Primitive Hominid Canine from Tanzania

Abstract. *A primitive hominid canine recovered at Laetoli by Louis Leakey in 1935 and stored at the British Museum of Natural History adds to our knowledge of dental anatomy in* Australopithecus. *The specimen was the first adult* Australopithecus *recovered and the first ancient hominid discovered in eastern Africa.*

The Pliocene paleontologic locality of Laetoli in northern Tanzania has yielded fossils and footprints of human ancestors dated to nearly 4.0×10^6 years ago (*1*). The fossils constitute part of the evidence for the species *Australopithecus afarensis* (*2*).

Louis Leakey recovered fossil mammals from Laetoli in 1935 including some monkeys that were sent to the British Museum of Natural History. He reported no hominids. The 1939 Kohl-Larsen expedition found additional remains at Laetoli including evidence of the first hominids—a small maxilla fragment and an isolated molar (*3*). Leakey failed to find other hominids, but during the 1974 to 1979 expedition directed by M. D. Leakey, remains of 24 more hominid individuals were recovered (*1*). Work at Berkeley and the British Museum has shown that Louis Leakey, not Kohl-Larsen, found the first Laetoli hominid.

Louis Leakey collected specimen M. 18773, a left lower canine, in 1935. He identified it as a primate remain and sent it to the British Museum. E. Delson sent a cast of the specimen to Berkeley as part of the Laetoli monkey collection (*4*). I recognized its hominid status in March 1979 and contacted Peter Andrews at the British Museum of Natural History who had independently reached a similar conclusion.

The color, state of preservation, and the distinctive aeolian tuff matrix adhering to the mesial root surface of specimen M. 18773 (Fig. 1) indicate derivation from the Laetolil Beds. The specimen is a worn, permanent left lower canine. The crown is damaged and the distal half of the root is missing. Both crown and root are oval in horizontal section. The labiolingual crown axis is 10.3 mm, but the mesiodistal diameter is incomplete. Wear and breakage have reduced the crown height by about 2.0 mm, but a direct measure from buccal enamel line to the apex of the worn crown is 13.6 mm. The distal third of the crown is highly worn with a nearly vertical, flat wall of exposed dentine bounded by thin enamel strips. Microscopic striae from wear on labial and lingual crown faces are oriented vertically. Wear reaches the distal enamel line as the vertical dentine wall turns distally and horizontally, contributing to a scooped-out profile of the crown. Lack of a distal interproximal facet suggests an open lower canine-third premolar ($\bar{C}/P_3$) diastema.

Most occlusal wear on M. 18773 results from contact with the mesial occlusal edge of the upper canine. The canine-premolar (C/P_3) complex of Pliocene hominids is now documented by other specimens from Laetoli and Hadar; for example, A.L. 200-1a and L.H.-5 have upper canines with broad facets along the mesial occlusal edges formed by contact with the distal lower canine (*2, 5*).

The morphology of M. 18773 is primitive for a hominid but not unexpected in comparison with the primitive nature of the dental complex described for other Pliocene hominids from Hadar and Laetoli (*2*). Specimen M. 18773 is now assigned to *Australopithecus afarensis* (*6*). Dentine is less exposed on other specimens of this species, but the occlusal mechanics were clearly the same. Modern lower canines in humans differ markedly. They are normally spatulate in labial outline, do not project significantly above the tooth row, and display apical occlusal wear (Fig. 1). *Australopithecus robustus*, *A. africanus*, and *Homo habilis* follow a more human pattern and no specimens assigned to these taxa display lower canines with morphology like that described for M. 18773 (*7*).

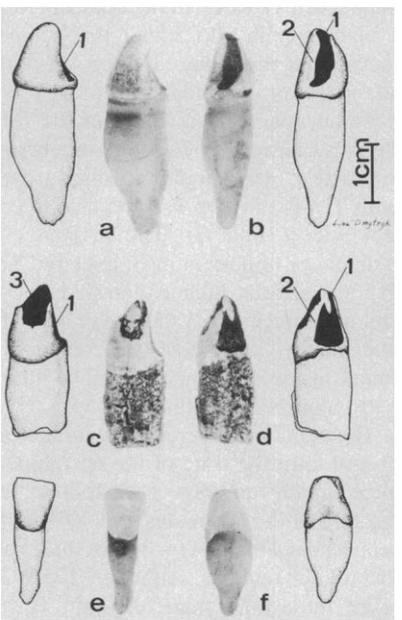

Fig. 1. Left lower canines ($\bar{C}$) from a female chimpanzee (top row), from a cast of a Pliocene hominid (middle row), and from a modern human (bottom row). (a) Labial aspect of the $\bar{C}$ of *Pan troglodytes*; (b) distal aspect of (a); (c) labial aspect of $\bar{C}$ specimen BMNH M. 18773 from *A. afarensis*; (d) distal aspect of (c); (e) labial aspect of $\bar{C}$ from *Homo sapiens* (Eskimo); (f) distal aspect of (e). The numeral 1 indicates dentine exposed by wear; 2, a worn enamel rim; and 3, postmortem enamel flake missing.

Lower canines similar to M. 18773 in occlusal projection and wear are found in modern and Miocene apes. Old female chimpanzees often show lower canines similar to M. 18773 (Fig. 1). Among the fossil apes, male *Sivapithecus* specimens recovered such as R.P.L.-56 from Macedonia and *Gigantopithecus blacki* from China have wear similar to that seen on this Laetoli hominid (*8*). Hominoid specimens recovered from the Miocene of Pakistan (GSP-9905 and GSP-8679) and from Pasalar in Turkey (BP-55 and BP-57) are functionally and morphologically similar (*9*).

The M. 18773 specimen confirms the primitive nature of the lower canine–third premolar complex in *A. afarensis* and provides another link with middle Miocene hominoids.

It also has historical implications. It was the first australopithecine recovered after Dart's discovery of the Taung child (*10*) and the first found in eastern Africa. It is the first adult specimen of *Australopithecus* ever recovered. Yet it lay on the shelves of the British Museum of Natural History during the controversy over Piltdown—a fake that included a lower canine artificially altered to resemble a heavily worn ape canine (*11*).

Because of its demonstrably apelike anatomy, M. 18773 might, in 1935, have seemed to contradict Dart's claim that *Australopithecus* was a hominid (*10*). The fossil now comfortably fits the conception of Pliocene hominid form. It reminds us that the intervening 45 years of fieldwork and laboratory study have significantly heightened our perception of hominid phylogeny.

TIM D. WHITE
Department of Anthropology,
University of California,
Berkeley 94720

References and Notes

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3. L. Kohl-Larsen, *Auf den Spuren des Vormenschen, Forschungen, Fahrten und Erlenbnisse in Deutsch-Ostafrika* (Strecker und Schröder Verlag, Stuttgart, Germany, 1943), band 1 and 2.
4. E. Delson also recognized a hominid lower incisor in the Berlin collections from Laetoli.
5. A full description of the C/P_3 complex of *A. afarensis* is in preparation by D. C. Johanson and T. D. White.

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6. Specimens of *A. afarensis* with wear on the distal edge of the lower canine include L.H.-14 (where there is more apical wear than on M. 18773), A.L. 128-23, A.L. 198-1, A.L. 333w-58, and A.L. 400-1a.
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Biopterin Cofactor Biosynthesis: Independent Regulation of GTP Cyclohydrolase in Adrenal Medulla and Cortex

Abstract. *Guanosine triphosphate cyclohydrolase, the enzyme that is apparently rate-limiting in biopterin biosynthesis, is increased in adrenal cortex and medulla of rats treated with insulin or reserpine. Denervation and hypophysectomy block the increase in medullary and cortical enzyme activity, respectively, whereas cycloheximide prevents the increase in both tissues. These results provide evidence for induction and regulation of guanosine triphosphate cyclohydrolase.*

L-Erythro-5,6,7,8-tetrahydrobiopterin (BH_4) is the putative cofactor for mixed function oxygenases participating in the synthesis of tyrosine, catecholamines, and serotonin (*1*) and in lipid metabolism (*2*). The low concentration of tissue BH_4 (*3*) relative to the Michaelis constants (K_m's) of tyrosine, tryptophan, and phenylalanine hydroxylases for BH_4 (*1*) indicates that availability of this cofactor could regulate the activity of these enzymes. Recently, large increases in the BH_4 content of rat adrenal medulla and cortex were observed after the administration of insulin and reserpine, and these increases were blocked by cycloheximide (*4*). These results suggested that the increase in cofactor concentration might be due to the induction of synthesis of one or more of the enzymes in the biopterin biosynthetic pathway. Reserpine and insulin have already been shown to induce the synthesis of adrenomedullary tyrosine hydroxylase and dopamine β-hydroxylase (*5*, *6*).

Reserpine acts on the adrenal medulla by blocking the uptake of catecholamines into the storage vesicles and indirectly, like insulin, by increasing splanchnic nerve discharge (*5*). Both drugs are also known to stimulate the adrenal cortex by enhancing the secretion of adrenocorticotropic hormone (ACTH) from the pituitary (*7*).

These observations led to the examination of the effect of these drugs in adrenal medullary and cortical guanosine triphosphate (GTP) cyclohydrolase activity (E.C. 3.5.4.16; D-erythrodihydroneopterin triphosphate synthetase), the first, and probably the rate-limiting, enzyme in the pathway leading from GTP to BH_4 (*8*). In this report, we describe a cycloheximide-sensitive increase in GTP cyclohydrolase activity of adrenal medulla and cortex following insulin or reserpine administration.

The specific activity of GTP cyclohydrolase is sixfold higher in the adrenal medulla than in the cortex (Table 1). Because of the larger mass of the cortex, the total enzyme activity is approximately the same in the two tissues. Significant increase in the activity of the enzyme in both tissues occurred 12 hours after administration of reserpine (Table 1) or 20 hours after administration of insulin (Fig. 1), the times at which maximum increases in BH_4 in medulla and cortex were observed (*4*). Reserpine treatment did not modify the apparent K_m's of the cortical or medullary enzyme for GTP. To test whether the increase in maximum velocity (V_{max}) after reserpine administration was due to induction of synthesis of the enzyme, we injected reserpine simultaneously with cycloheximide at doses previously shown to block the induction of synthesis of tyrosine hydroxylase and opioid peptides in the adrenal medulla (*5*, *6*, *9*). The protein synthesis inhibitor did not significantly affect the tissue mass of cortex or medulla but it decreased the specific activity of GTP cyclohydrolase in the medulla. Furthermore, cycloheximide completely prevented the reserpine-mediated increase in enzyme activity in both tissues. Reserpine and insulin are known to enhance secretion of ACTH from the pituitary (*7*), and hypophysectomy suppresses the increase in cortical, but not in medullary, BH_4 produced by these drugs (*4*). To determine if the increase in GTP cyclohydrolase was also hormonally mediated, we administered reserpine to hypophysectomized animals. The adrenal medulla showed no change, whereas the cortex showed an apparent increase in the specific activity of GTP cyclohydrolase after removal of the pituitary, presumably resulting from a faster loss of total tissue mass than loss of the activity of this enzyme (Table 1). Although reserpine produced its usual effect on the medulla of hypophysectomized animals, there was no effect on the cortex.

Both insulin-induced hypoglycemia

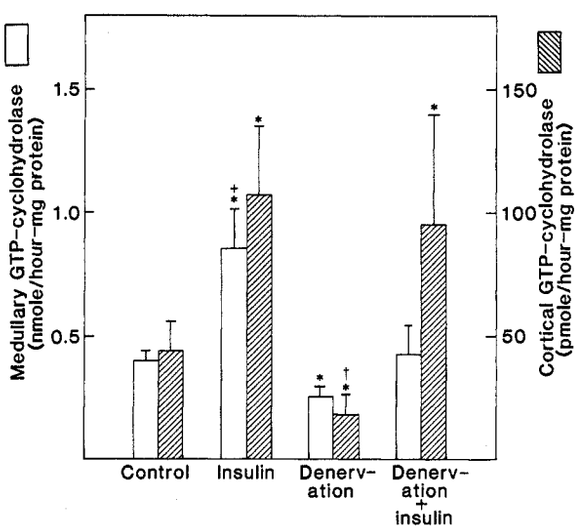

Fig. 1. Effect of denervation on the response of adrenal medullary and cortical GTP cyclohydrolase to insulin hypoglycemia. Increased splanchnic activation was obtained by injection of 10 units of insulin subcutaneously to fasted rats. After 4 hours the hypoglycemic shock was interrupted by administration of 1.0 ml of 40 percent sucrose by means of gastric tube and free access to food. The animals were killed 20 hours later. Splanchnic nerves were transected bilaterally between the diaphragm and coeliac ganglia 14 days before the experiment. Enzyme activity was measured as indicated in Table 1. Values are means ± standard error; $N = 5$ except for the group indicated by denervation plus insulin, where $N = 3$. $^*P < .05$ when compared to control groups. $^\dagger P < .005$ when compared to denervation plus insulin.

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