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A NEW SPECIES OF THE GENUS *AUSTRALOPITHECUS* (PRIMATES: HOMINIDAE) FROM THE PLIOCENE OF EASTERN AFRICA

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ABSTRACT

Hominid fossils have recently been recovered from Pliocene age deposits at Hadar, Ethiopia, and Laetolil, Tanzania. These fossils share an array of distinctive morphological characteristics which suggests that they belong to a single species of the genus *Australopithecus*, differing significantly from those previously described. The binomen *Australopithecus afarensis* sp. nov. is therefore assigned to this collection of early hominid remains.

A substantial collection of hominid fossils has recently been recovered from two Pliocene sites in eastern Africa. Hominid specimens from Hadar in Ethiopia (11°N, 40°30'E) and Laetolil in Tanzania (3°12'S, 35°11'E) have been dated to between ca. 2.9 and ca. 3.7 million years before present (Aronson et al., 1977; Leakey et al., 1977). The strong morphological continuity between these two samples suggests that they are best considered as representing a single taxon; hence, the Hadar and Laetolil fossils currently constitute the oldest indisputable evidence of the family Hominidae.

Some of these specimens have been provisionally allocated to *Homo* sp. indet. (Johanson and Taieb, 1976; Leakey et al., 1977) while others have been referred to *Australopithecus* aff. *africanus* (Johanson and Taieb, 1976). Subsequent to this preliminary assessment, more detailed study of the entire hominid sample from Laetolil and Hadar has provided us with new information indicating that 1) the specimens belong to only a single taxon, and 2) they differ significantly from previously recognized species of Plio/Pleistocene Hominidae. The Hadar and Laetolil hominids exhibit many morphological features found in specimens attributed to the genus *Australopithecus* (*sensu lato*) (as defined by Le Gros Clark, 1955) and they are therefore assigned to this taxon. Careful evaluation of the material has led to the recognition of a distinctive suite of morphological traits distinguishing the Laetolil and Hadar remains from other hominid taxa. Such study indicates the necessity of assigning these fossils to a new and more primitive species of *Australopithecus*.

Order PRIMATES Linnaeus 1758

Superfamily HOMINOIDEA Simpson 1931

Family HOMINIDAE (Le Gros Clark 1955)

Genus *Australopithecus* Dart 1925

Australopithecus afarensis sp. nov.

Synonymy:

1950 *Meganthropus africanus* Weinert, H.: 139

1955 *Praeanthropus africanus* Şenyürek, M.: 33

Holotype:

Laetolil Hominid (L.H.-) 4, mandibular corpus with broken RC, M₁, M₂; intact R and LP₄; RP₃, M₃; LM₁, M₂.

Locality:

Locality 7 of the Laetolil Site, Tanzania, collected in 1974 by M. Muluila.

Horizon:

Laetolil Beds between Aeolian Tuffs b and c, Pliocene age (3.6–3.7 m.y. b.p.)

Paratypes:

Laetolil Beds, Tanzania:

L.H.-1, RP⁴; L.H.-2, immature mandibular corpus with permanent and deciduous teeth; L.H.-3(a-t), isolated upper and lower deciduous and permanent teeth; L.H.-3/6a, b, Rdc-, Ldm¹; L.H.-5, R. maxillary row, I²-M¹; L.H.-6(a-e), isolated permanent and deciduous upper teeth; L.H.-7, RM⁻ frag.; L.H.-8, RM², RM³; L.H.-10, L. edentulous mandibular frag.; L.H.-11, LM^{1/2}; L.H.-12, LM^{2/3} frag.; L.H.-13, R. edentulous mandibular corpus frag.; L.H.-14(a-h), isolated lower teeth; Garusi maxilla, RP³-P⁴.

Hadar Formation, Ethiopia:

Sidi Hakoma Member:

A.L. 128-1, L. prox. femur frag.; A.L. 128-23, R. mandibular corpus, C-M₂; A.L. 129-1a, b, c, femur and tibia frags.; A.L. 129-52, L. ischium; A.L. 137-48a, R. distal humerus; A.L. 137-48b, R. distal ulna; A.L. 145-35, L. mandibular corpus, P₃-M₂; A.L. 166-9, L. temporal frag.; A.L. 198-1, L. mandibular corpus, C-M₃; A.L. 198-17a, b, LI¹, LI²; A.L. 198-18, RI₂; A.L. 199-1, R. maxilla, C-M³; A.L. 200-1a, maxilla, complete dentition; A.L. 200-1b, RM₁; A.L. 211-1, R. prox. femur frag.; A.L. 228-1, R. diaphysis femur; A.L. 266-1, mandibular corpus, LP₃-M₁, RP₃-M₃; A.L. 277-1, L. mandibular corpus, C-M₂; A.L. 311-1, L. mandibular corpus, P₃; A.L. 322-1, L. distal humerus; A.L. 400-1a, mandibular corpus, LI₁-M₃, RI₂-M₃; A.L. 400-1b, RC⁻; A.L. 411-1, R. mandibular corpus, M₁-M₃.

Denan Dora Member:

A.L. 161-40, LM³; A.L. 188-1, R. mandibular corpus, M₂-M₃; A.L. 207-13, L. mandibular corpus, P₃-M₂; A.L. 241-14, LM₋; A.L. 366-1, LM₃; A.L. 388-1, LM³.

A.L. 333-1, facial frag. and maxilla, RP³-P⁴, LC-P³; -2, maxilla, RC-M¹, LI²-P⁴; -3, R. prox. femur; -4, R. distal femur; -5, L. prox. tibia frag.; -6, L. distal tibia; -7, L. distal tibia; -8, R. calcaneum frag.; -9a, -9b, R. and L. distal fibulae; -10, L. mandibular corpus frag., P³; -11, R. prox. ulna frag.; -12, R. distal ulna; -13, L. prox. V metatarsal (MT); -14, R. V metacarpal (MC); -15, L. prox. II MC; -16, L. III MC; -17, R. distal V MC; -18, R. distal IV MC; -19, prox. hand phalanx; -20, prox. hand phalanx frag.; -21, distal MT; -22, prox. hand phalanx frag.; -23, cranial frag.; -25, intermed. hand phalanx; -26, prox. phalanx; -27, R. distal II MC; -28, R. medial cuneiform frag.; -29, L. distal humerus; -30, Rdm₁; -31, prox. hand phalanx frag.; -32, intermed. hand phalanx; -33, prox. hand phalanx; -34, immature metapodial; -35, Rdc₋; -36, R. foot navicular; -37, R. calcaneum frag.; -38, L. immature distal ulna; -39, L. immature prox. tibia; -40, R. capitate; -41, R. med. femoral condyle frag.; -42, L. prox. tibia; -43a, b, L. and R. mandibular corpi, R. and L. dm₁-dm₂; -44, LM⁻; -45, partial cranium; -46, intermed. hand phalanx; -47, R. foot navicular; -48, L. II MC; -49, prox. hand phalanx frag.; -50, R. hamate; -51, body thoracic vertebra; -52, frag. M₋; -53, thoracic vertebra frag.; -54, L. prox. I MT; -55, L. calcaneum frag.; -56, L. IV MC; -57, prox. hand phalanx; -58, R. prox. I MC frag.; -59, R. mandibular corpus frag., M₂-M₃; -60, prox. phalanx; -61, L. distal femur frag.; -62, prox. hand phalanx; -63, prox. hand phalanx; -64, intermed. hand phalanx; -65, R. prox. III MC; -66, Ldc⁻; -67, Rdi²; -68, Ldi₂; -69, L. prox. hand phalanx; -70, immature metapodial; -71, prox. foot phalanx; -72, MT frag.; -73, body lumbar vertebra; -74, L. mandibular corpus frag., M₁-M₃; -75, head R. talus; -76, Ldi₂; -77, Ldc₋; -78, L. prox. V MT; -79, L. lateral cuneiform; -80, R. trapezium; -81, body immature thoracic vertebra; -82 LI¹; -83 atlas vertebra frag.; -84, R. temporal frag.; -85, L. distal fibula; -86, maxilla, L. and R. dm¹-dm², M¹; -87, L. prox. humerus frag.; -88, intermed. hand phalanx; -89, L. V MC; -90, LC₋; -92, immature long bone frag.; -93, prox. hand phalanx; -94, L. clavicle frag.; -95, R. prox. femur; -96, L. distal tibia; -97, L. mandibular corpus frag.; -98, R. prox. radius; -99, Ldc⁻; -100, L. coronoid process mandible; -101, axis vertebra; -102, prox. hand phalanx; -103, RC₋; -104, Rdc⁻; -105, partial immature cranium, Rdm¹-dm²;

-106, cervical vertebra; -107, R. prox. humerus; -108, L. ascending ramus; -109, humerus shaft frag.; -110, L. immature distal femur frag.; -111, R. immature distal femur frag.; -113, immature long bone frag.; -115, associated foot bones.

A.L. 333w-la-e, R. and L. mandibular corpi, LP₃-M₂, RP₃-M₂, RM₃ frag., R. condyle; -2, LC⁻; -3, LI₂; -4, prox. hand phalanx; -5, R. distal II MC; -6, R. prox. III MC; -7, immature prox. hand phalanx; -8, vertebra frag.; -9a, b, LI₁, LI₂; -10, RC₋; -11, distal hand phalanx; -12, R. mandibular corpus frag., M₁; -13, prox. fibula; -15, R. coronoid process mandible; -16, L. mandibular condyle; -17, -18, -19, rib frags.; -20, immature prox. hand phalanx frag.; -21, immature phalanx; -22 R. distal humerus frag.; -23, R. immature II MC; -25, prox. hand phalanx frag.; -26, L. prox. V MC; -27, L. mandibular corpus, M₂; -28, RI²; -29, immature prox. phalanx frag.; -30, rib; -31, L. distal humerus frag.; -32, R. mandibular corpus, M₃; -33, R. prox. radius; -34, intermed. hand phalanx frag.; -35, L. prox. V MC; -36, L. prox. ulna; -37, L. distal fibula -38, intermed. hand phalanx; -39, R. I MC; -40, R. prox. femur frag.; -41, rib frag.; -42, RP⁴; -43, immature prox. I MT frag.; -45, rib frag.; -46, R. mandibular corpus, P₃; -47, rib frag.; -48, RM₂; -50, distal hand phalanx; -51, prox. hand phalanx frag.; -52, L. mandibular condyle; -53, intermed. hand phalanx frag.; -54, prox. hand phalanx frag.; -55, MT frag.; -56, R. distal femur; -57, L. mandibular corpus, M₂-M₃; -58, mandibular corpus frag., LI₁-P₄, RI₁-C₋; -59, L. mandibular corpus, M₂-M₃; -60, mandibular corpus, LP₃-M₃, RI₁-C₋.

A.L. 333x-1, RM³; -2, LI²; -3, LC⁻; -4, RI¹; -5, R. prox. ulna; -6, -9, R. clavicle frags.; -12, thoracic vertebra; -13a, prox. hand phalanx; -13b, intermed. hand phalanx; -14, -15, prox. radial epiphyses; -17, RI²; -18, intermed. hand phalanx; -20, RI¹; -21a, b, intermed. hand phalanges; -25, di_{1/2}; -26, R. prox. tibia.

Kada Hadar Member:

A. L. 288-1, partial skeleton.

Horizon:

Laetolil Beds, Tanzania. Known hominid sample from between strata dated to 3.59 and 3.77 m.y.

Hadar Formation, Ethiopia. Sidi Hakoma Member dated to older than ca. 3.0 m.y., but less than ca. 3.3 m.y. Denan Dora and Kada Hadar Members dated to younger than ca. 3.0 and older than ca. 2.6 m.y. with the latter member stratigraphically above the former.

Diagnosis:

A species of *Australopithecus* distinguished by the following characters:

Dentition

Upper central incisors relatively and absolutely large; upper central and diminutive lateral incisors with strong lingual basal tubercles, upper incisors with flexed roots; strong variation in canine size, canines asymmetric, lowers with strong lingual ridge, uppers usually with exposed dentine strip along distal edge when worn; P_3 occlusal outline elongate oval in shape with main axis mesiobuccal to distolingual at 45° – 60° to tooth row, dominant mesiodistally-elongate buccal cusp, small lingual cusp often expressed only as inflated lingual ridge; diastemata often present between I^2/C^- and C_-/P_3 ; C^-/P_3 complex not functionally analogous to pongid condition.

Mandible

Ascending ramus broad, not high; corpus of larger specimens relatively deep anteriorly and hollowed in region of low mental foramen which usually opens anterosuperiorly; moderate superior transverse torus; low rounded inferior transverse torus; anterior corpus rounded and bulbous; strong posterior angulation of symphyseal axis; postcanine teeth aligned in straight rows; arcade tends to be sub-rectangular, smaller mandibles with relatively narrow incisor region.

Cranium

Strong alveolar prognathism with convex clivus; palate shallow, especially anteriorly; dental arcade long, narrow, straight sided; facial skeleton exhibiting large, pillar-like canine juga separated from zygomatic processes by deep hollows, large zygomatic processes located above P^4/M^1 and oriented at right angles to tooth row with inferior margins flared anteriorly and laterally; occipital region characterized by compound temporal/nuchal crest (in larger specimens), concave nuchal plane short anteroposteriorly; large, flattened mastoids; shallow mandibular fossae with weak articular eminences placed only partly under braincase; occipital condyles with strong ventral angulation.

Postcranium

See remarks.

Description:

Dentition

Large canines project beyond tooth rows and possess massive, long roots; buccal face of P_3 's often with vertical wear striae caused by occlusion with upper canines; P_3 's often with two distinct roots, the mesial one round and angulated mesio-buccally, the distal one plate-like and oriented transverse to the tooth row; P^3 's sometimes three rooted, with pointed buccal cusp, extensive and asymmetric buccal face, buccal cervicoenamel line projecting towards mesio-buccal root, and the lingual cusp situated mesial to buccal cusp, P^3 's tend to be larger than P^4 's and the latter do not show mesiodistal elongation of the buccal crown half; lower molars, especially M_1 and M_2 tend to be square with cusps arranged in Y-5 pattern; wide occlusal foveae on all molars; strong molar size gradient of $M_3 > M_2 > M_1$; hypocones and hypoconulids large; deciduous canines similar to the permanent ones in form and occlusal projection; dm_1 's molarized, with lingually facing anterior foveae and deep buccal grooves; substantial variation in tooth size.

Mandible

Ascending ramus slopes posteriorly and joins corpus at high position defining narrow extramolar sulcus; broad condyles; mandibular canal immediately below distal M_3 root; base of corpus everted.

Cranium

Incisors procumbent; lower margin of pyriform aperture marked laterally by raised borders; tooth rows tend to converge posteriorly; strong muscle markings on vault and cranial base, temporal lines converge anteriorly, but presence of sagittal cresting unknown; lateral portion of cranial base highly pneumatized; occipital condyles placed below external auditory meatus in lateral view; estimated cranial capacity small relative to *Homo* sp.; broad mandibular fossae, laterally projecting postglenoid process; pyramid process angles anteriorly relative to more transverse tympanic plate.

Postcranium

Strong dimorphism in body size; all skeletal elements with high

level of robusticity in muscle and tendon insertions; pelvic region and lower limbs indicate adaptation to bipedal locomotion; "waisted" appearance of capitate; third metacarpal lacking styloid process; phalanges strongly longitudinally curved; foot navicular with cuboideonavicular facet; deep peroneal grooves on distal fibulae; anterior margin of ilium between anterior superior and inferior spines relatively straight; cervical vertebrae with long spinous process; relatively high humerofemoral index compared to modern humans.

Etymology:

The species name *afarensis* derives from the Afar depression of northeastern Ethiopia, where the largest portion of the paratype series was recovered.

REMARKS

Laetolil Hominid-4 was selected as the holotype both because of its distinctive, diagnostic morphology and because it has previously been fully described and illustrated (White, 1977). The generic name *Praeanthropus* originally proposed by Hennig (1948) is invalid because no species designation was given. Şenyürek (1955) used the generic nomen *Praeanthropus* and utilized Weinert's (1950) specific name *africanus*, designating the original Garusi maxillary fragment as *Praeanthropus africanus*. The present authors do not consider the original Garusi maxillary fragment or the new Laetolil and Hadar material to represent a hominid genus distinct from *Australopithecus*.

The authors recognize that individual traits and even single specimens in the new collections can be matched in other samples representing different taxa (e.g., *Australopithecus africanus* Dart 1925, *Homo habilis* Leakey, Tobias and Napier 1964). However, the overall character complex seen in the Hadar and Laetolil fossils is distinct from other previously found and described species. Care has been taken in the diagnosis to follow Mayr's suggestion to "list the most important characters or character combinations that are peculiar to the given taxon and by which it can be differentiated from other similar or closely related ones" (1969: p. 266). In the description of *Australopithecus afarensis* we have chosen to present a characterization of the entire hypodigm. This should insure that the presentation not be viewed as typological and should also given some indication of the variation recognized in this new taxon.

It is important to recognize that certain traits or complexes were not considered in the diagnosis but placed in the description due to the lack of comparable anatomical specimens from other species of *Australopithecus*.

Some of the traits, such as the morphology of the hand and foot bones, may be diagnostic of the new species, but this cannot be ascertained until pertinent new material is recovered from other sites.

The Hadar and Laetolil fossils appear to represent a distinctive early hominid form characterized by substantial size variation which is interpreted as reflecting sexual dimorphism. Members of this new taxon display a complex of primitive dental, cranial, and possibly postcranial characteristics. Recognition of the new species *Australopithecus afarensis* has important implications for interpretations of early hominid phylogeny. These implications will be considered in forthcoming publications.

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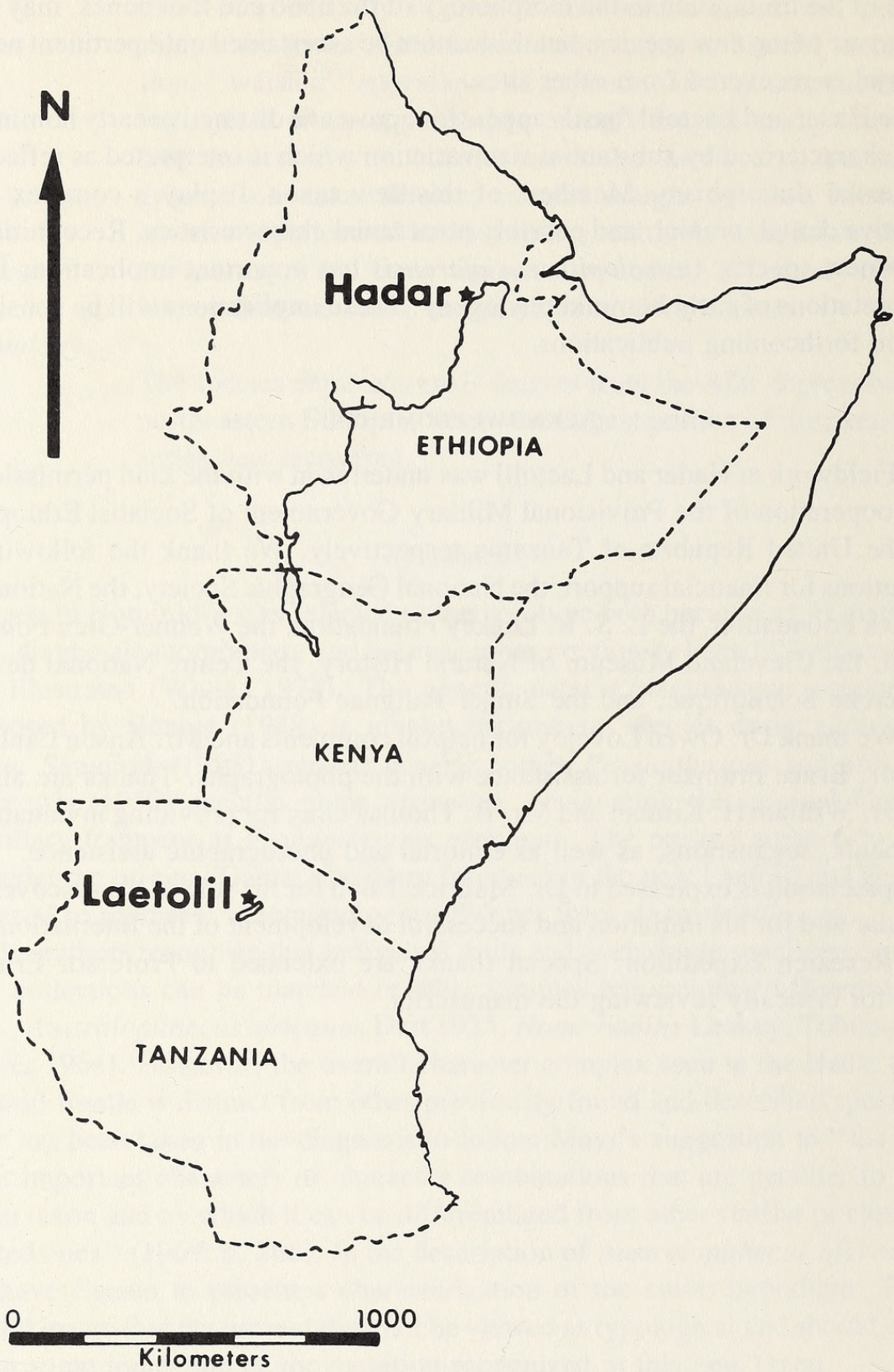


Fig. 1. Map of eastern Africa showing the locations of Hadar and Laetolil.

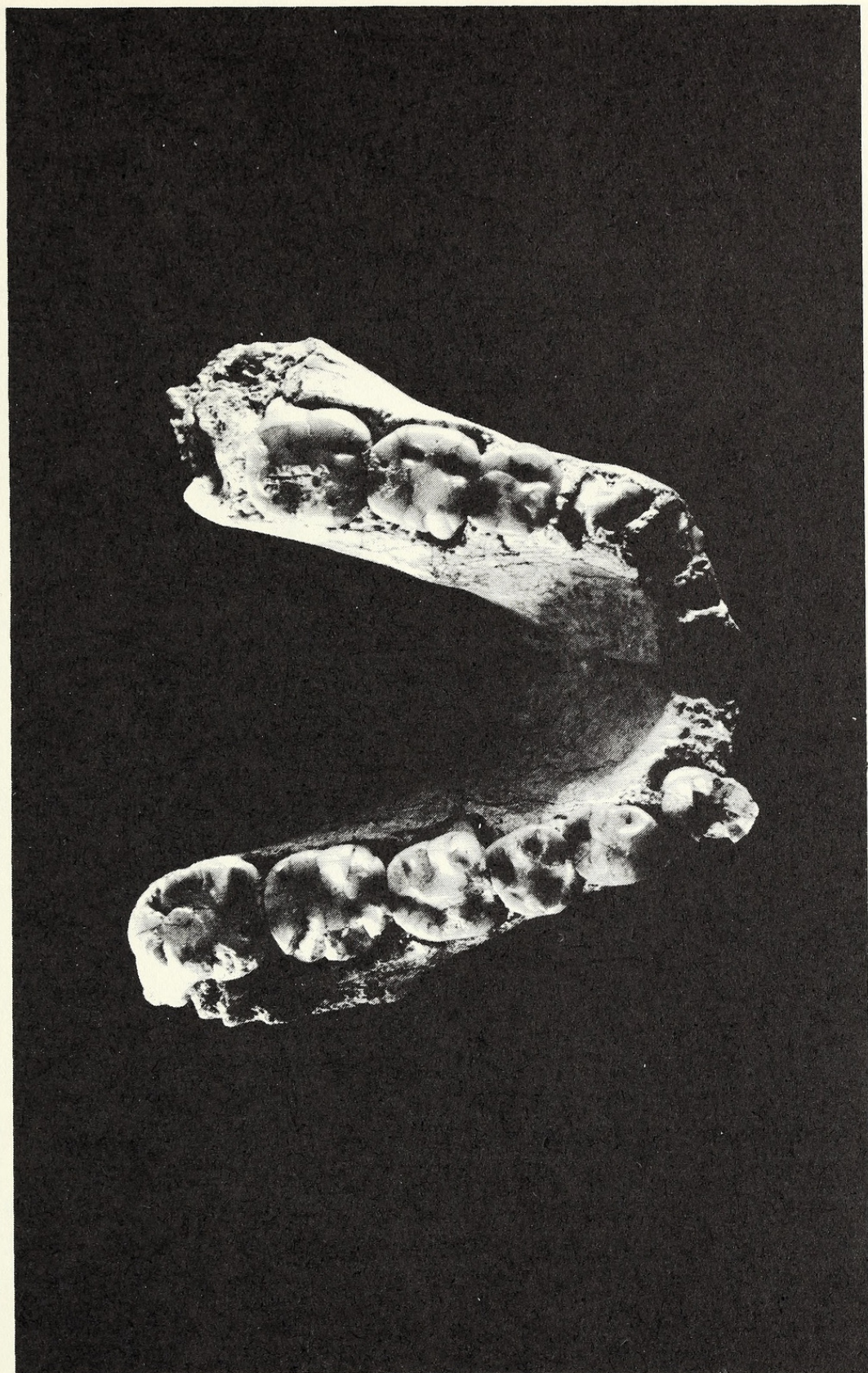


Fig. 2. Type specimen of the new species *Australopithecus afarensis*, the mandible L.H.-4 from Laetolil, Tanzania. Occlusal view. Natural size.



Fig. 3. Two distal femora from Hadar, Ethiopia (A.L. 333-4, left; A.L. 129-1a, right) indicating the size variation within the new species. Anterior view.

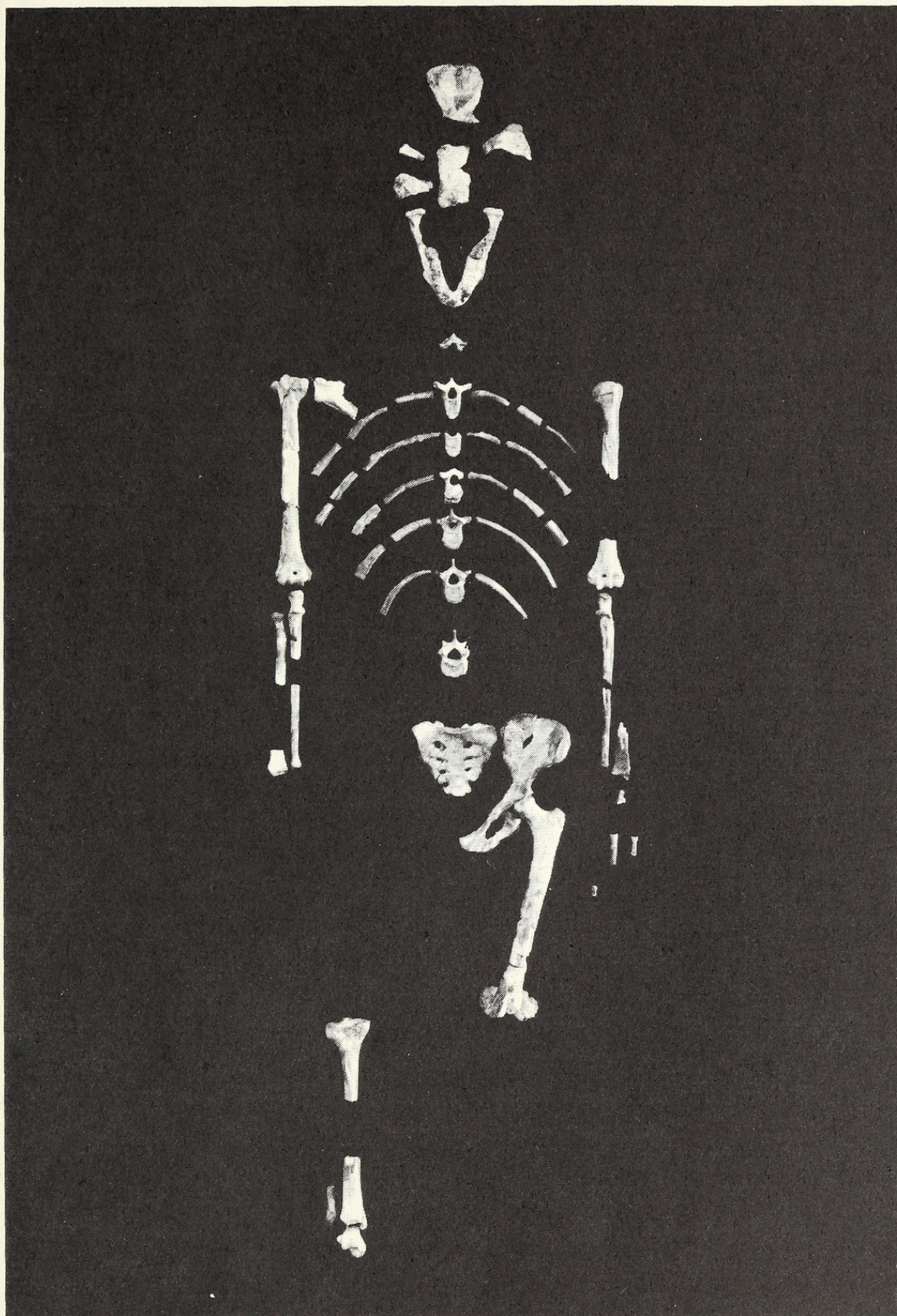


Fig. 4. The partial skeleton from Hadar, Ethiopia A.L. 288-1. The total length of the left femur is approximately 280 mm.

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