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A 3.8–million–year–old hominin cranium from Woranso–Mille, Ethiopia

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Supplementary Note 1. MRD-VP-1/1: Detailed description of discovery and preservation

1.1. *Recovery.* MRD was recovered from the surface in two major pieces. The facial component was found on February 10, 2016 by an Afar worker (Ali Bereino) at a place locally known as “Miro Dora” (11°32’59.5” N; 40°27’54.6” E). The rest of the cranium was found on the same day by YHS ca. 3m northeast of the face. After the discovery of the two major pieces (the face and the neurocranium), a sieving operation was carried out to recover more pieces that might have broken away from the specimen. The team first crawled the area in the immediate vicinity of the two major pieces and then surface swept an area of ca. 30 m². While the specimen eroded out from a sandstone horizon (based on the matrix adhered to it) and the amount of loose original sediment on top of it was minimal, the main area that had to be sieved was covered by up to 30 cm deep goat droppings piled up for many years, indicating that there was a lot of animal movement in the area and some of the fragments of MRD-VP-1/1 may have been destroyed by trampling.

The sieving operation resulted in the recovery of many fragments including two pieces of the left zygomatic bone. The larger piece constituted most of the malar region including the frontal process and some part of the frontal bone at the superolateral corner of the orbit. The other piece was a small fragment that joined to the bigger piece at the anterior origin of the zygomatic arch. One small but critical piece, that joined the left zygomatic bone with the frontal, was also found from the sieve. Other pieces that were found as a result of the sieving operation include a small fragment of the left zygomatic arch, which joined the temporal bone at the posterior end of the arch. Two more fragments of the zygomatic arch from mid-section were also recovered even though their position on the arch is unknown. A larger piece from the base of the right zygomatic was also recovered. This fragment has the entire masseteric origin preserved but did not join the

main specimen due to abrasion of its broken edge. Finally, the distal one-third of the right M³ was also recovered.

1.2. *Missing parts.* The right zygomatic bone, except for some parts at the inferolateral corner of the orbit, is entirely missing. A small piece from the masseter origin area was recovered from surface scraping but does not join the rest of the specimen. Most of the malar region on this side, especially the infraorbital region, is preserved intact. The right supraorbital ridge is also missing except for some part on its medial corner close to midline. The left malar region is missing a 6-15 mm long vertical stretch of bone extending from the inferior orbital rim to the zygomaticoalveolar crest. However, most of the lateral malar region, including the masseter origin, is preserved intact despite a minor displaced bone surface around the inferolateral corner of the orbit. The frontal process of the zygomatic bone is preserved intact except for a small part missing around jugale. The anterior and posterior roots of the zygomatic arch are also preserved on this side.

The floor of the left orbit and roof of the right orbit are also largely missing. The medial, superior and lateral margins of the left orbit are preserved intact. However, its inferolateral margin has undergone minimal plastic deformation and the inferolateral wall of the orbit is slightly pushed medially and superiorly, creating a small overlap on bone. The right orbit has its medial and inferior margins preserved intact but the lateral and superior margins are missing.

The frontal processes of the maxilla, the nasals, the nasal aperture, nasoalveolar clivus, and palate are preserved intact. However, the left dental row, especially its posterior half, is pushed medially. The maxillary bone immediately below the left malar region starting at the infraorbital

foramen is crushed and depressed medially. The root of the zygomatic process of the maxilla is better preserved on the right side. On the left side, this region is crushed and/or missing.

There is substantial loss of cortical bone along the alveolar margins on both sides, especially at left C-M1 level. However, based on the preserved parts of the margins, the buccal roots of the posterior teeth (M2-3) naturally protruded lateral to the wall of the alveolar margin even though the cortical bone that covered the roots is abraded. Most of the labial alveolar bone around the incisors is also abraded exposing the roots of all the incisors. It appears that all of the incisor crowns were broken postmortem although some portions of the crowns are present on the left first and second incisors. However, they are vertically sheared and lack most of the enamel surface. The preserved part of the left central incisor shows a clean break on its occlusal surface below the cervicoenamel junction and the remaining enamel on its labial crown surface is extensively chipped. The root of the right second incisor is coronally sliced exposing the entire length of the root canal. The anterior face of the left second incisor root is also exposed. However, the bony septum between it and the central incisor is intact. It is entirely damaged on the right side. There is enough preserved of the roots and crown parts of the incisors to indicate that they were not procumbent. The roots start curving downward before reaching the cervicoenamel junction. The alveolar bone in the region of the diastema is intact. The anterior face of left canine jugum is also exposed revealing the extremely long canine root. The bone around the vertical depression between it and the second incisor is preserved intact. The tips of the incisor roots are clearly seen protruding above the floor of the nasoalveolar clivus anterior to the entrance to the nasal opening.

The frontal squama is preserved intact except in the area of the right supraorbital region and some minor exfoliations of surface bone. The sagittal crest is sinuous and continues all the way to the nuchal crest, even though it is chipped at various places across its length. Postmortem deformation has resulted in the superior edge of the sphenoid greater wing, together with the anterior part of the temporal squama and part of the anterior inferior parietal region, being pushed medially and superiorly under the left frontal squama behind the orbit. The overlap is ca. 4.5 mm anteriorly. As a result of this deformation, there are three cracks in this region. One of them is an oblique crack close to the coronal suture where the sphenoid and temporal bones join the frontal (25 mm long). The second crack is sagittally oriented and it is a result of the anteroinferior corner of the parietal riding under the rest of the parietal (24 mm long). The third crack starts inferiorly at the junction of the two cracks and course superiorly on the parietal bone for 16 mm. The right parietal has two prominent circular pit-like depressions on its posterior part between the sagittal crest and the squamosal suture. The anterior depression has a maximum diameter of 9.5 mm and it is ca. 2 mm deep. The posterior depression has a maximum diameter of 9 mm and it is ca. 2 mm deep.

The temporal bones are more or less preserved intact except for some minor abrasion on the left mastoid face and along the supramastoid crests, particularly on the left side. The lateralmost rims of both left and right external auditory meatus are also broken, more so on the right side than the left side. The origin of the temporal processes of the zygomatic is also broken off on both sides all the way from above the EAM (auriculare is not preserved on either side), except for a small piece of bone recovered by sifting and which joined anteriorly on the left side. The tympanic plates are preserved intact on both sides. The petrous regions require further cleaning to see how much is preserved.

1.3. *Deformation.* The area around the posterior part of the left temporal squama near the occipitosquamosal suture is depressed as a result of what appears to be an impact from a blunt force. As a result, the anterior portion of the left temporal and sphenoid are displaced anteriorly, medially and superiorly to lie beneath the left side of frontal and left parietal. A small piece of the left parietal superior to TMJ is also displaced laterally. The impact has also created a narrow longitudinal crack running from mid-parietal obliquely to the nuchal crest on the left side. A number of hairline cracks run in different directions around the distal parietal and occipital regions. Such hairline cracks are apparent mostly on the left side of the cranium but do not obliterate any morphology in that region. The alveolar bone and associated teeth on the left side are twisted medially and transversely by ca. 5° posterior to the canine. There is substantial bone loss on the lateral alveolar region of the left maxilla below the base of the zygomatic origin.

The basicranial region of MRD shows misalignment of bilateral elements and a major sagittally oriented crack. This is largely caused by the displacement of bones around the left corner behind the orbit and the depression of the left posterior temporal squama. A wide crack runs sagittally starting from anterior to the TMJ on the left side to the midline and crossing over to the right side leaving midline to the left. This crack is caused by the displacements in the sphenotemporal region on the left side.

Supplementary Note 2. Symmetrization landmarks. List of anatomical landmarks and curves of the template for MRD symmetrization.

Unpaired landmarks	Paired landmarks*	Curve names	<i>N</i>	Smlm count**
Glabella (g)	Foramen infraorbitale (fori)	Anterior nasal aperture right	1	10
Nasion (n)	Frontomalare-orbitale (fmo)	Anterior nasal aperture left	2	10
Inion (i)	Condylus occipitalis	Orbital rim right	3	19
Staphylion (sta)	Entoglenoid mesial (egm)	Orbital rim left	4	19
Orale (ora)	Mastoid process (mp)	R_Temp	5	19
Rhinion (rh)	Frontomalare-temporale (fmt)	L_Temp	6	19
Temporal lines contact (tlc)	Jugale (ju)	R_Front_temp_zyg	7	9
	Entoglenoid distal (egd)	L_Front_temp_zyg	8	9
	Condylus occipitalis	rh_to_n	9	4
	P ⁴ _M ¹ lingual	n_to_g	10	4
	M ¹ _M ² lingual	Midsagittal	11	39
	M ² _M ³ lingual	i to (opistion)	12	20
	P ³ root	copR to cop antR	13	9
	P ⁴ root	cop_antR to copR	14	9
	M ² root	copL to cop antL	15	9
	M ³ root	cop_antL to copL	16	9
	M1 root 1st	Total semilandmarks on curves		217
	M1_root 2nd	Total semilandmarks on surface		490
	Canine Vestibular (Cv)			
	Canine Lingual			

* Landmarks identifiable on the left and right sides.

** Semilandmarks identified on the curves.

Supplementary Note 3. Landmarks used for missing part integration-Sts 5. List of anatomical landmarks and curves of the Sts 5 template (*A. africanus* = 632 (semi)landmarks).

Unpaired landmarks	Paired landmarks*	Curve names	N	Smlm count**
Glabella (g)	Anterior eminence (ae)	Anterior nasal aperture left	1	10
Inion (i)	Condylus occipitalis posterior (cop)	Anterior nasal aperture right	2	10
Staphylion (sta)	Entoglenoid (eg)	Median nuchal line	3	9
Rhinion (rh)	Frontomale-orbitale (fmo)	Foramen magnum rim left	4	9
Basion (ba)	Frontomale-temporale (fmt)	Foramen magnum rim right	5	9
Opisthion (op)	Frontotemporale (ft)	Lower zygomatic arc left	6	20
Incisive foramen (if)	Mastoid process (mp)	Lower zygomatic arc right	7	20
	Porion (po)	Midsagittal	8	39
		Orbital rim left	9	19
		Orbital rim right	10	19
		Palatine suture	11	19
		Rhinion_to_glabella (Sellion)	12	9
		Temporal line left	13	9
		Temporal line right	14	9
		Upper zygomatic arc and superior nuchal line left	15	39
		Upper zygomatic arc and superior nuchal line right	16	39
		Total semilandmarks on curves		288
		Total semilandmarks on surface		320

* Landmarks identifiable on the left and right sides.

** Semilandmarks identified on the curves.

Supplementary Note 4. Landmarks used for missing part integration-A.L. 444-2. List of anatomical landmarks and curves of the A.L. 444-2 template (*A. afarensis* = 549 (semi)landmarks).

Unpaired landmarks	Paired landmarks*	Curve names	N	Smlm count**
Rhinion (rh)	Frontomolare-orbitale (fmo)	Midsagittal	1	19
Nasion (n)	Frontomolare-temporale (fmt)	Glabella to nasion	2	1
Glabella (g)	Frontotemporale (ft)	Nasion to rhinion	3	2
Inion (i)	Jugale (ju)	Median nuchal line	4	4
Opisthion (o)	Anterior eminence (ae)	Palatine suture	5	9
Basion (ba)	Porion (po)	Orbital rim right	6	9
Stafilion (sta)	Entoglenoid distal (egd)	Orbital rim left	7	9
Incisive foramen (if)	Entoglenoid mesial (egm)	Anterior nasal aperture right	8	5
	Condylus occipitalis anterior (coa)	Anterior nasal aperture left	9	5
	Condylus occipitalis posterior (cop)	R_coa_to_cop_int	10	4
	Mastoid process (mp)	R_cop_to_coa_ext	11	4
	M2_M3	L_coa_to_cop_int	12	4
	M1_M2	L_cop_to_coa_ext	13	4
	P4_M1	Temporal line left	14	4
		L_fmt_to_ju	15	4
		Temporal line right	16	4
		R_fmt_to_ju	17	4
		L_lower_zy_arch	18	20
		R_lower_zy_arch	19	20
		Upper zygomatic arc and superior nuchal line left	20	39
		Upper zygomatic arc and superior nuchal line right	21	39
		Total semilandmarks on curves		213
		Total semilandmarks on surface		300

* Landmarks identifiable on the left and right sides.

** Semilandmarks identified on the curves.

Supplementary Note 5. Landmarks used for missing part integration-KNM-WT 17000. List of anatomical landmarks and curves of the KNM-WT 17000 template (*P. aethiopicus* = 313 (semi)landmarks).

Landmarks	Curve names	N	Smlm count**
Glabella (g)	Rhinion to nasion	1	4
Nasion (n)	Nasion to glabella	2	4
Inion (i)	Glabella to temporal line contact	3	9
Porion (po)	Midsagittal (tlc to i)	4	19
Rhinion (rh)	Temporal line	5	19
Temporal line contact (tlc)	Orbital rim	6	19
Frontomalare-orbitale left (fmol)	Lower zygomatic arc	7	30
Frontomalare-temporale left (fntl)	Anterior nasal aperture	8	10
Anterior eminence left (ael)	Upper zygomatic arc and superior nuchal line	9	39
Entoglenoid external left (egl)	Total semilandmarks on curves		153
Foramen infraorbitale (foril)	Total semilandmarks on surface		147
Incisive foramen (if)			
Anterior nasal spine (ans)			

* Landmarks identifiable on the left and right sides.

** Semilandmarks identified on the curves.

Supplementary Note 6. Morphological comparisons with *A. anamensis*

Comparisons between the MRD cranium and *A. anamensis* are limited due to minimal anatomical overlap between the samples. Diagnostic morphology of the upper canine, maxilla, and a small portion of the temporal can be evaluated. The majority of comparative work has focused on differentiating *A. anamensis* from *A. afarensis*, whereas differences among *A. anamensis* and more primitive taxa are less well characterized.

6.1. Canine morphology

Previous work has established that the upper canines of *A. anamensis* and more primitive hominins are relatively larger and more MD elongated than those of *A. afarensis* and later species¹⁻⁴. Differences in qualitative features of the crown have also been described. These evolutionary changes have long been related to the loss of the C-P₃ honing complex—a transformation that began at or near the origins of the Hominini and continued over millions of years.

The MRD canine exhibits morphology that is most similar to *A. anamensis*, and clearly more primitive than *A. afarensis*. With regard to relative size ($\sqrt{\text{MD} \times \text{BL}} / \text{M}^1 \text{MD}$), the MRD value falls between *A. ramidus* and *A. anamensis*, and more than five standard deviations larger than the *A. afarensis* mean (see main text, Fig. 3b). The MRD value is most similar to an *A. ramidus* specimen from the Western Margin of Gona (GWM9N/P51)^{5,6} and slightly larger than ASI-VP-2/334 (the relatively largest *A. anamensis* canine preserving the measured dimensions)⁷. The MRD canine is also MD elongated, with basal dimensions most similar to ASI-VP-2/334. Previous work used regression analysis to quantify differences in basal dimensions among taxa and showed that a relatively MD elongated shape characterizes *A. anamensis*^{1,8}, a feature which

also distinguishes it from *A. ramidus* as well⁷. The MRD canine falls very close to the regression line describing the *A. anamensis* pattern (see Figure 3a in Main Text).

Qualitative morphological features of the MRD canine crown are also consistent with *A. anamensis*. In lingual view, a basal bulge (the lingual basal tubercle) connects short, stub-like mesial and distal basal tubercles. The tubercles diverge occlusally, so that these structures connect in a parabolic shape. In *A. afarensis*, the homologous mesial and distal structures are sub-parallel so that a U-shape is produced (Figure 3c in Main Text). A further difference is that in *A. afarensis* the mesial shoulder is longer than the distal one, which also appears to be true of *A. ramidus*⁸⁻¹⁰.

6.2 Canine Orientation

In the initial diagnosis, *A. anamensis* was distinguished from *A. afarensis* in possessing a vertically oriented upper canine and midface¹¹. This characterization of *A. anamensis* was based on a single specimen (KNM-KP 29283). Subsequent work described the existence of some overlap in these features, following the recognition of considerable variation in the *A. afarensis* sample⁸ and the discovery of additional *A. anamensis* maxillae^{7,12}. The two maxillae currently known from Kanapoi (an older and younger individual) both exhibit the vertical morphology, but it is not as pronounced in the *A. anamensis* maxilla from the Middle Awash. The balance of current evidence suggests that Kanapoi *A. anamensis* differs from *A. afarensis* on average, though the samples overlap in range of variation. However, sample size is small and it remains unclear whether this vertical morphology is diagnostic of the species generally or characterizes the Kanapoi site-sample specifically.

The MRD canine and midface are posteriorly inclined, differing qualitatively from KNM-KP 29283 and -KP 58579. To further investigate the magnitude of this difference and its taxonomic significance, we compared canine implantation angle in MRD, KNM-KP 29283 and a comparative sample of extant *G. gorilla* (n=15) and *P. troglodytes* (n=18). Canine implantation was measured as the 2D angle formed between the canine root and the internal alveolar plane (Extended Data Figure 5). Data were collected using CT scans (MRD and the extant comparative sample) and a surface scan of KNM-KP 29283. The internal alveolar plane was defined as the plane best-fit to three landmarks lying at the apex of the alveolar bone visible between tooth crowns (lingually). These landmarks are positioned 1) between left P³ and P⁴, 2) between right P³ and P⁴, and 3) between left M¹ and M². Upper canines were segmented from CT scans and landmarks placed at the root tip and at the occlusal-most incursion along the distal enamel line. The landmarks can be securely estimated from KNM-KP 29283 in its preserved state, because the alveolar bone is flaked away on the right side and the root is exposed. To assess the effect of the uncertainty of this estimation, we considered other possible placements of the KNM-KP 29283 canine landmarks, but the angular measurement was affected only minimally.

Canine implantation between MRD and KNM-KP 29283 differ by about 12° (Extended Data Figure 5; Supplementary Table S6.1). We used a permutation approach (n = 500) to investigate the probability that two randomly sampled conspecific individuals could differ by the magnitude observed between the fossils. Permutation was implemented in the R statistical platform. Using a *Pan troglodytes* comparative sample, we found that such a magnitude (or larger) occurred in 6.6% of our permutations. The probability was higher for the more variable *Gorilla gorilla* comparative sample, at 19%. These comparisons suggest that the difference in canine orientation

between MRD and KNM-KP 29283 is consistent with the magnitude of variation in a single living species.

This approach uses extant comparative samples as the ‘yardstick’ by which differences between fossils are judged. Extant samples lack the geographic and chronological variation inherent in different fossil site-samples and will tend to underrepresent the magnitude of variation acceptable in a fossil species¹³⁻¹⁵. This issue would lead to the tendency to reject the null hypothesis of conspecificity when a paleospecies is varying through time and space. However, even using this conservative approach, we failed to reject the null hypothesis. Qualitative observations suggest that other fossil hominins like *A. afarensis* exhibit similar levels of variation⁸.

Still, the difference of 12° between MRD and KNM-KP 29283 is notable. It is equivalent to two or more standard deviations in the comparative samples. These comparisons are consistent with multiple explanations. One possibility is that the fossils come from *A. anamensis* populations that differed slightly in their average morphology due to differences in time or space. Another possibility is that the fossils fall toward opposite extremes of an *A. anamensis* distribution that is similarly variable as described here for extant African apes

Supplementary Table S6.1. Upper canine implantation measurements. Measured implantation angle in extant African apes, the *A. anamensis* paratype KNM-KP 29283 and MRD. SD: standard deviation.

	<i>Gorilla gorilla</i>	<i>Pan troglodytes</i>	KNM-KP 29283	MRD-VP-1/1
<i>n</i>	15	18	--	--
mean	80.7	76.9	88.9	76.4
SD	6.4	5.0	--	--
min	72.2	68.1	--	--
max	94.1	84.4	--	--

6.3 Maxillary arcade shape

The *A. anamensis* maxilla exhibits narrow-set, roughly parallel postcanine tooth rows. The canine is aligned with the postcanine row so that these teeth comprise a nearly straight line. These features make the *A. anamensis* arcade shape more primitive than *A. afarensis*, which shows wider-set and more divergent postcanine rows in conjunction with a canine that is slightly medially offset^{8,12}. The palate shape index (internal breadth at M² / ol-sta length × 100) indicates that the MRD maxilla is narrower than in *A. afarensis* and later hominins (Supplementary Note 7). The MRD canine is also aligned with the postcanine row (similar to KNM-KP 29283, but not to the extent seen in KNM-KP 58759 and KNM-ER 30745), rather than medially offset as in *A. afarensis* specimens like A.L. 199-1 and A.L. 444-2 (Extended Data Figure 6). Calculation of palatal wedging indicates that the MRD arcade is slightly more divergent than *A. anamensis* specimens KNM-KP 29283 and KNM-ER 30745, but the collective range from the three specimens is consistent with intraspecific variation in the comparative samples (Supplementary Note 7).

6.4 Nasoalveolar morphology

A. anamensis is further distinguished from *A. afarensis* in the structure of the lateral nasal margin. This margin tends to be thin and sharp in *A. afarensis*¹⁶, but rounded in *A. anamensis* due to the confluence of a pronounced canine jugum^{8,11,12}. This margin is also rounded in MRD—the canine root is located well lateral to the lateral nasal margin but the jugum and its superior extension tilt superomedially to contribute to the margin beginning just below the level of alare. *A. africanus* also shows a rounded lateral nasal margin, but this is due to a distinct morphological pattern associated with the “anterior pillar”^{17,18}. MRD morphology is distinct from the anterior pillar of *A. africanus* in that a “maxillary furrow” does not demarcate the lateral limit of the canine jugum, the P³ and canine juga are separated, the canine jugum surface is directed predominately laterally (rather than anteriorly), and there is a fairly smooth transition between the lateral nasal and infraorbital surfaces.

6.5 Temporal morphology

The squamosal suture of MRD is low and only slightly arched unlike in *A. afarensis*. It also has weakly developed articular tubercles and a postglenoid process that is fused to the tympanic. Some of these features are variably expressed in earlier and later hominins. Only a handful of cranial fragments are known for *A. anamensis*. Of these, the most informative is a temporal fragment (KNM-KP 29281B) associated with the holotype mandible¹¹. MRD and KNM-KP 29281B have a small external acoustic meatus (EAM), though the dimensions cannot be measured precisely on MRD due to damage (but see Main Text). The temporal squama and posterior origin of the zygomatic process are highly pneumatized in both specimens. Both of these features are interpreted as plesiomorphic for hominins. The articular tubercles are only weakly developed and the postglenoid process is fused to the tympanic.

Supplementary Note 7. Measurements of the maxilla in early hominins and African apes.
Deformation has slightly altered the MRD maxilla. We provide values for the original MRD specimens, as preserved, and from the symmetrized reconstruction (MRD-sym). Also see Supplementary Note 4.

	Palate Depth ¹					Palatal Wedging ²					Palate Shape Index ³				
	n	mean	SD	min	max	n	mean	SD	min	max	n	mean	SD	min	max
<i>P. troglodytes</i>						24	-3.0	3.0	-8.7	3.8					
<i>G. gorilla</i>						24	-5.9	2.7	-11.2	-0.7					
<i>A. anamensis</i>															
KNM-KP 29283	1	11.5	--	--	--	1	-1.4	--	--	--	--	--	--	--	--
KNM-ER 30745	--	--	--	--	--	1	0.3	--	--	--	--	--	--	--	--
MRD (original)	1	17.4	--	--	--	1	1.1	--	--	--	1	46.5	--	--	--
MRD-sym	--	--	--	--	--	1	4.6	--	--	--	1	47.5	--	--	--
<i>A. afarensis</i>	6	11.3	1.8	8.5	14.0	7	7.0	4.4	-1.7	12.9	4	53.7	4.4	49.1	59.3
<i>A. africanus</i>	3	16.2	1.8	14.5	18.0	3	10.2	3.5	6.4	13.4	3	55.2	3.8	51.7	59.3
<i>P. robustus</i>	5	13.8	1.4	12.2	15.5	--	--	--	--	--	1	57.7	--	--	--
<i>P. boisei</i>	3	21.0	1.0	20.0	22.0	--	--	--	--	--	4	52.3	9.2	48.3	56.7

¹ Depth at M¹/M². Data from ref. 16, for most comparative specimens. The KMN-KP 29283 value is the averaged the M¹ and M² depths reported by ref. 8. The *A. africanus* sample includes values for Sts 5 and StW 73/22 reported by ref. 16 and an estimate for Sts 17 made by the authors.

² Comparative data from ref. 8 and references therein for all comparative samples except *A. africanus*. Data for the latter species were collected by the authors and include observations for Sts 5, Sts 17 and StW 73/22.

³ Internal breadth at M²/ol-sta × 100. Comparative data from ref. 16.

Supplementary Note 8. Masticatory Indices. Indices expressing the configuration of the masticatory system^{16,18}. Values reported for MRD-sym represent the average from left and right sides. Parentheses indicate estimation.

	Palate protrusion anterior to sellion			Position of anterior masseter			Overlapping index			Masseteric height / vertical facial height		
	n	mean	SD (range)	n	mean	SD (range)	n	mean	SD (range)	n	mean	SD (range)
<i>P. troglodytes</i>	12	67	6 (58-77)	12	90	6.5 (79-102)	12	15	3 (10-18)	20	27	4 (21-34)
<i>G. gorilla</i>	12	67	5 (58-78)	12	91	9 (79-106)	12	17	5 (8-24)	20	30	4 (24-38)
MRD-sym	1	69	--	1	118	--	1	46	--	1	36	--
<i>S. tchadensis</i>	1	(47)	--	--	--	--	--	--	--	1	28	--
<i>A. ramidus</i>	--	--	--	--	--	--	1	(26)	--	1	27	--
<i>A. afarensis</i>	2	57	-- (55-59)	1	97	--	1	26	--	2	31	-- (29-32)
<i>A. africanus</i>	2	55	-- (43-68)	2	98	-- (93-103)	2	31	-- (22-40)	2	36	-- (35-37)
<i>P. aethiopicus</i>	1	82	--	1	148	--	1	28	--	1	36	--
<i>P. robustus</i>	1	46	--	1	119	-- 15	1	50	--	1	40	--
<i>P. boisei</i>	3	43	9 (35-53)	3	113	(100- 130)	3	50	7 (43-57)	3	34	-- (30-37)

Supplementary Note 9. Phylogenetic analyses

Cladistic methods are commonly used to investigate the phylogenetic position of early hominin taxa^{16,19,20}. Although the anatomical composition of the *A. anamensis* hypodigm has been a limiting factor in inferring its evolutionary relationships, it is consistently placed phylogenetically between the more primitive species *A. ramidus* and the more derived *A. afarensis*^{4,7,8,11,20,21}. The anagenetic series *A. ramidus*- *A. anamensis*- *A. afarensis* has been proposed, and the latter relationship is widely accepted^{4,7,22}. Few apomorphies are known for *A. anamensis*^{8,22} and this species is generally understood as a plesiomorphic extension of the *A. afarensis* lineage²². The addition of MRD to the *A. anamensis* hypodigm allows a more complete analysis of its phylogenetic position. Given previous work, we were particularly interested in whether these new observations continue to support the portrayal of *A. anamensis* as a species lacking apomorphies, and the hypothesized anagenetic relationship with *A. afarensis*.

Using Kimbel et al. (ref. 16) and Strait and Grine (ref. 20) character traits and scores, we conducted cladistic analyses in two ways: by combining MRD with the known *A. anamensis* material (K-combined and S&G-combined) and by treating MRD as its own operational taxonomic unit (K-separate and S&G-separate). Further information about the analysis is presented in the Methods section and in Extended Data Table 1.

9.1 Topology

The K-combined and S&G-combined analyses both return a single most parsimonious tree in which the MRD-*A. anamensis* operational taxonomic unit (OTU) appears as the sister taxon to a clade including *A. afarensis* and all later hominins (Figure 5 in main text, Extended Data Figure 9). The results reinforce widely accepted topology and are consistent with geochronological data.

The results of the K-separate and S&G-separate analyses differ only slightly (Extended Data Figure 9). In the K-separate analysis, two equally parsimonious trees result (Extended Data Figure 9a-b). The first has topology identical to the K-combined analysis and the second places *A. afarensis* as the most basally branching taxon (with MRD appearing in the clade with later hominins). The S&G-separate analysis returns three equally parsimonious trees that differ only in the relative positions of MRD and the pre-2004 *A. anamensis* OTUs (Extended Data Figure 9c-e). These results show that the phylogenetic position of *A. anamensis* is generally stable, regardless of whether cranial, dentognathic, or overall skull morphology is considered.

9.2 Pattern of morphological evolution

The inclusion of MRD in *A. anamensis* alters our understanding of the pattern of the evolution of cranial morphology in early australopiths. The portrayal of *A. anamensis* as a more primitive predecessor of the *A. afarensis* lineage is based primarily on dentognathic observations.

Following this line of reasoning, one might also expect that any cranial differences between *A. anamensis* and *A. afarensis* would be a matter of the former exhibiting slightly more ape-like morphology. The MRD cranium meets this expectation in some ways. Supplementary Table S9.1 provides a list of features that are more primitive in MRD than in *A. afarensis* and most other australopiths, according to the K-combined and S&G-combined results. Additional plesiomorphic features of MRD not included in these analyses include the transverse convexity of the cranial base and length of nuchal plane relative to its breadth (see Extended Data Figures 7-8).

However, cranial morphology of MRD suggests that *A. anamensis* exhibited more apomorphic features than previously recognized. The apomorphy list for the MRD-*A. anamensis* OTU is

provided in Supplementary Table S9.2. The K-combined analysis implies that the anterior position of the masseter origin and the topographic relief of the infraorbital region in MRD- *A. anamensis* are apomorphic. The S&G-combined analysis implies a longer list of apomorphies that similarly includes infraorbital topography and aspects of masseter origin position.

Results of the K-combined and S&G-combined analyses differ such that the most parsimonious solution from the K-combined dataset indicates that a majority of the differences between *A. anamensis* and *A. afarensis* accumulated along the *A. afarensis* lineage (Extended Data Figure 9f), while results from the S&G-combined dataset imply more apomorphic features for *A. anamensis* (Extended Data Figure 9g). The difference is likely due to the fact that the character matrices differ in the number of terminal taxa. Fewer taxa are included in the Kimbel dataset, so the addition of MRD tends to strongly influence the morphology reconstructed at nodes common to early hominins (i.e. nodes A and B in Extended Data Figure 9f-g). As a result, stem hominin morphology more closely resembles MRD in the K-combined results, compared to the S&G-combined results.

Thus, the phylogenetic analyses presented above suggest that the *A. anamensis* cranium (as newly documented by MRD) possessed multiple apomorphies, which are concentrated in the facial region. The apomorphic features may be limited to masseter position and facial topography or they may be more extensive and include aspects of zygomatic shape and temporal line position. Their appearance in MRD is unexpected due to their traditional association with masticatory robusticity. Although these features in MRD anticipate morphology present in *A. africanus* and some robust species, the most parsimonious solution indicates that they are independently derived in *A. anamensis* and in later hominins.

9.2.1 Apomorphies of *A. afarensis*

The apomorphy list for *A. afarensis* is provided in Supplementary Table S9.3. The K-combined apomorphy list is largely consistent with previous results, but notable differences are present in the form of polarity changes. Kimbel et al. (ref. 16) recognize the low masseter origin (low, arched zygomaticoalveolar crest) and the posterior emphasis of the temporalis muscle present in *A. afarensis* as primitive features. Our results, in contrast, depict these features as being derived in *A. afarensis* and homoplastic with *Pan/Gorilla*. The MRD cranium thus raises some questions about the polarity of features of the hominin face. Future discoveries will hopefully clarify whether the morphology present in MRD face is generally characteristic of *A. anamensis* and the primitive condition for the *Australopithecus* lineage.

A notable feature appearing on the K-combined apomorphy list is reduced postorbital constriction. Kimbel and colleagues¹⁶ hypothesized that a lack of pronounced postorbital constriction is derived in *A. afarensis*, but noted that the polarity could change depending on future discovery of an *A. anamensis* frontal^{16,22}. The frontal morphology of MRD supports this hypothesis. Both K-combined and S&G-combined results imply that pronounced constriction is the primitive condition (present in node A) and a wider postorbital region is derived in *A. afarensis*. However, due to differences in the way these authors scored *A. africanus*, a wider postorbital region appears as an independently derived feature of *A. afarensis* in the K-combined results, but as a derived feature shared between *A. afarensis* and *A. africanus* in the S&G-combined results.

Supplementary Table S9.1. MRD-*A. anamensis* plesiomorphy list. These features are more primitive in MRD and at node A, compared to *A. afarensis* and node B. See Extended Data Figure 9f-g for labeled nodes.

Character Label	Description of MRD- <i>A. anamensis</i> plesiomorphy
<u>K-combined</u>	
9	Pronounced subnasal prognathism‡
11	Pronounced midfacial prognathism‡
14	Somewhat flattened squamosal suture
20	A large canine accompanied by dull nasal margins
75	Relatively large canine
<u>S&G-combined</u>	
SG26	Pronounced postorbital constriction
SG65	Small external auditory meatus

‡ indicates plesiomorphies that are homoplastic *P. aethiopicus*.

Supplementary Table S9.2. MRD-*A. anamensis* apomorphy list. These features are derived along the MRD-*A. anamensis* branch, relative to node A. See Extended Data Figure 9f-g for labeled nodes.

Character Label	Description of MRD- <i>A. anamensis</i> apomorphy
<u>K-combined</u>	
10	The masseter origin projects more anteriorly (high masseter position index)*
22	Topographic changes in the infraorbital region are present (“nasomaxillary basin”-like morphology)
<u>S&G-combined</u>	
SG9	High masseter origin*
SG11	Unique topography of the midface
SG12	Variable presence of anterior palatal shelving*
SG19	Strong anteromedial incursion of the superior temporal lines*
CW2	Very long and inclined post-incisive planum
CW20	More frontal orientation of the zygomatic bone

* indicates evolutionary changes that are homoplastic with later hominins

Supplementary Table S9.3. *Australopithecus afarensis* apomorphy list. These features are derived along the *A. afarensis* branch, relative to node B. See Extended Data Figure 9f-g for labeled nodes.

Character Label	Description of <i>A. afarensis</i> apomorphy
<u>K-combined</u>	
4	Posterior “segmentation” of calvarial contour*
7	Very anterior position of foramen magnum*
16	Relatively high squamosal suture*
18	Low masseter origin (low, arched zygomaticoalveolar crest)†
19	Face very broad across the zygomatics (measured in the orbital plane)*
21	Vertical infraorbital plate*
25	Narrow interorbital breadth
30	Posterior emphasis of the temporalis muscle†
32	Marginal venous sinus pattern*
33	Tucked cerebellum*
35	Thick calvarial bone*
40	Wide postorbitally*
52	Postglenoid process and tympanic separate*
65	Deeply excavated temporal surface of the zygomatic
77	Molar cusps positioned near occlusal margins†
<u>S&G-combined</u>	
SG18	Occipito-marginal sinus present in high frequency*
SG33	Postglenoid process is large and positioned anteriorly†
SG69	Articular eminence positioned near occlusal plane

* indicates evolutionary changes that are homoplastic with later hominins

† indicates evolutionary changes that are homoplastic with the outgroup or more primitive nodes

Supplementary Note 10. Taxonomic affinity of the BEL-VP-1/1 frontal bone

The Belohdelie frontal (BEL-VP-1/1) was described by Asfaw and colleagues and later precisely dated to $3.89 \pm 0.02 - 3.85 \pm 0.03^{23,24}$. Asfaw²³ assigned the specimen to *A. aff. afarensis*, which was the oldest hominin species known at the time. However, the taxonomic assignment was provisional because only a small sample of comparative specimens were available from Hadar and even these were considerably younger than BEL-VP-1/1. The discovery of *A. anamensis* showed that another hominin species in eastern Africa was closer to BEL-VP-1/1 in age, but no morphological comparisons were possible due to the lack of an *A. anamensis* frontal bone^{16,22}. The MRD cranium has a well-preserved frontal associated with maxilla and canine morphology that is diagnostic of *A. anamensis* and presents the first opportunity to reconsider the taxonomic attribution of BEL-VP-1/1.

Kimbel et al.¹⁶ described similarities (see above) between BEL-VP-1/1 and known *A. afarensis* frontals^{16,22}. The discovery of the A.L. 444-2 cranium from Hadar, further confirmed the observation that *A. afarensis* frontals and the specimen from Belohdelie lack pronounced postorbital constriction²⁵. However, Kimbel et al.²² also noted that an *A. anamensis* frontal would be required to determine whether the similarities were taxonomically informative or simply shared primitive features. MRD (as well as the *S. tchadensis* cranium) is characterized by the primitive state of pronounced constriction, whereas BEL-VP-1/1 shares derived morphology with other *A. afarensis* specimens such as A.L. 444-2. This observation supports its original assignment to *A. afarensis*. Therefore, the phylogenetic considerations presented above indicate that postorbital constriction is indeed informative in differentiating *A. afarensis* from *A.*

anamensis. Further, postorbital constriction is minimally dimorphic²⁶, making it unlikely that the differences between BEL-VP-1/1 and MRD-VP-1/1 are results of sexual dimorphism.

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