Evolution, 41(4), 1987, pp. 705–720

GRADUAL CHANGE IN HUMAN TOOTH SIZE IN THE LATE PLEISTOCENE AND POST-PLEISTOCENE

C. Loring Brace, Karen R. Rosenberg, and Kevin D. Hunt
Museum of Anthropology, University of Michigan, Ann Arbor, MI 48109

Abstract.—Starting with the onset of the last glaciation approximately 100,000 years ago and continuing to the end of the Late Pleistocene approximately 10,000 years ago, human tooth size began to reduce at a rate of 1% every 2,000 years. Both the mesial-distal and the buccal-lingual dimensions of mandibular and maxillary teeth were undergoing the same rate of reduction. From the beginning of the Post-Pleistocene until the present, the overall rate of dental reduction doubled, becoming approximately 1% per thousand years. Buccal-lingual dimensions are now reducing twice as fast as mesial-distal dimensions, and maxillary teeth are reducing at an even more rapid rate than mandibular teeth. Late Pleistocene rates are comparable in Europe and the Middle East. The Post-Pleistocene rates are also the same for Europe, the Middle East, China, Japan, and Southeast Asia. It is suggested that the cookery at the beginning of the Late Pleistocene allowed the earlier changes to occur. The use of pottery within the last 10,000 years further reduced the amount of selection that had previously maintained usable tooth substance. Reduction then occurred as a consequence of the Probable Mutation Effect (Brace, 1963; McKee, 1984).

Received June 13, 1986. Accepted January 2, 1987

There is a widespread assumption that human evolution effectively ceased with the appearance of "anatomically modern" *Homo sapiens* just over thirty thousand years ago (Wallace, 1864, 1870, 1871, 1903; Bergson, 1907; Hooton, 1931; Haldane, 1932; Howells, 1959; Coon, 1962; Mayr, 1963; Fishbein, 1976; Tattersall and Eldredge, 1977; Stanley, 1981; Eldredge and Tattersall, 1982; R. E. Leakey in Fisher [1983]). In virtually every case, however, this assumption is based on theoretical expectations rather than empirical analysis of actual data distributed through time.

Studies of long-bone robustness (Lovejoy and Trinkaus, 1980) and cranial-vault reinforcements (Smith and Ranyard, 1980; Wolpoff et al., 1981; Trinkaus and LeMay, 1982; F. Smith, 1982) show that change has indeed taken place, but the scattered and incomplete nature of the evidence has left open the question of whether that change occurred throughout the hominid gene pool as some have suggested (Brace, 1964, 1979*a*, 1979*b*; Frayer, 1978; Wolpoff, 1980; F. Smith, 1982), or by a sequence of invasions and extinctions as traditionally assumed (Boule and Vallois, 1957; Howells, 1973) and recently reasserted (Tattersall and Eldredge, 1977; Bräuer, 1981, 1984*a*, 1984*b*; Stanley, 1981; Eldredge and Tattersall, 1982; Stringer, 1982, 1985; Rightmire, 1983*a*, 1983*b*; Stringer et al., 1984).

In the present paper, we consider data from the most readily preserved portion of the skeleton, namely the dentition. Teeth are preserved in greater numbers than are other parts of the skeleton, they are a closer reflection of the genotype, they are more directly affected by the forces of natural selection, and they are easily treated by quantitative methods (Brace, 1979*a*, 1980).

Materials and Methods

Since teeth have adaptive value only so long as usable crown substance is preserved, the most meaningful measures are those of crown size. The crown is a three-dimensional object, and ideally it would be best represented by dimensions of length, width, and height. However, the widespread occurrence of occlusal wear, especially on the teeth of prehistoric populations, means that crown height is almost always reduced by an unknowable amount (Brace, 1967). Our assessment is based on a study of the standard mesial-distal and buccal-lingual crown dimensions of human teeth (Brace, 1979*a*, 1980). Because interproximal wear may reduce the mesial-distal dimensions to a marked extent, we did not use teeth when we judged that wear would significantly have reduced the original dimension. Nevertheless, we continue to consider mesial-distal measurements because they yield useful results when treated in conjunction with buc-

cal-lingual measures, and also because the rate of change of the two dimensions appears to have diverged in the recent past. If we had used only the dimension least affected by wear, we could not have discovered this divergence.

Each dimension of the 32 teeth in the normal dental arch can be considered, which involves 64 separate variables. Since the left and right antimeres can be regarded as products of the same genetic background, the mean of both may be a better reflection of the genotype than each taken separately. Useful comparisons can also be made by examining the product of the mesial-distal and buccal-lingual measurements, a statistic that has been called the "cross-sectional area" (Brace and Mahler, 1971). For all but the Neanderthal samples, the data used for comparison are mid-sex means, that is, the sum of the separate male and female means divided by two. Since most of the Neanderthal material cannot be sexed, the figures used are total-sample means. For our most basic comparisons, then, we use 16 mesial-distal and 16 buccal-lingual means per population.

For ease of graphic comparison, we also sum the upper and lower cross-sectional areas of each tooth category to produce what has been called a "composite tooth-size profile" for each group (Brace, 1980). The use of this is illustrated in the comparisons displayed in Figure 1. Finally, if we sum the eight means in the composite tooth-size profile we get a single number referred to as "summary tooth-size" (TS) that can be used as a crude index of total occlusal area in each population (Brace, 1978; Brace and Hinton, 1981). The results lend themselves to the kind of treatment illustrated in Figure 2.

For those who may feel that such a treatment obscures what might be separate rates of change for the anterior and posterior teeth, rates of cross-sectional area change for each of the individual maxillary and mandibular teeth are presented in Figure 3. Even this, however, obscures what might be separate individual mesial-distal and buccal-lingual rates of change. The Late Pleistocene and Post-Pleistocene change rates for these individual dimensions are presented in Figures 4 and 5, and it is clear that separate consideration is warranted if we wish to understand what has happened in detail.

Samples Compared

Research efforts concerned with human prehistory have been pursued more intensively and for a longer period of time in Europe than anywhere else, and consequently there is more evidence on which to base our assessment of European dental change through time than there is for any other part of the world. The material used to determine tooth size at the beginning of the Late Pleistocene is from Krapina, in Yugoslavia. This is the only site from which complete data are available for Early Neanderthal tooth size (Brace, 1979*a*). The majority of the teeth are not implanted so it was not possible to make a determination of sex.

The Late Neanderthal material is from western Europe and includes isolated teeth and unsexable specimens (Wolpoff, 1971). Such included specimens as Le Moustier, La Ferrassie, and La Quina from France and Spy from Belgium were excavated before a detailed knowledge of stratigraphy and dating was possible. Our attempts to assess antiquity, then, are approximate at best. With the new realization that the Mousterian toolmaking tradition associated with the Neanderthals stretched over a time span almost twice as long as that previously accepted, dates of approximately 100,000 years ago for the Early Neanderthals and 50,000 years ago for the Late Neanderthals of Würm II are about the best that we can do (Dennell, 1983).

The situation for the European Upper Paleolithic, Mesolithic, and Neolithic, is a little better, although in many instances the material, as with the Neanderthal specimens, was excavated at a time when its exact antiquity could not be determined, and stratigraphic information was not preserved to allow us to calculate this in retrospect. The associated archaeology, however (Frayer, 1978), does allow us to posit the dates used in Figure 2.

RESULTS

Figure 1 portrays the change in tooth size for the available European samples starting

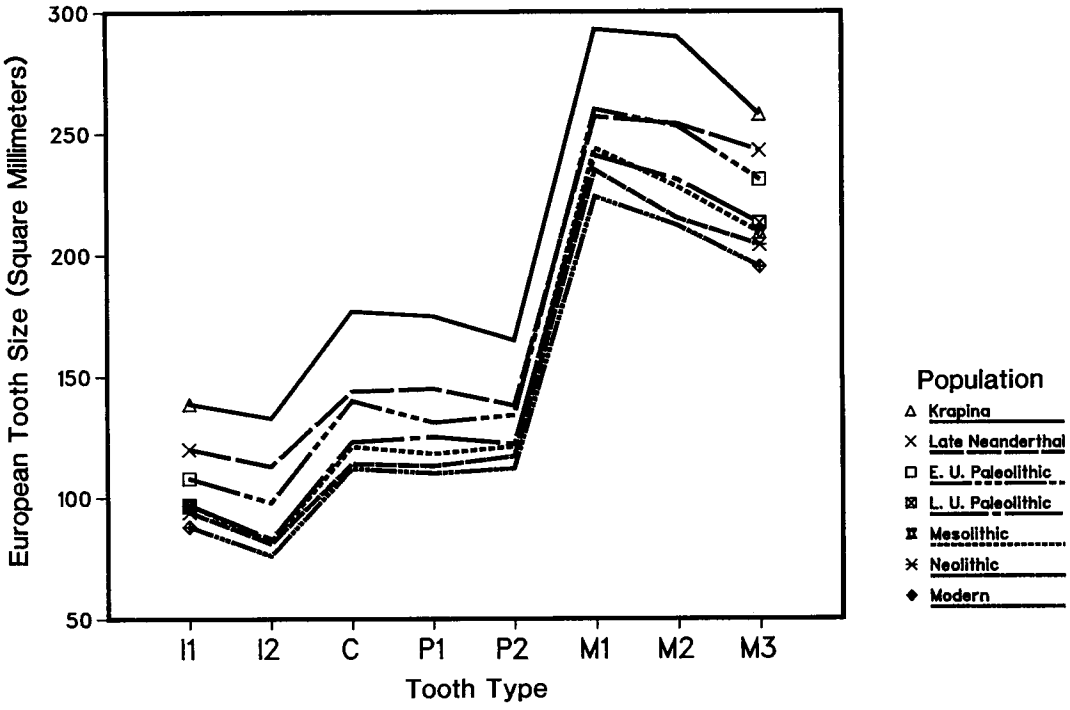

FIG. 1. Composite tooth-size profiles (Brace, 1980) for available European samples from the beginning of the Late Pleistocene to the present. The vertical axis represents cross-sectional area in mm^2 of the tooth categories noted on the horizontal axis. The lines connecting the tooth-type points provide the tooth-size profiles for the populations indicated by the symbols in the legend. The Early Neanderthals are from Krapina in Yugoslavia (Brace, 1979*a*), the Late Neanderthals are from approximately 50,000 years ago (Wolpoff, 1971; Brace, 1979*a*). The Early Upper Paleolithic is from between 28,000 and 33,000 years ago, and the Late Upper Paleolithic is from 12,000–15,000 years ago (Frayer, 1978). The Mesolithic figures are from French material between 8,000 and 10,000 years old (Frayer, 1978). The Neolithic figures are from English, French, and Swiss material between 4,000 and 6,000 years old and the "modern" European figures were compiled by combining data from Medieval and post-Medieval samples from England, France, Germany, Switzerland, Italy, and Yugoslavia measured by the senior author at the British Museum (Natural History) in London (courtesy of Dr. C. B. Stringer), the Duckworth Laboratory at Cambridge University (courtesy of Dr. J. P. Garlick), the Musée de l'Homme in Paris (courtesy of Dr. J.-L. Heim), The Département d'Anthropologie at the Université de Genève (courtesy of Prof. M.-R. Sauter and Dr. C. Kramar-Gerster), the Peabody Museum at Harvard University (courtesy of Prof. D. R. Pilbeam) and the von Luschan collection at the American Museum of Natural History in New York (courtesy of Dr. I. Tattersall).

with the beginning of the Late Pleistocene somewhere between 70,000–115,000 years ago and continuing up to the present. There has been a marked reduction since the beginning of the Late Pleistocene. If the data in Table 1 are used as a basis for comparison, then the reduction in total crown area from the Krapina Neanderthals to an average "modern" European amounts to some 45%. The reduction from Krapina to the Medieval Swiss figure is over 50%. It is also evident that tooth-size reduction is roughly proportional to time, a matter we shall return to again shortly.

Tooth Size and Body Size

For some human groups, low but positive correlations between tooth-size and body-size measures have been noted, and some of the correlations are significant (Garn et al., 1968*a*, 1968*b*; Henderson and Corruccini, 1976; Lavelle, 1977). For at least one group of Australian aborigines the correlations are markedly higher ranging between 0.24 and 0.51, although, even there, the allometric exponents are less than half the size of those recorded for the other primates for which such data are available (Wolpoff, 1985). However, even if the nature of the

TABLE 1. Summary Tooth Size (TS) in mm^2, average N and range of N for the European samples used.

Sample	TS	Mean N	Range of N (per tooth)
Krapina	1,631	13	(9–18)
Late Neanderthal	1,415	13	(5–20)
Early Upper Paleolithic	1,355	14	(5–27)
Late Upper Paleolithic	1,235	19	(9–34)
Mesolithic	1,220	49	(25–62)
Neolithic			
English	1,196	39	(17–57)
French	1,180	36	(7–56)
Swiss	1,138	15	(12–18)
Modern (17th century)			
English	1,120	32	(5–44)
French	1,128	52	(19–80)
German	1,141	30	(12–39)
Swiss	1,078	28	(21–34)
Italian	1,149	23	(7–39)
Yugoslav	1,140	79	(43–97)

allometric relation between tooth and body size in other organisms (Kurtén, 1954, 1967; Gould, 1966, 1968, 1971; Gould and Garwood, 1969; Gingerich, 1977, 1981; Gingerich et al., 1982; Gingerich and Smith, 1985) had been observed, it is clear that if differences in human tooth size are to be thus accounted for, then the amount of body-size change would have to have been an order of magnitude beyond that which actually took place. There is evidence to suggest that the recent human physique is less robust than that of the Neanderthals of 50,000 years ago and earlier (Trinkaus, 1978, 1981, 1983*a*; Lovejoy and Trinkaus, 1980; Rosenberg 1986*a*, 1986*b*), and there are abundant indications that tooth size has also undergone substantial reduction (Brace, 1964, 1979*a*). Consequently, it is important to consider whether the observed tooth-size reduction is simply an allometric result of body-size changes.

While there is no way to deal directly with body size for most of the groups we have considered, we do have cranial measurements for some of them. If in fact there is an allometric relation between body size and brain size within a given group as many have noted (Jerison, 1973; Riska and Atchley, 1985), then there is some reason to use those cranial measurements that can be combined to give an approximation to brain size as the basis for an appraisal of the extent to which body and dental dimensions covary. The product of the length, width, and height of the brain case gives a crude approximation of brain size, especially in *Homo sapiens* where the configuration of the cranium corresponds more closely to the dimensions of the brain itself than is true for the majority of mammals.

For four of our modern samples, two Asian and two European, we have produced correlations and regressions of tooth size on brain size as indicated by the product of those three cranial dimensions. The highest within-group r values between brain size and the dental dimensions with which it is most highly correlated (namely first and second lower and upper molars used separately and/or together, whichever produces the highest figure) are 0.12 for the Ainu ($N = 62$), 0.38 for Italians ($N = 11$), 0.54 for Hong Kong Chinese ($N = 27$) to 0.60 ($N = 18$) for Germans. Only the German figure is significantly different from zero.

The regression coefficients on log-transformed data range from 0.012 for the Ainu to 0.07 for the Hong Kong Chinese, with the Germans and Italians at 0.037 and 0.038, respectively. Only the Hong Kong slope is significant. When the several modern regressions are used to predict Neanderthal tooth size from the available data for Neanderthal brain size (cranial measurements from Suzuki [1970]), the modern regressions underestimate the observed extent to which Neanderthal tooth size exceeds modern levels by percentages ranging from 45% using Germans to over 90% using Ainu data. Looked at the other way around, there is no way that we could use the reduction in human cranial size recorded in the recent geological past to predict the magnitude of decrease in dental dimensions that in fact occurred during that same period of time.

There has been some previous reflection on the possibility that brain and body size have become "decoupled" in the course of primate evolution (Pilbeam and Gould, 1974; Gould, 1975; Lande, 1979). Our data suggest that in contrast to other mammalian groups, tooth size and body size have become notably decoupled in recent prehistoric and modern human populations. From this we can conclude that our findings are in keeping with previous observations on

tooth size and body size in fossil hominids, namely that the relationship is "effectively nil" (Garn and Lewis, 1958; Henderson and Corruccini, 1976).

Rates of Change in Tooth Size

When European summary tooth-size (TS) is plotted against time (see Fig. 2), the slope is not only significant ($r > 0.98$, $P < 0.01$), but the Post-Pleistocene regression line is twice as steep as that for the Late Pleistocene. The Early Neanderthal material from Krapina comes from the boundary between the last interglacial and the onset of the last glaciation (Malez, 1970*a*, 1970*b*), but whether that date is 70,000, 75,000, 100,000, 110,000, or 115,000 years ago is still a matter of debate (Bowen, 1978; van Eysinga, 1978; Ruddiman and McIntyre, 1979; Woillard and Mook, 1982). If the beginning is considered to be at 70,000 years ago, the regression slope is -0.0066 mm^2/yr and the r value is 0.982 ($P = 0.003$). At 110,000 years ago, the slope is -0.0041 mm^2/yr and the r value is 0.992 ($P = 0.0009$), and at 100,000 years ago, the slope is -0.0046 mm^2/yr and the r value is 0.996 ($P < 0.0001$). In contrast, the Post-Pleistocene slope is -0.0123 mm^2/yr and the r value is 0.888 ($P = 0.0003$). When the regressions are calculated on pooled unsexed data instead of using the mid-sex means, the Late Pleistocene slope is reduced by 0.0002 mm^2/yr and the Post-Pleistocene slope is reduced by 0.002 mm^2/yr because of the weighting of the larger male dimensions. However, the change in slope is not significant in either case and makes virtually no discernible difference in the nature of the overall picture.

Depending on which terminus post quem is used for the onset of the Late Pleistocene, the Post-Pleistocene rate of dental reduction is between two and three times the Late Pleistocene rate. In contrast, there is no evidence that there was any reduction at all from the earlier Middle Pleistocene populations to the levels visible at the beginning of the Late Pleistocene (Brace, 1967, 1979*a*, 1980). Figure 2 shows the plot of TS against time where the beginning date is arbitrarily set at 100,000 years ago and separate regression lines are calculated for the Late Pleistocene and Post-Pleistocene data points.

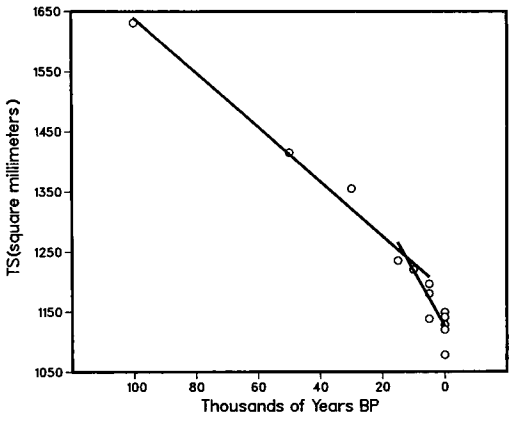

FIG. 2. TS regression lines for Early Neanderthal, Late Neanderthal, Early Upper Paleolithic, Late Upper Paleolithic, and Mesolithic European samples (slope = -0.0046, $r = 0.996$, intercept = 1181.7, $P < 0.0001$), and Mesolithic, Neolithic, and modern European samples (slope = -0.0123, $r = 0.888$, intercept = 1115.2, $P = 0.0003$). The TS data are listed in Table 1.

Furthermore, as can be seen in Table 2 and also in Figure 5, the Post-Pleistocene acceleration of dental reduction is largely the result of change in the buccal-lingual dimensions in general and the maxillary teeth in particular. The rates of reduction in both maxillary and mandibular teeth and in both length and width were essentially the same during the Late Pleistocene (see also Fig. 4). In the Post-Pleistocene, however, the maxillary teeth are reducing twice as fast as the mandibular teeth (this confirms the previous observation of this trend based on a more limited sample by LeBlanc and Black [1974]), and the buccal-lingual dimensions are reducing more than twice as fast as the mesial-distal dimensions (Fig. 5). The Late Pleistocene and Post-Pleistocene rates of reduction in cross-sectional areas are graphically depicted in Figure 3 where

TABLE 2. Average regression slopes (change per thousand years) for mesial-distal and buccal-lingual dimensions calculated separately for the maxillary and mandibular teeth of Late Pleistocene and Post-Pleistocene European samples.

	Mesial-Distal	Buccal-Lingual
Late Pleistocene maxilla	−0.018	−0.017
Late Pleistocene mandible	−0.015	−0.016
Post-Pleistocene maxilla	−0.035	−0.049
Post-Pleistocene mandible	−0.016	−0.041

TABLE 3. Rate of Dental Reduction (cross-sectional area in darwins[1]) in Late and Post-Pleistocene Europe.

	Krapina-Mesolithic	Mesolithic-Modern
Maxilla		
I1	1.70	6.83
I2	2.87	5.62
C	1.73	4.16
P1	2.23	4.91
P2	1.70	4.54
M1	1.30	3.89
M2	1.00	4.64
M3	1.25	4.99
Mandible		
I1	2.04	2.28
I2	2.15	2.88
C	2.08	2.70
P1	1.87	4.01
P2	1.60	2.48
M1	0.71	3.83
M2	1.50	3.47
M3	1.05	2.69

[1] Darwins of areas are divided by 2 to make them comparable with rates for linear dimensions.

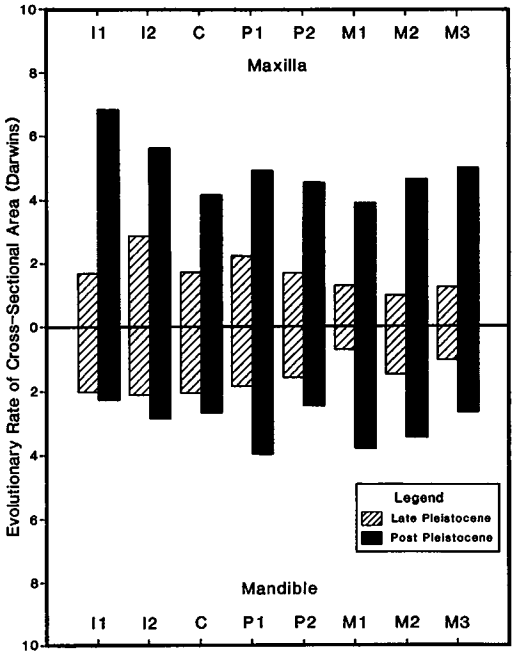

FIG. 3. Rates of change (in darwins) of maxillary and mandibular cross-sectional area for each tooth category. The shaded bars represent Post-Pleistocene rates and the unshaded bars depict Late Pleistocene rates. The figure is based on the data in Table 3 from the sources noted in Figure 1.

the bar representing change for each tooth extends above (for maxillary teeth) or below (for mandibular teeth) the zero line in darwin units where one darwin is a change by a factor of e in one million years (Haldane, 1949). The rate of mandibular tooth-size change nearly doubles while that of maxillary tooth size change nearly triples ($P = 0.0001$).

The increase in the rate of change for individual tooth dimensions in the Post-Pleistocene relative to that for the Late Pleistocene can be seen by comparing Figures 4 and 5. While the rate of change increases for most dimensions, it is most marked for the buccal-lingual measurements in general ($P = 0.005$) and the maxillary teeth in particular ($P < 0.0001$). As can be seen in Figure 5, the obvious exception to this generalization is the large change in the mesial-distal dimensions of the Post-Pleistocene maxillary incisors. This is the dimension most strongly affected by interproximal wear, especially in the anterior dentition of earlier populations. This does not mean that the pattern shown in Figure 5 is incorrect, but it suggests that the earlier pattern for maxillary incisor change shown in Figure 4 is an underestimate of what may have been taking place.

Although it can be no more than speculation, we can at least suggest that the constraints of maintaining regular interproximal contacts and a functioning occlusion indicate that mesial-distal dimensions are less free to vary than buccal-lingual dimensions. The role of approximal relationships in maintaining an effective occlusion may indicate that a component of selection continues to affect mesial-distal dimensions. There are no such constraints affecting buccal-lingual dimensions, and when selection for maintaining usable crown substance is suspended, the subsequent predictable reduction should be most marked in the buccal-lingual diameters.

The Non-European Evidence

The Middle East.—Although the actual evidence presents a picture of gradual and accelerating reduction in Europe, the traditional explanation has been to regard this as caused, not by change in situ, but by invasion of new populations from the east and, initially, by replacement of the resident Neanderthals (Spencer and Smith, 1981; El-

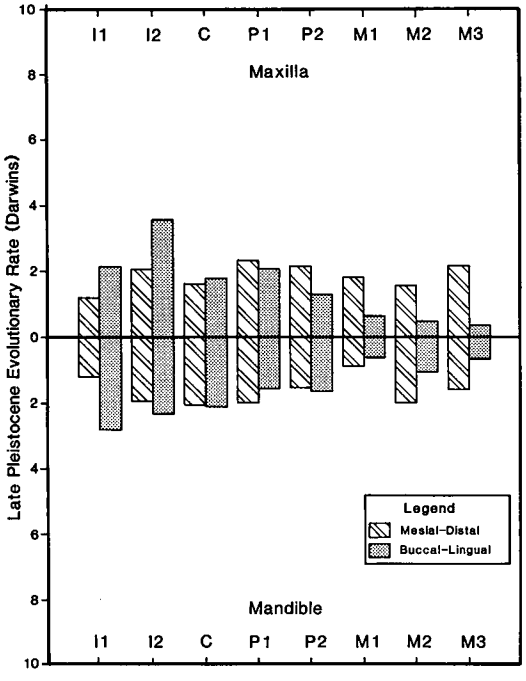

FIG. 4. Late Pleistocene rates of change (in darwins) for mesial-distal and buccal-lingual dimensions of maxillary and mandibular teeth in Europe. The figure is based on the data in Table 4 from the same sources noted in Figure 1.

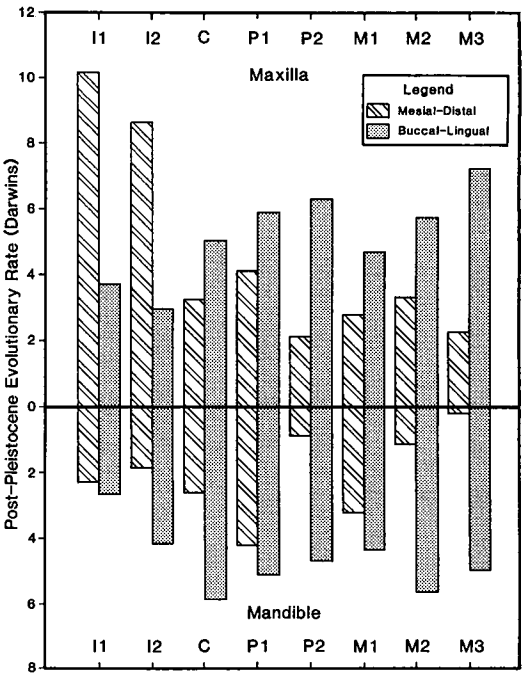

FIG. 5. Post-Pleistocene rates of change (in darwins) for mesial-distal and buccal-lingual dimensions of maxillary and mandibular teeth in Europe. The figure is based on the data in Table 4 from the same sources noted in Figure 1.

dredge and Tattersall, 1982; Rightmire, 1983*a*, 1983*b*; Stringer et al., 1984). Such a view assumes that modern form, in this case dental reduction, should occur earlier to the east than in Europe. Fortunately, the Middle East is the only other part of the world where Late Pleistocene human skeletal remains occur in sufficient quantity and datable context so that a comparison can be made. Neanderthals from Shanidar Cave in Iraq are temporal equivalents of European Late or "classic" Neanderthals, and they are also strikingly similar in form (Brace, 1979*a*; Trinkaus, 1983*b*). Furthermore, with a TS of 1,400 mm^2 (calculated from Trinkaus [1983*b*]), they have teeth of the same size. By 35,000 years ago, the "Neanderthaloids" at Skhūl, Mount Carmel (Israel), had a TS of 1,353 mm^2 (calculated from McCown and Keith [1939]). By 12,000 years ago (Henry and Servello, 1974), TS for the Mesolithic Natufians in Israel was down to between 1,273 mm^2 (calculated from Dahlberg [1960]) and 1,306 mm^2 (from measurements made on samples from Kebara, Shukba, and El Wad, stored in the collections at the Peabody Museum, Harvard University, with the permission of Professor W. W. Howells: sample sizes ranged from 30 to 65 and averaged 50; as with the Neanderthals, sexing was not possible because much of the collection consists of loose teeth).

We have used the term "Neanderthaloid" in the sense preferred by the late Sir Arthur Keith (McCown and Keith, 1939): that is, to denote specimens that "recall genuine Neanderthals in many respects, but in other features deviate in the modern direction" (Brace, 1979*b*). The Skhūl individuals are the best representatives of intermediate morphology available, and, at 35,000 years ago (Brothwell, 1961; Higgs, 1961*a*, 1961*b*; Oakley, 1962; Solecki, 1963; Trinkaus and Howells, 1979; Jelinek, 1982), they are intermediate between Neanderthals and Upper Paleolithic "moderns" in time as well as form.

There is another collection from Israel that has been considered "Neanderthaloid"

TABLE 4. Rate of Dental Reduction (mesial-distal [MD] and buccal-lingual [BL] dimensions in darwins) in Late and Post-Pleistocene Europe.

	Krapina-Mesolithic		Mesolithic-Modern	
	MD	BL	MD	BL
Maxilla				
I1	1.22	2.16	10.17	3.72
I2	2.10	3.59	8.65	2.97
C	1.65	1.80	3.26	5.07
P1	2.36	2.09	4.14	5.92
P2	2.18	1.32	2.14	6.34
M1	1.85	0.67	2.83	4.73
M2	1.60	0.51	3.35	5.79
M3	2.19	0.39	2.30	7.27
Mandible				
I1	1.21	2.83	2.29	2.66
I2	1.95	2.33	1.88	4.18
C	2.07	2.12	2.64	5.86
P1	1.99	1.55	4.23	5.13
P2	1.53	1.64	0.87	4.70
M1	0.88	0.61	3.24	4.37
M2	2.00	1.04	1.13	5.67
M3	1.59	0.66	0.19	4.98

in the same sense. This is the series of specimens found at Qafzeh starting in 1934 (Neuville, 1934–1935; Vandermeersch, 1970). In many aspects of morphology, they are clearly intermediate between fully Neanderthal and "modern" forms (Vandermeersch, 1981), but there remains an unresolved problem concerning their date. There is an amino acid racemization date of 33,000 years ago (Bada and Helfman, 1976) which fits with the archaeological assessment of one authority (Jelinek, 1982). Another archaeological assessment suggests a date nearer to 50,000 years ago (Trinkaus, 1983*b*), while sedimentological studies (Farrand, 1979) and evaluations of the fossil rodents (Bar Yosef and Vandermeersch, 1981) support a date of 70,000 or 80,000 years ago or older. The dentition is the one area where the Qafzeh specimens are not intermediate between the Neanderthal and modern conditions. With a TS of 1,503 mm^2 (calculated from Vandermeersch, 1981), they are intermediate between the Early and the Late Neanderthals. From this perspective, we would prefer the earlier dates. However, our whole thesis is compromised if we use morphology to determine date, so, since there is so much disagreement between those who have dealt with the data on which a date could be independently established, we have chosen to omit Qafzeh from the samples on which our calculations are based.

When reliably dated samples are used, the regression slope calculated from the Late Pleistocene teeth in the Middle East is -0.003 mm^2/yr which changes to -0.0165 mm^2/yr ($P = 0.04$) when the reduction from Mesolithic to Neolithic to modern is plotted (Dahlberg, 1960; Rosenzweig and Zilberman, 1967; Arensburg et al., 1980). Although the Late Pleistocene slope is not quite the same as that for Europe, there is a dramatic change at the end of the Pleistocene, and the Post-Pleistocene slopes are essentially identical. From this we can conclude that the Middle East, rather than being the earliest locus of the reductions that result in modern European form, gradually witnessed such reductions at precisely the same time that they were taking place in Europe.

Nubia.—Similar trends of Post-Pleistocene dental reduction are also visible beginning in the Mesolithic in Nubia (Calcagno, 1983*a*, 1983*b*), although there is reason to suspect that Mesolithic tooth size there was as much as 100 mm^2 larger than it was in the Middle East and Europe (Greene et al., 1967).

The Far East.—While usable Late Pleistocene samples have yet to be found from elsewhere in the world, there are several places where Post-Pleistocene samples from Mesolithic to modern can be compared. In China, although data from only three Mesolithic individuals are available, large Neolithic (average N's of 35, 51, and 75) and modern (average N's of 30, 81, and 107) samples have been measured (Brace et al., 1984). The Chinese regression line has a slope of -0.0129 mm^2/yr and an r value of 0.922 ($P = 0.003$), almost exactly the same as that in Post-Pleistocene Europe. The only difference is in the fact that TS at each stage averages nearly 50 mm^2 larger. This suggests that either Chinese teeth were slightly larger in the Late Pleistocene than European teeth or that the Late to Post-Pleistocene reduction trend began later. In Japan, from the Early Jōmon of about 7,000 years ago, to Middle and Late Jōmon, and finally to their modern descendants, the Ainu of Hokkaido, the rate of dental reduction involves a slope of -0.0105 mm^2/yr and an r value of 0.745 ($P = 0.03$) (Brace and Brace, 1987).

In Southeast Asia, usable Mesolithic samples are available for Sarawak, Laos, and the Malay Peninsula. Neolithic and modern samples are available for Sarawak, Laos, and Vietnam (Brace and Vitzthum, 1984). For these, the regression line has a slope of -0.017 mm^2/yr and an r value of 0.947 ($P < 0.0001$). Evidently the Post-Pleistocene rate of reduction in Southeast Asia was comparable to that in China, Japan, Europe, and the Middle East.

India.—Work is still in preliminary stages for India, but the first report on Neolithic remains (Lukacs, 1983) shows that TS was comparable to European Neolithic figures. The one modern datum gives a TS of 1,144 mm^2 (from measurements on a sample of 15 Bengalis in the American Museum of Natural History in New York, through the courtesy of Dr. Ian Tattersall), again quite in line with modern European figures.

Australia.—Post-Pleistocene dental reduction clearly was taking place among Australian aborigines, although it is not yet possible to determine how much was the result of in situ change and how much was the result of gene flow from the north, where it had begun much earlier (Brace, 1980). However, it is quite clear that Middle Pleistocene levels of tooth size were preserved in Australia right up to the end of the Pleistocene before the processes of reduction began (Thorne, 1976; Freedman and Lofgren, 1979; Brace and Ryan, 1980).

The New World.—No skeletal remains in the Western Hemisphere can be assigned to the Late Pleistocene, and there is little reason to believe that inhabitants had entered the Americas much before the end of the Pleistocene (Haynes, 1982; Owen, 1984). While there is some reason to suggest that Post-Pleistocene dental reductions were proceeding in a fashion analogous to that of the Old World (Brace and Mahler, 1971), the evidence is not sufficient to warrant treatment here.

Discussion

From the larger paleontological perspective, our time intervals are so short and our samples so limited that we may not be able to transcend the problem of the effects of time and temporal scaling that have been discussed for other examples (Gingerich, 1983, 1984; Gould, 1984). It is indeed possible, however, that failure to accept Neanderthals as being in the lineage of modern Europeans is just such a case of losing the sense of relationship because of the problem caused by seeing a rapidly changing picture at widely spaced points in time, while the failure to perceive change in the more recent human fossil record is due to instances of minor reversals of those long-term trends that appear over very short time intervals.

The problem remains of whether the rates and changes we have documented are comparable with those discussed for other mammals, specifically those noted for mandibular first and second molars (Kurtén, 1959; Gingerich, 1974, 1980). Our data all fall within Gingerich Domains III and IV (moderate) (Gingerich, 1983). More specifically, our Late Pleistocene European rates all fall within Kurtén's B rate calculated for Pleistocene bears, while our Post-Pleistocene rates, especially the maxillary teeth and their buccal-lingual dimensions, fall within the lower limits of Kurtén's A rate of tooth size change reported for postglacial mammals (Kurtén, 1959).

The Mesolithic data from southern Southeast Asia (Brace, 1978; Brace and Vitzthum, 1984) and from southward in the Nile Valley into Africa (Calcagno, 1983*a*, 1983*b*; Greene et al., 1967) suggest that the Late Pleistocene reductions had lagged in areas south of those where our picture of Late Pleistocene reduction is best demonstrated. The circumstances that are connected with the onset of that reduction, then, should be associated with the conditions of Late Pleistocene life along the northern reaches of human habitation, and specifically those particular aspects of life that alter chewing requirements. The elaboration of food-processing practices changed the nature of the selective forces that had once operated to maintain the jaws and teeth. This is what was meant when Brace (1977 p. 199) observed that, "The important thing to look to is not so much the food itself, but what was done to it before it was eaten." It has been observed that the adoption of "earth oven" cooking techniques, which allowed the use of frozen food early in the last glaciation, not only enabled humans to survive in the northerly parts of the Old World,

but also incidentally reduced the amount of necessary chewing (Brace, 1977, 1978, 1979*a*, 1979*b*; Brace and Hinton, 1981).

Until recently, earth ovens were used throughout the world. From the New England clambake to the Polynesian luau, the essentials of construction were the same. A pit of varying depth was scooped out in the ground, fist-sized rocks were placed in it, and a fire of wood and brush made over these. As the fire burned down, the ashes were raked aside and joints of meat, whole animals, or packets of food were installed among the rocks. A cover of hides or leaves was placed over the food, and the oven was sealed by being covered with dirt. The food then would steam without loss of moisture to a succulence treasured by the devotees of gastronomic excellence from the beaches of tropical Australia to the former imperial Chinese court, with the most sophisticated of the world's cuisines (Graebner, 1913; Lin and Lin, 1972). But beyond the extent to which such procedures are valued for the tastes they produce, they also materially reduce the amount of chewing necessary and thus lessen the intensity of selection for maintaining tooth size.

The consequences of relaxation of selective forces were noted by the late H. J. Muller over a generation ago (Muller, 1949) and have been independently realized by a number of others since that time (Kosswig, 1960, 1963; Post, 1962; Brace, 1963; King and Jukes, 1969; McKee, 1984). Reductions have been noted for light-related attributes of cave organisms (Wilkens, 1971, 1973), sexual behavior of fruit flies after generations of parthenogenesis (Carson et al., 1982), and molecular segments whose functions have been duplicated or usurped (Kimura, 1968, 1979*a*, 1979*b*, 1983*a*, 1983*b*; Kimura and Ohta, 1974; Ohno, 1970, 1972; Ohta, 1974, 1980; Nei, 1975, 1983). It seems plausible to us that the reductions we document were produced by the Probable Mutation Effect (Brace, 1963); that is, they resulted from mutations alone, when the forces of selection were less stringent than those which had maintained Middle Pleistocene levels of human dental substance (Brace, 1967, 1978, 1979*a*, 1980; Brace and Mahler, 1971; Brace and Hinton, 1981; Brace et al., 1984; McKee, 1984).

We are aware that such an interpretation is not favored by those who, following Fisher (1930), regard all evolutionary change as having been produced by natural selection (Prout, 1964; Clarke, 1970*a*, 1970*b*; Stebbins and Lewontin, 1972; Armelagos and Van Gerven, 1980). Some indeed have suggested that human dental reductions have been the secondary consequences of face-size reduction (Bailit and Friedlaender, 1966; Sofaer et al., 1971), although just why the latter should be the controlling trait and what led to its reduction remains unknown. Others have suggested that the metabolic energy or calcium saved by generating a fraction of a millimeter less dental substance per generation was the driving force (Jolly, 1970; P. Smith, 1981, 1982). It is difficult to see how this could produce the requisite differential survival, and, recalling that Darwin ended the Introduction to the first four editions of *The Origin of Species* with the words "I am convinced that Natural Selection has been the main but not exclusive means of modification" (Darwin, 1964; Gould, 1980), we suggest that this may be one of those instances in which natural selection is not the main agency.

Conclusions

Human tooth size, crudely considered, was maintained at the same level throughout the Middle Pleistocene. With the onset of the last glaciation in the Late Pleistocene between 75,000 and 100,000 years ago, dental reduction began to occur among the northernmost inhabitants of the Old World for which we have evidence. Tooth size then began to reduce at a rate of roughly 1% per 2,000 years until the end of the Pleistocene approximately 10,000 years ago. From that point on, wherever we can test the evidence, reduction has proceeded at twice the previous rate and can be reckoned at about 1% per 1,000 years.

It is interesting that this rate of change is exactly the same as that documented for the divergence in dental morphology for a series of recent Asian, Pacific and Amerindian groups (Turner, 1986). In the latter case, the morphological change has been used to establish what are called "dentochronological separation estimates," although no theoretical expectations are offered to account either

for the nature or the direction of the changes observed. In the present analysis, we suggest that metric reduction is just what we would expect to find following relaxation in the intensity of selective forces. It may be no coincidence that both dental metrics and dental morphology have been changing in these populations at the same rate of speed after the intensity of selection had been reduced.

If we only had populations from the beginning and the end of a 50,000-year time span during which such a rate of change had been taking place, the groups would be perceived as specifically distinct, using the criteria derived from other paleontological instances (Gingerich, 1983). Such a case would be accepted as evidence that a punctuation event had occurred, and indeed this is the interpretation preferred by many (Stanley, 1979; Trinkaus and Howells, 1979; Bräuer, 1981, 1984*a*, 1984*b*; Stringer, 1982, 1985; Eldredge and Tattersall, 1982; Rightmire, 1983*a*; Stringer et al., 1984). From the perspective of a human life span, or even the extent of recorded history, the total amount of change has been so small that few have perceived it at all, and everyone would agree that it has been proceeding in a fashion that is so gradual as to be generally unrecognized.

If, however, that gradual Post-Pleistocene rate were projected backwards 100,000 years, the predicted human ancestor at the beginning of the Late Pleistocene would have had teeth not just of *Homo erectus* or Neanderthal dimensions but would have had a fully Australopithecine TS of 2,056 mm^2. This is greater than the 1,934 mm^2 figure for the Pliocene hominids of more than three million years back (White et al., 1983), and almost identical to the 2,089 mm^2 figure for the South African hominids from the Pliocene/Pleistocene boundary some two million years ago (Brace et al., 1973). Whatever the outcome of the arguments concerning the names and relationships of those early hominids, most authorities agree that the genus to which they belong—*Australopithecus*—is ancestral to the genus *Homo* (Howells, 1973; Brace, 1979*a*, 1979*b*; Wolpoff, 1980). Given the recent rate of change for which we have produced evidence, the metric characteristics of the modern human dentition could have evolved from a fully Australopithecine condition after the end of the Middle Pleistocene. However, the evidence suggests that the transition from *Australopithecus* to *Homo* actually took place between 2 and 1.5 million years ago (Howells, 1973; Brace, 1979*b*; Wolpoff, 1980) at a rate that was far less than that visible in the Late Pleistocene and Post-Pleistocene record. From one perspective, then, it could be argued that we are currently living in the midst of a punctuation event, which, from another perspective, is a classic manifestation of gradualism.

We suggest that it was not a dietary change but a change in food-processing techniques that provided the conditions for the occurrence of Late Pleistocene dental reduction (Brace and Mahler, 1971; Brace, 1977, 1979*a*, 1980). The question remains concerning why that reduction should double in rate after the Pleistocene had ended. Again, we suggest that this was the result, not of dietary change but of further developments in the realm of food processing, since trace-element analysis of skeletal material from the Middle East has shown that a change in the proportion of plant to animal components in the diet had occurred well before the escalation of dental reduction began at the end of the Pleistocene (Schoeninger, 1980, 1981, 1982). In this instance, the development and widespread utilization of pottery after the end of the Pleistocene completely changed the previous requirement that a person should maintain a functional dentition throughout the normal reproductive life span (Brace and Mahler, 1971; Brace, 1977, 1978, 1979*a*; Brace and Hinton, 1981; Brace et al., 1984). Pottery enables the users to process foods to drinkable consistency, and it is no accident that human skeletal collections from the Neolithic and subsequent periods contain the remains of individuals who had survived for years in a completely edentulous state. No such evidence is available for any human population that did not use pottery.

Pounding, grinding, and milling tools also become common late in the Pleistocene in many parts of the world as human populations exploited previously unutilizable plant foods, and it seems likely that this may also have contributed to the relaxation of

Pleistocene levels of selection, which had maintained large amounts of tooth substance. Pottery, however, may have been the key factor that led to a doubling of the rate of tooth-size reduction within the past 10,000 years, a phenomenon that appears to have occurred independently in Europe (Brace, 1979*a*), Asia (Brace and Nagai, 1982; Brace et al., 1984; Brace and Vitzthum, 1984; Brace and Brace, 1987), and possibly in Meso-America (Brace and Mahler, 1971). It is possible that similar arguments can be applied to account for the reduction of levels of muscularity and skeletal robustness by which Middle Pleistocene hominids were converted into modern human form, but this must remain the subject for other investigators and further studies.

Acknowledgments

The research on which this report is based was supported in part by the Rackham School for Graduate Studies at the University of Michigan in 1968, 1973, 1974, 1977, 1980, and 1983, by the University of Michigan Museum of Anthropology in 1985, and by the Committee for Scholarly Communication with the People's Republic of China in 1980 and 1985. We gratefully acknowledge contributions from the late A. J. Crozier and E. B. Hoagland, and from Prof. and Mrs. G. W. Brace and M. L. Brace. Essential support has also been provided by M. A. Gordon, Chacma, Inc., and G. Brace. The rest was sustained by loans from the American Express Co., the National Bank of Detroit, the Ann Arbor Bank, and the Great Lakes Federal Savings and Loan Association. We gratefully acknowledge the comments and criticisms made by S. M. Garn, P. D. Gingerich, D. C. Fisher, B. H. Smith, and J. N. Spuhler on previous drafts of this paper. Finally, the criticisms and suggestions made by anonymous reviewers have enabled us to strengthen the thesis presented.

Literature Cited

Arensburg, B., M. S. Goldstein, H. Nathan, and Y. Rak. 1980. Skeletal remains of Jews from the Hellenistic, Roman and Byzantine periods in Israel. Bull. Mém. Soc. Anthropol. Paris (sér. XIII) 7:175–186.

Armelagos, G. J., and D. P. Van Gerven. 1980. Sexual dimorphism and human evolution: An overview. J. Hum. Evol. 9:437–446.

Bada, J., and P. Helfman. 1976. Application of amino-acid racemization in paleoanthropology. Colloque Union Internat. Sci. Préhist. Protohist. IX Congr. 1:39–62.

Bailit, H. L., and J. S. Friedlaender. 1966. Tooth size reduction: A hominid trend. Amer. Anthropol. 68:665–672.

Bar Yosef, O., and B. Vandermeersch. 1981. Notes concerning the possible age of the Mousterian layers in Qafzeh Cave, pp. 281–285. *In* P. Sanlaville and J. Cauvin (eds.), Préhistoire du Levant. Centre National pour la Recherche Scientifique, Paris, France.

Bergson, H. 1907. L'Évolution Créatrice. Felix Alca, Paris, France.

Boule, M., and H. V. Vallois. 1957. Fossil Men. Dryden, N.Y.

Bowen, D. Q. 1978. Quaternary Geology: A Stratigraphic Framework for Multidisciplinary Work. Pergamon, Oxford, U.K.

Brace, C. L. 1963. Structural reduction in evolution. Amer. Natur. 97:39–49.

———. 1964. The fate of the "classic" Neanderthals: A consideration of hominid catastrophism. Curr. Anthropol. 5:3–43.

———. 1967. Environment, tooth form, and size in the Pleistocene. J. Dent. Res. 46:809–816.

———. 1977. Occlusion to the anthropological eye, pp. 179–209. *In* J. A. McNamara (ed.), The Biology of Occlusal Development. Center for Human Growth and Development, Univ. Michigan, Ann Arbor.

———. 1978. Tooth reduction in the Orient. Asian Persp. 19:203–219.

———. 1979*a*. Krapina, "Classic" Neanderthals, and the evolution of the European face. J. Hum. Evol. 8:527–550.

———. 1979*b*. The Stages of Human Evolution, 2nd Ed. Prentice-Hall, Englewood Cliffs, NJ.

———. 1980. Australian tooth-size clines and the death of a stereotype. Curr. Anthropol. 21:141–164.

Brace, C. L., and M. L. Brace. 1987. Reflections on the face of Asia. Amer. J. Phys. Anthropol. 27: 181.

Brace, C. L., and R. J. Hinton. 1981. Oceanic tooth-size variation as a reflection of biological and cultural mixing. Curr. Anthropol. 22:549–569.

Brace, C. L., and P. E. Mahler. 1971. Post-Pleistocene changes in the human dentition. Amer. J. Phys. Anthropol. 34:191–204.

Brace, C. L., P. E. Mahler, and R. B. Rosen. 1973. Tooth measurements and the rejection of the taxon "*Homo habilis*." Yearb. Phys. Anthropol. 16:50–68.

Brace, C. L., and M. Nagai. 1982. Japanese tooth size, past and present. Amer. J. Phys. Anthropol. 59:399–411.

Brace, C. L., and A. S. Ryan. 1980. Sexual dimorphism and human tooth size differences. J. Hum. Evol. 95:417–435.

Brace, C. L., Shao Xiang-qing, and Zhang Zhen-biao. 1984. Prehistoric and modern tooth size in China, pp. 485–516. *In* F. H. Smith and F. Spencer (eds.), The Origins of Modern Humans: A World Survey of the Fossil Evidence. Liss, N.Y.

Brace, C. L., and V. J. Vitzthum. 1984. Human tooth size at Mesolithic, Neolithic and modern levels

at Niah Cave, Sarawak: Comparisons with other Asian populations. Sarawak Mus. J. 33:75–82.

BRÄUER, G. 1981. New evidence on the transitional period between Neanderthal and modern man. J. Hum. Evol. 10:467–474.

———. 1984*a*. A craniological approach to the origin of anatomically modern *Homo sapiens* in Africa and implications for the appearance of modern Europeans, pp. 327–410. *In* F. H. Smith and F. Spencer (eds.), The Origins of Modern Humans. Liss, N.Y.

———. 1984*b*. The "Afro-European *sapiens*-hypothesis," and hominid evolution in East Asia during the late Middle and Upper Pleistocene, pp. 145–165. *In* P. Andrews and J. L. Franzen (eds.), The Early Evolution of Man With Special Emphasis on Southeast Asia and Africa. Courier Forschungsinstitut, Senckenberg, W. Ger.

BROTHWELL, D. R. 1961. The people of Mount Carmel. Proc. Prehist. Soc. 27:155–159.

CALCAGNO, J. N. 1983*a*. Human dental evolution in Post-Pleistocene Nubia. Ph.D. Diss. Univ. Kansas, Lawrence.

———. 1983*b*. Odontometric trends in Post-Pleistocene Nubia. Amer. J. Phys. Anthropol. 60:181.

CARSON, H. L., L. S. CHANG, AND T. W. LYTTLE. 1982. Decay of female sexual behavior under parthenogenesis. Science 218:68–70.

CLARKE, B. 1970*a*. Darwinian evolution of proteins. Science 168:1009–1011.

———. 1970*b*. Selective constraints on amino-acid substitutions during the evolution of proteins. Nature 228:159–160.

COON, C. S. 1962. The Origin of Races. Knopf, N.Y.

DAHLBERG, A. A. 1960. The dentition of the first agriculturalists (Jarmo, Iraq). Amer. J. Phys. Anthropol. 18:243–256.

DARWIN, C. 1964. On the Origin of Species. A Facsimile of the First Edition, with an Introduction by Ernst Mayr. Harvard Univ. Press, Cambridge, MA.

DENNELL, R. 1983. A new chronology for the Mousterian. Nature 301:199–200.

ELDREDGE, N., AND I. TATTERSALL. 1982. The Myths of Human Evolution. Columbia Univ. Press, N.Y.

FARRAND, W. R. 1979. Chronology and palaeoenvironment of Levantine prehistoric sites as seen from sediment studies. J. Archaeol. Sci. 6:369–392.

FISHBEIN, H. D. 1976. Evolution, Development and Children's Learning. Goodyear, Pacific Palisades, CA.

FISHER, H. E. 1983. Richard Leakey's time machine. Omni 5:94–104, 142–145.

FISHER, R. A. 1930. The Genetical Theory of Natural Selection. Oxford Univ. Press, Oxford, U.K.

FRAYER, D. W. 1978. Evolution of the Dentition in Upper Paleolithic and Mesolithic Europe. Univ. Kansas, Lawrence.

FREEDMAN, L., AND M. LOFGREN. 1979. Human skeletal remains from Cossack, Western Australia. J. Hum. Evol. 8:283–300.

GARN, S. M., AND A. B. LEWIS. 1958. Tooth size, body size, and "giant" fossil man. Amer. Anthropol. 60:874–880.

GARN, S. M., A. B. LEWIS, AND R. KEREWSKY. 1968*a*. The magnitude and implications of the relationship between tooth size and body size. Arch. Oral Biol. 13:129–131.

GARN, S. M., A. B. LEWIS, AND A. J. WALENGA. 1968*b*. Two-generation confirmation of crown-size body-size relationships in human beings. J. Dent. Res. 47:1197.

GINGERICH, P. D. 1974. Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. J. Paleontol. 48:895–903.

———. 1977. Correlation of tooth size and body size in living hominoid primates with a note on relative brain size in *Aegyptopithecus* and *Proconsul*. Amer. J. Phys. Anthropol. 47:395–398.

———. 1980. Evolutionary patterns in early Cenozoic mammals. Ann. Rev. Earth Planet. Sci. 8:407–424.

———. 1981. Cranial morphology and adaptations in Eocene Adapidae. I. Sexual dimorphism in *Adapis magnus* and *Adapis parisiensis*. Amer. J. Phys. Anthropol. 56:217–234.

———. 1983. Rates of evolution: Effects of time and temporal scaling. Science 22:159–161.

———. 1984. Smooth curve of evolutionary rate: A psychological and mathematical artifact. Science 226:995–996.

GINGERICH, P. D., AND B. H. SMITH. 1985. Allometric scaling in the dentition of primates and insectivores, pp. 257–272. *In* W. L. Jungers (ed.), Size and Scaling in Primate Biology. Plenum, N.Y.

GINGERICH, P. D., B. H. SMITH, AND K. ROSENBERG. 1982. Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. Amer. J. Phys. Anthropol. 58:81–100.

GOULD, S. J. 1966. Allometry and size in ontogeny and phylogeny. Biol. Rev. 41:587–640.

———. 1968. Ontogeny and the explanation of form: An allometric analysis. J. Paleontol. 42:81–98.

———. 1971. Geometric similarity in allometric growth: A contribution to the problem of scaling in the evolution of size. Amer. Natur. 105:113–136.

———. 1975. Allometry in primates, with emphasis on scaling and the evolution of the brain, pp. 244–292. *In* F. S. Szalay (ed.), Approaches to Primate Paleobiology. Karger, Basel, Switzerland.

———. 1980. Wallace's fatal flaw. Nat. Hist. 89:26–40.

———. 1984. Smooth curve of evolutionary rate: A psychological and mathematical artifact. Science 226:994–995.

GOULD, S. J., AND R. A. GARWOOD. 1969. Levels of integration in mammalian dentitions: An analysis of correlations in *Nesophontes micrus* (Insectivora) and *Oryzomys couesi* (Rodentia). Evolution 23:276–300.

GRAEBNER, F. 1913. Der Erdofen in der Südsee. Anthropos 8:801–809.

GREENE, D. L., G. H. EWING, AND G. J. ARMELAGOS. 1967. Dentition of a Mesolithic population from Wadi Halfa, Sudan. Amer. J. Phys. Anthropol. 27: 41–56.

HALDANE, J. B. S. 1932. The Causes of Evolution. Longmans Green, N.Y.

———. 1949. Suggestions as to quantitative measurements of rates of evolution. Evolution 3:51–56.

HAYNES, C. V. 1982. Were Clovis progenitors in Beringia? pp. 383–398. *In* D. M. Hopkins, J. V. Matthews, C. E. Schweger, and S. B. Young (eds.), Paleoecology of Beringia. Academic Press, N.Y.

HENDERSON, A. M., AND R. S. CORRUCCINI. 1976. Relationship between tooth size and body size in American blacks. J. Dent. Res. 55:94–96.

HENRY, D. A., AND A. F. SERVELLO. 1974. Compendium of C-14 determinations derived from Near Eastern prehistoric sites. Paleorient 2:19–44.

HIGGS, E. S. 1961*a*. North Africa and Mount Carmel: Recent developments. Some Pleistocene fauna of the Mediterranean coastal areas. Man 61:138–139.

———. 1961*b*. Some Pleistocene faunas of the Mediterranean coastal areas. Proc. Prehist. Soc. 27:144–154.

HOOTON, E. A. 1931. Up from the Ape. Macmillan, N.Y.

HOWELLS, W. W. 1959. Mankind in the Making. Doubleday, N.Y.

———. 1973. Evolution of the Genus Homo. Addison-Wesley, Reading, MA.

JELINEK, A. J. 1982. The Tabun Cave and Paleolithic man in the Levant. Science 216:1369–1375.

JERISON, H. J. 1973. Evolution of the Brain and Intelligence. Academic Press, N.Y.

JOLLY, C. J. 1970. The seed eaters: A new model of hominid differentiation based on a baboon analogy. Man 5:5–26.

KIMURA, M. 1968. Evolutionary rate at the molecular level. Nature 217:624–626.

———. 1979*a*. Model of effectively neutral mutations in which selective constraint is incorporated. Proc. Nat. Acad. Sci. USA 76:3440–3444.

———. 1979*b*. The neutral theory of molecular evolution. Sci. Amer. 241:98–126.

———. 1983*a*. The neutral theory of molecular evolution, pp. 208–233. *In* M. Nei and R. K. Koehn (eds.), Evolution of Genes and Proteins. Sinauer, Sunderland, MA.

———. 1983*b*. The Neutral Theory of Molecular Evolution. Cambridge Univ. Press, N.Y.

KIMURA, M., AND T. OHTA. 1974. On some principles governing molecular evolution. Proc. Nat. Acad. Sci. USA 71:2848–2852.

KING, J. L., AND T. H. JUKES. 1969. Non-Darwinian evolution. Science 164:788–798.

KOSSWIG, C. 1960. Darwin und die degenerative Evolution. Abhandl. Verhandl. Naturwiss. Ver. Hamburg 4:21–42.

———. 1963. Genetische Analyse konstruktiver und degenerativer Evolutionsprozesse. Zeit. Zool. Syst. Evol. 1:205–239.

KURTÉN, B. 1954. Observations on allometry in mammalian dentitions: Its interpretation and evolutionary significance. Acta Zoologica Fennica 85: 1–13.

———. 1959. Rates of evolution in fossil mammals. Cold Spr. Harb. Symp. Quant. Biol. 24:205–214.

———. 1967. Some quantitative approaches to dental microevolution. J. Dent. Res. 46:817–828.

LANDE, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain : body size allometry. Evolution 33:402–416.

LAVELLE, C. L. B. 1977. Relationship between tooth and long bone size. Amer. J. Phys. Anthropol. 46: 423–426.

LEBLANC, S. A., AND B. BLACK. 1974. A long term trend in tooth size in the eastern Mediterranean. Amer. J. Phys. Anthropol. 41:417–422.

LIN, H. J., AND T. LIN. 1972. Chinese Gastronomy. Pyramid, N.Y.

LOVEJOY, C. O., AND E. TRINKAUS. 1980. Strength and robusticity of the Neandertal tibia. Amer. J. Phys. Anthropol. 53:465–470.

LUKACS, J. R. 1983. Human dental remains from early Neolithic levels at Mehrgarh, Baluchistan. Curr. Anthropol. 24:390–392.

MALEZ, M. 1970*a*. Novi pogledi na stratigrafiju Krapinskog nalazišta, pp. 13–33. *In* M. Malez (ed.), Krapina 1899–1969. Jugoslav. Akad. Znan. Umjen. Zagreb, Yugoslavia.

———. 1970*b*. Rezultati revizije Pleistocenske faune iz Krapine, pp. 45–50. *In* M. Malez (ed.), Krapina 1899–1969. Jugoslav. Akad. Znan. Umjen. Zagreb, Yugoslavia.

MAYR, E. 1963. Animal Species and Evolution. Belknap, Cambridge, MA.

MCCOWN, T. D., AND A. KEITH. 1939. The Stone Age of Mount Carmel, Vol. 2. The Fossil Remains from the Levalloiso-Mousterian. Clarendon, Oxford, U.K.

MCKEE, J. K. 1984. A genetic model of dental reduction through the probable mutation effect. Amer. J. Phys. Anthropol. 65:231–241.

MULLER, H. J. 1949. The Darwinian and modern conceptions of natural selection. Proc. Amer. Phil. Soc. 93:459–470.

NEI, M. 1975. Molecular Population Genetics and Evolution. North Holland, Amsterdam, Neth.

———. 1983. Genetic polymorphism and the role of mutation in evolution, pp. 165–190. *In* M. Nei and R. K. Koehn (eds.), Evolution of Genes and Proteins. Sinauer, Sunderland, MA.

NEUVILLE, R. 1934–1935. Le préhistorique de Palestine Rev. Bibl. 42:237–259.

OAKLEY, K. P. 1962. Dating the emergence of man. Adv. Sci. 18:415–426.

OHNO, S. 1970. Evolution by Gene Duplication. Springer-Verlag, N.Y.

———. 1972. So much "junk" DNA in our genome, pp. 366–370. *In* H. H. Smith (ed.), Evolution of Genetic Systems, Brookhaven Symposia in Biology 23. Gordon and Breach, N.Y.

OHTA, T. 1974. Mutational pressure as the main cause of molecular evolution and polymorphism. Nature 252:351–354.

———. 1980. Evolution and Variation of Multigene Families. Springer-Verlag, N.Y.

OWEN, R. C. 1984. The Americas: The case against an ice-age human population, pp. 517–563. *In* F. H. Smith and F. Spencer (eds.), The Origins of Modern Humans: A World Survey of the Fossil Evidence. Liss, N.Y.

PILBEAM, D., AND S. J. GOULD. 1974. Size and scaling in human evolution. Science 186:892–901.

POST, R. H. 1962. Population differences in red and green color vision deficiency: A review, and a query on selection relaxation. Eugen. Quart. 9:131–146.

PROUT, T. 1964. Observations on structural reduction in evolution. Amer. Natur. 98:239–249.

RIGHTMIRE, G. P. 1983*a*. The Lake Ndutu cranium and early *Homo sapiens* in Africa. Amer. J. Phys. Anthropol. 61:245–254.

———. 1983*b*. Stone Age life in Africa. Review of The Middle Stone Age at Klasies River Mouth in South Africa by R. Singer and J. Wymer. Science 220:835–836.

RISKA, B., AND W. R. ATCHLEY. 1985. Genetics of growth predict patterns of brain-size evolution. Science 229:668–671.

ROSENBERG, K. R. 1986*a*. The functional significance of Neandertal pubic morphology. Ph.D. Diss. Univ. Michigan, Ann Arbor.

———. 1986*b*. Sexual dimorphism in the Neandertal pelvis. Amer. J. Phys. Anthropol. 59:257.

ROSENZWEIG, K. A., AND Y. ZILBERMAN. 1967. Dental morphology of Jews from Yemen and Cochin. Amer. J. Phys. Anthropol. 26:15–22.

RUDDIMAN, W. F., AND A. MCINTYRE. 1979. Warmth of the subpolar north Atlantic ocean during northern hemisphere ice-sheet growth. Science 204:173–175.

SCHOENINGER, M. J. 1980. Changes in human subsistence activities from the Middle Paleolithic to Neolithic Period in the Middle East. Ph.D. Diss. Univ. Michigan, Ann Arbor.

———. 1981. The agricultural "revolution": Its effect on human diet in prehistoric Iran and Israel. Paleorient 7:73–92.

———. 1982. Diet and the evolution of modern human form in the Middle East. Amer. J. Phys. Anthropol. 58:37–52.

SMITH, F. H. 1982. Upper Pleistocene hominid evolution in south-central Europe: A review of the evidence and analysis of trends. Curr. Anthropol. 23: 667–703.

SMITH, F. H., AND G. C. RANYARD. 1980. Evolution of the supraorbital region in Upper Pleistocene fossil hominids from south-central Europe. Amer. J. Phys. Anthropol. 53:589–610.

SMITH, P. 1981. Comment on "Oceanic tooth-size as a reflection of biological and cultural mixing" by C. L. Brace and R. J. Hinton. Curr. Anthropol. 22: 561.

———. 1982. Dental reduction: Selection or drift? pp. 366–379. *In* B. Kurtén (ed.), Teeth: Form, Function and Evolution. Columbia Univ. Press, N.Y.

SOFAER, J. A., H. L. BAILIT, AND C. J. MACLEAN. 1971. A developmental basis for differential tooth reduction during hominid evolution. Evolution 25:509–517.

SOLECKI, R. S. 1963. Prehistory in Shanidar Valley, northern Iraq. Science 139:179–193.

SPENCER, F., AND F. H. SMITH. 1981. The significance of Aleš Hrdlička's "Neanderthal phase of man": A historical and current assessment. Amer. J. Phys. Anthropol. 56:435–459.

STANLEY, S. M. 1979. Macroevolution: Pattern and Process. Freeman, San Francisco, CA.

———. 1981. The New Evolutionary Timetable: Fossils, Genes and the Origin of Species. Basic Books, N.Y.

STEBBINS, L., AND R. C. LEWONTIN. 1972. Comparative evolution at the levels of molecules, organisms and populations, pp. 23–42. *In* L. M. LeCam, J. Neyman, and E. L. Scott (eds.), Proceedings of the Sixth Berkeley Symposium on Mathematical Statistics and Probability, Vol. 5. Darwinian, NeoDarwinian and NonDarwinian Evolution. Univ. California Press, Berkeley.

STRINGER, C. B. 1982. Towards a solution to the Neanderthal problems. J. Hum. Evol. 11:431–438.

———. 1985. Middle Pleistocene hominid variability and the origins of Late Pleistocene humans, pp. 289–295. *In* E. Delson (ed.), Ancestors: The Hard Evidence. Liss, N.Y.

STRINGER, C. B., J. J. HUBLIN, AND B. VANDERMEERSCH. 1984. The origin of anatomically modern humans in western Europe, pp. 51–135. *In* F. H. Smith and F. Spencer (eds.), The Origin of Modern Humans. Liss, N.Y.

SUZUKI, H. 1970. The skull of the Amud man, pp. 123–206. *In* H. Suzuki and F. Takai (eds.), The Amud Man and His Cave Site. Univ. Tokyo Press, Tokyo, Japan.

TATTERSALL, I., AND N. ELDREDGE. 1977. Fact, theory, and fantasy in human paleontology. Amer. Sci. 65:204–211.

THORNE, A. G. 1976. Morphological contrasts in Pleistocene Australians, pp. 95–112. *In* R. L. Kirk and A. G. Thorne (eds.), The Origin of the Australians. Humanities Press, Atlantic Highlands, NJ.

TRINKAUS, E. 1978. Hard times among the Neanderthals. Nat. Hist. 87:58–63.

———. 1981. Neanderthal limb proportions and cold adaptation, pp. 187–224. *In* C. B. Stringer (ed.), Aspects of Human Evolution. Taylor and Francis, London, U.K.

———. 1983*a*. Neandertal postcrania and the adaptive shift to modern humans, pp. 165–200. *In* E. Trinkaus (ed.), The Mousterian Legacy: Human Biocultural Change in the Upper Pleistocene. Brit. Archaeol. Rep., Oxford, U.K.

———. 1983*b*. The Shanidar Neandertals. Academic Press, N.Y.

TRINKAUS, E., AND W. W. HOWELLS. 1979. The Neanderthals. Sci. Amer. 241:118–133.

TRINKAUS, E., AND M. LEMAY. 1982. Occipital bunning among later Pleistocene hominids. Amer. J. Phys. Anthropol. 57:27–35.

TURNER, C. G., II. 1986. Dentochronological separation estimates for Pacific rim populations. Science 232:1140–1142.

VANDERMEERSCH, B. 1970. Une sépulture moustérienne avec offrandes découverte dans la grotte de Qafzeh. Compt. Rend. Séances Acad. Sci. Paris 270: 298–301.

———. 1981. Les Hommes Fossiles de Qafzeh (Israël). Centre National de la Recherche Scientifique, Paris, France.

VAN EYSINGA, F. W. B. 1978. Geological Time Table, 3rd Ed. Elsevier, Amsterdam, Neth.

WALLACE, A. R. 1864. The origin of human races and the antiquity of man deduced from the theory of 'natural selection.' J. Anthropol. Soc. Lond. 2: 158–187.

———. 1870. Contributions to the Theory of Natural Selection. Macmillan, London, U.K.

———. 1871. The Action of Natural Selection on Man. Chaffield. New Haven, CT.

———. 1903. Man's Place in the Universe: A Study

of the Results of Scientific Research in Relation to the Unity or Plurality of Worlds, 3rd Ed. Chapman and Hall, London, U.K.

WHITE, T. D., D. C. JOHANSON, AND W. H. KIMBEL. 1983. *Australopithecus africanus*: Its phyletic position reconsidered, pp. 721–780. *In* R. L. Ciochon and R. S. Corruccini (eds.), New Interpretations of Ape and Human Ancestry. Plenum, N.Y.

WILKENS, H. 1971. Genetic interpretation of regressive evolutionary processes: Studies on hybrid eyes of two *Astyanax* cave populations (Characidae, Pisces). Evolution 25:530–544.

———. 1973. Über das Phylogenetische Alten von Höhlentieren Untersuchungen über die cavernische Süsswasserfauna Yucatans. Sond. Zeit. Zool. Syst. Evol. 11:49–60.

WOILLARD, G. M., AND W. G. MOOK. 1982. Carbon-14 dates at Grand Pile: Correlation of land and sea chronologies. Science 218:159–161.

WOLPOFF, M. H. 1971. Metric Trends in Hominid Dental Evolution. Case Western Reserve Univ. Press, Cleveland, OH.

———. 1980. Paleoanthropology. Knopf, N.Y.

———. 1985. Tooth size-body size scaling in a human population: Theory and practice of an allometric analysis, pp. 273–318. *In* W. L. Jungers (ed.), Size and Scaling in Primate Biology. Plenum, N.Y.

WOLPOFF, M. H., F. H. SMITH, M. MALEZ, J. RADOVČIĆ, AND D. RUKAVINA. 1981. Upper Pleistocene human remains from Vindija cave, Croatia, Yugoslavia. Amer. J. Phys. Anthropol. 54:499–545.

Corresponding Editor: D. Jablonski