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HOMININ EVOLUTION

Expanded geographic distribution and dietary strategies of the earliest Oldowan hominins and *Paranthropus*

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The oldest Oldowan tool sites, from around 2.6 million years ago, have previously been confined to Ethiopia's Afar Triangle. We describe sites at Nyayanga, Kenya, dated to 3.032 to 2.581 million years ago and expand this distribution by over 1300 kilometers. Furthermore, we found two hippopotamid butchery sites associated with mosaic vegetation and a C₄ grazer-dominated fauna. Tool flaking proficiency was comparable with that of younger Oldowan assemblages, but pounding activities were more common. Tool use-wear and bone damage indicate plant and animal tissue processing. *Paranthropus* sp. teeth, the first from southwestern Kenya, possessed carbon isotopic values indicative of a diet rich in C₄ foods. We argue that the earliest Oldowan was more widespread than previously known, used to process diverse foods including megafauna, and associated with *Paranthropus* from its onset.

The appearance of Oldowan tools around 2.6 million years ago (Ma) was a technological breakthrough that used systematically produced, sharp-edged flakes for cutting and cobbles or cores for percussion (1). Although the Oldowan is often attributed to the genus *Homo*, multiple hominin taxa overlapped temporally and geographically with these early tools, and it is possible that other genera, such as *Paranthropus*, made and/or used them. Some have linked emergent Oldowan technology to the first access to or more efficient processing of nutrient-rich animal carcasses [for example, (2, 3)]. Others have argued that plant food processing was the primary goal of early Oldowan stone tool usage, with increased carnivory (and butchery with stone tools) being added to the behavioral repertoire after 2 Ma (4, 5). The evolutionary benefits connected with the emergence of Oldowan technology are unclear because of the paucity of late Pliocene Oldowan sites,

hitherto known only from the Afar Triangle of Ethiopia at Gona and Ledi-Geraru, localities found approximately 50 km away from each other (6, 7). In this study, we report 3.032–2.595 Ma deposits at Nyayanga, Kenya, that expand the geographic range of the earliest Oldowan by more than 1300 km and the range of *Paranthropus* by approximately 230 km to southwestern Kenya. Archeological findings demonstrate that hominins used tools to butcher a variety of animals, including megafauna, and process diverse plants at the Oldowan's inception.

Nyayanga (0° 23.909'S, 34° 27.115'E) is an archeological and paleontological locality on the western shoreline of the Homa Peninsula (Fig. 1A) [(8), section 1]. The peninsula is located on the southern margin of the Winam Gulf of Lake Victoria, within the east-west-oriented Nyanza Rift between the two main branches of the East African Rift System (9). It is dominated by the Homa Mountain car-

bonatite complex, which on its flanks bears alluvial, fluvial, and lacustrine sediments that range in age from 6 Ma through the Holocene (10–13). Sediments at Nyayanga are exposed in a 40,000 m² amphitheater and a gully that can be traced for 500 m upslope (Fig. 1). Excavations and surface collection focused on the top half of the oldest bed (Fig. 1, NY-1), which yielded Oldowan artifacts, *Paranthropus* sp. fossils, and faunal fossils in overbank deposits from a westward-flowing paleochannel [(8), section 2].

The age of the Nyayanga Beds is constrained by (U-Th)/He dating of apatite crystals, magnetostratigraphy, lithostratigraphic correlation with the Rawi Fm (11, 13) deposited north of Homa Mountain, and biostratigraphy. The (U-Th)/He dating of apatite crystals yielded ages of 2.87 ± 0.79 Ma and 2.98 ± 0.50 Ma from two tuffaceous silts in NY-1 (fig. S1 and table S1) [(8), section 3]. Magnetostratigraphic sampling was carried out on the excavation 3 slope and in trenches 9 and 11 (Fig. 1) [(8), section 4]. The Nyayanga sequence shows reversed polarity in unit A, intermediate-normal to normal polarity from basal to middle NY-1, normal polarity from middle NY-1 through NY-2, intermediate normal polarity in the base of NY-3, and reversed polarity at the top of NY-3 (Fig. 1, fig. S2, and table S2). The (U-Th)/He apatite crystal dates suggest that the normal interval corresponds to the C2An.In Subchron between 3.032 and 2.595 Ma (14). This is similarly indicated by the lithostratigraphic correlation of the Nyayanga Beds with the Rawi Fm (11, 13), which was also deposited during the C2An.In Subchron. Biostratigraphy [(8), section 6] is consistent with a late Pliocene age, including more archaic examples of two pig species, the suine *Metridiochoerus andrewsi* and the tetraconodont *Notochoerus cf. scotti*, than the nearby locality of Kanjera South from 2 Ma (13), as well as an equid sample composed exclusively of hipparionin (*Eurygnathohippus* sp.) fossils. The latter indicates a date earlier than the 2.3 Ma dispersal of *Equus* across Africa (15). Acknowledging the wide 1σ uncertainty, the combination of (U-Th)/He apatite

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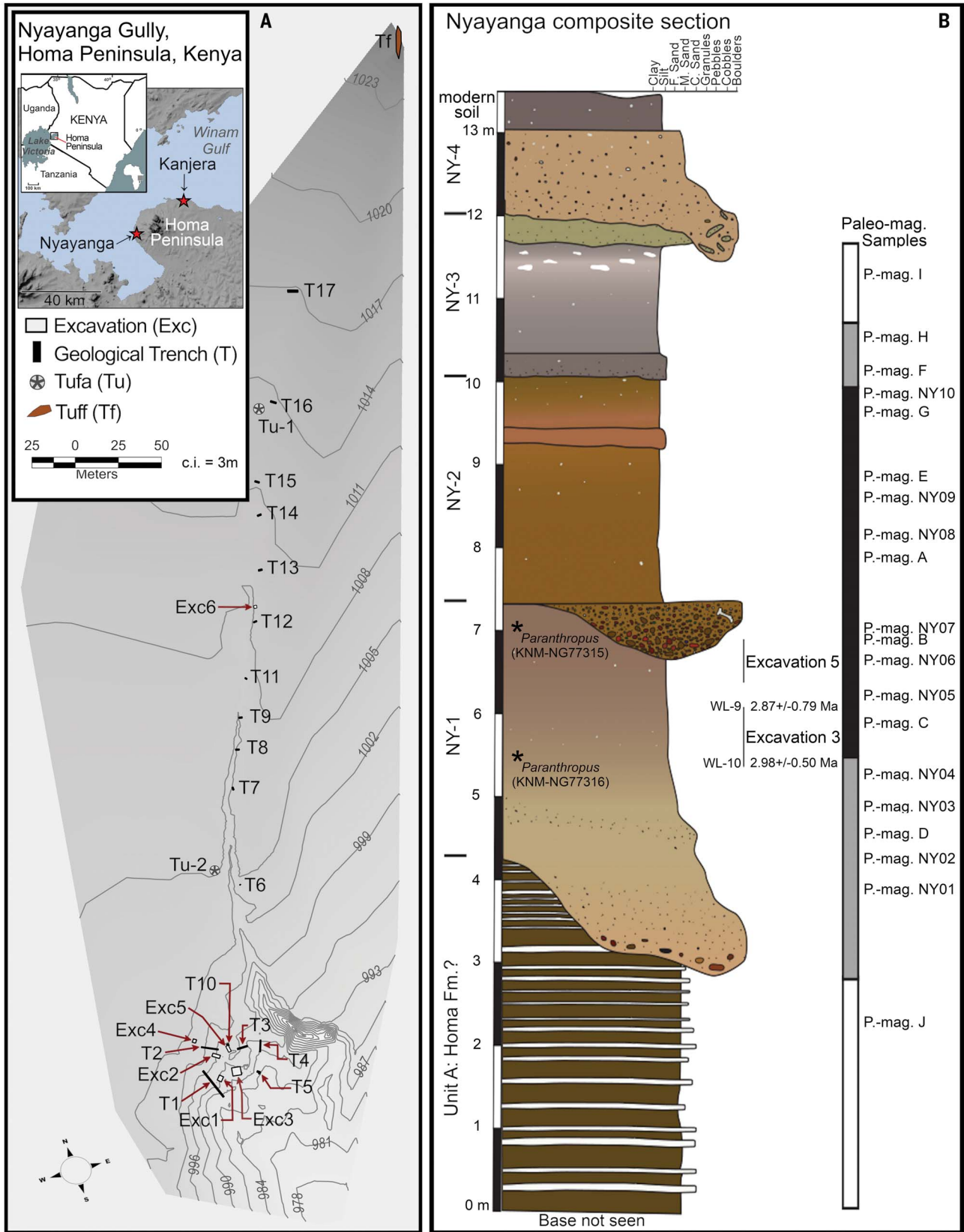


Fig. 1. Nyayanga gully, stratigraphy, magnetostratigraphic data, and apatite crystal dating results. (A) Topographic map of the gully system showing the locations of geologic trenches and excavations. **(B)** Composite stratigraphic column of the Nyayanga Beds showing the stratigraphic placement of excavations 3 and 5 and the magnetostratigraphic profile. Reversed polarity is shown in white, intermediate normal polarity in gray, and normal polarity in black.

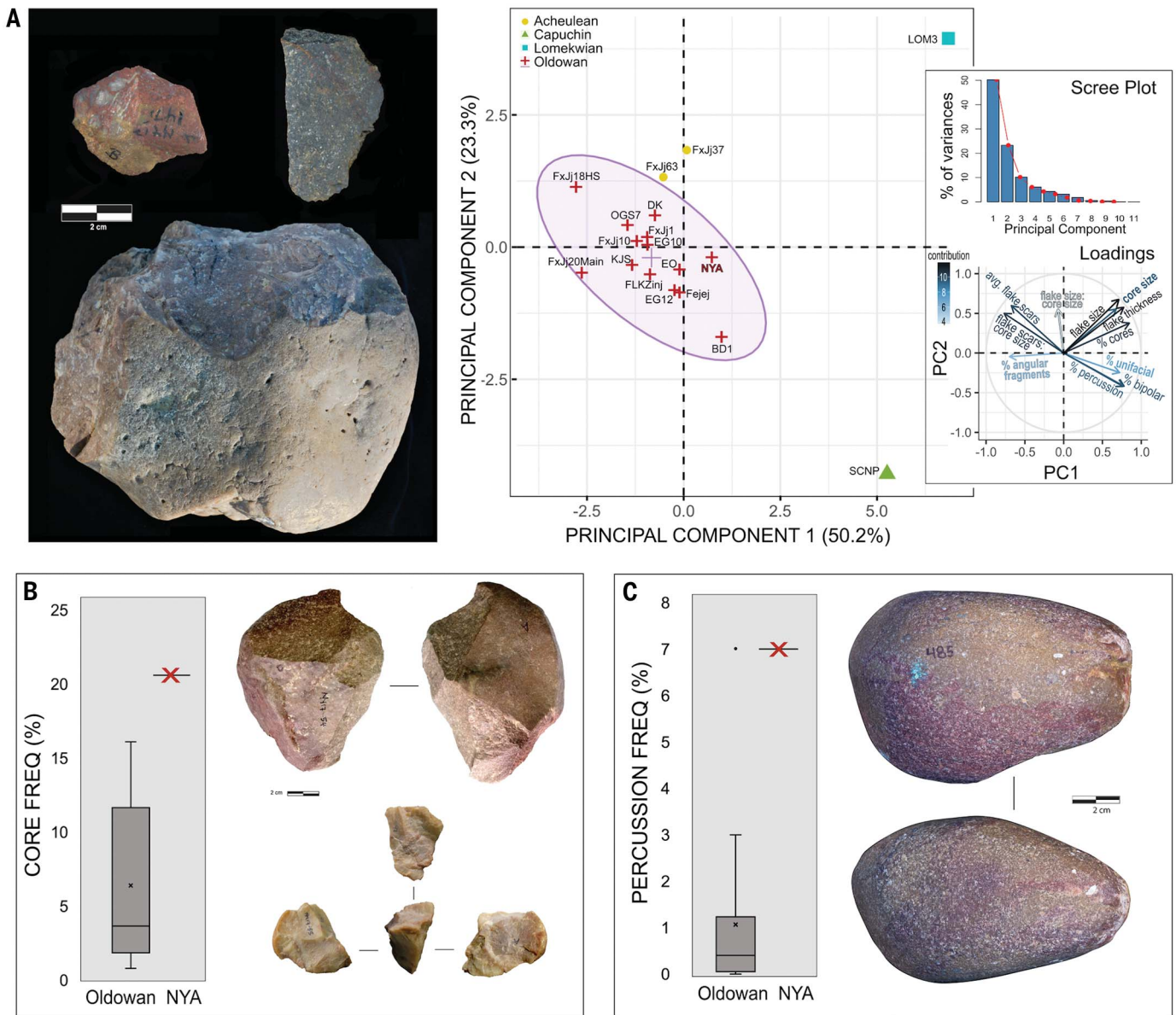


Fig. 2. Oldowan artifact technological analysis. (A) Photos of a dorsal flake (Exc3-1475), ventral flake (Exc3-1413), and core (NY17-128) from Nyayanga next to a principal component analysis based on major technological attributes of Early Stone Age artifact assemblages and a capuchin-derived assemblage (table S4) [(8), section 9]. Assemblages are plotted according to principal component 1 (x axis) and principal component 2 (y axis). The Nyayanga assemblage (NYA) falls within the shaded ellipse that represents the 95% confidence interval for Oldowan

sites. A scree plot with eigenvalue percentage of variance for principal components 1 through 11, and a loadings plot showing the contribution of each variable are shown to the right. **(B)** The frequency of cores in other Oldowan assemblages compared with those of Nyayanga (table S4) and photos of two Nyayanga cores (NY17-54, top; NY17-55, bottom). **(C)** The frequency of artifacts with percussion damage in other Oldowan assemblages compared with those of Nyayanga (table S4) with photos of a Nyayanga pounded piece (Exc3-485).

crystal dates, biostratigraphy, and the transitional nature of the magnetostratigraphy of lower NY-1 supports deposition early in the temporal range of the C2An.1n Subchron.

We recovered 330 artifacts from the upper half of NY-1; 135 were recovered in situ from excavations 3 and 5, and 195 were recovered from the surface [(8), section 7]. The overall technological attributes of tools, such as core and flake sizes and the number of flake scars on cores, are similar to other Oldowan as-

semblages (Fig. 2A and table S4). Nyayanga hominins efficiently removed flakes from cores using unifacial, bifacial, and multifacial reduction that is also comparable with technology at other Oldowan localities (7). The presence of cortical flakes and hammerstones with battering damage is consistent with on-site flake production through hard hammer percussion. Artifacts were manufactured from a diverse array of raw materials, including rhyolite, quartzite, and quartz. The Nyayanga assemblage is

distinct in containing a high frequency of cores (20.6%, $n = 68$) (Fig. 2B) and a large percentage of artifacts preserving evidence of percussive activities (7.0%, $n = 23$) (Fig. 2C).

A total of 1776 bones were recovered in situ from NY-1 in excavation 3 ($n = 1580$) and excavation 5 ($n = 196$). The most common taxa in excavations 3 and 5 are hippopotamids [57.1 and 61.9% of the number of identified specimens (NISP), respectively] followed by bovinds (19.2 and 22.2% of the NISP, respectively) (fig. S4

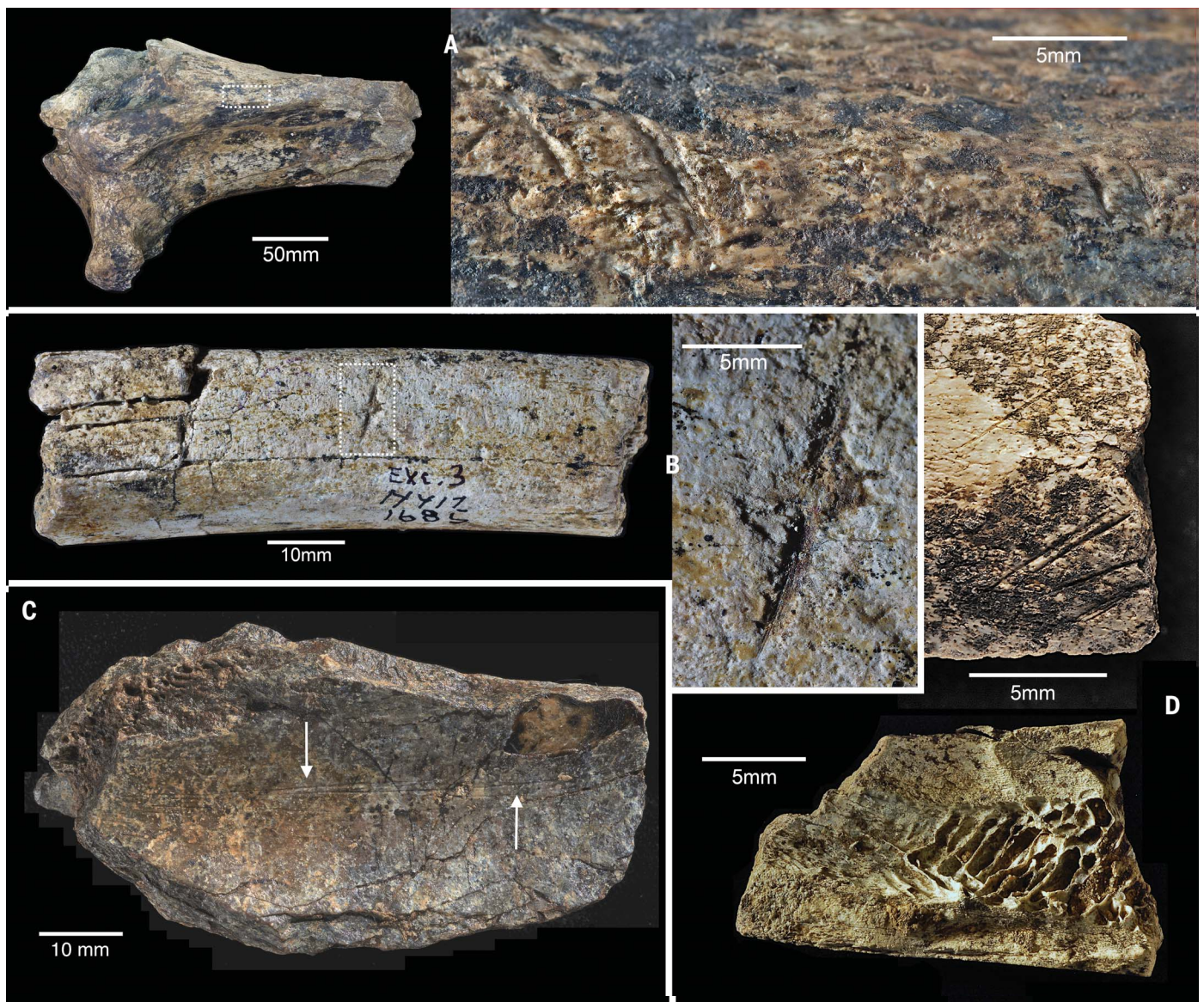


Fig. 3. Stone tool–damaged fossilized bones from Bed NY-1. (A) Hippopotamid tibia (Exc5-170, proximal end oriented to left) displaying a series of identically oriented cut marks with striae on anterior tibial crest. (B) Cut mark on a hippopotamid rib (Exc3-1685) displaying striae and a concretion filling the

middle of the mark. (C) Parallel cut marks extending along the spine of size three bovid scapula NY17-1. (D) A series of parallel cut marks (top) as well as percussion load points and flake scars created during marrow processing (bottom) visible on a size three bovid long bone shaft fragment (NY15-61).

and tables S5 and S6) [(8), section 8]. The high in situ frequencies of animals preferring near-water habitats [such as hippopotamids, turtles, crocodylians, and cane rats (*Thryonomys*)] reflect a riparian depositional context. Bone surface preservation was highly variable, but more than 85% of the sample in both excavations showed no or minimal weathering, which is consistent with the results of rapid burial by fluvial sediments (fig. S7).

Hippopotamid butchery is documented in both excavation 3 and excavation 5. A minimum of two hippopotamid individuals were recovered from excavation 3 (fig. S5). The more complete individual is composed of 241 bone

fragments from across the skeleton, including a large axial bone concentration likely marking its death site. Stone tools ($n = 42$) were closely associated with the skeleton, including several tools recovered in direct physical contact with hippopotamid bones. Despite the varied bone preservation, one hippopotamid rib fragment exhibits a deep cutmark with clearly preserved internal striations (Fig. 3B), and three stone flakes (detached pieces) exhibit use-wear indicative of butchery.

In excavation 5, 39 hippopotamid bones, likely from a single individual, were found spatially associated with 14 artifacts (fig. S6). One cluster of bones consisted of girdle elements (scapula,

innominate), appendicular elements (proximal half of tibia, calcaneum), a flake, and a split cobble with percussion damage. The anterior tuberosity of the tibia has a series of four short, parallel cutmarks (Fig. 3A). A second cluster of bones, located 2 m away, consists of a broken humerus, a flake, a rib fragment, and a man-upt. The nonanatomical placement of these bones, some with hominin damage, and associated artifacts (one with use-wear indicative of butchery) in a fine silt suggests that the bones may have been moved by hominins while butchering the carcass.

Tool-damaged bones of nonhippopotamid taxa were also found in the excavations and

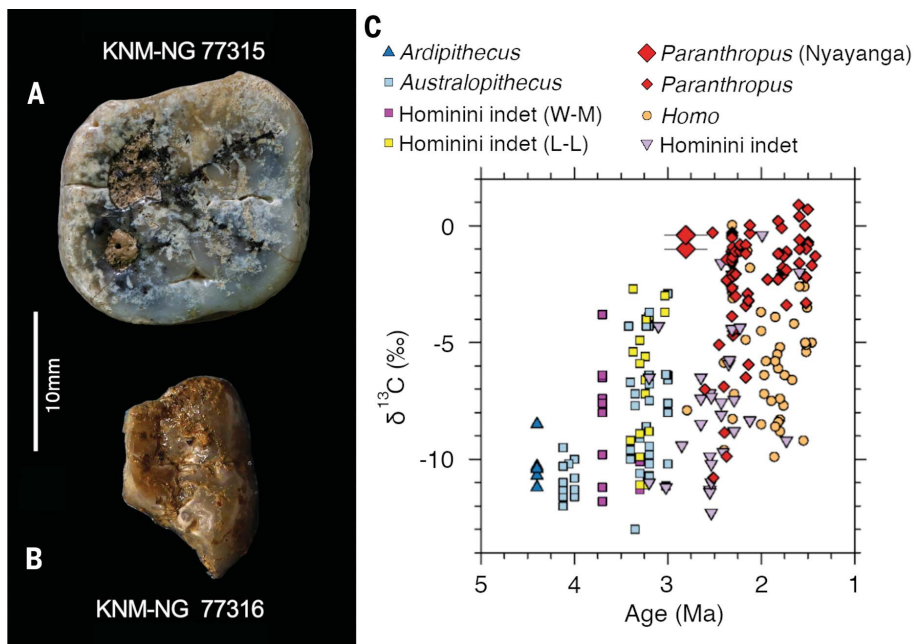


Fig. 4. *Paranthropus* finds from Nyayanga. (A) *Paranthropus* sp. left upper molar KNM-NG 77315 found on the surface of NY-1. (B) *Paranthropus* sp. left lower molar KNM-NG 77316 found in situ in NY-1 in excavation 3. (C) Tooth enamel $\delta^{13}\text{C}$ of Nyayanga hominins and previously published $\delta^{13}\text{C}$ data from eastern African hominins (19, 25–34). Pliocene hominin teeth from Woranso-Mille are identified as “hominini indet (W-M).” Mid-Pliocene hominin teeth from Lomekwi and Lothagam in the Turkana Basin previously attributed to *K. platyops* (28) are identified here as “hominini indet (L-L)” (35). Hominin teeth from other areas of the Omo-Turkana Basin that cannot be confidently attributed to a genus are identified as “hominini indet.”

eroding out of NY-1 in the amphitheater. A size three bovid scapular spine fragment with cut marks was found eroding from an in-situ context at about the same level as the excavation 5 hippopotamid (Fig. 3C). Other bones from NY-1 with cut marks or percussion damage show that hominins were consuming both meat and marrow (Fig. 3D), a finding supported by use-wear analysis. Overall frequencies of hominin damage from the excavations are low: 0.9 and 1.9% at excavations 3 and 5, respectively (table S7). In part, this reflects poor surface preservation of many of the fossils as well as fragmentation of ribs.

Use-wear observed on 30 quartz, quartzite, granite, carbonatite, and rhyolite tools from NY-1 confirm hominin processing of faunal remains and plant tissue (18, section 9). Use-wear found on six pounded pieces (16) and 17 flaked pieces (cores) show macro- and microtraces related to pounding activities (fig. S8). Percussive stone tools were heavily used, showing deep pits and developed polishes and striations at low and high magnification, which, based on modern experiments, require at least several hours of use to emerge. On the basis of experimental analogs (figs. S9 and S10 and tables S8 and S10), the quartzite and rhyolite Oldowan percussive tools at Nyayanga were used to process soft (such as soft tubers,

vegetables, or fruits) and hard (such as fibrous tubers or woody parts) plant tissues (fig. S11 and table S11). Macro- and microtraces related to cutting and scraping on six detached pieces (flakes) and one flaked piece show that similar materials were being cut and pounded (fig. S12 and tables S9 and S12). Five quartz detached pieces from excavation 3 show traces indicative of underground storage organ, wood, and animal processing. A rhyolite flaked piece from excavation 5 and a NY-1 surface collected detached piece also have use-wear related to butchery (fig. S12 and table S12).

Stable carbon isotopic analysis of pedogenic carbonates, dietary reconstruction by using tooth enamel isotopes, and bovid taxonomic frequencies indicate that hominin activities took place in a wooded grassland to grassy woodland, bushland, or shrubland along a stream channel within a mesic savanna biome characterized by an abundance of C_4 grasses and herbaceous plants (figs. S13 to S17 and tables S13 and S14) [(8), sections 10 to 12]. Similar C_4 grazer-dominated ecosystems are documented at the Ethiopian sites of Ledi-Geraru (~2.8 Ma) (17) and Mille-Logya (~2.8 to ~2.4 Ma) (18), indicating that early representatives of both *Paranthropus* and *Homo* were found in substantially open ecosystems. The riparian setting, nearby freshwater spring, and

ecotone with open habitats provided Nyayanga hominins with a diverse array of plant and animal foods, shelter, and potable water.

Two hominin individuals from Bed NY-1 are assigned to *Paranthropus* sp. (Fig. 4) [(8), section 13]. KNM-NG 77315 is a relatively complete left upper molar, probably M^2 (second upper molar), from surface collection, with a crown area above the range of that of *P. boisei* and *P. robustus* samples (tables S17 and S18). KNM-NG 77316 is a nearly complete lingual portion of a left lower molar, probably M_1 (first lower molar), found in situ in excavation 3, spatially associated with Oldowan artifacts and a butchered hippopotamid. The Nyayanga *Paranthropus* teeth have an average $\delta^{13}\text{C}_{\text{enamel}}$ value of $-0.7 \pm 0.4\text{‰}$ (Fig. 4C), which demonstrates a heavy reliance on C_4 foods. Thus, the emergence of C_4 specialist diets coincided with the appearance of at least one major aspect of robust masticatory morphology (large post-canine teeth) relatively early in the evolution of *Paranthropus* [as opposed to (19)].

Paranthropus molar KNM-NG 77316 from the excavation 3 hippopotamid butchery site is a clear association of a hominin fossil with artifacts, raising the possibility that *Paranthropus* made and/or co-opted stone tools. Although its skull anatomy was not preserved, Nyayanga *Paranthropus* was megadont and had flat molars with poor shearing capability. However, its specialized gnathic morphology may not have precluded tool use. Extraoral cutting and pounding with stone tools could have provided access to carcasses and within bone nutrients, and made plant and animal tissue easier to chew and digest (20), potentially allowing *Paranthropus* to expand its diet. Although not found at Nyayanga, *Homo* was also present in eastern Africa at about the time of Nyayanga deposition (21), so the Nyayanga artifacts cannot be definitively attributed to a specific hominin genus.

Deposits at Nyayanga dated between 3.032 and 2.581 Ma show that at its earliest onset the Oldowan was geographically more widely dispersed than previously known, a finding consistent with a recently described Oldowan site from around 2.4 Ma in North Africa (22). Nyayanga artifacts were used to cut, scrape, and pound large mammal and plant tissue, demonstrating that at their emergence Oldowan tools were used in a variety of actions to access a broad array of food types. By 2 Ma, Oldowan sites are found from northern to southern Africa in both grassy and wooded habitats (23), suggesting that one of the key attributes of the technology was the flexibility to process foods with different physical properties in a diversity of habitats.

The behaviors preserved at Nyayanga are at least 600,000 years older than prior evidence of megafaunal carcass and plant processing and substantially predate the increase in absolute brain size documented in the genus *Homo*

after 2 Ma (24). The late Pliocene expanded geography of the earliest Oldowan, and new evidence of its use in diverse tasks amplifies our understanding of the adaptive advantage of early stone technology in hominin diet and foraging ecology.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
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