CT-based study of internal structure of the anterior pillar in extinct hominins and its implications for the phylogeny of robust *Australopithecus*

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The phylogeny of the early African hominins has long been confounded by contrasting interpretations of midfacial structure. In particular, the anterior pillar, an externally prominent bony column running vertically alongside the nasal aperture, has been identified as a homology of South African species *Australopithecus africanus* and *Australopithecus robustus*. If the anterior pillar is a true synapomorphy of these two species, the evidence for a southern African clade of *Australopithecus* would be strengthened, and support would be given to the phylogenetic hypothesis of an independent origin for eastern and southern African "robust" australopith clades. Analyses of CT data, however, show that the internal structure of the circumnasal region is strikingly different in the two South African australopith species. In *A. africanus* the anterior pillar is a hollow column of cortical bone, whereas in *A. robustus* it is a column of dense trabecular bone. Although *Australopithecus boisei* usually lacks an external pillar, it has internal morphology identical to that seen in *A. robustus*. This result supports the monophyly of the "robust" australopiths and suggests that the external similarities seen in the South African species are the result of parallel evolution.

Facial anatomy has played a prominent role in the elucidation of the systematics and adaptations of the australopiths, the extinct group of hominins that flourished in Africa between *ca*. 4.2 and 1.4 Mya (reviewed in ref. 1; for the purposes of this paper, we treat the genera *Paranthropus* and *Kenyanthropus* as synonymous with *Australopithecus*). Taxonomic variation in the morphology of the midface, including the subnasal plate, nasal aperture margins, and position of the maxillary zygomatic process, as well as the expanded, morphologically derived postcanine dental battery, have supported the inference of dietary specialization in the so-called "robust" species, *Australopithecus boisei* of eastern Africa and *Australopithecus robustus* of southern Africa (2–4). The presence of "anterior pillars," distinctive bony columns bordering the nasal aperture in *A. robustus*, at least one specimen of *A. boisei*, and *Australopithecus africanus*, the oldest and otherwise most symplesiomorphic of the three, was thought by Rak (3) to unite these species in a monophyletic group characterized by progressive specialization of the masticatory system. Rak (3) hypothesized that the anterior pillars structurally buttressed the midface to counter high-magnitude loading of the molarized premolars in these species. Results of a recent finite-element analysis of a model *A. africanus* face have been interpreted as support for Rak's functional hypothesis (5), although this study has been challenged (6).

Implicit in the phylogenetic and functional evaluation of the anterior pillar is that it is compositionally identical among the taxa in which it appears. Here we report the results of a CT-based study of the australopith midface and show that, on the contrary, the internal composition of the anterior pillar varies taxonomically among the australopiths. This finding raises questions about the homology and functional significance of a structure that has been central to debates about early hominin phylogeny and adaptation.

In one of his first surveys of australopith discoveries made after the Taung child, Robert Broom (7) noted the "curious bony ridge [that] runs down from the inner border of the large infraorbital foramen" on the face of the type specimen (TM 1517) of *A. robustus* from Kromdraai (*ca*. 1.5–2.0 Mya). Shortly thereafter, Gregory and Hellman (8) drew attention to the similarity in morphology of the area bordering the nasal aperture in TM 1517 and the *A. africanus* (*ca*. 2.5–3.0 Mya) maxilla TM 1512: "A slightly defined ridge posterior to the elevation of the canine socket extends upward, ending just below the infraorbital; this seems to be homologous with the sharp ridge that bounds the flattened lower nasal plate in the type of *A. robustus*." Broom and Robinson (9) characterized the facial plate lateral to the nasal cavity in *A. africanus* (Sts 5) as a "rounded angle which runs up towards the side of the nostril and divides the premaxillary anterior plane from the lateral part of the maxilla," and on *A. robustus* specimen SK 12 they observed "two slightly raised bony ridges, which pass downwards and slightly outwards to below the level of the infraorbital foramina and then almost straight down over the region of the canine roots. … These ridges form the lateral walls of the nasal opening" (10).

Rak's (3) formal designation of this morphology as the anterior pillar underscored the restricted distribution of the character among the australopiths. As with the extant great apes, *Australopithecus afarensis* (*ca*. 3.7–3.0 Mya) does not display this structure; here, the large maxillary canine root plays the major role in shaping the facial plate alongside the nasal aperture (11). The pillar also is absent from the *Australopithecus aethiopicus* cranium KNM-WT 17000 (*ca*. 2.5 Mya) (12) and the *Australopithecus garhi* type specimen ARA-VP 12/130 (*ca*. 2.5 Mya) (13), which, given the strongly divergent maxillary anatomies of these two specimens, would seem to reinforce the phylogenetically derived status of the pillar's presence in *A. africanus* and *A. robustus*. Although most *A. boisei* crania lack the anterior pillar, Rak (3) asserted that this species actually was situated at the most derived end of the feature's morphocline of expression. The basis for this conclusion was Rak's linking taxonomically congruent morphoclines in anterior pillar expression, maxillary prognathism, and maxillary zygomatic position in a functional complex designed to resist deformation of the variably prognathic snout in the face of high-magnitude occlusal loads imposed on the relatively large, molarized premolars. For *A. boisei*, the extreme anterior position of the zygomatics obviated the need for anterior pillars, because the peripheral face itself served

as the buttress against loading of the extraordinarily large, molarized premolars.

The absence of the pillar in the KNM-WT 17000 cranium of *A. aethiopicus* is important, because this middle Pliocene species usually is interpreted as cladistically basal to the later "robust" australopiths and thus critical to the phylogenetic reconstruction of this group. Different investigators have interpreted the absence of pillars in *A. aethiopicus* and *A. boisei* differently, depending on whether they accept Rak's (3) functional model. For example, Skelton and McHenry (14) considered pillars in these two taxa to be present (but "obscured by infilling") and thus derived a priori, whereas Strait et al. (15) identified them as being absent. The phylogenetic consequences of these kinds of distinctions are not trivial. A "robust" clade comprising *A. aethiopicus*, *A. robustus,* and *A. boisei* (as in refs. 11 and 16) would imply that the development of the anterior pillars in *A. robustus* and *A. africanus* is homoplastic, whereas McCollum's (17) proposal of separate eastern and southern African australopith clades, essentially an argument for a polyphyletic origin of robust australopiths, would concede that anterior pillars in *A. africanus* and *A. robustus* are synapomorphies and that their absence in *A. aethiopicus* and *A. boisei* is symplesiomorphic.

All the research on the australopith circumnasal region has assumed that the anterior pillar conforms to Rak's (3) description of a solid column of bone. Both phylogenetic and functional conclusions about the pillar are susceptible to the finding, as we report here, that the internal structure of the pillar in fact varies among taxa that manifest it topographically on the external aspect of the facial skeleton (Table 1).

Analysis

Australopithecus afarensis. We examined CT scans of A.L. 444–2 (11). The fragmentary nature of other maxillae attributed to this species allowed direct examination of the maxillary sinus walls ("non-CT" in Table 1). Externally, on all these specimens, the lateral margin of the nasal aperture is sharp. Laterally, the external contour of the midface reflects the bulging contour of the canine jugum which, at a level approximating one-third the

Table 1. *Australopithecus* species and specimens examined for this study

Species	Specimen
A. africanus	Sts 5
	Sts 17
	Sts 52
	Sts 71
	Stw 73 (cast)
	Stw 183 (cast)
A. boisei	OH 5
	KNM-ER 406
	KNM-ER 732
A. robustus	SK 11
	SK 12
	SK 13/14
	SK 46
	SK 48
	SK 52
	SK 79
	SK 83
	SKW 11
A. aethiopicus	KNM-WT 17000
A. afarensis	AL 200–1 (non-CT)
	AL 417–1 (non-CT)
	AL 444–2
	AL 922–1 (non-CT)

height of the nasal aperture, forms part of the lateral nasal margin. Internally, the area lateral to the nasal aperture is formed by the hollowed maxillary sinus and the internal contour of the canine root and socket. On A.L. 922–1, damage exposes the canine root, broken just below the tip, immediately above the inferolateral corner of the nasal aperture. *A. afarensis* is the only hominin species examined for this study in which the canine root extends above the inferior nasal margin (clearly visible in CT scans of A.L. 444–2) to influence the form of the external facial contour [although this condition is reported in *A. anamensis* as well (18)]. The canine jugum strongly influences the form of the facial contour in extant apes, and this morphology is likely the ancestral condition for early hominins.

Australopithecus africanus. In many specimens, the anterior pillar is the most prominent topographic feature of the *A. africanus* midface, forming the sides of the "nasoalveolar triangular frame" of Rak (3). The anterior pillar dulls the lateral margin of the nasal aperture for all, or nearly all, of the aperture's height. In horizontal CT sections above the nasal cavity floor the external aspect of the pillar is composed of a thin, curved plate. Internal to the curved plate, the anterior pillar is hollow, rather than solid, forming part of the anterior wall of maxillary sinus cavity. This morphology can be seen clearly in a horizontal section of Sts 5 (Fig. 1) and Sts 71 (Fig. S1). The matrix infilling of the maxillary sinus cavity in Sts 17 makes interpretation more challenging, but this specimen appears to match the pattern of Sts 5 and Sts 71. In all cases the external contour surrounds the internal hollow space, and in no case is the pillar formed by solid cortical or cancellous bone (Figs. 2 and 3 and Fig. S2).

Maxillae Stw 73 and Stw 183 follow this pattern, but in these specimens the alveoli for the canine roots reach further superiorly than in other specimens of *A. africanus* we examined for this study, extending along the subnasal plate to terminate approximately at the level of the inferior nasal margin (see canine roots of Sts 71 in Fig. S3). On other specimens the trabecular bone of the alveolus does not extend superiorly as far as the nasal aperture, whereas on these two specimens maxillary trabecular bone extends slightly above the inferior nasal margin. It therefore appears that the presence of trabecular bone above the level of the nasal cavity floor, protruding into the maxillary sinus, is in *A. africanus* related to the height of the canine root (and so is not similar to the condition found in *A. robustus*; see below).

Australopithecus robustus. In CT images of the anterior margin of the nasal margin in a horizontal plane above the nasal floor, the lateral margin of the nasal aperture can be seen readily in SK 12, SK 13/14, SK 46, SK 48, SK 52, SK 79, SK 83, and SKW 11. As is apparent in Fig. 1, on SK 12 the facial plate of the maxilla immediately lateral to the nasal aperture is composed of a column of trabecular bone, triangular in cross-section, immediately lateral to which is the anterior compartment of the maxillary sinus. Even on specimens where the maxillary sinus is filled with matrix (e.g., SK 48, SK 13/14, and SK 11) this trabecular column is clearly visible. On specimens SK 12, SK 52, and SK 83 matrix does not fill the maxillary sinus, and the CT scan provides more resolution. On all these specimens, the triangle of bone is clear (Figs. S4 and S5).

Superiorly, the triangular column extends to about one-half the height of the nasal aperture in SK 48 and SK 12 (Figs. 2 and 3). In other specimens breakage precludes determining the vertical extent of the triangular column. Externally on SK 48 the anterior pillar terminates midway up the nasal aperture, corresponding to the superior extent of the trabecular column visible in CT scans, but on SK 12 the anterior pillar is visible externally running along the entire vertical extent of the nasal aperture. Thus in *A. robustus* there is not a close relationship between the external topographic manifestation of the anterior pillar and the extent of the internal trabecular column. The column of trabec-
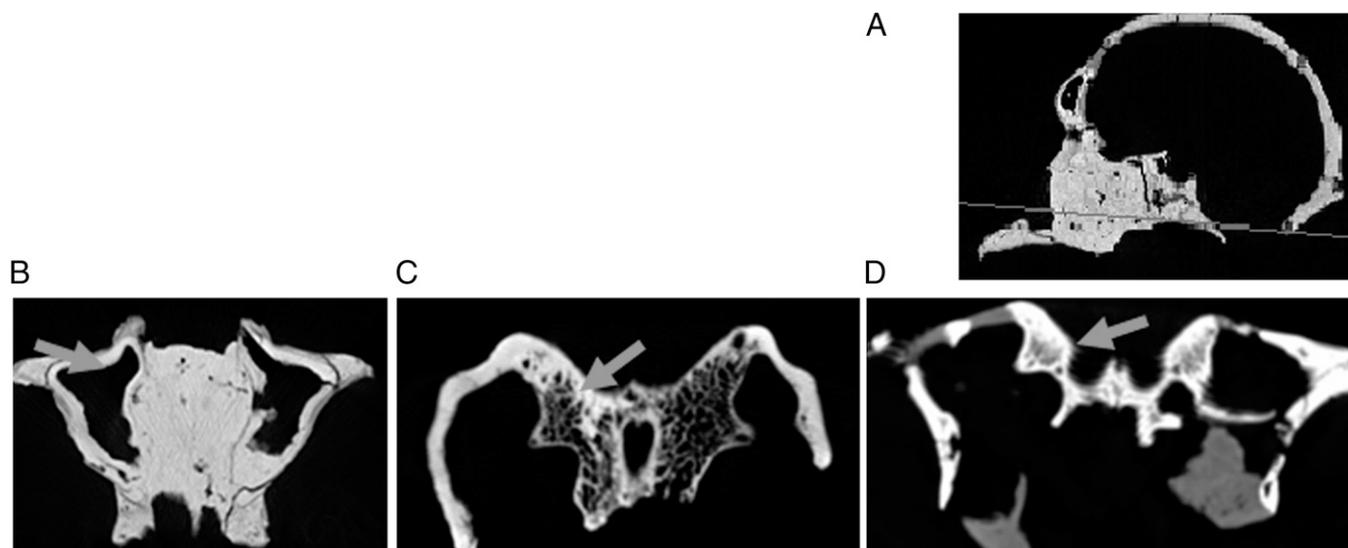
Fig. 1. The horizontal line in *A* indicates the alveolar plane. Sts 5 (*B*), SK 12 (*C*), and OH 5 (*D*) are shown in horizontal section parallel with the alveolar plane, 5 mm above the nasospinale. The hollow anterior pillar is visible on both sides of the nasal margin in Sts 5 (arrow). In SK 12 and OH 5 a cross-section of the column of trabecular bone is visible (arrows). See also Fig. S1.

ular bone forming the interior of the anterior pillar is contiguous with the trabecular bone that makes up the canine alveolus and is visible in a coronal section of SK 12 just posterolateral to the nasal spine (Fig. 3).

Australopithecus boisei. As noted by Rak (3), externally there is no anterior pillar in *A. boisei* (with the exception of KNM-ER 732). On OH 5, there is no exterior column of bone along the nasal margin topographically distinguishable from the infraorbital plate immediately lateral to it. However, as observed in the horizontal CT section above the nasal cavity floor (Fig. 1) of OH 5, the lateral margin of the nasal aperture is formed by a thickened column of cortical and trabecular bone that is very similar in form and location to that seen in *A. robustus*. As in SK 12, the column extends superiorly approximately half the height of the nasal aperture, as seen in sagittal and coronal sections (Figs. 2 and 3).
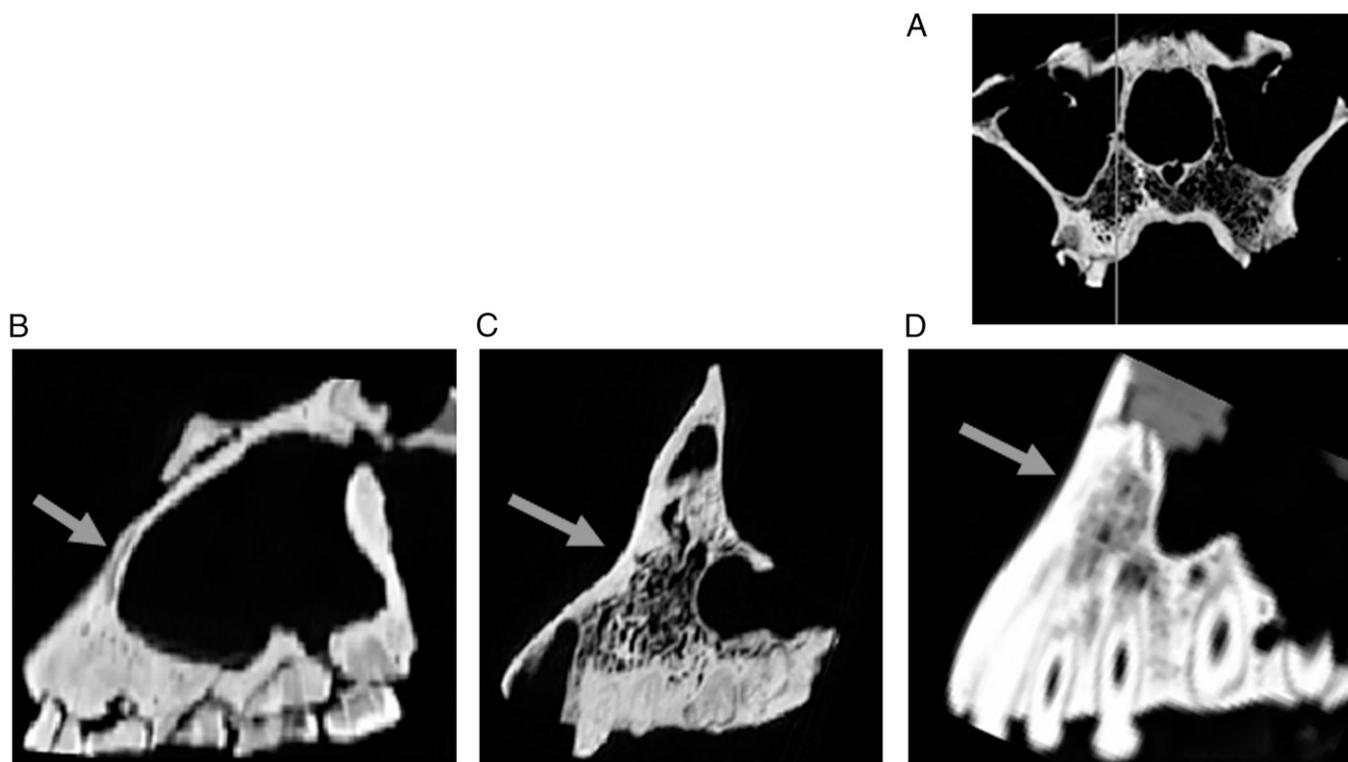

Fig. 2. The vertical line in *A* shows the plane of the coronal section posterior to the nasospinale. Note the lack of trabeculae at inferior corner of nasal aperture in Sts 71 (*B*) and the trabecular column in SK 12 (*C*) and OH 5 (*D*). See Fig. S2 for Sts 5 and Fig. S5 for SK 52.
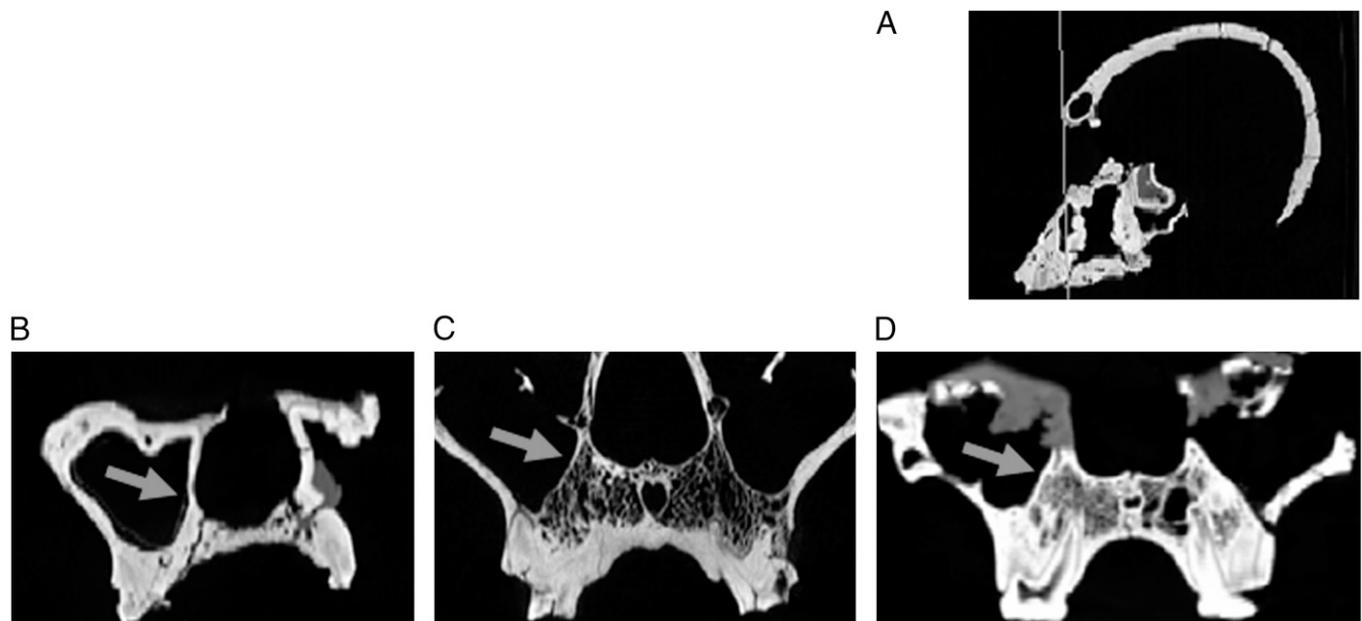
Fig. 3. The vertical line in *A* shows the plane of the coronal section posterior to the nasospinale in Sts 71 (*B*), SK 12 (*C*), and OH 5 (*D*). Note lack of trabeculae at inferior corner of nasal aperture in Sts 71 (arrow) and the trabecular column in SK 12 and OH 5 (arrows). See Fig. S2 for Sts 5 and Fig. S5 for SK 52.

Specimens KNM-ER 406 and KNM-ER 732 are not as well preserved as OH 5, and infilling matrix is not as distinct from the fossilized bone in CT scans. In KNM-ER 406 the facial surface below the orbits is eroded, so we cannot make any interpretation of the external morphology, and in coronal CT sections the distribution of trabecular bone cannot be identified in the eroded region. However, in a horizontal section slightly below the level of the nasal cavity floor, it is possible to identify the base of the trabecular column (Fig. 4), which separates the maxillary sinus cavity into anterior and posterior chambers in OH 5 and KNM-ER 406, exactly as in *A. robustus*. Preservation around the nasal aperture in KNM-ER 732 is poor also. However, the same pattern seen in the maxillary sinus cavity of KNM-ER 406 is visible in CT scans of the internal structure of the maxillary sinus of KNM-ER 732, with trabecular bone separating the maxillary sinus into two chambers. Because this trabecular formation is

clearly the base of the trabecular column bordering the nasal aperture in OH 5 (and in *A. robustus*), we infer that KNM-ER 406 and KNM-ER 732 possessed the same internal bony column.

Australopithecus aethiopicus. The KNM-WT 17000 cranium suffers damage to the face, including breakage at the left margin of the nasal aperture (12); however, it is possible to determine the morphology in this region both by studying the CT scans and examining the interior directly through breaks in the bone of the midface. Although much of the maxillary sinus cavity remains filled with matrix, the CT scan clearly discriminates between the fossilized bone and the matrix, so determining the internal morphology is straightforward. There is no external manifestation of an anterior pillar on the face of KNM-WT 17000 (12, 19), and it lacks the broadly rounded lateral margins found low on the nasal aperture of *A. boisei*. Superiorly, the nasal margin is sharp, whereas inferiorly, for about the lower third, it is more rounded. Examining the interior via CT scans shows the region bordering the nasal aperture is formed by the maxillary sinus antrum. There is no internal column of trabecular bone as seen in *A. robustus* and *A. boisei*, and there is no separate hollow column as in *A. africanus* (Fig. S6). This anatomy appears to be most similar to that of *A. afarensis*, except that the canines are reduced, and the canine roots have less influence on the external and internal morphology.

Discussion

Rak's (3) recognition of the anterior pillar in South African *Australopithecus* focused attention on the phylogenetic and functional significance of the australopith midface. The anterior pillar was incorporated into the body of evidence supporting a phylogenetic hypothesis that linked *A. africanus* exclusively to the "robust" australopith clade, with *A. afarensis* as the generalized mid-Pliocene ancestor to both the "robust" and *Homo* clades (20), and bolstered the explanatory scheme that linked these species, via postcanine megadontia, premolar molarization, and derived facial morphology, to an adaptation for specialized feeding (21–23). In this scheme, the "absence" of pillars in *A. boisei* actually was interpreted as a "presence," although subsequent demonstration of their absence in the more symplesiomorphic cranium of *A. aethiopicus* created ambiguity regarding
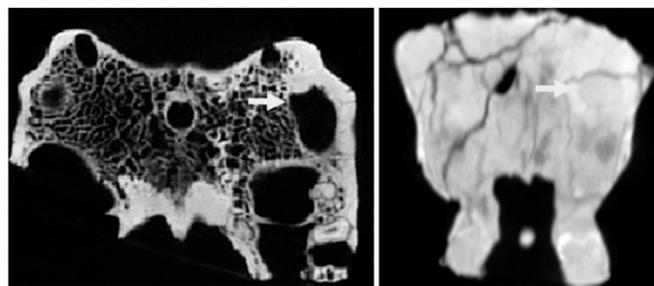

Fig. 4. Base of trabecular column in (*Left*) *A. robustus* (SK 12a) and (*Right*) *A. boisei* (KNM-ER 406) (not to scale). Although KNM-ER 406 is infilled by matrix, a circular sinus cavity (marked by arrow) is visible on right of the specimen and also is visible in SK 12. Similar morphology is present on OH 5 and KNM-ER 732. This sinus is formed at the base of the trabecular column bordering the nasal aperture in *A. robustus* and OH 5 and suggests that the trabecular column is present in all specimens of *A. boisei*, even though damage to Koobi Fora specimens makes identification of the column impossible above the nasal floor. Section is horizontal at the level of the nasospinale (5 mm below plane shown in Fig. 1). The sinus also is visible a few millimeters higher on the left side of SK 12.
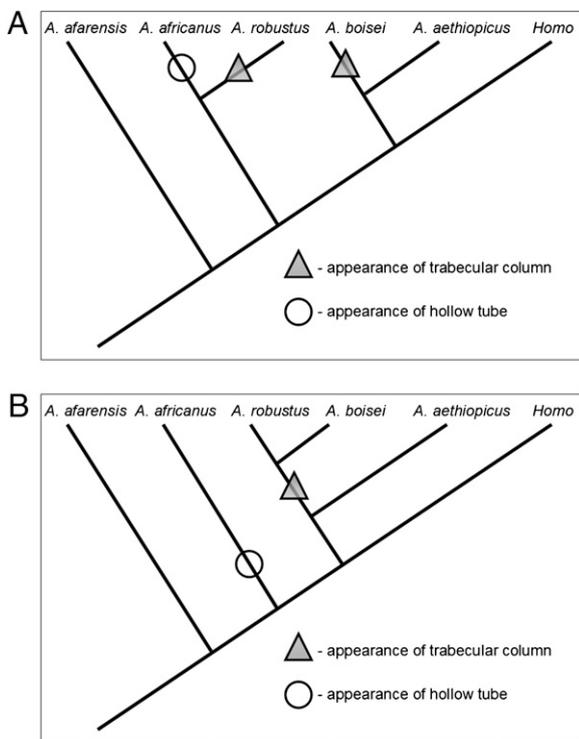
Fig. 5. Two models for the evolution of the anterior pillar. *A* shows distinct East African and South African clades; however, this model requires convergences for the trabecular column in *A. boiei* and *A. robustus*. *B* shows a phylogenetic model that is consistent with recent phylogenetic analyses (11, 16), and does not require any homoplasy.

the state of the structure in the east African "robust" australopiths (14, 19). Our examination of the internal structure of the anterior pillar clarifies the role of this feature in phylogenetic research on early hominins.

A pattern of internal circumnasal structure is shared uniquely by *A. robustus* and *A. boisei*. In crania of both species the facial plate lateral to the nasal aperture is composed of dense trabecular bone. However, this underlying structural similarity belies differences in external morphology, because the largest *A. boisei* specimens (OH 5 and KNM-ER 406) lack a distinct pillar, whereas *A. robustus* invariably has it. Rak's (3) observation of a rudimentary external pillar in the female *A. boisei* cranium KNM-ER 732 now attains greater significance as a sign of common descent: The "layer" of internal structural similarity in the faces of these species is consistent with their derivation from a taxon with the same internal morphology (*contra* ref. 17). *A. aethiopicus* is symplesiomorphic in the internal structure of the region surrounding the nasal aperture and in this respect is more similar to *A. afarensis* than to *A. robustus* and *A. boisei*. Our CT-based findings support the monophyly of the two late "robust" australopiths, *A. robustus* and *A. boisei*, and highlight the morphological gap, noted by others (12, 14, 19), between the craniofacial anatomy of *A. aethiopicus* and that expected of the last common ancestor of *A. robustus* and *A. boisei*.

Unexpectedly, the internal morphology of the anterior pillar in *A. africanus,* the species that initially drew Rak's (3) attention to this feature, is singular among the australopiths. Despite the relative prominence of the external pillar in many crania of this species, and in contrast to Rak's (3) description of it as a solid column of bone, CT reveals it to be a hollow tube, at least in the specimens examined in this study, notably including Sts 5, which has the most prominent external pillars of any *A. africanus* specimen. This finding suggests that the anterior pillars of *A. africanus*

and the anterior pillars of *A. robustus* are not homologous, as was implied already by phylogenetic hypotheses that position a species with the facial structure of *A. aethiopicus* as the sister taxon to *A. robustus* and *A. boisei* (e.g., 11, 16, 19) (Fig. 5).

Rak's (3) functional hypothesis assumed that anterior pillars comprise solid bone. Our finding that uniquely in *A. africanus*—the species in which they are best developed externally—the pillars are hollow tubes rather than solid columns means that disparate functional causes could underlie the development of the structurally nonhomologous pillars among the australopith species. Our results do not address directly the functional basis of the anterior pillars, but recent debate about the functional interpretation of finite element analysis of the model *A. africanus* midface (5, 6) will need to incorporate questions of homology raised by the discovery of diversity in the internal composition of the anterior pillar.

Conclusion

Patterns of similarity in midfacial morphology among extinct Plio-Pleistocene hominins have drawn paleoanthropologists' attention since the 1930s. Rak's (3) identification of the anterior pillar in mid-Pliocene *A. africanus* constituted evidence of an exclusive phylogenetic relationship between this species and the late hypermegadont "robust" australopiths. His functional hypothesis, linking the pillars to high-magnitude biting on the premolars, attempted to account for the persistence of this structure in *A. robustus* and its near-disappearance in *A. boisei*, species with much more derived masticatory configurations than *A. africanus*. Rak's interpretation and most subsequent analyses of the distribution (14–16, 24–26) and function (5, 6, 27) of the anterior pillar have assumed that the structure is composed of solid bone. Here we have shown that this assumption is false. Our CT-based study demonstrates that the pillar in *A. africanus* is hollow, whereas in *A. robustus* it comprises dense trabecular bone; in *A. boisei* the comparable midfacial zone also is composed of trabecular bone, even though usually there is no discernible trace of the anterior pillar externally. The primitive hominin condition is exemplified by *A. afarensis*, in which the presence of the long maxillary canine root adjacent to the nasal aperture shapes the midface, as in extant great apes.

Our results indicate that the anterior pillar, a frequently cited synapomorphy of the midface in *A. africanus* and *A. robustus,* actually may be a homoplasy, which cedes support to hypotheses of a monophyletic rather than a polyphyletic origin of the geologically late "robust" australopith species (Fig. 5). The anterior pillar in *A. africanus* is likely an autapomorphy, highlighting the ambiguous phylogenetic position of this taxon, as noted by others (11, 14–16). These findings also may complicate biomechanical interpretations, because they raise suspicions that different functional causes correspond to the different patterns of internal bone distribution beneath the anterior pillar.

Materials and Methods

We examined the fossil specimens using direct observation and/or examination of CT data to examine the internal morphology of the nasal margin, maxillary sinus, and maxilla (Table 1). CT data were collected from a variety of sources and include all available CT scans of relevant specimens from the species analyzed. For specimens SK 11, SK 12, SK 46, SK 79, SK 83, and SKW11, scans (0.33-mm slices; voxel size 0.3222) were made by Chris Williams at Moot Algemen Hospital, Pretoria, Republic of South Africa, on a Phillips Brilliance 40 CT scanner. Specimens SK 13/14, SK 48, SK 52, Sts 17, and Sts 52 were scanned by Stephany Potze of the Transvaal Museum at Little Company of Mary Hospital in Pretoria on a Siemens Sensation 16 CT scanner (0.75-mm slices; voxel sizes ranging from 0.2929–0.3476). Other scans (Sts 5, Sts 71, OH 5, KNM-ER 406, KNM-ER 732, KNM-WT 17000, and A.L. 444–2) are from the digital archives at the University of Vienna and the National Museums of Kenya. We used ImageJ 1.42 (National Institutes of Health) and Amira 4.1.2 (Mercury Computer Systems) to examine the CT data.

The small sample sizes of well-preserved taxa that have been CT scanned limit the potential resolution of statistical analyses. To capture the internal

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