length (*x* axis): **left**, females; **right**, males. Both axes represent size free variables (residuals) derived from scaling tooth size against body size across a wide range of anthropoids (*2*). A value of zero represents the average female catarrhine condition. Positive and negative residuals represent relatively large and small tooth sizes, respectively. The diagonal line indicates the direction of equivalent canine and postcanine proportions independent of size. The five great ape taxa plotted are from left to right: *P. paniscus*, *P. t. troglodytes*, *P. t. schweinfurthi*, *Gorilla gorilla*, and *Pongo pygmaeus*. *Ar. ramidus* is plotted by using mean postcanine size and canine crown heights of probable female (*ARA-VP-6/500*) and male (*ARA-VP-1/300*) individuals. A hypothetical female body weight of 45 kg or 50 kg was used (right and left stars, respectively). *Ar. ramidus* is shown to have small postcanine tooth sizes, similar to those of *Ateles*, *Presbytis* sensu stricto, and *Pan*. Relative canine height of *Ar. ramidus* is lower than that of the smallest-canined nonhuman anthropoids, *P. paniscus* and *Brachyteles arachnoides*. See SOM text S2 for further details.

The relative timing of canine eruption in *Ar. ramidus* is revealed by two juveniles. The *ARA-VP-6/1* holotype, a probable male (table S6), includes an unworn UC whose perikymata count is 193, higher than that in *Au. africanus/afarensis* (maximum 134, *n* = 4) (*36*) and lower than those in small samples of female *P. troglodytes* and *Gorilla* (minimum 204, *n* = 10) (*37*). The *ARA-VP-6/1* UC crown formation time was 4.29 or 4.82 years, depending on estimates of enamel formation periodicity (fig. S26). This is a comparatively short formation time, around the minimum reported for modern female apes (*38*).

The eruption pattern of a second individual, *ARA-VP-1/300*, can be assessed from the presence or absence of wear facets and/or polish. The *ARA-VP-1/300* canines were just completing eruption, its M2s were worn occlusally, and its unerupted M3 crowns were barely complete (Fig. 1 and fig. S27). Compared with extant apes, both its UC and LC development are advanced relative to M2 and M3 (fig. S28) (*39*).

The combined morphological and developmental evidence suggests that selection for delayed canine eruption had been relaxed in *Ar. ramidus*. We hypothesize that canine prominence had ceased to function as an important visual signal in male competitive contexts.

Tooth size and diet. We consider relative incisor and postcanine sizes to be potentially useful in inferring dietary adaptations, although consistent patterns across primates have not been obtained (*40*). In particular, postcanine megadontia has been considered a defining feature of *Australopithecus* (*41*). We evaluated incisor and molar sizes of *Ar. ramidus* in comparison to those of *Pan* and *Australopithecus*. Among anthropoids, *Pan* and *Pongo* are unique in having large incisors relative to both postcanine and body size, a condition not shared by *Ar. ramidus* (fig. S29). This suggests that *Ar. ramidus* was not as intensive a frugivore as are *Pan* and *Pongo*, incisor length probably being functionally related to removal of fruit exocarp (*42*) and/or feeding behavior such as wadging.

Although the M1 area, normalized by individual postcranial metrics, lies well within the range of extant chimpanzees, the total postcanine area of *ARA-VP-6/500* falls between *Pongo* and *P. troglodytes* (Fig. 3). *Ar. ramidus* is not only less megadont than *Pongo* and *Au. afarensis* but, together with *Pan*, *Ateles*, and some *Presbytis* species, lies at the small end of the range of variation of large-bodied anthropoids (fig. S30). The most megadont anthropoids include robust *Australopithecus*, such as *Au. boisei*, as well as papionins and *Alouatta*. *Ouranopithecus* was probably as megadont as *Australopithecus* species, whereas *Dryopithecus* and *Pierolapithecus* probably had relative postcanine sizes closer to *Ar. ramidus* and thus better approximate the dentition–to–body size relationship of the last common ancestor of humans and chimpanzees. We conclude that *Ar. ramidus* was substantially less megadont than *Australopithecus*.

Molar structure and enamel thickness. Molar structure, enamel thickness, and tooth wear further illuminate dietary adaptation in *Ar. ramidus*. Compared with the distinct occlusal structure of the molars of each of the modern ape species (see below), *Ardipithecus* occlusal morphology is more generalized, with low, bunodont cusps and moderate to strong basal crown flare. Such morphology also characterizes *Australopithecus* as well as a diversity of Miocene apes (*43*). *Gorilla* molars have much more salient occlusal topography and enhanced shearing crests. *Pan* molars are characterized by broad, capacious occlusal basins flanked by moderately tall cusps, effective in crushing relatively soft, fluidal mesocarp while retaining the ability to process more fibrous herbaceous materials (Fig. 4) (*44*, *45*). These features are accentuated in *Pan* by the characteristically thin enamel of its occlusal basin (*45*, *46*).

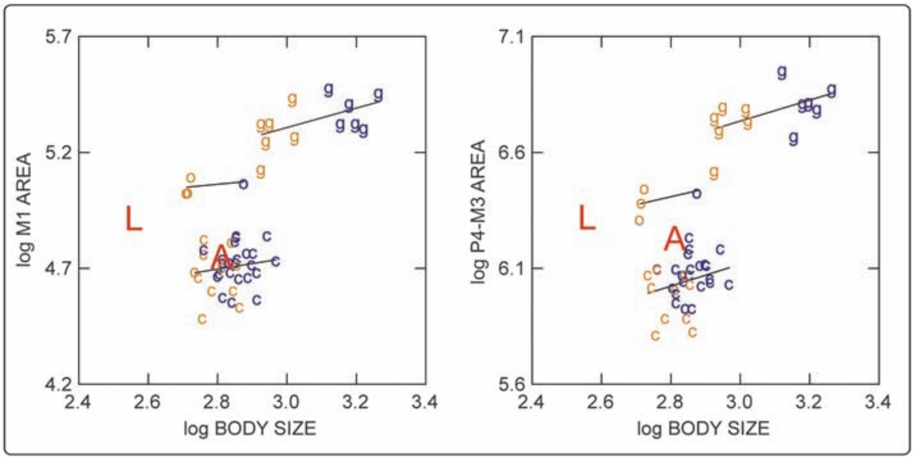

Fig. 3. Relative postcanine dental size in *Ar. ramidus*. Postcanine size is compared directly in reference to associated postcranial elements; *x* axis is natural log of the size variable (body size proxy) of Lovejoy *et al.* (*23*), derived from four metrics of the talus and five metrics of the capitate; *y* axis is natural log of the square root of the sum of calculated areas (mesiodistal length multiplied by buccolingual breadth) of lower M_1 (**left**) and lower P_4 to M_3 (**right**). A, *Ar. ramidus ARA-VP-6/500*; L, *Au. afarensis A.L. 288-1*; c, *Pan troglodytes troglodytes*; g, *Gorilla gorilla gorilla*; o, *Pongo pygmaeus* (males blue, females red).

To further elucidate molar structure and dietary adaptations of *Ar. ramidus*, particularly in comparison with *Pan* and *Australopithecus*, we used micro–computed tomography (micro-CT) to study molar enamel thickness and underlying crown structures (*2*). Although the weak contrast of fossil enamel and dentin makes micro-CT–based evaluations difficult, we were able to assess several *Ar. ramidus* molars with this method. These and analyses of CT sections and natural fracture data (*2*) indicate that *Ar. ramidus* enamel is considerably thinner than that of *Australopithecus* but not as thin as in *Pan* [as originally reported in (*1*)] (Fig. 4 and figs. S31 and S32).

Of particular importance is that *Ar. ramidus* molars do not exhibit enamel distribution patterns characteristic of *P. troglodytes* and *P. paniscus*. Both *Pan* species have similar crown structure and enamel distribution patterns (Fig. 4), although *P. paniscus* molars exhibit a higher cuspal topography, perhaps related to greater reliance on fibrous food (*46*, *47*). *Ar. ramidus* lacks the thin occlusal fovea enamel of *Pan* and in this regard is similar to both *Australopithecus* and Miocene forms such as *Dryopithecus* (Fig. 4). The *Pan* condition is most likely derived, probably associated with an increased reliance on higher-canopy ripe fruit feeding.

Despite the generalized molar structure common to both *Ar. ramidus* and *Australopithecus*, the adaptive difference between the two is expressed by enamel tissue volume, which we consider to broadly track net resistance to abrasion. Modern ape species exhibit a near-isometric relation between molar durability (measured as volume of enamel tissue available for wear per unit occlusal area) and tooth size, despite diverse dietary preferences and crown anatomy (Fig. 4). *Ar. ramidus* falls near this isometric continuum, but *Australopithecus* does not. *Australopithecus* molars achieve greater functional durability from increased enamel volume. *Au. boisei* occupies an extreme position distant from the modern ape baseline. Thus, both tooth size and enamel thickness and volume suggest a substantial adaptive shift from *Ardipithecus* to *Australopithecus*.

This is further expressed in molar macro- and microscopic wear patterns. In contrast to *Australopithecus*, *Ar. ramidus* molars did not wear flat but instead retained stronger buccolingual wear slopes. The Aramis *Ar. ramidus* dentition also exhibits consistently weak M1 to M3 wear gradients (*48*). Microwear of the *Ar. ramidus* molars tends to differ from that of *Au. afarensis*, the latter characterized by a dominance of buccolingually oriented scratches (*49*). In contrast, the *Ar. ramidus* molars tend to exhibit finer and more randomly oriented striae (fig. S33). Collectively, the wear evidence suggests that *Ar. ramidus* consumed a less abrasive diet and engaged in less masticatory grinding than *Australopithecus*.

Enamel thickness and phylogenetic implications. Since the initial description of *Ar. ramidus* as a new species of Hominidae (*1*), its relatively thin molar enamel has been a focus of attention. Some authors have suggested that its thin enamel might be a shared derived feature with *Pan* (*7*). The fuller study of molar enamel thickness and patterns outlined above establishes the following: (i) Although *Ar. ramidus* enamel is thinner than that of *Australopithecus*, it is not as thin as *Pan's*; (ii) the thin enamel of *Pan* molars can be considered a part of a structural adaptation to ripe fruit frugivory (*46*) and therefore differs from the *Ar. ramidus* condition. Furthermore, the distinct internal structure of *Pan* molars seems lacking in *Ar. kadabba*, *O. tugenensis*, and *S. tchadensis* (*4*, *8*, *10*). Hence, the *Pan* condition is best considered derived relative to the ancestral and early hominid conditions.

Conclusions. Multiple lines of morphological evidence suggest that *Ar. ramidus* was a generalized omnivore and frugivore that did not rely heavily on either ripe fruits (as in *Pan* or *Pongo*), fibrous plant foods (as in *Gorilla*), or hard and

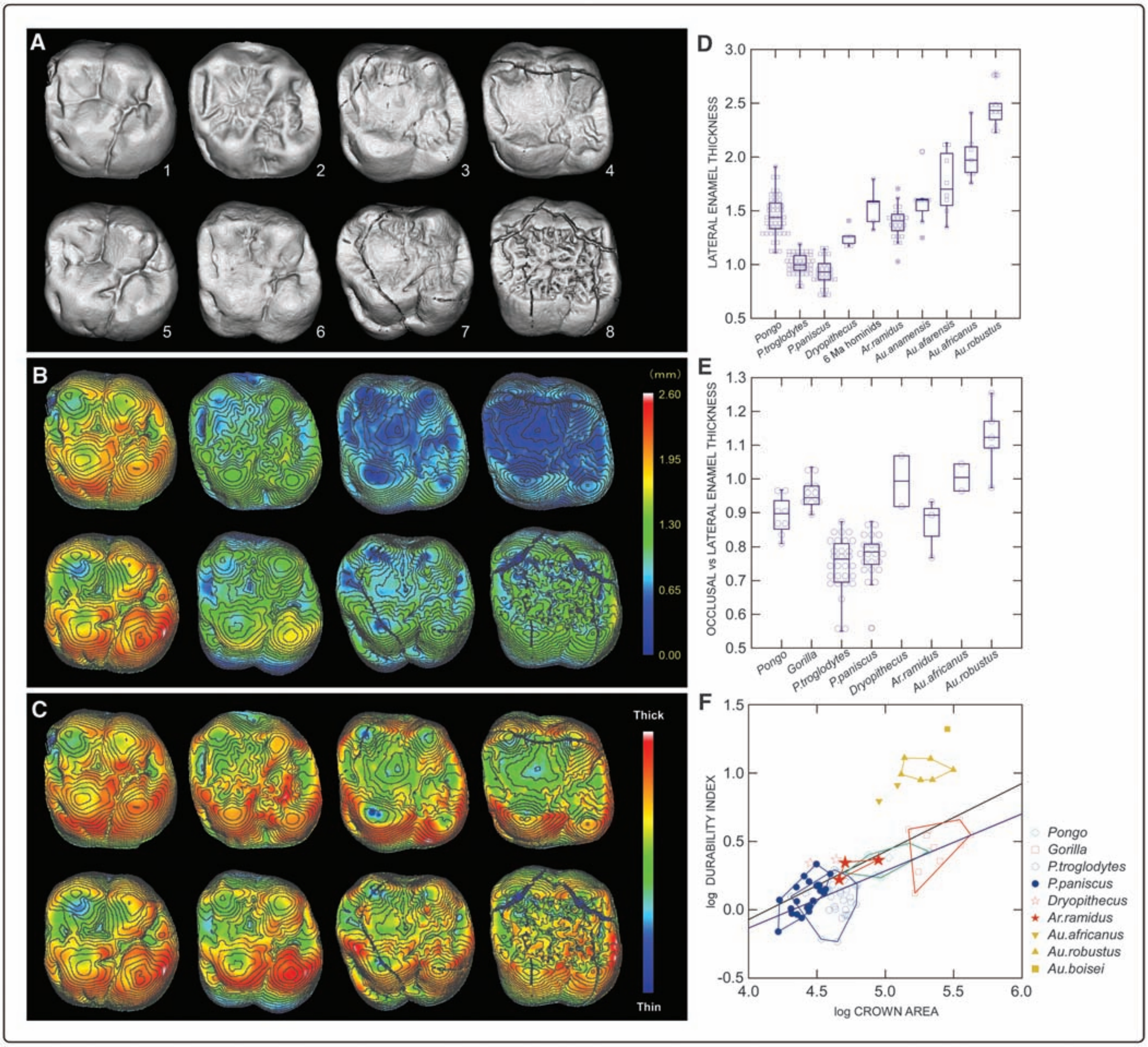

Fig. 4. Enamel thickness and distribution patterns in *Ar. ramidus*. Left panels: micro-CT–based visualizations of maxillary first molars in arbitrary size. (**A**) Outer enamel surface; (**B**) enamel thickness in absolute thickness scale superimposed on topographic contours; (**C**) enamel thickness in relative scale to facilitate comparison of pattern. The molars [labeled in (A)] are as follows: 1 and 5, *Au. africanus Sts 24* (mirrored) and *Sts 57*; 2, *Dryopithecus brancoi*; 6, *Ar. ramidus ARA-VP-1/3288*; 3, *Pan troglodytes*; 4, *Pan paniscus*; 7, *Gorilla gorilla*; 8, *Pongo pygmaeus*. The *Pan* species share a broad occlusal basin and thin occlusal enamel. Both *Ar. ramidus* and *D. brancoi* are thinner-enameled than *Australopithecus* but share with *Australopithecus* a generalized distribution pattern. (**D**) Maximum lateral enamel thickness, showing that *Ar. ramidus* enamel is thicker than those of *Pan* and *D. brancoi* and thinner than that of *Australopithecus* species. Horizontal line is median; box margins are central 50% range. (**E**) Ratio of occlusal (volume/surface area) to lateral (average linear) enamel thicknesses, showing that *Pan* is unique in its distinctly thin occlusal enamel. (**F**) Molar durability (enamel volume per unit occlusal view crown area) plotted against projected occlusal view crown area. An isometric line (slope of 0.5) is fitted through the centroid of the three measured *Ar. ramidus* molars. The least squares regression ($y = 0.418x - 1.806$) of the combined modern ape sample is also shown. This slope does not differ significantly from isometry. *Ar. ramidus* and *D. brancoi* are close to, and *Australopithecus* species considerably above, the regression line, indicating greater enamel volume available for wear in *Australopithecus* molars. See (*2*) for further details.

tough food items (as in *Pongo* or *Australopithecus*). *Ar. ramidus* also lacked adaptations to abrasive feeding environments (unlike *Australopithecus*). These inferences are corroborated by the isotopic analysis of enamel, which indicates that *Ar. ramidus* predominantly consumed (~85 to 90%) C$_3$ plant sources in woodland habitats and small patches of forest (*50*), thus differing from both savanna woodland-dwelling chimpanzees (>90% C$_3$) and *Australopithecus* spp. (>30% C$_4$) (*51*).

Conversely, extant *Pan* and *Gorilla*, each with its distinctive dental morphology, are best considered derived in their dietary and dental adaptations. This is consistent with the *Ar. ramidus* postcranial evidence and its interpretations (*11*, *23*) and strengthens the hypothesis that dental and locomotor specializations evolved independently in each extant great ape genus. This implies that considerable adaptive novelty was necessary to escape extinction in the Late Miocene forest and woodland environments.

These analyses also inform the social behavior of *Ar. ramidus* and its ancestors. The dental evidence leads to the hypothesis that the last common ancestors of African apes and hominids were characterized by relatively low levels of canine, postcanine, and body size dimorphism. These were probably the anatomical correlates of comparatively weak amounts of male-male competition, perhaps associated with male philopatry and a tendency for male-female codominance as seen in *P. paniscus* and ateline species (*52*, *53*).

From this ancestral condition, we hypothesize that the *P. troglodytes* lineage secondarily enhanced its canine weaponry in both sexes, whereas a general size reduction of the dentition and cranium (*25*) occurred in the *P. paniscus* lineage. This suggests that the excessively aggressive intermale and intergroup behavior seen in modern *P. troglodytes* is unique to that lineage and that this derived condition compromises the living chimpanzee as a behavioral model for the ancestral hominid condition. The same may be the case with *Gorilla*, whose social system may be a part of an adaptation involving large body size, a specialized diet, and marked sexual dimorphism.

In the hominid precursors of *Ar. ramidus*, the predominant and cardinal evolutionary innovations of the dentition were reduction of male canine size and minimization of its visual prominence. The *Ar. ramidus* dental evidence suggests that this occurred as a consequence of selection for a less projecting and threatening male upper canine. The fossils now available suggest that male canine reduction was well underway by 6 million years ago and continued into the Pliocene. Further fossils will illuminate the tempo and mode of evolution before 6 million years ago.

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Supporting Online Material

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References

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