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[1] Warren, H. V., and Delavault, R. E., *Trans. Roy. Soc. Chem.*, Sect. III, **54**, 11 (1960).
[2] Cannon, H. L., and Bowles, J. M., *Science*, **137**, 765 (1962).
[3] Murozumi, M., Chow, T. J., and Patterson, C. C., *Geochim. Cosmochim. Acta*, **33**, 1247 (1969).
[4] Chow, T. J., and Johnstone, M. S., *Science*, **147**, 502 (1965).

Rates of Evolutionary Change in the Hominid Canine Teeth

RATES of evolutionary change in the size and shape of hominid cheek teeth were not constant during the Pleistocene[1]. Because of the widespread interest in the relationship between the use of tools and the evolution of human canine teeth, I now present data for rates of evolutionary change in hominid canines. Evolutionary rates should be rapid at times of strong selective pressure for larger or smaller canines. My data, however, do not support the orthodox view[2] that a reduction in size of the canine accompanied the appearance or early development of tool making by the precedessors of man.

The earliest hominid for which dental measurements and reliable estimate of age are available is the *Ramapithecus* maxilla from Fort Ternan, Kenya. The material has been dated by K/Ar at 14 million years[3]. Although there is disagreement about the taxonomic status of the Fort Ternan specimens, it is generally agreed that *Ramapithecus*, including the closely similar Asian material[4], is a reasonable ancestor for later hominid forms.

Younger fossil hominids (the oldest known australopithecines) have been reported from Omo Basin, Ethiopia. A mandibular fragment including a canine belonging to *Australopithecus* was obtained from locality 74 immediately below a layer dated at 1·87 m.y.[5]. The estimated age of this hemimandible was placed at 2·0 m.y. Further fossil hominids of known age for which canine and premolar measurements were available included the *Homo erectus* (Pithecanthropus IV) maxilla from Java[6] (700,000 yr), and the *Homo erectus* material from Choukoutien (Pekin), China[7] (370,000 yr). The dates are as given by Bilsborough[1], as are the parameters for teeth of *Homo sapiens* derived from the average of values for Australian aborigines[8] and African bushmen[9]. A phylogenetic series of hominid dentitions is thus provided from before the known existence of stone tools to the present—a period of 14 m.y.

The mesiodistal (MD) and buccolingual (BL) dimensions, shape index (100 BL/MD), and crown size ($MD \times BL$) were calculated to provide comparisons with previous data on premolars and molars[1]. Canine–premolar ratios (100 C/P^4) were also calculated for the module ($MD + BL/2$), and for crown size; the validity of these comparisons was demonstrated by Tobias[10].

Evolutionary rates were calculated according to Haldane's formula[11]

$$\text{Rate of change} = \frac{\log_e x_2 - \log_e x_1}{t_2 - t_1}$$

where x_1 and x_2 are the mean values for a parameter at times t_1 and t_2. Rates were expressed in millidarwins (one darwin is an increase or decrease in a parameter by a factor of e per m.y.).

Rates of change in the hominid canines and canino–premolar ratios are presented in Tables 1 and 2. Before *Homo erectus* appeared in the Middle Pleistocene, the rate of change was low in all parameters. It was less than 50 millidarwins even for reduction in canine size before 700,000 yr ago. Low rates of change for premolars and molars were also obtained[1] for the Lower Pleistocene.

Table 1. RATES OF EVOLUTIONARY CHANGE OF HOMINID MAXILLARY CANINE TEETH

Interval		Parameter	Rate
Ramapithecus (Fort Ternan)—*Homo erectus* (Java) (13·3 m.y.)	MD	9·25– 9·5	+2
	BL	8·0 – 11·8	+29
	I	86·5 –124·2	+27
	A	74·0 –112·1	+31
	C/P^4M	106·2 –103·4	−2
	C/P^4A	120·3 –109·6	−7
Homo erectus (Java)—*Homo erectus* (Pekin) (0·33 m.y.)	MD	9·5 – 9·4	−22
	BL	11·8 – 10·2	−456
	I	124·2 –107·6	−434
	A	112·1 – 95·7	−479
	C/P^4M	103·4 –101·5	−56
	C/P^4A	109·6 –106·3	−94
Homo erectus (Pekin)—*Homo sapiens* (0·37 m.y.)	MD	9·4 – 8·0	−456
	BL	10·2 – 8·4	−511
	I	107·6 –105·5	−55
	A	95·7 – 66·9	−967
	C/P^4M	101·5 –101·1	−10
	C/P^4A	106·3 –104·6	−43

MD = mesiodistal diameter; BL = buccolingual diameter; I = shape index; A = crown area; M = module; C/P^4 = ratio of canine to upper posterior premolar.

Table 2. RATES OF EVOLUTIONARY CHANGE OF HOMINID MANDIBULAR CANINE TEETH

Interval		Parameter	Rate
Australopithecus (Omo)—*Homo erectus* (Pekin) (1·63 m.y.)	MD	8·8 – 8·6	−16
	BL	9·7 – 9·2	−32
	I	110·2 –107·4	−16
	A	85·4 – 78·9	−48
Homo erectus (Pekin)—*Homo sapiens* (0·37 m.y.)	MD	8·6 – 7·2	−470
	BL	9·2 – 7·7	−498
	I	107·4 –106·3	−29
	A	79·1 – 55·1	−968

MD = mesiodistal diameter; BL = buccolingual diameter; I = shape index; A = crown area.

Not until the Middle Pleistocene, when the process of tool making had become a highly refined skill associated with specialized lithic industries, was the rate of reduction in canine size rapid. From *Homo erectus* at Choukoutien to *H. sapiens* the rate of decrease in both upper and lower canines was nearly 1 darwin, while the change in shape and in relative size was negligible. Strongly selective factors clearly produced markedly rapid reduction in absolute size of the canine from *H. erectus* to *H. sapiens*, and at rates comparable with those for reduction of the upper and lower premolars[1] during the same time period.

Before, and perhaps during, the time of rudimentary tool development in the Pliocene, and during the time of primitive pebble tool use in the Early Pleistocene when, according to the orthodox view, the canine should have been responding to strong selective pressure, the rate of change was at its lowest.

These data suggest that the development of tool making among the earliest hominids was not associated with rapid change in size and shape of the canine teeth. When rapid dental reduction finally occurred during and after the Middle Pleistocene, it seems to have come about as a result of factors other than the development of tool making.

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[1] Bilsborough, A., *Nature*, **223**, 146 (1969).
[2] Washburn, S. L., *Scientific American*, **253**, 62 (1960).
[3] Leakey, L. S. B., *Ann. Mag. Nat. Hist.*, **4**, 689 (1962).
[4] Simons, E. L., *S. Afric. J. Sci.*, **64**, 92 (1968).
[5] Howell, F. C., *Nature*, **223**, 1234 (1969).
[6] Weidenreich, F., *Anthrop. Pap. Amer. Mus.*, **40**, 1 (1945).
[7] Weidenreich, F., *The Dentition of Sinanthropus Pekinensis, Palaeontologica Sinica* (NS D1, Pekin, 1937).
[8] Campbell, T. D., *Dentition and Palate of the Australian Aboriginal* (Publ. Keith Sheridan Foundation Medical Research 1, Adelaide, 1925).
[9] Drennan, M. R., *Ann. S. Afric. Mus.*, **24**, 61 (1929).
[10] Tobias, P. V., *The Cranium and Maxillary Dentition of Australopithecus (Zinjanthropus) boisei* (Cambridge Univ. Press, 1967).
[11] Haldane, J. B. S., *Evolution*, **3**, 51 (1949).