New hominin genus from eastern Africa shows diverse middle Pliocene lineages

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Most interpretations of early hominin phylogeny recognize a single early to middle Pliocene ancestral lineage, best represented by *Australopithecus afarensis,* which gave rise to a radiation of taxa in the late Pliocene. Here we report on new fossils discovered west of Lake Turkana, Kenya, which differ markedly from those of contemporary *A. afarensis*, indicating that hominin taxonomic diversity extended back, well into the middle Pliocene. A 3.5 Myr-old cranium, showing a unique combination of derived facial and primitive neurocranial features, is assigned to a new genus of hominin. These findings point to an early diet-driven adaptive radiation, provide new insight on the association of hominin craniodental features, and have implications for our understanding of Plio–Pleistocene hominin phylogeny.

The eastern African hominin record between 4 and 3 Myr is represented exclusively by a single species, *A. afarensis*, and its possible ancestor, *Australopithecus anamensis*, which are commonly thought to belong to the lineage ancestral to all later hominins[1,2]. This apparent lack of diversity in the middle Pliocene contrasts markedly with the increasingly bushy phylogeny evident in the later hominin fossil record. To study further the time interval between 4 and 3 Myr, fieldwork in 1998 and 1999 focused on sites of this age at Lomekwi in the Nachukui Formation, west of Lake Turkana. New hominin discoveries from Lomekwi, as well as two mandibles and isolated molars recovered previously[3] (Table 1), indicate that multiple species existed between 3.5 and 3.0 Myr. The new finds include a well-preserved temporal bone, two partial maxillae, isolated teeth, and most importantly a largely complete, although distorted, cranium. We assign the latter specimen to a new hominin genus on the basis of its unique combination of primitive and derived features.

Description of *Kenyanthropus platyops*

Order Primates LINNAEUS 1758
Suborder Anthropoidea MIVART 1864
Superfamily Hominoidea GRAY 1825
Kenyanthropus gen. nov.

Etymology. In recognition of Kenya's contribution to the understanding of human evolution through the many specimens recovered from its fossil sites.

Generic diagnosis. A hominin genus characterized by the following morphology: transverse facial contour flat at a level just below the nasal bones; tall malar region; zygomaticoalveolar crest low and curved; anterior surface of the maxillary zygomatic process positioned over premolars and more vertically orientated than the nasal aperture and nasoalveolar clivus; nasoalveolar clivus long and both transversely and sagittally flat, without marked juga; moderate subnasal prognathism; incisor alveoli parallel with, and only just anterior to, the bicanine line; nasal cavity entrance stepped; palate roof thin and flexed inferiorly anterior to the incisive foramen; upper incisor (I^1 and I^2) roots near equal in size; upper premolars (P^3, P^4) mostly three-rooted; upper first and second molars (M^1 and M^2) small with thick enamel; tympanic element mediolaterally long and lacking a petrous crest; external acoustic porus small. *Kenyanthropus* can be distinguished from *Ardipithecus ramidus* by its buccolingually narrow M^2, thick molar enamel, and a temporal bone with a more cylindrical articular eminence and deeper mandibular fossa. It differs from *A. anamensis*, *A. afarensis*, *A. africanus* and *A. garhi* in the derived morphology of the lower face, particularly the moderate subnasal prognathism, sagittally and transversely flat nasoalveolar clivus, anteriorly positioned maxillary zygomatic process, similarly sized I^1 and I^2 roots, and small M^1 and M^2 crowns. From *A. afarensis* it also differs by a transversely flat midface, a small, external acoustic porus, and the absence of an occipital/marginal venous sinus system, and from *A. africanus* by a tall malar region, a low and curved zygomaticoalveolar crest, a narrow nasal aperture, the absence of anterior facial pillars, a tubular, long and crestless tympanic element, and a small, external acoustic porus. *Kenyanthropus* lacks the suite of derived dental and cranial features found in *Paranthropus aethiopicus*, *P. boisei* and *P. robustus* (Table 2), and the derived cranial features of species indisputably assigned to *Homo* (For example, *H. erectus s.l.* and *H. sapiens*, but not *H. rudolfensis* and *H. habilis*)[4].

Type species *Kenyanthropus platyops* sp. nov.

Etymology. From the Greek *platus*, meaning flat, and *opsis*, meaning face; thus referring to the characteristically flat face of this species.

Specific diagnosis. Same as for genus.

Types. The holotype is KNM-WT 40000 (Fig. 1a–d), a largely complete cranium found by J. Erus in August 1999. The paratype is KNM-WT 38350 (Fig. 1e), a partial left maxilla found by B. Onyango in August 1998. The repository is the National Museums of Kenya, Nairobi.

Localities. Lomekwi localities are situated in the Lomekwi and Topernawi river drainages in Turkana district, northern Kenya (Fig. 2). The type locality LO-6N is at 03° 54.03′ north latitude, 035° 44.40′ east longitude.

Horizon. The type specimen is from the Kataboi Member, 8 m below the Tulu Bor Tuff and 12 m above the Lokochot Tuff, giving an estimated age of 3.5 Myr. The paratype is from the lower Lomekwi Member, 17 m above the Tulu Bor Tuff, with an estimated age of 3.3 Myr.

Cranial description and comparisons

The overall size of the KNM-WT 40000 cranium falls within the range of *A. afarensis* and *A. africanus*. It is preserved in two main parts, the neurocranium with the superior and lateral orbital margins, but lacking most of the cranial base; and the face, lacking the premolar and anterior tooth crowns and the right incisor roots. Most of the vault is heavily distorted, both through post-mortem diploic expansion and compression from an inferoposterior direction (Fig. 1a, b). The better preserved facial part shows some lateral skewing of the nasal area, anterior displacement of the right canine, and some expansion of the alveolar and zygomatic processes (Fig. 1c–d), but allows for reliable assessment of its morphology.

Only the right M^2 crown is sufficiently preserved to allow reliable metric dental comparisons. It is particularly small, falling below the known ranges of other early hominin species (Fig. 3a). Likewise, the

Table 1 Hominin specimens from the lower Lomekwi and Kataboi Members

KNM-WT	Description	Year	Discoverer	Locality	Measurements (mm)
8556	Mandible fragment: symphysis, right body with RP_3–RM_1, isolated partial RM_2, RM_3, LP_3	1982	N. Mutiwa	LO-5	RP_3, 9.8, 12.4; RP_4, 11.3, 12.6; RM_1, 13.7, 12.9; RM_2, NA, NA; RM_3, (17.5), (14.1); LP_3, 9.8, 12.5
8557	$LM_{1/2}$	1982	N. Mutiwa	LO-4	NA, (11.5)
16003	RM^3	1985	M. Kyeva	LO-5	13.3, 14.6
16006	Left mandible fragment with M_2 fragment and M_3	1985	N. Mutiwa	LO-4E	M_2, NA, NA; M_3, 15.3, 13.1
38332	Partial RM^3 crown	1999	M. Eregae	LO-4E	NA, 14.8
38333	$LM_{1/2}$ crown	1999	M. Eregae	LO-4E	13.1, 12.1
38334	$LM_{1/2}$	1999	M. Eregae	LO-4W	12.1, 11.5
38335	$RM_{1/2}$ crown fragment	1999	M. Eregae	LO-4E	NA
38337	$RM^{1/2}$	1999	R. Moru	LO-4E	11.5, 12.3
38338	Partial $RM^{1/2}$ crown	1999	N. Mutiwa	LO-4E	NA
38339	$LM_{1/2}$ crown	1999	J. Erus	LO-4W	12.8, 12.7
38341	Partial $LM_{2/3}$	1999	G. Ekalale	LO-4E	NA
38342	$LM_{1/2}$ crown	1999	J. Erus	LO-4E	12.8, (11.3)
38343	Right maxilla fragment with I^2 and P^3 roots and partial C; mandible fragment with partial P_4 and M_1 roots	1999	J. Erus	LO-4W	NA
38344	$RM_{1/2}$ crown	1998	M. Eregae	LO-9	12.8, 12.2
38346	Partial $RM^{1/2}$	1998	M. Mutiwa	LO-5	NA
38347	LdM_2 crown	1998	R. Moru	LO-5	11.7, 9.6
38349	$RM_{1/2}$ crown	1998	W. Mangao	LO-5	13.5, 12.6
38350	Left maxilla fragment with P^3 and P^4 roots and partial M^1	1998	B. Onyango	LO-5	LM^1: (10.5), (12.0)
38352	Partial $RM_{1/2}$	1998	W. Mangao	LO-5	NA, 11.5
38355	Partial $RM^{1/2}$ crown	1998	M. Eregae	LO-9	NA
38356	Partial $RM^{1/2}$ crown	1998	M. Eregae & J. Kaatho	LO-9	12.8, NA
38357	$RM_{1/2}$	1998	G. Ekalale	LO-5	12.8, 11.8
38358	Associated RI^2, LM_2 fragment, LM_3, RM^3 fragment, four crown fragments	1998	G. Ekalale	LO-5	RI^2, 7.5, 7.5, 9.1; LM_3, 15.3, 13.2
38359	Associated RM_1, RM_2	1998	M. Eregae	LO-5	RM_1, 12.7, 11.6; RM_2, 13.9, 12.2
38361	Associated (partial) germs of I^1, LI^2, $R\underline{C}$, LRP^3, LRP^4	1998	R. Moru	LO-5	I^1, NA, (8.0), (11.5); LI^2, 7.6, >5.9, 8.3; LP^3, (9.3), (12.0)
38362	Associated partial $LM^{1/2}$, $RM^{1/2}$	1998	R. Moru	LO-5	$RM^{1/2}$, 12.9, 14.3
39949	Partial LP_4	1998	R. Moru	LO-5	NA
39950	RM_3	1998	R. Moru	LO-5	16.0, 14.5
39951	$RM_{1/2}$ fragment	1998	R. Moru	LO-5	NA
39952	$LM_{1/2}$	1998	R. Moru	LO-5	NA
39953	$LM_{1/2}$ fragment	1998	R. Moru	LO-5	NA
39954	Two tooth fragments	1998	R. Moru	LO-5	NA
39955	L_C fragment	1998	R. Moru	LO-5	NA
40000	Cranium	1999	J. Erus	LO-6N	RM^2, 11.4, 12.4
40001	Right temporal bone	1998	P. Gathogo	LO-5	NA

Dental measurements taken as in ref. 34. Mesiodistal crown diameter followed by buccolingual or labiolingual diameter, and for incisors and canines, labial crown height. Values in parentheses are estimates. NA, Not available. L or R in the 'Description' column indicates the left or right side. $\underline{C}$, upper canine; d, deciduous.

Table 2 Derived cranial features of *Paranthropus*, and their character state in *K. platyops* and *H. rudolfensis*

	Paranthropus aethiopicus	*Paranthropus boisei*	*Paranthropus robustus*	*Kenyanthropus platyops*	*Homo rudolfensis*
Upper molar size	Large	Large	Moderate	Small	Moderate
Enamel thickness	Hyperthick	Hyperthick	Hyperthick	Thick	Thick
Palatal thickness	Thick	Thick	Thick	Thin	Thin
Incisor alveoli close to bicanine line*	Present	Present	Present	Present	Present
Nasoalveolar clivus	Gutter	Gutter	Gutter	Flat	Flat
Midline subnasal prognathism	Strong	Moderate	Moderate	Weak	Weak
Upper I^2 root to lateral nasal aperture	Medial	Medial	Medial	Lateral	Lateral
Nasal cavity entrance	Smooth	Smooth	Smooth	Stepped	Stepped
Zygomaticoalveolar crest	Straight, high	Straight, high	Straight, high	Curved, low	Curved, low
Anteriorly positioned zygomatic process of maxilla*	Present	Present	Present	Present	Present
Midface transverse contour	Concave, dished	Concave, dished	Concave, dished	Flat	Flat
Malar region	Wide	Wide	Wide	Tall	Tall
Malar orientation to lateral nasal margin	Aligned	Aligned	Aligned	More vertical	More vertical
Facial hafting, frontal trigone	High, present	High, present	High, present	Low, absent	Low, absent
Postorbital constriction	Marked	Marked	Marked	Moderate	Moderate
Initial supraorbital course of temporal lines	Medial	Medial	Medial	Posteromedial	Posteromedial
Tympanic vertically deep and plate-like	Present	Present	Present	Absent	Absent
Position external acoustic porus	Lateral	Lateral	Lateral	Medial	Medial
Mandibular fossa depth	Shallow	Deep	Deep	Moderate	Moderate
Foramen magnum heart shaped	Present	Present	Absent	Absent	Absent
Occipitomarginal sinus	Unknown	Present	present	Absent	Absent

Hypodigm of *H. rudolfensis* as in ref. 35. See refs 1, 8, 11, 36–40 for detailed discussions of the features.
* Character states shared by *Paranthropus* and *K. platyops*.

estimated M^1 crown size of KNM-WT 38350 (Table 1) corresponds to minima for *A. anamensis*, *A. afarensis* and *H. habilis*, and is below the ranges for other African early hominins[5–7]. Molar enamel thickness in both specimens is comparable to that in *A. anamensis* and *A. afarensis*. CT scans show that both P^3 and P^4 of KNM-WT 40000 have a lingual root and two well-separated buccal roots. This morphology, thought to be the ancestral hominoid condition[8], is commonly found in *Paranthropus*, but is variable among species of *Australopithecus*. The P^3 of KNM-WT 38350 has three well-separated roots (Fig. 1e). Its P^4 seems to be two-rooted, but the deeply grooved buccal root may split more apically. Relative to M^2 crown size, the canine roots of KNM-WT 40000 are smaller in cross-section at the alveolar margin than in *Ardipithecus ramidus* and *A. anamensis*, similar in size to *A. afarensis*, *A. africanus* and *H. habilis*, and larger than in *P. boisei*. Exposed surfaces and CT scans demonstrate that the I^1 and I^2 roots in KNM-WT 40000 are straight and similar in size. At the level of the alveolar margin the cross-sectional area of the I^2 root is about 90% of that of the I^1 root, whereas this is typically 50–70% in other known hominid taxa.

The incisor alveoli of KNM-WT 40000 are aligned coronally, just anterior to the bicanine line, and the overlying nasoalveolar clivus is flat both sagittally and transversely. There is no canine jugum visible on the preserved left side, reflecting the modest size of the canine root. At 32 mm (chord distance nasospinale to prosthion) the clivus is among the longest of all early hominins. Subnasal prognathism is moderate, expressed by a more vertically orientated clivus than in nearly all specimens of *Australopithecus* and *Paranthropus* (Fig. 3b). The nasal aperture lies in the same coronal plane as the nasoalveolar clivus and there are no anterior facial pillars (Fig. 1a–c). The nasal aperture is small and narrow, in contrast to the large, wide aperture in *A. africanus* and *P. robustus*. The midface of KNM-WT 40000 is dominated by the tall malar region (Fig. 3c) with a low and curved zygomaticoalveolar crest. At a level just below the nasal bones the transverse facial contour is flat (Fig. 1b). In both KNM-WT 40000 and KNM-WT 38350 the anterior surface of the zygomatic process of the maxilla is positioned between P^3 and P^4 (Fig. 1a, d, e), as is commonly seen in *Paranthropus*, but more anteriorly than in most *Australopithecus* specimens[9] or in *H. habilis*. The supraorbital region is *Australopithecus*-like, lacking both a frontal trigon as seen in *Paranthropus*, and a supratoral sulcus as seen in *H. habilis* (but not *H. rudolfensis*). Relative postorbital constriction (frontofacial index) of KNM-WT 40000 is similar to that in *Australopithecus*, *H. rudolfensis* and *H. habilis*, and less than in *P. boisei* (estimated frontofacial index[9] = 70). Its temporal lines converging on the frontal squama have a posteromedial course throughout (Fig. 1b). Around bregma the midline morphology is not well preserved, but the posterior half of the parietals show double, slightly raised temporal lines about 6 mm apart. These contribute posteriorly to indistinct compound temporal/nuchal lines. The original shape of the severely distorted mastoids cannot be reconstructed, but other

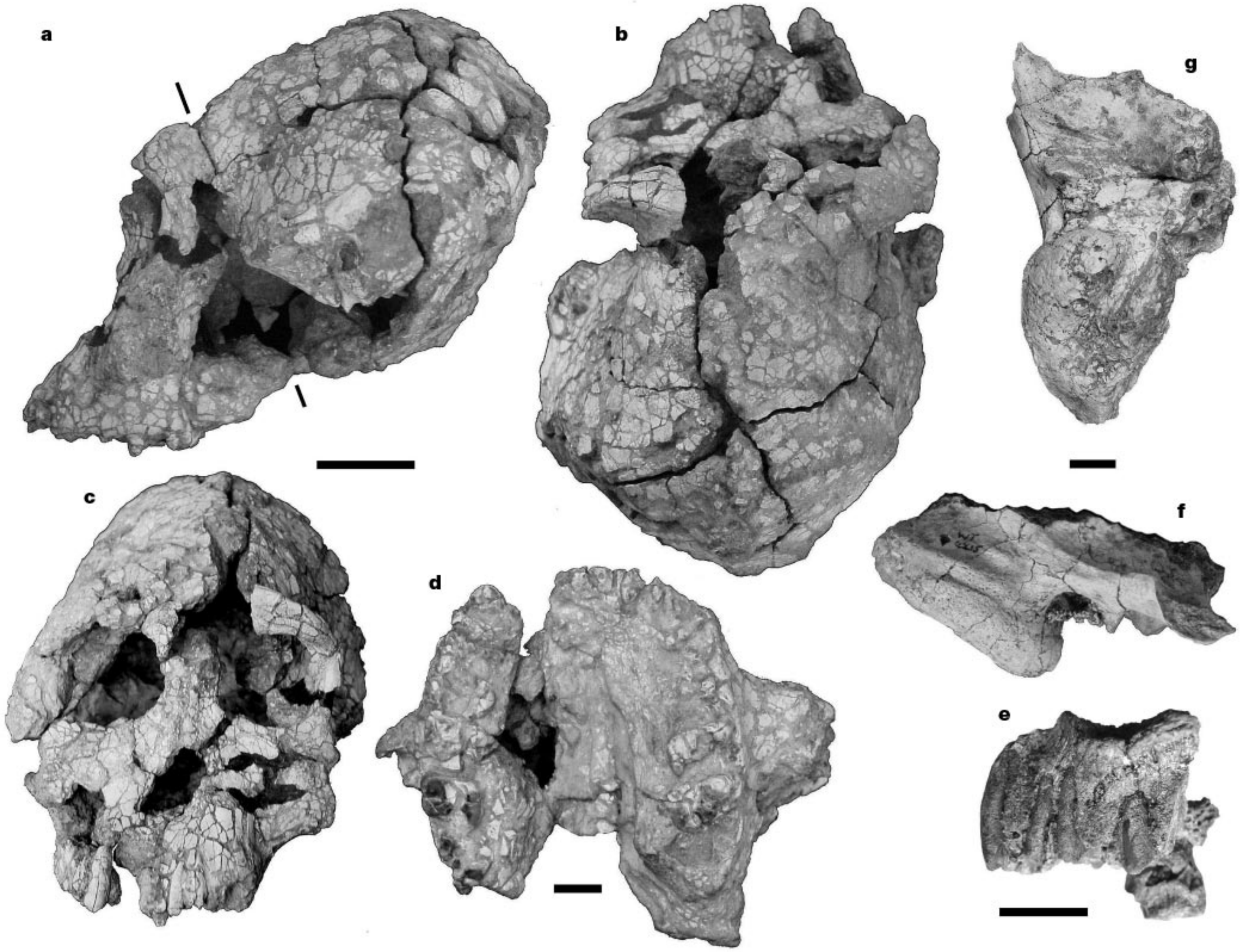

Figure 1 Holotype KNM-WT 40000 **a**, left lateral view (markers indicate the plane separating the distorted neurocranium and the well-preserved face). **b**, Superior view. **c**, Anterior view. **d**, Occlusal view of palate. Paratype KNM-WT 38350. **e**, Lateral view. KNM-WT 40001. **f**, Lateral view. **g**, Inferior view. Scale bars: **a**–**c**, 3 cm; **d**–**g**, 1 cm.

parts of the left temporal are well preserved. The tubular tympanic lacks a petrous crest and forms a narrow external acoustic meatus with a small aperture. This combination constitutes the primitive hominin morphology, also seen in *Ar. ramidus* and *A. anamensis* (Fig. 3d). The mandibular fossa resembles that of specimens of *A. afarensis* and *A. africanus*. It is moderately deep, and the articular eminence, missing its lateral margin, is cylindrical with a moderately convex sagittal profile. The preserved posterior half of the foramen magnum suggests that it was probably oval in shape, rather than the heart shape seen in *P. boisei* and probably *P. aethiopicus*. Regarding the endocranial aspect, the reasonably well preserved occipital surface lacks any indication of the occipital/marginal venous sinus system characteristic of *A. afarensis*, *P. boisei* and *P. robustus*. Bilateral sulci suggest that the transverse/sigmoid sinus system was well developed. Endocranial capacity is difficult to estimate because of the distorted vault. However, comparing hominin glabella–opisthion arc lengths[8] with that of KNM-WT 40000 (259 mm; an estimate inflated by diploic expansion) suggests a value in the range of *Australopithecus* or *Paranthropus*.

The sex of KNM-WT 40000 is difficult to infer. Interpretation of the canine root size proves inconclusive without a suitable comparative context. The small M^2 crown size could suggest that the specimen is female. However, the close proximity and slightly raised aspect of the temporal lines on the posterior half of the parietals is not seen in known female hominin crania, including the *Paranthropus* specimens KNM-ER 732, KNM-ER 407 and DNH7, and suggests that KNM-WT 40000 could be male.

With incisor alveoli close to the bicanine line and anteriorly positioned zygomatic processes, the face of KNM-WT 40000 resembles the flat, orthognathic-looking faces of both *Paranthropus* and *H. rudolfensis* cranium KNM-ER 1470. However, KNM-WT 40000 lacks most of the derived features that characterize *Paranthropus* (Table 2), and its facial architecture differs from the latter in much the same way as has been described for KNM-ER 1470 (refs 8, 10). Facial flatness in *Paranthropus* results from the forward position of the anteroinferiorly sloping malar region, whose main facial surface approximates the plane of the nasal aperture, but whose orientation contrasts with the more horizontally inclined nasoalveolar gutter[11]. In KNM-WT 40000 and KNM-ER 1470, it is the flat and orthognathic nasoalveolar clivus that aligns with the plane of the nasal aperture, whereas the anteriorly set, tall malar region is more vertically orientated. KNM-WT 40000 lacks the derived short nasal bones and everted lateral nasal margin of KNM-ER 1470, and is less orthognathic in the midfacial region than this specimen; however, on balance this is the hominin face that KNM-WT 40000 most closely resembles.

Additional material

The right maxilla fragment KNM-WT 38343A preserves three well-separated P^3 roots, and its damaged canine seems low-crowned when compared with *A. afarensis* canines of similar size and degree of wear. The right temporal bone KNM-WT 40001 lacks the squama and petrous apex, but is otherwise well preserved (Fig. 1f, g). It shows a combination of characters not seen in any other hominin specimen. The projecting mastoid process is rounded, with an anteriorly positioned tip. It has a well-developed digastric fossa in the form of a deep, narrow groove that runs posterolaterally from the stylomastoid foramen, fully demarcating the mastoid process from the adjacent nuchal plane. The tympanic element is long, inferosuperiorly shallow and lacks a petrous crest. The external acoustic porus is the smallest of any known hominin temporal bone (Fig. 3d). The articular eminence is as broad mediolaterally (38 mm) as in *P. aethiopicus* and *P. boisei*, and similar to the largest found in *A. afarensis*. Compared with KNM-WT 40000 the eminence is relatively flat sagittally, and the mandibular fossa is shallow.

The partial mandibles KNM-WT 8556 and KNM-WT 16006 have been assigned to *A. afarensis*[3]. However, KNM-WT 8556 shows a more derived morphology than this species by having a flat, more horizontal post-incisive plane, a more superiorly positioned genioglossal pit, a molarized lower fourth premolar (P_4) and a large M_3

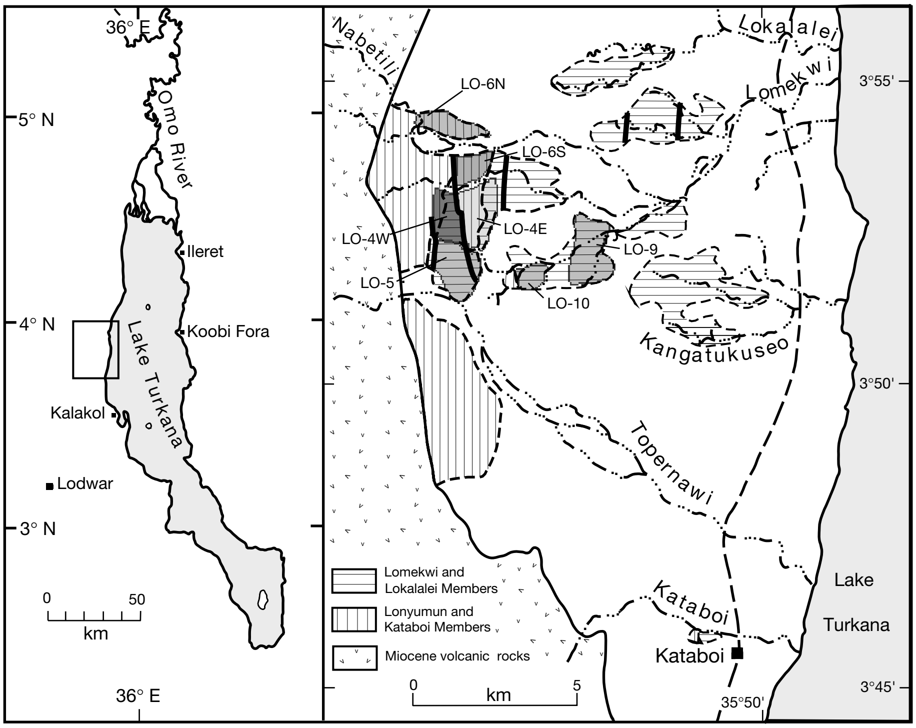

Figure 2 Map showing localities of fossil collection in upper Lomekwi and simplified geology. The boundary between the Kataboi and Lomekwi Members is the base of the Tulu Bor Tuff, indicated as a dashed line through LO-4E and LO4-W. Faults are shown as thick lines; minor faults are omitted. LO-4E and LO4-W are of different shades to distinguish them from each other.

(ref. 3). Indeed, relative to its *Australopithecus*-sized M_1 (refs 5, 6, 12, 13), the P_4 and M_3 crowns of KNM-WT 8556 are enlarged to an extent only seen in *P. boisei* (Fig. 3e, f). All unworn molars in the Lomekwi sample are characterized by low occlusal relief and numerous secondary fissures. Most of the lower molars, including the KNM-WT 16006 M_3, have a well-developed protostylid, a feature that is usually absent in *A. afarensis*, but common in *A. africanus*[14]. The two I^2s are lower crowned than in *A. afarensis*, *A. africanus*[14] and *P. robustus*[14]. Inability to distinguish between first and second molars makes meaningful intertaxon comparisons of these elements difficult.

Taxonomic discussion

The hominin specimens recovered from the Kataboi and lower Lomekwi Members show a suite of features that distinguishes them from established hominin taxa, including the only contemporaneous eastern African species, *A. afarensis*. Compared with the latter, the morphology of *K. platyops* is more derived facially, and more primitive in its small external acoustic porus and the absence of an occipital/marginal sinus system. These finds not only provide evidence for a taxonomically more diverse middle Pliocene hominin record, but also show that a more orthognathic facial morphology emerged significantly earlier in hominin evolutionary history than previously documented. This early faciodental diversity concerns morphologies that functionally are most closely associated with mastication. It suggests a diet-driven adaptive radiation among hominins in this time interval, which perhaps had its origins considerably earlier. Furthermore, the presence in *K. platyops* of an anteriorly positioned zygomatic process in combination with a small M^1 and M^2 indicates that such characters are more independent than is suggested by developmental and functional models that link such facial morphology in *Paranthropus* with postcanine megadontia[11,15].

At present it is unclear whether the Lomekwi hominin fossils sample multiple species. Apart from the paratype maxilla KNM-WT 38350 with its small molar size and anteriorly positioned zygomatic process, the other specimens cannot be positively associated morphologically with the *K. platyops* holotype. These are therefore not included in the paratype series, and are left unassigned until further evidence emerges. Differences between the tympanic and mandibular fossa morphologies of the KNM-WT 40000 and KNM-WT 40001 temporal bones can perhaps be accommodated within a single species, but their shared primitive characters do not necessarily imply conspecificity. Affiliation of the KNM-WT 8556 mandible with the *K. platyops* types is not contradicted by its molarized P_4, which is consistent with an anteriorly positioned zygomatic process. However, its M_1 is larger than would be inferred from the smaller upper molars of the types, and with a 177 mm^2 crown area it is also larger than any in the combined sample of ten isolated M_1s and M_2s (139–172 mm^2). One isolated $M^{1/2}$ (KNM-WT 38362) is significantly larger than the molars of the *K. platyops* types, whereas another (KNM-WT 38337) is similar in size to the holotype's M^2.

The marked differences of the KNM-WT 40000 cranium from established hominin taxa, both with respect to individual features

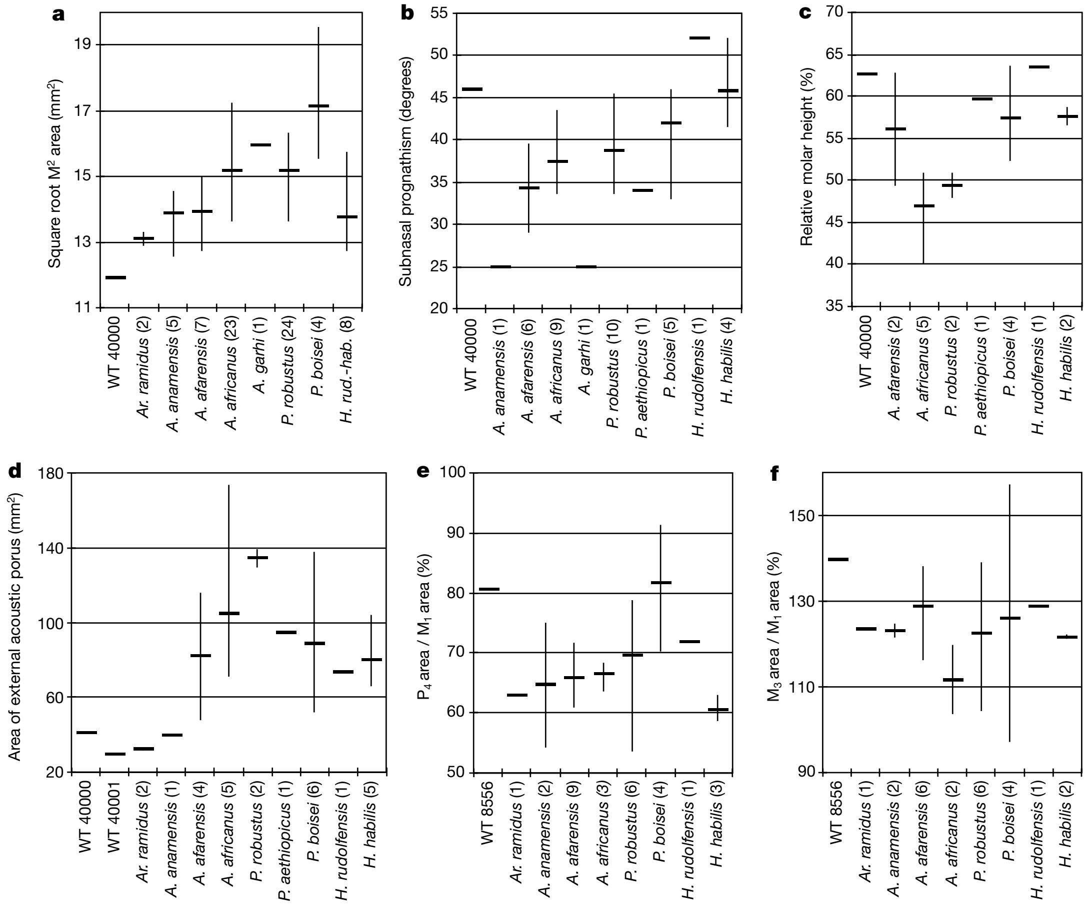

Figure 3 Mean and range of characters of specified hominins. **a**, Square root of M^2 crown area (buccolingual × mesiolingual diameters). **b**, Angle of subnasal prognathism (nasospinale–prosthion to postcanine alveolar plane). **c**, Malar height[8] relative to orbitoalveolar height (orbitale to alveolar margin aligned with malar surface). **d**, Area of the external acoustic porus (π × long axis × short axis). **e**, Crown area of P_4 relative to that of M^1 ×100. **f**, Crown area of M_3 relative to that of M_1 ×100. All measurements are taken from originals, directly or as given in refs 8, 9, 14, 18, 37, 41–44, except for some South African crania taken from casts. Numbers in parentheses indicate sample size.

and their unique combination, fully justify its status as a separate species. It is worth noting that comparisons with *Australopithecus bahrelghazali* cannot be made directly, because this species was named on the basis of the limited evidence provided by an anterior mandible fragment[16]. Specific distinction of *A. bahrelghazali* from *A. afarensis* has yet to be confirmed[17], and Lomekwi specimens differ from *A. bahrelghazali* in symphyseal morphology and incisor crown height.

The generic attribution of KNM-WT 40000 is a more complex issue, in the absence of consensus over the definition of the genus category[4]. The specimen lacks almost all of the derived features of *Paranthropus* (Table 2), and there are no grounds for assigning it to this genus unless it can be shown to represent a stem species. However, the fact that the facial morphology of KNM-WT 40000 is derived in a markedly different way renders this implausible. As KNM-WT 40000 does not show the derived features associated with *Homo*[4] (excluding *H. rudolfensis* and *H. habilis*) or the strongly primitive morphology of *Ardipithecus*[18], the only other available genus is *Australopithecus*. We agree with the taxonomically conservative, grade-sensitive approach to hominin classification that for the moment accepts *Australopithecus* as a paraphyletic genus in which are clustered stem species sharing a suite of key primitive features, such as a small brain, strong subnasal prognathism, and relatively large postcanine teeth. However, with its derived face and small molar size, KNM-WT 40000 stands apart from species assigned to *Australopithecus* on this basis. All it has in common with such species is its small brain size and a few other primitive characters in the nasal, supraorbital and temporal regions. Therefore, there is no firm basis for linking KNM-WT 40000 specifically with *Australopithecus*, and the inclusion of such a derived but early form could well render this genus polyphyletic. In a classification in which *Australopithecus* also includes the 'robust' taxa and perhaps even species traditionally known as 'early *Homo*'[4], this genus subsumes several widely divergent craniofacial morphologies. It could thus be argued that the inclusion of KNM-WT 40000 in *Australopithecus* would merely add yet another hominin species

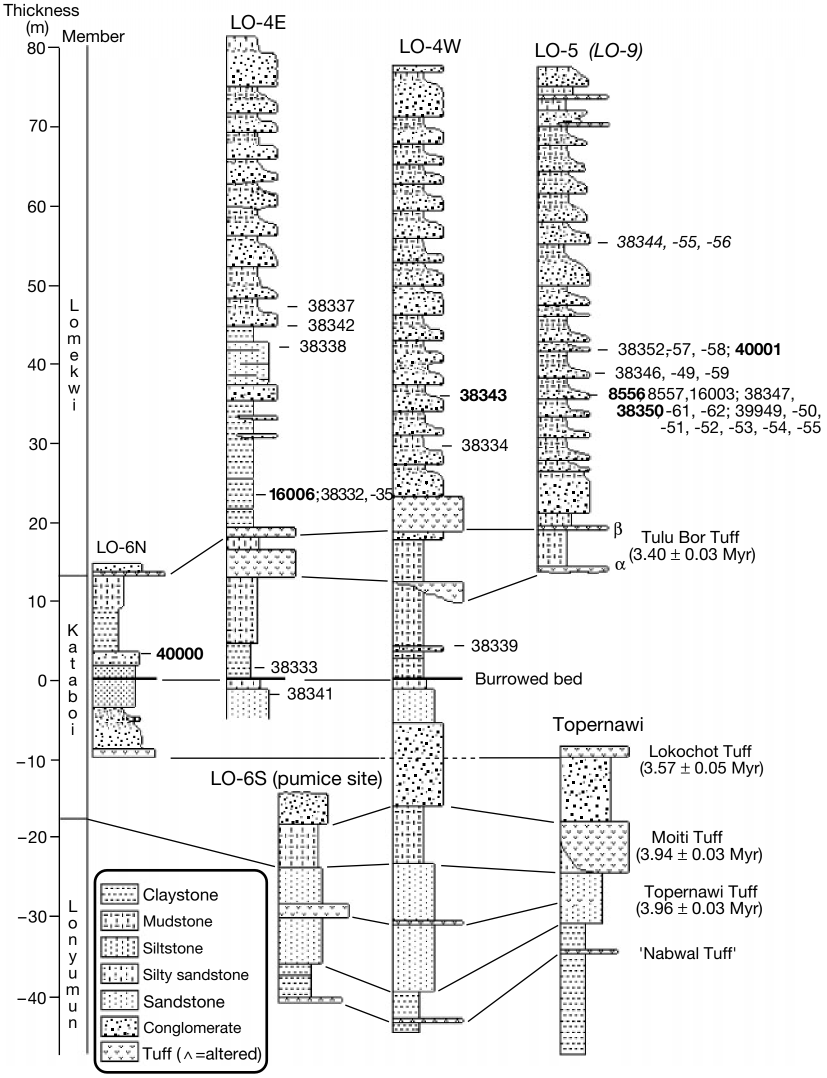

Figure 4 Stratigraphic sections and placement of hominin specimens at sites in upper part of the Lomekwi drainage, west of Lake Turkana, northern Kenya. Specimen numbers are given without the prefix KNM-WT, and those in bold are discussed in the text. Placement of specimens is relative to the nearest marker bed in the section. Italicized numbers show the relative placement of specimens at LO-9 on section LO-5. The burrowed bed, a useful local marker, is used as stratigraphic datum (0 m). Representative ^{40}Ar–^{39}Ar analytical data on the Moiti Tuff and on the Topernawi Tuff are given as Supplementary Information. The date for the Tulu Bor Tuff is taken as the age of the Sidi Hakoma Tuff at Hadar[25], which is consistent with the age of the Toroto Tuff (3.32 ± 0.03 Myr)[45] that overlies the Tulu Bor at Koobi Fora. The age of the Lokochot Tuff is assigned from its placement at the Gilbert/Gauss Chron boundary[24,46]. The tuff formerly thought to be the Moiti Tuff at Lomekwi[22] has been informally called the 'Nabwal tuff'[47]. Ages on the Tulu Bor and the Lokochot Tuffs are consistent with orbitally tuned ages of correlative ash layers in Ocean Drilling Program Core 722A in the Arabian Sea[48].

with a derived face. This amounts to defining *Australopithecus* by a single criterion, those hominin species not attributable to *Ardipithecus* or *Homo*, which in our view constitutes an undesirable approach to classification. Thus, given that KNM-WT 40000 cannot be grouped sensibly with any of the established hominin genera, and that it shows a unique pattern of facial and dental morphology that probably reflects a distinct dietary adaptive zone, we assign this specimen to the new genus *Kenyanthropus*.

Despite being separated by about 1.5 Myr, KNM-WT 40000 is very similar in its facial architecture to KNM-ER 1470, the lectotype of *H. rudolfensis*. The main differences amount to the more primitive nasal and neurocranial morphology of KNM-WT 40000. This raises the possibility that there is a close phylogenetic relationship between the two taxa, and affects our interpretation of *H. rudolfensis*. The transfer of this species to *Australopithecus* has been recommended[4,19], but *Kenyanthropus* may be a more appropriate genus. The identification of *K. platyops* has a number of additional implications. As a species contemporary with *A. afarensis* that is more primitive in some of its morphology, *K. platyops* weakens the case for *A. afarensis* being the sister taxon of all later hominins, and thus its proposed transfer to *Praeanthropus*[1,20]. Furthermore, the morphology of *K. platyops* raises questions about the polarity of characters used in analyses of hominin phylogeny. An example is the species' small molar size, which, although probably a derived feature, might also imply that the larger postcanine dentition of *A. afarensis* or *A. anamensis* does not represent the primitive hominin condition. Finally, the occurrence of at least one additional hominin species in the middle Pliocene of eastern Africa means that the affiliation of fragmentary specimens can now be reassessed. For example, the attribution of the 3.3 Myr old KNM-ER 2602 cranial fragment to *A. afarensis*[21] has been questioned[8], and evaluating its affinities with *K. platyops* is now timely.

Geological context and dating

KNM-WT 40000 was collected near the contact of the Nachukui Formation with Miocene volcanic rocks in the northern tributary of Lomekwi (Nabetili). It is situated 12 m above the Lokochot Tuff, and 8 m below the β-Tulu Bor Tuff (Fig. 4). Along Nabetili, the Lokochot Tuff is pinkish-grey and contains much clay and volcanic detritus. It is overlain by a volcanic pebble conglomerate, followed by a pale brown quartz-rich fine sandstone that includes a burrowed fine-sandstone marker bed 10–15 cm thick. The Lokochot Tuff is replaced by a thick volcanic clast conglomerate in the central part of Lomekwi. The contact between the fine sandstone and the overlying dark mudstone can be traced from Nabetili to the hominin locality. Locally the mudstone contains volcanic pebbles at the base, and it has thin pebble conglomerate lenses in the upper part at the hominin locality, and also contains $CaCO_3$ concretions. The hominin specimen and other vertebrate fossils derive from this mudstone. Overlying the dark mudstone at the hominin site is a brown mudstone (8 m) that directly underlies the β-Tulu Bor Tuff.

New ^{40}Ar–^{39}Ar determinations on alkali feldspars from pumice clasts in the Moiti Tuff and the Topernawi Tuff, stratigraphically beneath the Lokochot Tuff, were instrumental in re-investigating the lower portion of this section. The new results yield a mean age for the Topernawi Tuff of 3.96 ± 0.03 Myr; this is marginally older than the pooled age for the Moiti Tuff of 3.94 ± 0.03 Myr. Previous investigations[22,23] placed the Topernawi Tuff above the Moiti Tuff, mainly on the basis of the K/Ar ages on alkali feldspar from pumice clasts in the Topernawi Tuff (3.78, 3.71, 3.76 and 3.97 Myr, all ± 0.04 Myr)[23]. The older determination (3.97 Myr) was thought to result from contamination by detrital feldspar. South of Topernawi, however, the Topernawi Tuff has now been shown to underlie the Moiti Tuff, and to be in turn underlain by a tephra informally termed the 'Nabwal tuff', previously thought to be a Moiti Tuff correlative. The correct sequence is shown in Fig. 4, and the new ^{40}Ar–^{39}Ar age data on the Moiti Tuff and Topernawi Tuff are provided as Supplementary Information.

Linear interpolation between the Lokochot Tuff (3.57 Myr old)[24] and Tulu Bor Tuff (3.40 Myr)[25] yields an age of 3.5 Myr for KNM-WT 40000, and 3.53 Myr for the burrowed bed. KNM-WT 38341 from immediately below the burrowed bed has an age near 3.53 Myr. KNM-WT 38333 and 38339, from between the burrowed bed and the α-Tulu Bor Tuff lie between 3.4 and 3.5 Myr. Other specimens from LO-4, LO-5, and LO-6 lie 16–24 m above the β-Tulu Bor Tuff, with ages near 3.3 Myr. Assuming linear sedimentation between the Tulu Bor Tuff and the Lokalalei Tuff (2.5 Myr)[23], specimens from LO-9 are around 3.2 Myr. The probable error on these age estimates is less than 0.10 Myr.

Palaeogeographically, the mudstone that contained KNM-WT 40000 at LO-6N was deposited along the northern margin of a shallow lake that extended to Kataboi and beyond[26,27]. Laterally discontinuous volcanic pebble conglomerates within the mudstone record small streams draining from hills to the west. Carbonate concretions at the hominin level are probably pedogenic, and indicate regional conditions with net evaporative loss. Other specimens between the burrowed bed and the Tulu Bor Tuff were also preserved in lake-margin environments, as is the case for KNM-WT 38341 that was collected below the burrowed bed. At LO-5, and in the upper part of LO-4E, strata were laid down by ephemeral streams draining the basin margin, principally the ancestral Topernawi, which deposited gravels in broad, shallow channels, and finer grained materials in interfluves. Specimens preserved in floodplain deposits of the ancestral Omo River that occupied the axial portion of the basin include those at LO-9, those less than 6 m above the Tulu Bor Tuff at LO-4E, and KNM-WT 38338. Thus, there is evidence for hominins occupying floodplains of major rivers, alluvial fans, and lake-margin environments 3.0–3.5 Myr ago. There is reasonable evidence that water sources were available to these hominins in channels of the ephemeral streams, and also possibly as seeps or springs farther out into the basin.

Palaeoecology and fauna

Faunal assemblages from Lomekwi sites LO 4, LO 5, LO 6 and LO 9 indicate palaeoenvironments that were relatively well watered and well vegetated. The relative proportions of the bovids in the early collections from these sites indicate a mosaic of habitats, but with predominantly woodland and forest-edge species dominating[22]. Comparisons of the Lomekwi faunal assemblages with those from the few known hominin sites of similar age, Laetoli in Tanzania, Hadar in Ethiopia and Bahr el Ghazal in Chad, are of interest in view of the different hominin taxa represented. Hadar and Bahr el Ghazal, like Lomekwi, represent lakeshore or river floodplain palaeoenvironments[28,29], whereas Laetoli was not located near a water source; no aquatic taxa nor terrestrial mammals indicative of swamp or grassy wetlands were recovered[30]. The faunal assemblages of all four sites indicate a mosaic of habitats that seems to have included open grasslands and more wooded or forested environments[22,28,29,31,32]; the assemblages differ primarily in the indication of the nature of the dominant vegetation cover.

Although the mammalian faunal assemblage from Lomekwi is more similar to that from Hadar than to that from Laetoli, some mammalian species represented are different. At Lomekwi, *Theropithecus brumpti* is common and is the dominant cercopithecid, as it is elsewhere in the Turkana Basin at this time. This species is generally considered to indicate more forested or closed woodland habitats. In the Hadar Formation, *Theropithecus darti* is the common *Theropithecus* species and is associated with lower occurrences of the water-dependent reduncines and higher occurrences of alcelaphines and/or *Aepyceros*, which indicates drier woodlands and grasslands[33]. Differences in the representation of other common species at the two sites that are less obviously linked to habitat include *Kolpochoerus limnetes*, *Tragelaphus nakuae* and *Aepyceros* *shungurensis* at Lomekwi, as opposed to *K. afarensis*, *T. kyaloae* and an undescribed species of *Aepyceros* at Hadar (K. Reed, personal communication). The general indication is that the palaeoenvironment at Lomekwi may have been somewhat more vegetated and perhaps wetter than that persisting through much of the Hadar Formation. At both sites more detailed analyses will be essential to further develop an understanding of how subtle temporal changes in the faunal assemblages relate to hominin occurrences.

Note added in proof: If the hominin status of the recently published Lukeino craniodental specimens[49] is confirmed, this would support the suggestion that small molar size is the primitive rather than the derived hominin condition. ☐

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