Australopithecus sediba: A New Species of *Homo*-Like Australopith from South Africa

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Despite a rich African Plio-Pleistocene hominin fossil record, the ancestry of *Homo* and its relation to earlier australopithecines remain unresolved. Here we report on two partial skeletons with an age of 1.95 to 1.78 million years. The fossils were encased in cave deposits at the Malapa site in South Africa. The skeletons were found close together and are directly associated with craniodental remains. Together they represent a new species of *Australopithecus* that is probably descended from *Australopithecus africanus*. Combined craniodental and postcranial evidence demonstrates that this new species shares more derived features with early *Homo* than any other australopith species and thus might help reveal the ancestor of that genus.

The origin of the genus *Homo* is widely debated, with several candidate ancestors being proposed in the genus Australopithecus (1-3) or perhaps Kenyanthropus (4). The earliest occurrence of fossils attributed to Homo (H. aff. H. habilis) at 2.33 million years ago (Ma) in Ethiopia (5) makes it temporally antecedent to all other known species of the genus Homo. Within early Homo, the hypodigms and phylogenetic relationships between H. habilis and another early species, H. rudolfensis, remain unresolved (6-8), and the placement of these species within *Homo* has been challenged (9). H. habilis is generally thought to be the ancestor of H. erectus (10-13), although this might be questioned on the basis of the considerable temporal overlap that existed between them (14). The identity of the direct ancestor of the genus Homo, and thus its link to earlier Australopithecus, remains controversial. Here we describe two recently discovered, directly associated, partially articulated Australopithecus skeletons from the Malapa site in South Africa, which allow us to investigate several competing hypotheses regarding the ancestry of Homo. These skeletons cannot be accommodated within any existing fossil taxon; thus, we establish a new species, Australopithecus sediba, on the basis of a com-

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bination of primitive and derived characters of the cranium and postcranium.

The following is a description of *Au. sediba*: Order Primates Linnaeus 1758; suborder Anthropoidea Mivart 1864; superfamily Hominoidea Gray 1825; family Hominidae Gray 1825; genus *Australopithecus* DART 1925; species *Australopithecus sediba* sp. nov. **Etymology**. The word *sediba* means "fountain" or "wellspring" in the seSotho language.

Holotype and paratype. Malapa Hominin 1 (MH1) is a juvenile individual represented by a partial cranium, fragmented mandible, and partial postcranial skeleton that we designate as the species holotype [Figs. 1 and 2, supporting online material (SOM) text S1, figs. S1 and S2, and table S1]. The first hominin specimen recovered from Malapa was the right clavicle of MH1 (UW88-1), discovered by Matthew Berger on 15 August 2008. MH2 is an adult individual represented by isolated maxillary teeth, a partial mandible, and partial postcranial skeleton that we designate as the species paratype. Although MH1 is a juvenile, the second molars are already erupted and in occlusion. Using either a human or an ape model, this indicates that MH1 had probably attained at least 95% of adult brain size (15). Although additional growth would have occurred in the skull and skeleton of this individual, we judge that it would not have appreciably altered the morphology on which this diagnosis is based.

Locality. The two *Au. sediba* type skeletons were recovered from the Malapa site (meaning "homestead" in seSotho), situated roughly 15 km NNE of the well-known sites of Sterkfontein, Swartkrans, and Kromdraai in Gauteng Province, South Africa. Detailed information regarding geology and dating of the site is in (*16*).



Fig. 1. Craniodental elements of *Au. sediba.* UW88-50 (MH1) juvenile cranium in (**A**) superior, (**B**) frontal, and (**C**) left lateral views. (**D**) UW88-8 (MH1) juvenile mandible in right lateral view, (**E**) UW88-54 (MH2) adult mandible in right lateral view, (**F**) UW88-8 mandible in occlusal view, (**G**) UW 88-54 mandible in occlusal view, and (**H**) UW 88-50 right maxilla in occlusal view (scale bars are in centimeters).

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Diagnosis. Au. sediba can be distinguished from other species of Australopithecus by a combination of characters presented in Table 1; comparative cranial measures are presented in Table 2. A number of derived characters separate Au. sediba from the older chronospecies Au. anamensis and Au. afarensis. Au. sediba exhibits neither the extreme megadontia, extensive cranial cresting, nor facial prognathism of Au. garhi. The suite of derived features characterizing Au. aethiopicus, Au. boisei, and Au. robustus, in particular the pronounced cranial muscle markings, derived facial morphology, mandibular corpus robusticity, and postcanine megadontia, are absent in Au. sediba. The closest morphological comparison for Au. sediba is Au. africanus, as these taxa share numerous similarities in the cranial vault, facial skeleton, mandible, and teeth (Table 1). Nevertheless, Au. sediba can be readily differentiated from Au. africanus on both craniodental and postcranial evidence. Among the more notable differences, we observe that although the cranium is small, the vault is relatively transversely expanded with vertically oriented parietal walls and widely spaced temporal lines; the face lacks the pronounced, flaring zygomatics of Au. africanus; the arrangement of the supraorbital torus, nasoalveolar region, infraorbital region, and zygomatics result in a derived facial mask; the mandibular symphysis is vertically oriented with a slight bony chin and a weak post-incisive planum; and the teeth are differentiated by the weakly defined buccal grooves of the maxillary premolars, the weakly developed median lingual ridge of the mandibular canine, and the small absolute size of the postcanine dentition. These exact differences also align Au. sediba with the genus Homo (see SOM text S2 for hypodigms used in this study). However, we consider Au. sediba to be more appropriately positioned within Australopithecus, based on the following craniodental features: small cranial capacity, pronounced glabelar region, patent premaxillary suture, moderate canine jugum with canine fossa, small anterior nasal spine, steeply inclined zygomaticoalveolar crest, high masseter origin, moderate development of the mesial marginal ridge of the maxillary central incisor, and relatively closely spaced premolar and molar cusps.

Postcranially, Au. sediba is similar to other australopiths in its small body size, its relatively



Fig. 2. Associated skeletal elements of MH1 (**left**) and MH2 (**right**), in approximate anatomical position, superimposed over an illustration of an idealized *Au. africanus* skeleton (with some adjustment for differences in body proportions). The proximal right tibia of MH1 has been reconstructed from a natural cast of the proximal metaphysis.

long upper limbs with large joint surfaces, and the retention of apparently primitive characteristics in the upper and lower limbs (table S2). Au. sediba differs from other australopiths, but shares with Homo a number of derived features of the os coxa, including increased buttressing of the ilium and expansion of its posterior portion, relative reduction in the distance between the sacroiliac and hip joints, and reduction of distance from the acetabulum to the ischial tuberosity. These synapomorphies with Homo anticipate the reorganization of the pelvis and lower limb in H. erectus and possibly the emergence of more energetically efficient walking and running in that taxon (17). As with the associated cranial remains, the postcranium of Au. sediba is defined not by the presence of autapomorphic features but by a unique combination of primitive and derived traits.

Cranium. The cranium is fragmented and slightly distorted. The minimum cranial capacity of MH1 is estimated at 420 cm³ (SOM text S4). The vault is ovoid, with transversely expanded, vertically oriented parietal walls. The widely spaced temporal lines do not approach the midline. Postorbital constriction is slight. The weakly arched supraorbital torus is moderately developed and laterally extended, with sharply angled lateral corners and a weakly defined supratoral sulcus. A robust glabelar region is evident, with only a faint depression of the supraorbital torus at the midline. The frontal process of the zygomatic faces primarily laterally and is expanded medially but not laterally. The zygomatic prominence does not show anterolateral expansion. The zygomatics are weakly flared laterally, resulting in an uninterrupted frontal profile of the facial mask that is squared superiorly and tapered inferiorly. The zygomaticoalveolar crests are long, straight, and steeply inclined, resulting in a high masseter origin. The root of the zygomatic begins at the anterior margin of M¹. The nasal bones are widened superiorly, become narrowest about one-third of the way down, and flare to their widest extent at their inferior margin. The nasal bones are elevated as a prominent ridge at the internasal suture, with an increasingly anterior projection inferiorly. The bone surface of the maxilla retreats gently away from the nasal aperture laterally, resulting in an everted margin of the superolateral portion of the aperture relative to the infraorbital region. The inferolateral portion of the nasal aperture becomes bluntly rounded. The infraorbital region is slightly convex (18) and is oriented at an approximately right angle to the alveolar plane. There is a trace of a premaxillary suture near the superolateral margin of the nasal aperture. Prominent canine juga delineate moderately developed canine fossae. Anterior pillars are absent. The inferior margin of the nasal aperture is marked by a stepped nasal sill and a small but distinct anterior nasal spine. The subnasal region is straight in the coronal plane and only weakly projecting relative

Table 1. List of characters used to diagnose *Au. sediba*. These characters are commonly used in hominin phylogenetic studies (11, 38–40) or have been recorded as diagnostic for various hominin taxa in the past (3, 10, 36). Recognizing the potential pitfalls of performing a cladistic analysis on possibly interdependent characters of uncertain valence, we produced a cladogram from the data in this table as a test of the phylogenetic position of *Au. sediba* (fig. 53). Our most parsimonious cladogram places *Au. sediba* at the stem of the *Homo* clade.

Numbers in parentheses in the first column refer to measures presented in Table 2; descriptions of these character states are provided in SOM text S3. Abbreviations are as follows: A-M, anteromedial; costa supr., costa supraorbitalis; intermed., intermediate; lat., lateral; med., medial; mesognath., mesognathic; mod., moderately; MMR, mesial marginal ridge; orthogn., orthognathic; procumb., procumbent; proj., projecting; TMJ, temperomandibular joint.

S3). Our most parsimonious clad	ogram places Au	<i>u. sediba</i> at the	stem of the H	omo clade.	dibular joint.					
Characters	Au. afarensis	Au. garhi	Au. africanus	Au. sediba	H. habilis	H. rudolfensis	H. erectus	Au. aethiopicus	Au. boisei	Au. robustus
Vault										
Cranial capacity (1)	Small	Small	Small	Small	Intermed.	Large	Large	Small	Small	Small
A-M incursion of	Strong	Moderate	Moderate	Weak	Weak	Weak	Weak	Strong	Strong	Strong
temporal lines on frontal bone (9)										
Position of temporal lines	Crest	Crest	Variable	Wide	Variable	Wide	Wide	Crest	Crest	Crest
on parietal bones										
Compound temporal	Extensive	ż	Absent	Absent	Variable	Absent	Absent	Extensive	Variable	Absent
nuchal crest (males)										
Postorbital constriction (5)	Marked	Moderate	Moderate	Slight	Moderate	Moderate	Slight	Marked	Marked	Marked
Pneumatization of	Extensive	ż	Extensive	Reduced	Reduced	Reduced	Reduced	Extensive	Variable	Reduced
temporal squama										
Facial hafting	Low	Low	Low	Low	Low	Low	Low	High	High	High
Frontal trigon	Present	Present	Absent	Absent	Absent	Absent	Absent	Present	Present	Present
Supraglenoid gutter width	Narrow	ż	Narrow	Narrow	Narrow	Narrow	Narrow	Wide	Wide	Wide
Horizontal distance	Long	ż	Long	Short	Short	Long	Short	Long	Long	Long
between TMJ and										
M2/M3 (6)										
Parietal transverse	Absent	Absent	Absent	Present	Present	Present	Present	Absent	Absent	Absent
expansion/tuber										
Facial skeleton										
Supraorbital expression	Costa supr.	Costa supr.	Intermed.	Torus	Torus	Intermed.	Torus	Costa supr.	Costa supr.	Costa supr.
Supraorbital contour	Less arched	Less arched	Variable	Arched	Arched	Arched	Arched	Less arched	Variable	Arched
Glabellar region forms as	No	No	Variable	Yes	No	Variable	No	No	Yes	Yes
prominent block										
Lat. half of infraorbital	No	ż	No	No	No	No	No	Yes	No	Yes
margin blunt										
and protruding										
Zygomatic arch relative to	Above	ż	Level	Level	Level	ż	Level	Above	Above	Above
interior orbital margin										
Convexity/concavity of infrantized region	ć	د:	Convex	Convex	Concave	Concave	Convex	Concave	Concave	Concave
		ſ					-	ŀ		
Nasal bone projection above frontomaxillary	Ехрапдед	~ .	Variable	NO	NO	NO	NO	lapered	Expanded	Expanded
suture										
Inferior width of	Wide	ż	Variable	Wide	Variable	Narrow	Wide	Not proj.	Not proj.	Not proj.
projecting nasat pone (CZ)	Lish Ari	~	Mariation	ц: чр	ц:~Р	6	Li.ch	100		
hill avi bleat 101 aniteri heicht (32)	прп	••	עמו ומוזוב	III	шбш		шбш	FOW	FOW	FOW

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Characters	Au. afarensis	Au. garhi	Au. africanus	Au. sediba	H. habilis	H. rudolfensis	H. erectus	Au. aethiopicus	Au. boisei	Au. robustus
Canine juga prominence/anterior nillarc	Prominent	Prominent	Variable	Prominent	Variable	Weak	Weak	Weak	Weak	Pillars
Patency of premaxillary	Obliterated	ż	Occasional	Trace	Obliterated	Obliterated	Obliterated	Obliterated	Obliterated	Occasional
suture Inferolateral nasal	Sharp	Sharp	Variable	Blunt	Variable	Sharp	Blunt	Blunt	Variable	Blunt
aperture margin Eversion of superior nasal	~	ć	None	Slight	Slight	Slight	Slight	Slight	Variable	None
aperture margin	Turner	ſ	Turner		, china cin F	, clusterin T	u na	, , , , , , , , , , , , , , , , , , , 	,	, , ,
hasuativeotat titangutat frame/dutter	IIIaIIyua		IIIaIIyua	IIIaIIyua	шапуца	шануца	IIIaIIgulai	ממונהו	ממונבו	ממונבו
Nasal cavity entrance	Stepped	Stepped	Stepped	Stepped	Variable	Stepped	Stepped	Smooth	Smooth	Smooth
Nasoalveolar clivus	Convex	Convex	Straight	Straight	Straight	Straight	Straight	Concave	Concave	Concave
contour in coronal plane	bodreM	hadren	oldeireV	JeelW	oldeireV	dealM	Jeem	hodreM	Moderate	Moderato
Canine fossa	Present	Present	Present	Present	Present	Absent	Absent	Absent	Absent	Absent
Maxillary fossula	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present
Incisor procumbency	Procumb.	Procumb.	Variable	Vertical	Variable	Vertical	Vertical	Vertical	Vertical	Vertical
Anterior nasal spine rel. to	Absent	ż	Anterior	Anterior	Anterior	ż	Enlarged	Posterior	Posterior	Posterior
nasal aperture Expansion of frontal	Med. and lat.	~	Med. and lat.	Medial	Medial	Medial	Medial	Med. and lat.	Med. and lat.	Med. and lat.
process of zygomatic bone										
Angular indentation of	ż	ذ	Indented	Curved	Curved	Curved	Curved	ż	Curved	Curved
lateral orbital margin		ſ		с I: - I- 1		ſ	c1:			
zygomatic prominence develonment	Prominent		Prominent	Inguc	Jugue		Jugue	Prominent	Prominent	Prominent
Lateral flaring of	Marked	ć	Marked	Slight	Slight	Slight	Slight	Marked	Marked	Marked
zygomatic arches									·	
Outline of superior	Tapered	ć	Tapered	Squared	Squared	Squared	Squared	Tapered	Tapered	Tapered
Tacial mask Zvrom atico algorite	Straight	~	Strainht	Strainht	Notch	Notch	Notch	Strainht	Straight	Straight
crest/malar notch	סנומוקוור	•	Juaigur	Judigine				Juaigur	Juagur	Jugan
Infraorbital plate angle	Obtuse	ż	Obtuse	Right	Right	Right	Right	Obtuse	Obtuse	Obtuse
relative to alveolar plane										
Zygomaticomaxillary	No	ć	No	No	No	No	No	No	No	Yes
steps and fossae present										
Height of masseter	Low	Low	High	High	Low	Low	Low	High	High	High
	H	ſ	H	H		ſ				
Matal Unickness (31) Projection of zvoomatics	Posterior	f Posterior	Variable	Posterior	Posterior	: eve	Posterior	Anterior	Anterior	Anterior
relative to nasal bones			5							
Facial prognathism (7) (sellion-prosthion angle)	Prognathic	Prognathic	Variable	Mesognath.	Mesognath.	Mesognath.	Orthogn.	Prognathic	Mesognath.	Mesognath.
Masseteric position	Anterior	ż	Posterior	Posterior	Posterior	ż	Posterior	Anterior	Anterior	Anterior
relative to sellion	Discritic	Disartito	ماطدتيدي	C+vicit+	oldeinett	Ctraintt	Ctrainst	Ctraintt	Ctraintt	C+vicht
Lateral anterior facial contour	ырагие	ырагие	vaпарle	วเาลเgn	Variable	Juraignu	Juraignu	Juraigin	วเโลเยทเ	วเโลเยูทเ

Characters	Au. afarensis	Au. garhi	Au. africanus	Au. sediba	H. habilis	H. rudolfensis	H. erectus	Au. aethiopicus	Au. boisei	Au. robustus
Palate										
Protrustion of incisors	Yes	Yes	Yes	Yes	Yes	No	Yes	No	No	No
beyond bi-canine line										
Anterior palatal depth	Shallow	Shallow	Deep	Deep	Variable	Deep	Variable	Shallow	Deep	Shallow
Dental arcade shape	Rectangle	Rectangle	Variable	Parabolic	Parabolic	Parabolic	Parabolic	Rectangle	Parabolic	Parabolic
Maxillary I2/C diastema	Present	Present	Absent	Absent	Variable	Absent	Absent	Absent	Absent	Absent
Mandible										
Orientation of mandibular	Receding	ż	Receding	Vertical	Vertical	Vertical	Vertical	Vertical	Vertical	Vertical
symphysis										
Bony chin	Absent	ż	Slight	Slight	Slight	Slight	Slight	Slight	Slight	Slight
(mentum osseum)										
Direction of mental	Variable	ż	Variable	Lateral	Lateral	Lateral	Lateral	Lateral	Lateral	Lateral
foramen opening										
Post-incisive planum	Prominent	ż	Prominent	Weak	Prominent	Weak	Weak	Prominent	Prominent	Prominent
Torus marginalis and	Prominent	ż	Moderate	Moderate	Moderate	Prominent	Prominent	ż	Prominent	Prominent
	=	ſ				· · · · · · · · · · · · · · · · · · ·			_	_
Mangibular corpus	Small		Small	Small	Small	Variable	Small	Large	Large	Large
cross-sectional area										
dt M1 (30) Teeth										
Incisor-to-nostranine ratio	arne	Moderate	Moderate	Moderate	Moderate	Moderate	arde	د	Small	Small
(maxillary) (60)	נייער					MOREIRE	rui ye			
Canine-to-postcanine ratio	Large	Large	Large	Large	Large	Large	Large	ż	Small	Small
(maxillary/mandibular) (61, 62)										
Postcanine crown area	Moderate	Large	Large	Moderate	Moderate	Large	Small	Large	Large	Large
(maxillary/mandibular) (57, 59)										
Maxillary 1 [±] : MMR	Moderate	ż	Moderate	Moderate	Weak	Weak	Weak	ż	Moderate	Moderate
gevelopment, ungual race										
Maxillary C: development	Marked	Marked	Marked	Weak	Weak	Marked	Marked	ż	Marked	Weak
or unguat riages				-				1 I MM	1	1 1 MM
Maxillary premolar molaritation	None	MINOL	MINOL	None	MINOL	MILLOL	None	Marked	Marked	Marked
ווטנוובא איבווטנון Muvillauri	hodron	hodren	hoduch	ALC: N	death	booken	1-010	ſ	droot	10001
Maximaly premorans.	Marken	Marken	Marken	WEAK	WEAK	MAIKEU	WEAK		WEAK	WEAK
Modian lingual video of	Drow	ç	Drom	JJM	J.co.M	J.co.M	Jeom	ç	JL00M	J-0/M
median ungaat nage of mandihular raning	LIUII.		LI 011.	WEAK	WEAK	WEAK	WEAK		WEAK	WEAK
	ſ	ſ	ſ	ſ		ſ	Ţ	ſ	ſ	ſ
Mandibular P ₃ root number	. 7 -	~. 1	. 7 -	7		7		~ 1	. 7 -	. 7 -
Protoconid/metaconid	Equal	<i>.</i> :	Equal	Protoconid	Protoconid	Protoconid	Protoconid	ż	Equal	Equal
more mesial cusp (molars)										
Peak of enamel forms	No	ż	Yes	Yes	No	No	No	ż	No	Yes
between roots of molars										
Relative enamel thickness	Thick	Thick	Thick	Thick	Thick	Thick	Thick	Hyper	Hyper	Hyper
Positions of apices of	LC at	LC at	LC slightly	LC slightly	LC at	LC at	LC at	LC mod.	LC mod.	LC mod.
lingual (LC) and buccal	margin, BC	margin, BC	buccal, BC	buccal, BC	margin, BC	margin, BC	margin, BC	buccal, BC	buccal, BC	buccal, BC
(BC) cusps of premolars	slightly	slightly	moderately	moderately	slightly	slightly	slightly	strongly	strongly	strongly
and molars relative to	lingual	lingual	lingual	lingual	lingual	lingual	lingual	lingual	lingual	lingual
occlusal margin										

The first metric for the sector of the sect	AutomaticationMeasurementAutomate3Mitherenelle bordiniMitherenelle bordini <td< th=""><th>Craniodental m ass otherwise e for specimen re estimated. es average va</th><th>assurements for early hominins in Africa. Au. sediba is represented b defined, measurements are based on (6). Some measures were s of Au. afarensis and Au. garhi, in which case the character states i several character states in Table 1 are recorded as variable, althoug lues are presented here. Measurements are in millimeters unles</th><th>oy other re meas in bregr gh g, gl ss prost</th><th>wise indicat urements fr na; ek, ecto abella; mf, hion; rhi, rh</th><th>ed. Descri om this ta conchion; maxillofre inion; zm,</th><th>ptions of ble are pr ekm, ecto ontale; n, zygomaxi</th><th>character sta ovided in SO molare; fmt, nasion; ns, llare; zy, zyg</th><th>tes presen M text S3. frontomola nasospina ion; zyo, zy</th><th>ted in Table 1 Abbreviations re temporale; f lle; or, orbital /goorbitale.</th><th>that are are as fo t, frontot e; po, p</th><th>based on ollows: br, emporale; orion; pr,</th></td<>	Craniodental m ass otherwise e for specimen re estimated. es average va	assurements for early hominins in Africa. Au. sediba is represented b defined, measurements are based on (6). Some measures were s of Au. afarensis and Au. garhi, in which case the character states i several character states in Table 1 are recorded as variable, althoug lues are presented here. Measurements are in millimeters unles	oy other re meas in bregr gh g, gl ss prost	wise indicat urements fr na; ek, ecto abella; mf, hion; rhi, rh	ed. Descri om this ta conchion; maxillofre inion; zm,	ptions of ble are pr ekm, ecto ontale; n, zygomaxi	character sta ovided in SO molare; fmt, nasion; ns, llare; zy, zyg	tes presen M text S3. frontomola nasospina ion; zyo, zy	ted in Table 1 Abbreviations re temporale; f lle; or, orbital /goorbitale.	that are are as fo t, frontot e; po, p	based on ollows: br, emporale; orion; pr,
Carriel capacity (arr ³)415442420631751Maximum parietal breath99910103114Perioribid constriction index (414 × 100)12699104104127Perioribid constriction index (414 × 100)12693137693134Perioribid constriction index (414 × 100)83616555655565Perioribid constriction index (414 × 100)83616365767878Perioribid constriction index (414 × 100)66718565767588Perioribid constriction index (414 × 100)66718666758887Minimum frontial breacht firth)67101807588877676Superior facial height (rept)71737374807175748776Superior facial height (rept)717374877676767676Superior facial height (rept)737487767676767676Superior facial height (rept)757487767676767676Superior facial height (rept)7574877676767676Superior facial height (rept)7574877676767676Superior facial height (rept)75<	Canisd caterly (m ³) Canisd caterly (m ³) (1)	. 9	Measurement	Au. afarensis	Au. africanus	Au. sediba	H. habilis	H. rudolfensis	H. erectus	Au. aethiopicus	Au. boisei	Au. robustus
Maximum partical breadth 90 99 100 103 114 Pestorbial constriction (accounce) point behind the orbits) 7 99 104 127 Pestorbial constriction (accounce) points behind the orbits) 7 95 70 75 Pestorbial constriction (accounce) points behind the orbits) 7 93 76 76 77 Pestorbial constriction (accounce) point behind the orbits) 63 71 85 70 75 Partorial distance beforem TMJ and W/M ³ 63 61 65 71 85 70 75 Infratemporal forsa depth 63 71 85 70 75 66 73 Superior facial heght (n-p) 101 89 73 86 80 90 101 Superior facial heght (n-p) 117 73 81 73 83 73 83 73 83 76 83 93 93 Superior facial breadth (mrt-fmt) 81 73 83 73 83 73	Relation partial health 90 100 103 114 12.6 94 99 100 Psycholic breadth (p_{200}) Disordisal constriction (marrower) point behind the orbid) 77 99 104 123 124 126 124 126 124 124 124 124 124 124 124 124 124 126 124 126 124 126 124 126 124 126 124 126 124 126 124 126 124 126		Cranial capacity (cm ³)	415	442	420	631	751	006	419	515	530
Bi-portonic breadth (pc-pd)12699104127Postorbital constriction intervers point behind the orbits 63 61 65 73 76 85 Postorbital constriction intervers point behind the orbits 61 61 65 71 85 71 85 Postorbital constriction intervers point behind the orbits 63 61 61 65 71 85 70 56 Postorbital constriction intervers between Mi and M*Ma 61 61 61 61 67 52 62 62 72 56 Infratemporal forsa depth 61 61 71 83 61 75 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 66 72 26 92			Maximum parietal breadth	60	66	100	103	114	126	94	66	100
Postorbital constriction (narrowest point behind the orbits) 77 69 73 76 85 70 72 Postorbital constriction (narrowest point behind the orbits) 77 69 73 75 76 73 75 75 75 75 75 75 75 75 75 75 75 75 75			Bi-porionic breadth (po-po)	126	66	104	104	127	121	125	116	Ι
Postorbital constriction index (4/14 × 100) 66 71 85 70 72 Postorbital constriction index (4/14 × 100) 66 71 85 70 72 Failal programation (selion-protition angle) 63 61 45 55 68 Failal program (rontal breadth (tr-th) 101 80 77 65 68 Superior facial height (ron-position angle) 101 80 73 68 83 80 93 Superior facial height (ron-position angle) 117 97 84 78 89 91 100 Superior facial height (ron-position angle) 157 126 102 117 9 94 97 113 Superior facial height (ron-position angle) 75 74 84 97 113 Superior facial height (ron-b) 117 97 113 113 114 113 113 Superior facial height (ron-b) 111 17 125 124 123 124 133 33 33			Postorbital constriction (narrowest point behind the orbits)	77	69	73	76	85	89	65	64	73
Horizontal distance between TM) and $M^2 M^3$ Bit is a possibility for eleveen TM) and $M^2 M^3$ Bit is a possibility for eleveen TM) and $M^2 M^3$ Bit is a possibility for eleveen TM) and $M^2 M^3$ Bit is a possibility for eleveen TM) and $M^2 M^3$ Bit is a possibility for eleveen TM) and $M^2 M^3$ Bit is a possibility for eleveen TM) and $M^2 M^3$ Bit is a possibility for eleveen TM) and $M^2 M^3$ Bit is a possibility for eleveen TM) and $M^2 M^3$ Bit is a possibility for eleveen TM) and $M^2 M^3$ Bit is a possibility for eleveen TM) and $M^2 M^3$ Bit is a possibility for eleveen TM) Bit is a possibility for eleveen TM) Bit is a possibility for eleveen TM) Bit is a possibility for eleveen TM (m-1M) Bit is a possibility for eleveen TM) Bit is a possibility for eleveen TM (m-1M) Bit is a possibility for eleveen TM (m-1M) Bit is a possibility for eleveen TM (m-1M) Bit is a possibility for the most is a possibility for eleveen TM (m-1M) Bit is a possibility for the most is a possibility for eleveen TM (m-1M) Bit is a possibility for the most is a possibility for eleveen TA (m-1M) Bit is a possibility for eleveen TM (m-1M) Bit is a possibility for the most is a possibility preading materion factorial creats Bit is a possibility for the most possibility preading materion factorial creats Bit is a possibility for the most possibility for the most possibility for the most possibility preading materion factorial creats Bit is a possibility for the most possibility for the most possibility for the mossibility preading for the most possibility for the most possib			Postorbital constriction index $(4/14 \times 100)$	99	71	85	70	72	80	65	61	68
Facial progratism (ellion-prostrition angle) 63 61 65 65 65 66 Tratemporal forse depth 61 61 67 66 75 83 86 Minimum frontal breadth (ft-th) 101 80 75 83 86 93 Superior facial height (r-p) 7 87 78 66 75 83 86 Superior facial height (r-p) 87 78 68 80 90 Superior facial height (r-p) 87 78 68 80 90 Superior facial height (r-p) 87 87 86 100 117 Superior facial height (r-p) 87 87 86 100 117 Superior facial height (r-p) 87 87 86 100 117 Superior facial height (r-p) 87 87 86 100 117 Superior facial height (r-p) 87 87 86 100 117 Superior facial height (rp-p) 87 87 86 100 117 Suportial breadth (mf-m) 75 74 84 85 100 Interorbial breadth (mf-m) 75 74 84 85 100 Nasal bridge height (rp-facion actests) -103 133 32 26 Nasal bridge height (rp-facion 100 117 83 36 27 28 28 Nasal bridge height (rp-facion 100 110 136 72 26 27 26 <tr< td=""><td>FieldFieldField6872416669find<td< td=""><td></td><td>Horizontal distance between TMJ and M²/M³</td><td>83</td><td>61</td><td>45</td><td>51</td><td>58</td><td>57</td><td>94</td><td>82</td><td>81</td></td<></td></tr<>	FieldFieldField6872416669find <td< td=""><td></td><td>Horizontal distance between TMJ and M²/M³</td><td>83</td><td>61</td><td>45</td><td>51</td><td>58</td><td>57</td><td>94</td><td>82</td><td>81</td></td<>		Horizontal distance between TMJ and M ² /M ³	83	61	45	51	58	57	94	82	81
Infratemporal foss depth - 31 21 27 - Infratemporal forsa depth (f+f) - 31 21 27 - Glabella to bregma (g-b) - 8 7 8 8 10 Supraoritation of (n-br) - 8 8 8 10 117 Suprior facial height (n-pr) 8 8 8 10 117 97 86 00 117 Superior facial height (n-pr) 8 8 7 8 8 100 117 Superior facial height (n-pr 137 12 12 13 13 3 3 100 117 117 117 117 117 117 113	Intervenolal for a depth (inc) and the depth (inc) and depth (inc) and depth (inc) and the depth (inc) and the depth (Facial prognathism (sellion-prosthion angle)	63	61	65	65	68	72	41	99	69
Minimum frontal fund (n-th) 40 54 70 66 72 Fignal to briggma (g-br) - 8 7 8 8 70 Superior facial breadth (fr-th) - 8 7 8 8 70 Superior facial breadth (fr-th) - 8 8 8 90 90 Superior facial breadth (fr-th) 117 7 7 8 8 90 100 Bi-orbital breadth (fr-th) 99 117 127 126 102 117 - Siportitial breadth (fr-th) 99 84 95 13 33 39 Orbital breadth (fr-th) 157 126 102 117 - - Simaxillary breadth (frr-th) 18 19 20 21 21 21 Orbital breadth (frr-th) 18 19 20 21 21 21 Nasal bridge length (frr-th) Nasal bridge length (frr-th) 23 23 26 27 <t< td=""><td></td><td></td><td>Infratemporal fossa depth</td><td>I</td><td>31</td><td>21</td><td>27</td><td>I</td><td>37</td><td>51</td><td>50</td><td>36</td></t<>			Infratemporal fossa depth	I	31	21	27	I	37	51	50	36
Glabella to bregma (g-br) 101 80 75 83 86 Fornal chord (nucl) - 84 74 80 93 Superior facial breght (n-pt) - 87 78 68 68 90 Superior facial breght (n-pt) 5 78 68 68 90 93 Superior facial breadth (mt-fmt) 117 97 86 100 117 9 9 90 90 93 90 100 117 9 75 74 86 100 117 7 24 97 113 1	Gladela (ref) 101 80 75 83 86 103 $-$ 87 $-$ 87 Grandal (red) (ref) $-$ 8 7 8 8 101 101 93 10 87 Superior facial length (ref) $-$ 8 8 8 100 117 100 103 103 Superior facial length (ref) $-$ 8 8 100 117 107 100 103 103 Superior facial length (ref) $-$ 8 8 100 117 107 100 103 103 Superior facial length $-$ 103 84 97 113 105 113 106 Superative length $-$ 103 84 87 113 105 113 106 Superative length $-$ 13 33 33 33 33 33 33 33 34 33 33 34 33 33 </td <td></td> <td>Minimum frontal breadth (ft-ft)</td> <td>40</td> <td>54</td> <td>70</td> <td>99</td> <td>72</td> <td>76</td> <td>33</td> <td>36</td> <td>35</td>		Minimum frontal breadth (ft-ft)	40	54	70	99	72	76	33	36	35
Forntal chord (n-br)=84748093Superior facial breadth (m+-im)Superior facial breadth (m+-im)=888100Superior facial breadth (m+-im)Superior facial breadth (m+-im)1179786100117Si-orbital breadth (m+-im)Si-orbital breadth (m+-im)89847889100117Si-orbital breadth index (14/16 × 100)7574849786100117Si-orbital breadth (m+-m)757484971131Dimaxillary breadth (m+-m)1819202724Si-orbital breadth (m+-m)1819202724100Binaxillary breadth (m+-m)181920272424Orbital breadth (m+-m)18192027242426Nasal bridge breadth superior383631333333Orbital breadth inferior-111510Nasal bridge breadth superior-111510Nasal bridge breadth inferior23313333Nasal bridge breadth inferior111510-Nasal bridge breadth inferiorNasal bridge breadth inferior-111131110Nasal bridge breadth inferiorNasal bridge breadth inferior-111131110<	Fortial chird (n-b)		Glabella to bregma (g-br)	101	80	75	83	86	103	I	87	I
Suprantital torus vertical thickness - 8 8 10 Superior facial headth (n-pr) Superior facial headth (n-pr) 87 78 68 68 90 Superior facial headth (n-pr) Superior facial headth (n-pr) 87 78 68 100 117 Bi-orbital breadth (net-mt) 157 126 102 117 - Superior facial headth (mt-mt) 157 126 102 117 - Bi-orbital breadth (net-mt) 75 74 84 85 - - Superior facial breadth (mf-mt) 18 19 20 27 24 Rimaxillary breadth (mf-mt) 18 19 20 27 24 Interothital breadth (mf-mt) 38 36 31 33	$ \begin{array}{rcccccccccccccccccccccccccccccccccccc$		Frontal chord (n-br)	I	84	74	80	93	66	I	84	I
Superior facial height (n-pt) 87 78 68 68 90 Superior facial height (n-pt) Bi-orbital breadth (m-fmt) Bi-orbital breadth (m-fmt) Bi B	Superior facial height (n=p) Sec 68 68 60 76 99 100 80 Superior facial height (n=p) Br-orbib levath (ge+of) Br-orbib levath (ge+of) 117 126 112 117 107 100 108 107 109 108 103 Br-orbib levath (ge+of) 118 125 124 125 133 133 133 133 133 133 133 133 133 133 133 133 133 143 106 118 109 109 109 109 109 109 109 109 109 109 109 109 103 133 23 24		Supraorbital torus vertical thickness	I	8	œ	8	10	12	10	12	6
Superior facial breadth (fmt-fmt) 117 97 86 100 117 Br-orbital breadth (ex-ek) Br 89 84 97 113 Br>opmatic breadth (ex-ek) Br 157 126 102 117 - Zygomatic breadth (mf-mf) 7_7 126 103 84 97 113 Interorbital breadth (mf-mf) $-$ 103 84 97 113 Interorbital breadth (mf-mf) $-$ 103 84 97 113 Orbital breadth (mf-ek) 38 36 31 33 39 Orbital breadth inferior $ 103$ 84 97 113 Nasal bridge breadth inferior $ 27$ 26 20 27 24 Nasal bridge breadth inferior $ 23$ 34 31 31 33 Nasal bridge breadth inferior Nasal bridge breadth inferior $ 27$ 26 27 26 27 Nasal bridge breadth inferior Nasat bridge breadth inferior $ 11$	Superior facial breadth (meth) 117 9 107 107 107 107 107 107 107 107 107 107 108 107 108		Superior facial height (n-pr)	87	78	68	68	60	76	66	100	80
Bi-orbital breadth (ek-ek) B)	Binotial breadth (efeek) Binotial breadth (efeek) Binotial breadth (efeek) Binotial breadth (efeek) Binotial breadth (ar-xi) Dite (ar-xi) <thdin (ar-xi)<="" <="" td=""><td></td><td>Superior facial breadth (fmt-fmt)</td><td>117</td><td>76</td><td>86</td><td>100</td><td>117</td><td>107</td><td>100</td><td>108</td><td>107</td></thdin>		Superior facial breadth (fmt-fmt)	117	76	86	100	117	107	100	108	107
Bizygomatic breadth (3γ - $2y$)157126102117-Zygomatic breadth index (14γ L6 × 100)75748485-Zygomatic breadth index (14γ L6 × 100)75748485-Dimaxillary breadth (mf -mf)18192121333Interolital breadth (mf -mf)3833363133Orbital breadth (mf -mf)3834323133Orbital breadth superior3432313133Orbital breadth superior-27261820Nasal bridge breadth superior111510-Nasal bridge breadth superior111510-Nasal bridge breadth superior11151010Nasal bridge breadth superior111510-Nasal bridge breadth superior111131110Nasal bridge breadth superior111131010Nasal bridge breadth superior1111310 <td>Bityonmatic breacht ($x_7 x_7$) 157 126 102 117 - 135 153 153 153 155 143 Zygomatic breacht inter($x_1 (x_1 6 \times 100)$) - 103 126 113 105 143 Proprint breacht inter($x_1 (x_1 1 6 \times 100)$) - 133 <</td> <td></td> <td>Bi-orbital breadth (ek-ek)</td> <td>89</td> <td>84</td> <td>78</td> <td>89</td> <td>100</td> <td>66</td> <td>101</td> <td>93</td> <td>82</td>	Bityonmatic breacht ($x_7 x_7$) 157 126 102 117 - 135 153 153 153 155 143 Zygomatic breacht inter($x_1 (x_1 6 \times 100)$) - 103 126 113 105 143 Proprint breacht inter($x_1 (x_1 1 6 \times 100)$) - 133 <		Bi-orbital breadth (ek-ek)	89	84	78	89	100	66	101	93	82
Zygomatic breadth index (14/16 × 100) 75 74 84 85 - Simuaxillary breadth (π -m) - 103 84 97 113 Interorbital breadth (π -m) - 103 84 97 113 Interorbital breadth (π -m) - 103 84 97 113 Orbital breadth (π -m) 38 36 31 33 39 Orbital height (π -m) 38 36 31 33 39 Orbital breadth superior - 27 26 18 20 Nasal bridge breadth superior - 11 5 10 - Nasal bridge breadth inferior - 11 5 11 10 Nasal bridge breadth inferior - - 4 9 8 - Nasal bridge breadth inferior - - 11 13 11 10 Nasal bridge breadth superior Nasal bridge breadth inferior - 4 9 8 -	Zygomatic breath index (14/16 × 100)75748485-847-6574Interonialiary breath (mr=m)1121038497113105126119106Interonialiary breath (mr=m)111111111222Orbital breath (mr=m)333333333333Orbital breath (mr=m)333333333333Orbital breath superior-588333323Nasal bridge breath superior588111111Nasal bridge breath superior11510-22424Nasal bridge breath superior11133328Nasal bridge breath superior111111111Nasal bridge breath superior1111111111112Nasal bridge breath superior11111111122Nasal bridge breath superior11111111 </td <td></td> <td>Bizygomatic breadth (zy-zy)</td> <td>157</td> <td>126</td> <td>102</td> <td>117</td> <td>I</td> <td>135</td> <td>153</td> <td>165</td> <td>143</td>		Bizygomatic breadth (zy-zy)	157	126	102	117	I	135	153	165	143
Bimaxillary breadth (π m- π m) - 103 84 97 113 Interorbital breadth (π f- π m) 18 19 20 27 24 Orbital breadth (π f- π m) 38 36 31 33 39 Orbital breadth (π f- π m) 38 36 31 33 39 Orbital breadth (π f- π m) 38 36 31 31 33 39 Orbital breadth midge breadth superior 27 26 18 20 27 26 18 20 Nasal bridge breadth at anterior lacrimal crests - 11 13 11 10 20 Nasal bridge breadth inferior - 11 13 11 10 26 27 26 57 5	Bimaxillary breadth (π m- π m)End (π m- π m)<		Zygomatic breadth index (14/16 \times 100)	75	74	84	85	I	84	I	65	74
Interorbital breadth (mf-mf) 18 19 20 27 24 Orbital breadth (mf-ek) 38 36 31 33 39 Orbital breadth (mf-ek) 38 36 31 33 39 Orbital breight (perpendicular to 20) 34 32 31 33 39 Nasal bridge length (n-rh) - 27 26 18 20 Nasal bridge breadth superior - 11 13 11 10 Nasal bridge breadth inferior - 11 15 10 - Nasal bridge breadth inferior - 11 13 11 10 Nasal bridge height (n-ns) - 11 13 11 10 Nasal height (n-ns) - - 4 9 8 - Nasal aperture height (n-ns) Nasal aperture width 23 26 27 27 Maximum nasal aperture width 23 23 26 25 27 Orbitoalveolar height (n-ns) Orbitoalveolar plane) - 12 13 14 47	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		Bimaxillary breadth (zm-zm)	I	103	84	76	113	105	126	119	106
Orbital breadth (mf-ek) 38 36 31 33 39 Orbital breadth (mf-ek) 34 32 31 31 33 39 Nasal bridge length (n-rhi) $-$ 27 26 18 20 Nasal bridge breadth superior $-$ 27 26 18 20 Nasal bridge breadth superior $-$ 11 13 11 10 Nasal bridge breadth inferior $-$ 11 13 11 10 Nasal bridge breadth inferior $-$ 11 13 11 10 Nasal bridge breadth inferior $-$ 11 13 11 10 Nasal bridge breadth inferior $-$ 4 9 8 $-$ Nasal aperture height (n-ns) Nasal aperture width 23 26 27 27 Maximum nasal aperture width $-$ 23 26 25 27 28 Orbitoalveolar height (n-ns) Orbitoalveolar plane) $-$ 12 13 14	Orbital breadth (mf-ek)3836313339363733Norbital height (perpendicular to 20)034323131313330Nasal bridge headth superior034323131313336313330Nasal bridge breadth superior01221115102241111Nasal bridge breadth superior011131110131178Nasal bridge breadth superior011131110131178Nasal bridge breadth superior0111311101178Nasal breadth superior0249455752726457Nasal aperture height (masion subtense at anterior lacrimal crests)2926222830333323Nasal aperture height (masion subtense at anterior lacrimal crests)1413138-121411Nasal aperture height (masion subtense at anterior lacrimal crests)23242452726457Nasal aperture height (masion subtense at anterior lacrimal crests)2324247224Nasal aperture height (masion subtense at anterior lacrimal crests)2324247224Nasal aperture height (masion subtense at anterior lacrimal crests)23<		Interorbital breadth (mf-mf)	18	19	20	27	24	25	23	24	24
Orbital height (perpendicular to 20) 34 32 31 31 33 Nasal bridge length (n-rhi) $ 5$ 8 8 8 Nasal bridge breadth superior $ 27$ 26 18 20 Nasal bridge breadth superior $ 11$ 5 10 $-$ Nasal bridge breadth inferior $ 11$ 13 11 10 Nasal bridge breadth inferior $ 11$ 13 11 10 Nasal bridge breadth inferior $ 4$ 9 8 $-$ Nasal bridge breadth inferior $ 11$ 13 11 10 Nasal bridge breadth inferior $ 4$ 9 8 $-$ Nasal aperture height (mi-ns) $ 4$ 9 8 $-$ Nasal aperture height (n-ns) $ 22$ 22 22 23 23 Nasal aperture height (n-alveolar plane) 23 23 23 24 47 55 Maximum nasal aperture width $233/34 \times 100$ $ 12$ 13 13 14 47 55 Malar thickness $ -$ Malar thickness $ -$ Malar thickness $ -$ Infrao	Orbital height (perpendicular to 20) 34 32 31 31 33 36 41 33 30 Nasal bridge headth superior $$ 27 26 18 20 18 11 -1 Nasal bridge headth superior $$ $ 11$ 5 26 11 -1 11 -1 Nasal bridge headth superior $$ $ 11$ 13 11 10 18 11 7 8 Nasal bridge headth superior $$ $ 11$ 13 11 10 18 11 7 8 Nasal height (n=io)subtense at anterior lacrimal crests) $$ $ 4$ 9 8 $ 24$ 9 11 7 8 Nasal height (n=io)subtense at anterior lacrimal crests) $$ 4 9 8 $$ 24 11 7 8 Nasal height (n=io)subtense at anterior lacrimal crests) $$ 4 9 8 $$ 24 9 11 7 8 Nasal aperture height (n=io)subtense at anterior lacrimal crests) $$ 4 4 7 9 24 4 7 8 Maximum asal aperture height (n=is)maximum asal aperture height (n=is) $$ 14 47 59 57 72 64 54 Maximum asal aperture height (neiterior orbital margin) $$ -12 13 13 $$ 14 47 59 <		Orbital breadth (mf-ek)	38	36	31	33	39	39	36	37	33
Nasal bridge length (n-thi) $ 27$ 26 18 20 Nasal bridge breadth superior $ 5$ 8 8 8 Nasal bridge breadth superior $ 11$ 13 11 10 Nasal bridge breadth inferior $ 11$ 13 11 10 Nasal bridge breadth inferior $ 11$ 13 11 10 Nasal bridge height (nasion subtense at anterior lacrimal crests) $ 4$ 9 8 $-$ Nasal bridge height (n-ns) $ 4$ 9 8 $-$ Nasal bridge height (n-ns) $ 4$ 9 8 $-$ Nasal aperture height (n-ns) $ 29$ 26 22 23 39 Maximum nasal aperture width 23 23 23 23 24 47 59 Main thickness $ 14$ 13 13 8 $-$ Infaorbital foramen height (to inferior orbital margin) $ 12$ 13 44 47 59 Prostino to zygomaxillare (pr-zw) $ 12$ 13 8 $ 14$ 9 8 $-$ Prostino to zygomaxillare (pr-zw) $ 12$ 13 13 12 75 55 59 Prostino to zygomaxillare (pr-zw) $ 12$ 12 12 12 12 12 Prostino to zygomaxillare (pr-zw) $ 12$ <	Nasal bridge length (n-rh)-2726182018353028Nasal bridge breadth superiorNasal bridge breadth superior-5888131111Nasal bridge breadth superior-111510-2419111Nasal bridge breadth superior-11131110181178Nasal bridge height (nasion subtense at anterior lacrimal crests)-498-9452Nasal bridge height (n-ns)585049455752726457Nasal aperture height (n-ns)23232326222839303125Maximum asal aperture width23232625275457575757575757Malar thickoss1113138-12111010Malar thickoss1113138-2769577576Malar thickoss111213138-121110Malar thickoss1113138-27262526Malar thickoss111313131447555757575756Prosthion to zygoowhitale (pr-zyo)-112113		Orbital height (perpendicular to 20)	34	32	31	31	33	36	41	33	30
Nasal bridge breadth superior $=$ 5 8 8 Nasal bridge breadth at anterior lacrimal crests $=$ 11 5 10 $=$ Nasal bridge breadth inferior $=$ 11 13 11 10 $=$ Nasal bridge height (nasion subtense at anterior lacrimal crests) $=$ 4 9 8 $=$ Nasal bridge height (n-ns) 58 50 49 45 57 Nasal aperture height (n-ns) 229 226 22 28 39 Nasal aperture width 23 23 24 47 59 Maximum nasal aperture width 23 23 26 25 27 Orbitoalveolar height (or-alveolar plane) 55 53 44 47 59 Malar thickness 14 13 13 8 $=$ Infraorbital foramen height (to inferior orbital margin) $=$ 12 15 15 14 Prosthion to zygoorbitale (pr-zyo) $=$ 60 50 57 55 53 44 47 55 Nasseler origin height index ($36/37 \times 100$) $=$ 112 112 104 96 92 Subnasale to prosthion (wertical projection) 15 21 17 187 106 57 Subnasale to prosthion (wertical projection) 15 21 17 187 106 57 Subnasale to prosthion (wertical projection) 15 21 17 18 106 57 Subnasale t	Nasal bridge breadth superior $=$ 5 8 8 13 12 14 11 Nasal bridge breadth superior $=$ 11 5 10 $ 24$ 11 7 8 Nasal bridge breadth at anterior lacrimal crests $ 11$ 13 11 10 12 11 7 8 Nasal bridge breadth at anterior lacrimal crests $ 4$ 9 8 $ 9$ 4 5 7 64 57 22 22 22 22 22 22 22 22 23 33 35 24 57 57 52 24 55 22 22 22 23 23 25 24 25 24 25 24 25 24 25 26 27 25 26 23 23 23 23 23 23 26 27		Nasal bridge length (n-rhi)	I	27	26	18	20	18	35	30	28
Nasal bridge breadth at anterior lacrimal crests-11510-Nasal bridge breadth inferior-11131110Nasal bridge height (nasion subtense at anterior lacrimal crests)-498-Nasal bridge height (n-ns)5850494557Nasal aperture height (rhi-ns)2926222839Nasal aperture height (rhi-ns)2323262527Nasal aperture width2323262527Orbitoalveolar height (or-alveolar plane)5553444759Malar thickness1413138Infraorbital foramen height (to inferior orbital margin)-121514Prosthion to zygoorbitale (pr-zw)1121049692Masseter origin height index ($33/34 \times 100$)1121049692Subnasale to prosthion (vertical projection)1521171830Subnasale to prosthion index ($36/37 \times 100$)-1871087610657Subnasale projection index ($36/37 \times 100$)13161514Incisor alveolar length-13161514Incisor alveolar length13161514Incisor alveolar length131617Incisor alveolar length-	Nasal bridge breadth at anterior lacrimal crests $ 11$ 5 10 $ 24$ 19 11 $-$ Nasal bridge breadth inferiorNasal bridge breadth inferior $ 11$ 13 11 10 18 11 7 8 Nasal bridge breadth inferior $ 4$ 9 8 $ 9$ 4 5 $-$ Nasal bridge freadth inferior $ 4$ 9 8 $ 9$ 4 5 $-$ Nasal aperture bright (n-ns) $ 29$ 49 45 57 32 24 47 55 53 24 47 55 52 27 Nasal aperture width $ 23$ 23 23 23 23 33 33 33 35 24 Nasal aperture width $ 23$ 44 47 59 51 53 69 57 Mair minasal aperture width $ 12$ 13 13 13 14 47 59 51 53 Orbitoalveolar height (or-alveolar plane) $ 12$ 13 13 14 47 59 51 53 26 Mair minasal aperture width $ 12$ 13 13 12 12 12 12 Infraorbital foramen height (or-alveolar plane) $ 12$ 13 12 12 12 12 12 Prosthion to zygo		Nasal bridge breadth superior	I	S	8	8	8	13	12	14	11
Nasal bridge breadth inferior-11131110Nasal bridge height (nasion subtense at anterior lacrimal crests)-498-Nasal height (n-ns)5850494557Nasal aperture height (rhi-ns)2926222839Nasal aperture width2323244759Maximum nasal aperture width2323244759Orbitoalveolar height (or-alveolar plane)5553444759Malar thickness1413138-14Prosthion to zygomaxillare (pr-zm)-1121151514Prosthion to zygoorbitale (pr-zm)-60505775Masseter origin height index ($33/34 \times 100$)-1121049692Subnasale to prosthion (vertical projection)1521171830Subnasale projection index ($36/37 \times 100$)-13161514Incisor alveolar length-13161514Horizor alveolar length13161514Nasseler origin height index ($36/37 \times 100$)131171830Subnasale projection index ($36/37 \times 100$)13161514Horizor alveolar length-13108761065757Nasseler origin keight index ($36/37 \times 100$)-	Nasal bridge breadth inferior-11131110181178Nasal bridge height (nasion subtense at anterior lacrimal crests)-498-945-Nasal bridge height (nasion subtense at anterior lacrimal crests)-498-9455-Nasal aperture height (nasion subtense at anterior lacrimal crests)-498-945524Nasal aperture height (nais)2323232333333125Mainum nasal aperture width232324475951536957Orbitoalveolar height (or-alweolar plane)555344475951536957Malar thicknes141313138-121818Infraorbital foramen height (no inferior orbital margin)-12151416302526Prosthion to zygoomatulae (pr-zm)605057757670717381Prosthion to zygoomatulae (pr-zm)1121131310101101103103Submasale to prosthion the cytoin the cyt		Nasal bridge breadth at anterior lacrimal crests	I	11	ъ	10	I	24	19	11	I
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Incisor alveolar length – 13 16 15 14	Incisor alveolar length – 13 16 15 15 13 Premolar alveolar length – 15 18 16 13 21 22 17		Subnasale projection index $(36/37 \times 100)$	187	108	76	106	57	79	192	108	122
	Premolar alveolar length – 15 18 16 16 13 21 22 17		Incisor alveolar length	I	13	16	15	14	16	15	15	13
Dremolar alveolar lenoth – 15 18 16 16			Premolar lavariar length	I	1 L	18	16	16	13	12		17

continued on next page

200

ltem	Measurement description in (6)	Measurement	Au. afarensis	Au. africanus	Au. sediba	H. habilis	H. rudolfensis	H. erectus	Au. aethiopicus	Au. boisei	Au. robustus
41	98	Intercanine distance	26	30	30	30	33	31	I	29	27
42	88	Palate breadth (ekm-ekm)	68	64	63	70	80	99	83	82	67
43	141	Mandibular symphysis height	39	38	32	27	36	34	I	47	42
44	142	Mandibular symphysis depth	60	20	19	19	24	19	I	28	25
45	147	Mandibular corpus height at P_4	34	33	28	30	38	30	I	42	38
46	148	Mandibular corpus depth at P_4	19	21	18	20	22	19	I	28	24
47	149	Cross-sectional area at P4 (calculated as an ellipse)	511	558	382	427	653	458	Ι	910	709
48	150	Mandibular corpus height at M ₁	33	32	28	29	36	30	35	41	37
49	151	Mandibular corpus depth at $M_{ m 1}$	19	21	18	20	23	20	26	28	26
50	152	Cross-sectional area at M_{1} (calculated as an ellipse)	488	532	396	421	667	469	715	913	759
51	154	Mandibular corpus height at M ₂	31	31	25	31	36	30	I	41	35
52	155	Mandibular corpus depth at M ₂	22	25	22	23	26	21	I	31	28
53	156	Cross-sectional area at M_2 (calculated as an ellipse)	536	612	436	537	745	504	I	980	770
54	162	Height of mental foramen relative to alveolar margin	20	19	13	13	17	13	I	20	20
55		Maxillary incisor crown area (I ¹ +I ²)	143	135	109	132	137	136	I	117	109
56		Maxillary canine crown area	107	104	79	95	118	96	I	76	79
57		Maxillary postcanine crown area	713	868	731	755	829	617	I	1012	941
58		Mandibular canine crown area	87	95	68	83	I	79	I	72	61
59		Mandibular molar crown area	550	651	536	565	668	466	I	781	678
60		Maxillary incisor to postcanine ratio	20.0	15.6	14.9	17.4	16.6	22.1	I	11.5	11.6
61		Maxillary canine to postcanine ratio	15.0	11.9	10.8	12.6	14.2	15.5	Ι	7.5	8.4
62		Mandibular canine to molar ratio	15.8	14.6	12.7	14.6	I	16.7	I	9.2	9.0

to the facial plane. The face is mesognathic. The palate is consistently deep along its entire extent, with a parabolic dental arcade.

Mandible. Descriptions apply to the more complete juvenile (MH1) mandible unless otherwise stated. The nearly vertical mandibular symphysis presents a weak lateral tubercle, resulting in a slight mental trigone, and a weak mandibular incurvation results in a slight mentum osseum. The post-incisive planum is weakly developed and almost vertical. Both mandibular corpora are relatively gracile, with a low height along the alveolar margin. The extramolar sulcus is relatively narrow in both mandibles. In MH1, a moderate lateral prominence displays its greatest protrusion at the mesial extent of M₂, with a marked decrease in robusticity to P₄; in MH2 the moderate lateral prominence shows its greatest protrusion at M₃, with a marked decrease in robusticity to M2. The alveolar prominence is moderately deep with a notable medial projection posteriorly. The anterior and posterior subalveolar fossae are continuous. The ramus of MH1 is tall and narrow, with nearly parallel, vertically oriented anterior and posterior borders; the ramus of MH2 is relatively broader, with nonparallel anterior and posterior borders (fig. S2). The mandibular notch is relatively deep and narrow in MH1 and more open in MH2. The coronoid extends farther superiorly than the condyle. The condyle is mediolaterally broad and anteroposteriorly narrow. The endocondyloid buttress is absent in MH1, whereas in MH2 a weak endocondyloid buttress approaches the condyle without reaching it.

Dental size and proportions. The dentition of the juvenile (MH1) is relatively small, whereas preserved molars of the adult (MH2) are even smaller (Fig. 3 and fig. S4). For MH1, the maxillary central incisor is distinguishable only from the reduced incisors of Au. robustus. The maxillary canine is narrower than all canines of Au. africanus except TM 1512, whereas the mandibular canine falls well below the range of Au. africanus. Premolars and molars are at the lower end of the Au. africanus range and within that of *H. habilis–H. rudolfensis* and *H. erectus*. Molar dimensions of the adult individual (MH2) are smaller than those of Au. africanus, are at or below the range of those of H. habilis-H. rudolfensis, and are within the range of those of H. erectus. Au. sediba mirrors the Au. africanus pattern of maxillary molars that increase slightly in size posteriorly, though it differs in that the molars tend to be considerably larger in the latter taxon. Conversely, the Au. sediba pattern varies slightly from that seen in specimens KNM-ER 1813, OH 13, and OH 65 and H. erectus, wherein the molars increase from M¹ to M² but then decrease to M³. In broad terms, the teeth of Au. sediba are similar in size to teeth of specimens assigned to Homo but share the closely spaced cusp apices seen in Australopithecus.

Postcranium. Preserved postcranial remains of *Au. sediba* (table S1) denote small-bodied

hominins that retain an australopith pattern of long upper limbs, a high brachial index, and relatively large upper limb joint surfaces (table S2). In addition to these aspects of limb and joint proportions, numerous other features in the upper limb are shared with sibling species of Australopithecus (to the exclusion of later Homo), including a scapula with a cranially oriented glenoid fossa and a strongly developed axillary border; a prominent conoid tubercle on the clavicle, with a pronounced angular margin; low proximal-to-distal humeral articular proportions; a distal humerus with a marked crest for the brachioradialis muscle, a large and deep olecranon fossa with a septal aperture, and a marked trochlear/capitular keel (19); an ulna with a pronounced flexor carpi ulnaris tubercle; and long, robust, and curved manual phalanges that preserve strong attachment sites for the flexor digitorum superficialis muscle.

Numerous features of the hip, knee, and ankle indicate that Au. sediba was a habitual biped. In terms of size and morphology, the proximal and distal articular ends of the femur and tibia fall within the range of variation of specimens attributed to Au. africanus. However, several derived features in the pelvis link the Malapa specimens with later Homo. In the os coxa (Fig. 4), Au. sediba shares with Homo a pronounced acetabulocristal buttress; a more posterior position of the cristal tubercle; a superoinferiorly extended posterior iliac blade, with an expanded retroauricular area; a sigmoid-shaped anterior inferior iliac spine; a reduced lever arm for weight transfer between the auricular surface and the acetabulum; an enlarged and rugose iliofemoral ligament attachment area; a tall and thin pubic symphyseal face; and a relatively short ischium with a deep and narrow tuberoacetabular sulcus. These features are present in taxonomically un-

assigned postcranial remains from Koobi Fora (KNM-ER 3228) and Olduvai Gorge (OH 28), which have been argued to represent early *Homo* (20), as well as in early *Homo erectus* (21). An os coxa from Swartkrans (SK 3155) has been considered by some to also represent early *Homo* (22) but can be seen to possess the australopith pattern in most of these features. In addition, *Au. sediba* shares with later *Homo* the humanlike pattern of low humeral-to-femoral diaphyseal strength ratios, in contrast to the ape-like pattern seen in the *H. habilis* specimen OH 62 (table S2).

Although aspects of the pelvis are derived, the foot skeleton is more primitive overall, sharing with other australopiths a flat talar trochlea articular surface with medial and lateral margins with equal radii of curvature, and a short, stout, and medially twisted talar neck with a high horizontal angle and a low neck torsion angle



Fig. 3. Dental size of a selection of *Au. sediba* teeth compared to other early hominin taxa; see fig. S4 for additional teeth. Dental measurements were taken as described by Wood (*6*). Owing to small sample sizes, *H. habilis* and *H. rudolfensis* were combined. (**A**) Upper central incisor mesiodistal (MD) length. (**B**) Upper canine MD length. (**C**) Lower canine MD length. (**D**) Square root of calculated [MD × BL (BL, buccolingual)] upper third premolar area. (**E**) Square root of calculated (MD × BL) upper second molar area. (**F**) Square root of calculated (MD × BL) lower second molar area. Measures were taken on original specimens by D.J.D. for *Au. africanus*, *Au. robustus*,

and *Au. sediba*. Measurements for *Au. afarensis*, *H. habilis*, *H. rudolfensis*, and *H. erectus* are from (6). P⁴ is not fully erupted on the right side of MH1, therefore measures of the maxillary postcanine dentition are presented for the left side only. Dental metrics for *Au. sediba* are as follows (MD, BL, in millimeters): Maxillary: MH1: RI1 10.1, 6.9; LI2 7.7 (damaged), 5.1; RC 9.0, 8.8; LP3 9.0, 11.2; LP4 9.2, 12.1; LM1 12.9, 12.0; LM2 12.9, 13.7; LM3 13.3, 14.1; MH2: RM3 11.3, 12.9. Mandibular: MH1: LC 8.0, 8.5; RM1 12.5, 11.6; RM2 14.4, 12.9; RM3 14.9, 13.8; MH2: RM1 11.8, 11.1; RM2 14.1, 12.2; RM3 14.2, 12.7; LM3 14.1, 12.5.



Fig. 4. Representative ossa coxae, in lateral view, from left to right, of *Au. afarensis* (AL 288-1), *Au. africanus* (Sts 14), *Au. sediba* (MH1), and *H. erectus* (KNM-WT 15000). The specimens are oriented so that the iliac blades all lie in the plane of the photograph (which thus leads to differences between specimens in the orientation of the acetabula and ischial tuberosities). MH1 possesses derived, *Homo*-like morphology compared to other australopithecines, including a relative reduction in the weight transfer distance from the sacroiliac (yellow) to hip (circle)

joints; expansion of the retroauricular surface of the ilium (blue arrows) (determined by striking a line from the center of the sphere representing the femoral head to the most distant point on the posterior ilium; the superior arrow marks the terminus of this line, and the inferior arrow marks the intersection of this line with the most anterior point on the auricular face); narrowing of the tuberoacetabular sulcus (delimited by yellow arrows); and pronouncement of the acetabulocristal (green arrows) and acetabulosacral buttresses.

(table S2 and fig. S5). The calcaneus is markedly primitive in its overall morphology: the bone is strongly angled along the proximodistal axis, with the point of maximum inflexion occurring at an enlarged peroneal trochlea; the lateral plantar tubercle is lacking; the calcaneal axis is set about 45° to the transverse plane; and the calcaneocuboid facet is vertically set and lacks an expanded posterior projection for the beak of the cuboid (23).

Discussion. The age and overall morphology of Au. sediba imply that it is most likely descended from Au. africanus, and appears more derived toward Homo than do Au. afarensis, Au. garhi, and Au. africanus. Elsewhere in South Africa, the Sterkfontein cranium Stw 53, dated to 2.0 to 1.5 Ma, is generally considered to represent either H. habilis (10, 24, 25) or perhaps an undiagnosed form of early Homo (26). It played an important role in the assignment of OH 62 to H. habilis (27). However, the derived craniodental morphology of Au. sediba casts doubt on the attribution of Stw 53 to early Homo [see also (28)]: Stw 53 appears to be more primitive than MH1 in retaining closely spaced temporal lines: marked postorbital constriction; a weakly developed supraorbital torus; narrow, nonprojecting nasal bones; anterior pillars; marked nasoalveolar prognathism; medial and lateral expansion of the frontal process of the zygomatic bone; and laterally flared zygomatics. If Stw 53 instead represents Au. africanus, the assignment of OH 62 to H. habilis becomes tenuous. Attribution of the partial skeleton KNM-ER 3735 to H. habilis was tentatively based, in part, on a favorable comparison with OH 62 and on the hypothesis that there were no other contemporaneous nonrobust australopith species to which it could be assigned in East Africa (29). As a result, the interpretation of KNM-ER 3735 as H. habilis also becomes uncertain.

The phylogenetic significance of the cooccurrence of derived postcranial features in Au. sediba, H. erectus, and a sample of isolated fossils generally referred to Homo sp. indet. (table S2) is not clear: The latter might represent early H. erectus, it might sample the postcranium of H. rudolfensis (which would then imply an evolutionary pathway from Au. sediba to H. rudolfensis to H. erectus), or it might represent the postcranium of H. habilis [which would suggest that OH 62 and KNM-ER 3735 (two specimens with ostensibly more primitive postcranial skeletons) do not belong in this taxon]. If the latter possibility holds, it could suggest a phylogenetic sequence from Au. sediba to H. habilis to H. erectus. Conversely, although the overall postcranial morphology of Au. sediba is similar to that of other australopiths, a number of derived features of the os coxa align the Malapa hominins with later Homo (H. erectus) to the exclusion of other australopiths. Additionally, Au. sediba shares a small number of cranial traits with H. erectus that are not exhibited in the H. habilis-H. rudolfensis hypodigm, including slight postorbital constriction and convexity of the infraorbital region (18). Following on this, MH1 compares favorably with SK 847 (H. erectus) in the development of the supraorbital torus, nasal bones, infraorbital region, frontal process of the zygomatic, and subnasal projection. However, MH1 differs from SK 847 in its relatively smaller size, the robust glabelar region, the weakly developed supratoral sulcus, the steeply inclined zygomaticoalveolar crests with a high masseter origin, and the moderate canine juga, all features aligning MH1 with *Australopithecus*. It is thus not possible to establish the precise phylogenetic position of *Au. sediba* in relation to the various species assigned to early *Homo*. We can conclude that combined craniodental and postcranial evidence demonstrates that this new species shares more derived features with early *Homo* than does any other known australopith species (Table 1 and table S2) and thus represents a candidate ancestor for the genus, or a sister group to a close ancestor that persisted for some time after the first appearance of *Homo*.

The discovery of a <1.95-million-year-old (16) australopith that is potentially ancestral to Homo is seemingly at odds with the recovery of older fossils attributed to the latter genus (5) or of approximately contemporaneous fossils attributable to H. erectus (6, 30). However, it is unlikely that Malapa represents either the earliest or the latest temporal appearance of Au. sediba, nor does it encompass the geographical expanse that the species once occupied. We hypothesize that Au. sediba was derived via cladogenesis from Au. africanus (\approx 3.0 to 2.4 Ma), a taxon whose first and last appearance dates are also uncertain (31). The possibility that Au. sediba split from Au. africanus before the earliest appearance of Homo cannot be discounted.

Although the skull and skeleton of *Au. sediba* do evince derived features shared with early *Homo*, the overall body plan is that of a hominin at an australopith adaptive grade. This supports the argument, based on endocranial volume and craniodental morphology, that this species is most parsimoniously attributed to the genus *Australopithecus*. The Malapa specimens dem-

onstrate that the evolutionary transition from a small-bodied and perhaps more arboreal-adapted hominin (such as Au. africanus) to a largerbodied, possibly full-striding terrestrial biped (such as H. erectus) occurred in a mosaic fashion. Changes in functionally important aspects of pelvic morphology, including a reduction of the sacroacetabular weight-bearing load arm and enhanced acetabulosacral buttressing (reflecting enhancement of the hip extensor mechanism), enlargement of the iliofemoral ligament attachment (reflecting a shift in position of the line of transfer of weight to behind the center of rotation of the hip joint), enlargement of the acetabulocristal buttress (denoting enhancement of an alternating pelvic tilt mechanism), and reduction of the distance from the acetabulum to the ischial tuberosity (reflecting a reduction in the moment arm of the hamstring muscles) (20, 32)occurred within the context of an otherwise australopith body plan, and seemingly before an increase in hominin encephalization [in contrast to the argument in (33)]. Relative humeral and femoral diaphyseal strength measures (table S2) also suggest that habitual locomotor patterns in Au. sediba involved a more modern human-like mechanical load-sharing than that seen in the H. habilis specimen OH 62 (34, 35). Mosaic evolutionary changes are mirrored in craniodental morphology, because the increasingly wide spacing of the temporal lines and reduction in postorbital constriction that characterize Homo first appeared in an australopith and before significant cranial expansion. Moreover, dental reduction, particularly in the postcanine dentition, preceded the cuspal rearrangement (wide spacing of postcanine tooth cusps) that marks early Homo.

The pattern of dental eruption and epiphyseal fusion exhibited by MH1 indicates that its age at death was 12 to 13 years by human standards, whereas in MH2 the advanced degree of occlusal attrition and epiphyseal closure indicates that it had reached full adulthood (SOM text S1). Although juvenile, MH1 exhibits pronounced development of the supraorbital region and canine juga, eversion of the gonial angle of the mandible, and large rugose muscle scars in the skeleton, all indicating that this was a male individual. And, although fully adult, the mandible and skeleton of MH2 are smaller than in MH1, which, combined with the less rugose muscle scars and the shape of the pubic body of the os coxa, suggests that MH2 was a female. In terms of dental dimensions, MH1 has mandibular molar occlusal surface areas that are 10.7% (M_1) and 8.1% (M_2) larger than those of MH2. Dimorphism in the postcranial skeleton likewise is not great, though the juvenile status of MH1 tends to confound efforts to assess adult body size. The diameter of the proximal epiphysis for the femoral head of MH1 (29.8 mm) is approximately 9.1% smaller than the superoinferior diameter of MH2's femoral head (32.7 mm). It is likely that MH1 would have experienced some appositional increase in joint size before maturity, thus this disparity would probably have decreased somewhat. The distal humeral epiphysis of MH1 is fully fused and its articular breadth (35.3 mm) is only marginally larger than that of MH2 (35.2 mm). Thus, although the dentition and postcranial skeleton are at odds in the degree of apparent size differences, the overall level of dimorphism, if these sex attributions are correct, appears slight in the Malapa hominins and was probably similar to that evinced by modern humans.

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- 19. Some humeri that are probably best attributed to Australopithecus lack marked development of the trochlear/capitular keel [or "lateral crest": see (37)], and thus the absence of a marked crest does not reliably differentiate Australopithecus from Homo. However, although some specimens of early Homo (such as KNM-WT 15000) have crests that are more strongly developed than those of modern humans, none exhibit the marked crests of the australopiths. Thus, the marked crest seen in the Malapa humeri can be seen to be shared with Australopithecus rather than Homo.
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- 41. We thank the South African Heritage Resources Agency for the permits to work at the Malapa site: the Nash family for granting access to the Malapa site and continued support of research on their reserve; the South African Department of Science and Technology, the South African National Research Foundation, the Institute for Human Evolution, the Palaeontological Scientific Trust, the Andrew W. Mellon Foundation, the AfricaArray Program, the U.S. Diplomatic Mission to South Africa, and Sir Richard Branson for funding: the University of the Witwatersrand's Schools of Geosciences and Anatomical Sciences and the Bernard Price Institute for Palaeontology for support and facilities; the Gauteng Government, Gauteng Department of Agriculture, Conservation and Environment and the Cradle of Humankind Management Authority; E. Mbua, P. Kiura, V. Iminjili, and the National Museums of Kenya for access to comparative specimens: Optech and Optron: Duke University; the Ray A. Rothrock Fellowship of Texas A&M University; and the University of Zurich 2009 Field School, Numerous individuals have been involved in the ongoing preparation and excavation of these fossils, including C. Dube, B. Eloff, C. Kemp, M. Kgasi, M. Languza, J. Malaza, G. Mokoma, P. Mukanela, T. Nemvhundi, M. Ngcamphalala, S. Jirah, S. Tshabalala, and C. Yates. Other individuals who have given significant support to this project include B. de Klerk, C. Steininger, B. Kuhn, L. Pollarolo, B. Zipfel, J. Kretzen, D. Conforti, J. McCaffery, C. Dlamini, H. Visser, R. McCrae-Samuel, B. Nkosi, B. Louw, L. Backwell, F. Thackeray, and M. Peltier. T. Stidham helped construct the cladogram in fig. S3, 1, Smilg facilitated computed tomography scanning of the specimens. R. Clarke and F. Kirera provided valuable discussions on these and other hominin fossils in Africa.

Supporting Online Material

www.sciencemag.org/cgi/content/full/328/5975/195/DC1 SOM Text 1 to 4 Figs. S1 to S5 Tables S1 and S2 References

19 November 2009; accepted 26 February 2010 10.1126/science.1184944