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Comparative biomechanics of Australopithecus sediba mandibles

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ABSTRACT

Fossils attributed to Australopithecus sediba are described as having phylogenetic affinities with early Homo to the exclusion of other South African australopiths. With respect to functional anatomy of mastication, one implication of this hypothesis is that A. sediba mandibles should exhibit absolutely and relatively reduced stiffness and strength in comparison to Australopithecus africanus and Paranthropus robustus jaws. Examination of cortical bone distribution in the MH 1 and MH 2 mandibles of A. sediba (evaluated against samples of Pan, early and modern Homo as well as A. africanus and P. robustus) indicate that the A. sediba mandibular corpus was geometrically similar to other South African australopiths. In particular, enhanced torsional rigidity is characteristic of all South African australopiths including A. sediba. These findings are consistent with a hypothesis that masticatory mechanics may have been similar to other australopiths (and distinct from exemplars of early Homo), and as such suggest that A. sediba's mandibles were functionally suited to consume hard and tough objects. Recent mechanical modeling of the A. sediba cranium, however, has been interpreted as indicating that this species was relatively poorly adapted to produce large bite forces and likely experienced relatively modest strains in its facial skeleton. This paradox – that the cranium signals a departure from the australopith morphotype whereas the mandibles conform to a hypodigm of australopith grade – can be resolved, in part, if it is acknowledged that mechanical performance variables offer imperfect insight into what constitutes feeding adaptations.

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The authors of the announcement of *Australopithecus sediba* (Berger et al., 2010) expressed the view that the Malapa hominins represented a late species of australopith that shared morphologically derived traits with early *Homo*. Since this time, additional comparative studies of mandibles (de Ruiter et al., 2013) and teeth (Irish et al., 2013) have supported this interpretation. Irrespective of the phylogenetic position of *A. sediba* and its role in the emergence of *Homo* (cf. Spoor, 2011; Berger, 2012; Kimbel, 2013; Dembo et al., 2015; Hawks et al., 2015; Villmoare et al., 2015a,b), understanding functional morphology of the *A. sediba* skull will presumably provide insight into the trophic adaptations of this hominin species, which themselves may facilitate interpretation of other aspects of ecology including habitat choice, geographic range, life history profile and even social behavior and locomotion (Walker, 2007).

Isotopic, phytolith and dental microwear data (Henry et al., 2012) have been collected for the Malapa hominins in order to infer diet in *A. sediba*. The isotopic data indicate reliance on C₃ resources to a degree unseen in other hominins, with values reminiscent of those in savannah, but not forest-dwelling, chimpanzees. Identifiable phytoliths harvested from the dentition of MH 1 are attributed to bark, sedge, grass, leaf, fruit and palm (in descending order of abundance). Microwear texture analysis of tooth surfaces places *A. sediba* within the range of wear fabrics of other early hominins, but with relatively high complexity values that have been associated with hard-object feeding in living primates (Scott et al., 2005). These three lines of evidence have been taken to







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indicate that *A. sediba* had an eclectic diet, which likely included tough (given recovery of bark phytoliths) and hard (given microwear complexity) foods.

Henry et al.'s (2012) dietary inferences are drawn independently from consideration of skull anatomy in *A. sediba* and thus speak more directly to the question of dietary preferences rather than dietary adaptations that might be inferred from analysis of the form of the dentition and craniofacial skeleton. Ledogar et al.'s (2016) analysis of the MH 1 cranium suggested that masticatory stresses were reduced relative to *Australopithecus africanus* (Sts 5 in particular), and MH 1 is argued to have experienced architectural constraints that limited the production of large bite forces; specifically, MH 1 could have produced bite forces on par with Sts 5, but only at a cost of incurring distractive forces at the working-side temporomandibular joint TMJ. In any case, a relatively low level of masticatory strain in the MH 1 facial skeleton is inferred.

Analysis of structural and geometric properties of the mandibular corpus provides direct insight into biomechanical competence in mastication (Hylander, 1979, 1988), and may inform inferences into feeding adaptations within certain limits (Daegling and Grine, 2007; Ross et al., 2012). Under the premise that A. sediba is derived toward an early Homo morphotype, but is itself derived from australopith precursors (Berger et al., 2010; de Ruiter et al., 2013; Irish et al., 2013), three hypotheses can be articulated that address the question of whether the A. sediba mandibles (MH 1 and MH 2) are functionally and mechanically intermediate between those of South African australopiths on the one hand and early and modern Homo on the other. First, MH 1 and MH 2 mandibles should be derived relative to primitive hominids (here represented by a sample of Pan troglodytes) in the same manner as A. africanus and Paranthropus robustus. Second, measures of mechanical stiffness and strength in MH 1 and MH 2 should be reduced relative to the other South African australopiths while approaching those observed in early Homo (here represented by SK 15 and SK 45) and, to a lesser extent, modern humans. Finally, corpus geometry has long been recognized as a distinguishing feature of the australopith radiation (Wolpoff, 1977; Chamberlain and Wood, 1985; Wood and Aiello, 1998), and the underlying cortical bone distribution indicative of enhanced torsional strength is one hallmark of australopith mandibular functional morphology (Daegling and Grine, 1991). A third hypothesis, then, is that MH 1 and MH 2 are expected to fall intermediate between australopiths and Homo in terms of torsional strength if they are functionally and mechanically derived toward the human condition.

1. Materials and methods

Structural mechanical properties were estimated from cortical bone contours obtained from computed tomography (CT) scans of modern *Homo sapiens* (n = 20: 10m, 10f), *P. troglodytes* (n = 20: 10m, 10f), two South African representatives of early *Homo* (SK15 and SK 45 [see Grine, 2005, for justification of the incertae sedis specific status of these fossils]), and specimens of *A. africanus* and *P. robustus*. The modern human sample was drawn from the anatomical sciences collection at Stony Brook University (10 individuals, no identifying information) and the Pueblo San Cristobal archaeological collection (10 individuals) at the American Museum of Natural History (AMNH). The chimpanzee sample was drawn equally from collections at the Museum of Comparative Zoology (*Pan troglodytes verus*) and the AMNH (subspecies indeterminate owing to missing provenience data).

Coronal cross-sections taken at the mesiodistal midpoint of M_3 , M_1 and P_4 as well as a midsagittal section (i.e., at the mandibular symphysis) were examined. Specimens were oriented so that minimum sections were sampled (Fig. 1). The choice of sections

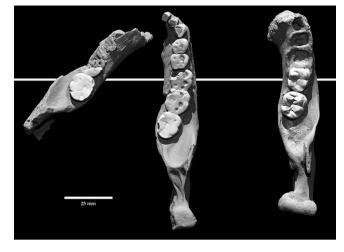


Figure 1. Occlusal view of the MH 1 (right) and MH 2 (left) mandible renderings. Plane of section through the M_1 is indicated by the solid white line running behind the mandibular corpora. At the M_1 and other sampled sections (M_3 , P_4 and midsagittal, sections not shown), specimens were oriented in order to sample minimum areas.

was motivated by preservational status of MH 1 and MH 2. At the three selected postcanine sections, both Malapa individuals could be sampled. The midsagittal section is preserved in only MH 1. Inclusion of comparative australopith and early *Homo* fossils was also constrained by preservational status (specimens included are provided in Table 1). Measurements of mandibular length (supraangular incisure to infradentale) are only available for Sts 36, Sts 52, SK 12, SK 23, SK 34 and SKW 5.

Cortical geometry for MH 1 was imaged via synchrotron X-ray tomography on ID19 at the European Synchrotron Radiation Facility (ESRF). For the MH 1 mandible scans performed at the ESRF, a polychromatic beam with a propagation distance of 900 mm was used. A wiggler source set was used with a gap of 73 mm, filtered with aluminum (3 mm) and copper (1 mm), and coupled with a

Table 1			
Comparative	fossil	hominin	sample. ^a

Section	Included specimens			
	Australopithecus africanus	Paranthropus robustus	Early Homo	
M ₃	MLD 18	SK 12 ^b	SK 45	
	MLD 40	SK 23 ^b		
		SK 34 ^b		
		SKW 5 ^b		
		TM 1517		
M ₁	MLD 18	SK 6	SK 15 ^b	
	MLD 34	SK 12 ^b		
	MLD 40	SK 23 ^b		
	Sts 36 ^b	SK 34 ^b		
	Stw 404	SKW 5 ^b		
		SKX 4446		
		SKX 5013		
		TM 1517		
P ₄	MLD 40	SK 12 ^b	SK 15 ^b	
	Sts 36 ^b	SK 23 ^b		
	Sts 52 ^b	SKX 4446		
	Stw 404	TM 1517		
Midsagittal	Sts 36 ^b	SK 23 ^b	None	
	Sts 52 ^b	SKW 5 ^b		

^a Only MH 1 was analyzed in midsagittal (symphyseal) section. Cross-sectional properties are based on minimum planes of section taken through the midpoint of the buccal margins of M₃, M₁ and P₄. Samples of modern *Homo sapiens* and *Pan troglodytes* (n = 20 each) were also included for comparison to the Malapa hominins. ^b Denotes specimens that include mandibular length measurements for analyses.

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