

Advances in Dental Anthropology

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4 What Big Teeth You Had Grandma! Human Tooth Size, Past and Present

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INTRODUCTION

More than 20 years ago, the complaint was voiced that systematically collected information on the nature and extent of variation in human biological dimensions was in woefully short supply, and that we did not even have a coherent body of data on such an obvious and easily treated matter as the basic sizes of human teeth, past and present (Brace, 1967). Australian aborigines, ever the subject when the focus of concern is on what used to be called "primitive man," had indeed been studied in exemplary fashion, but, even in that case, Australia was treated as though it were a single typological entity and as though one local group of aborigines would give us all the information we needed to understand the continent as a whole (Campbell, 1925).

Other living groups with a comparable claim to "exotic" status in the eyes of Occidental investigators have received similar attention. Thus it was that, among others, both South African Bantus (Jacobson, 1982) and Bushmen (Drennan, 1929), Japanese (Miyahara, 1916; Yamada, 1932), East Greenland Eskimos (Pedersen, 1949) and Aleuts (Moorrees, 1957) have all received treatment. Recently, John Lukacs has been adding to our knowledge concerning dental metrics on the Indian subcontinent (Lukacs, 1984, 1985) (see also Chapter 6, *this volume*). To date, however, nothing fully comparable exists for such major geographic blocs as Europe, Russia, China, Mexico, or any part of South America. There seems to be some sort of tacit feeling that these all constitute that curious abstraction, "anatomically modern" *Homo sapiens*, which presumi-

ably is such a known and invariant commodity that further study would be redundant.

If this is true where the issue is the comparison of dental dimensions of the various living human populations, then it has classically been even more the case where the populations concerned are distributed in terms of temporal as opposed to geographical separation. So it is that the Neanderthal dentition has received its full share of attention (Partic, 1962), but, with a few notable exceptions (Brabanti, 1970; Frayer, 1978), there has been no comparable interest in treating the dentition of Upper Paleolithic and succeeding human populations in any given area. The general feeling was well-expressed a few years ago in a presentation in Ann Arbor by the celebrated commentator on matters of evolutionary biology, Stephen Jay Gould (October 30, 1986). He had just declared that the late Pleistocene human fossil sequence is a fine demonstration of his favorite generalization concerning the course of organic evolution—punctuated equilibrium. And, in response to a question concerning the aspects of Upper Paleolithic anatomy that are intermediate between Neanderthal and modern size and shape, he expatiated: "But the Upper Paleolithic is represented by the Cro-Magnons, and they are us" (and see also in Glieck, 1983:64). By analogy, again, further consideration presumably would be redundant.

But, are Cro-Magnons really "us," and, if so, how did they get to be that way? What were the forces that shaped the emergence of that form? Where in fact did "we" come from? Does the prehistoric record in Europe where they are found give us any answers to these questions? And of what rel-

evance is this to the evolution of the "modern" human condition wherever we find it in the world today? This chapter focuses on what can be regarded as a single adaptive trait—human tooth size—and considers the circumstances that have influenced its maintenance and change in an attempt to gain a perspective on the larger issues that lie behind the questions raised above.

IMMACULATE CONCEPTION IN THE GARDEN OF EDEN

The answers that are currently accepted as the view of "normal science" in the Kuhnian sense (Kuhn, 1962) bear a startling similarity to those offered a generation before the publication of Darwin's *Origin* to account for the picture of organic succession provided in broad terms by an examination of the geological record (Cuvier, 1826). Specifically, some postulated catastrophe had presumably overwhelmed the previous inhabitants of the area in question, and their successors, who had been thriving elsewhere beyond the scope of scrutiny, moved in as replacements. The processes by which these successors had been shaped could not be assessed, since these had occurred in a region remote from the area under observation. Such matters, then, were considered beyond the scope of proper "science" and ultimately knowable only to *l'auteur du monde* (Topinard, 1888:473).

Even before Darwin developed his vision of evolution in the organic world produced by the operation of discoverable natural forces (Darwin, 1859), the assumption that such changes were spastic in nature and produced by forces that were essentially unknowable was labelled "catastrophism" (Whewell, 1832:126). The re-emergence of this as a general paradigm in "modern" paleontology has been recognized by some as deserving of the appellation "neocatastrophism" (Brace, 1978:983; Godfrey, 1981:6), and its application to the human fossil record had been referred to previously as "hominid catastrophism" (Brace, 1964).

As was true a generation ago, research on human origins is almost exclusively concerned with the discovery and naming of categorical distinctions, and the consequent proliferation of specific names based on trivial differences has recently been presented as a virtue rather than a vice (Tattersall, 1986). A concern for the study of the mechanics of evolutionary process has been explicitly rejected (Gaffney, 1979:88) in favor of a faith in the unexamined "speciation event" by which "equivalent" taxa emerge, as it

were, by "special creation" (Hennig, 1966; Gish, 1979). Truly, as Tuttle has warned, a new age of taxonomic splitting is upon us (Tuttle, 1987, 1988:397).

Thus the possibility that the Middle Pleistocene fossils of Java and China and the Neanderthals of Europe and the Middle East could have been the ancestors of the modern inhabitants of each of these areas is summarily dismissed (Stringer, 1974, 1984, 1985, 1989; Stringer and Andrews, 1988; Stringer et al., 1984; Rightmire, 1983; Bräuer, 1984a,b, 1989; Cann et al., 1987; Diamond, 1989; Mellars, 1989). Instead, modern human form is presumed to have arisen somewhere in sub-Saharan Africa.

No reason is suggested for why this should have occurred in Africa and nowhere else in the world. No process has been suggested that would have generated modern form. No archaeological evidence has been advanced to indicate the subsistence strategy of the emergent "modern" population. When nonmodern candidates have been identified as potential ancestors, they are done so by being redefined as "sapiens" even when they lack the one trait essential for that designation; namely a modern-sized brain. And finally, there is no unequivocal evidence even for the existence of these presumed early "moderns."

In regard to the last point, among the most prominent sites mentioned is Border Cave in Natal (Beaumont, 1973, 1980; Beaumont et al., 1978; Butzer, 1978). Although the material is extremely scrappy, it is clearly "modern" in form (de Villiers, 1973, 1976), and most closely related to the current inhabitants of southern Africa (Rightmire, 1979). However, there is no certainty that the human skeletal elements are actually contemporary with the strata in which they were found, and so far there has been no convincing response to Klein's expostulation that "Those Border Cave remains didn't come out of excavations. They came out of dumps" (Rensberger, 1980:7; Klein, 1983:34). The two Omo Kibish skulls are also referred to although, again, the casual manner of their discovery (Leakey, 1984:91) and the questions concerning their dating and affinities make them dubious props for such a wide-ranging hypothesis (Klein, 1983:35).

Finally, the material from just east of Klasies River Mouth on the southern coast of South Africa is cited as support for the idea that humans of modern form were living there more than 100,000 years ago (Singer and Wymer, 1982; Stringer et al., 1989). Similarly, the morphology is clearly "modern," but once again there is a problem with assessments of antiquity. The principal direct dating of the site

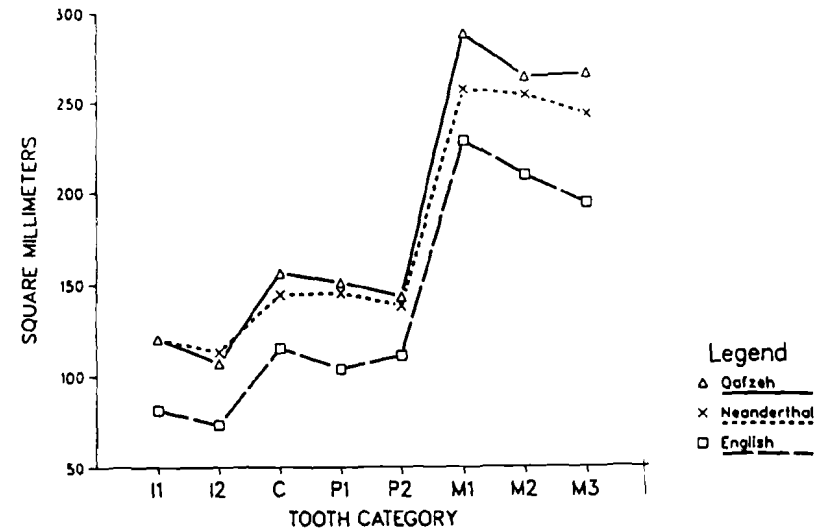


Fig. 1. Tooth size profiles comparing Qafzeh, European "classic" Neanderthals and modern western Europeans (English). Each point represents the mean cross-sectional (MD × BL) area of the tooth listed on the horizontal axis where that figure is the sum of the maxillary and mandibular tooth category mentioned. The points for Qafzeh are from Vandermeersch (1981), and the ones for Neanderthals and for modern English are from Brace (1979b).

(Bada and Decms, 1975) was by the same technique that had been used to proclaim an antiquity of perhaps 70,000 years for modern human form in California (Bada and Helfman, 1975). The latter, as has subsequently been shown, is post-Pleistocene (Taylor et al., 1983, 1985). Other aspects of confusion concerning the stratigraphy and relationships have also been voiced (Deacon and Geleijnse, 1988).

The most widely cited evidence for the "out-of-Africa" hypothesis, however, is not even from Africa itself but from Israel, namely the discoveries made over the last half century at Qafzeh near Nazareth (Köppel, 1935; Vandermeersch, 1966, 1981; Stringer and Andrews, 1988; Mellars, 1989). Presumably, Qafzeh represents the first step of the spread beyond the assumed African cradle of origin en route to the establishment of "modern" human form in the rest of the Old World.

No serious challenge has been raised yet concerning the antiquity of Qafzeh, which has been dated from 90,000 to 115,000 years on the basis of two different techniques (Schwarz et al., 1988; Valladas et al., 1988), but some other very real problems remain. First, the Mousterian industry with which they are associated is the same as that later found with

undoubted Neanderthals all the way from Iraq to southern Russia and western Europe (Garrod and Bate, 1937; Blanc, 1958; Rust, 1958; Ullrich, 1958; Solecki, 1963; Bordes, 1977). The people at Qafzeh, then, practiced the same kind of subsistence strategy as did the "classic" Neanderthals 50,000 years later. In fact, their life ways were identical since, if we can trust the archaeological evidence, it would appear that they shared the same culture.

Second, from an odontometric point of view, there is nothing "modern" about the dentition of Qafzeh. Summary tooth size (TS) for Qafzeh is 1,494 mm² (calculated from Vandermeersch, 1981:176-177), while that for the "classic" Neanderthals of western Europe is 1,415 mm² (Brace, 1979b:537). The difference in these figures is derived solely from the fact that the postcanine teeth in Qafzeh are even larger than those found in the Neanderthals (Fig. 1). In the latter, the anterior teeth contribute 27% of the cross-sectional area, whereas the anterior tooth size contribution in Qafzeh is 26% of TS. In modern human populations (Africans, Amerindians, Asians, Australians, Eskimos, Europeans, India, Oceania), our data show that the anterior teeth in each case make up 24% of TS.

Finally, a metric assessment of the Qafzeh 6 craniofacial skeleton using multiple discriminant function assessment of 15 craniofacial measurements shows that it is significantly different ($p \leq 0.01$) from modern human craniofacial form in six of the eight major geographic clusters tested (Brace, in press; Brace et al., in press b). The only modern human populations from which it could not be excluded were from sub-Saharan Africa (Dahomey, Gabon, and the Haya of Tanzania $p = 0.663$), and Australia-Melanesia ($p = 0.317$). If Qafzeh represents a form that can be ancestral to anything, it must represent the appearance of the precursors of modern sub-Saharan Africans, less likely the Australo-Melanesians, but no one else. The same can also be said for the material from Border Cave and Klasies River Mouth after a general assessment of their morphological affinities.

The continued enthusiasm for finding an identifiable sub-Saharan African cradle for the origin of all "modern" human form, then, owes more to the Judeo-Christian faith in the traditions of a Garden of Eden than it does to anything that can be called science (Brace, 1979b:539, 1986, 1989; Brace et al., in press b). There is virtually no unequivocal evidence to support that faith, and no processes or dynamics are considered by which such an origin could have occurred. As it is generally presented (Cann et al., 1987; Stringer and Andrews, 1988), this model of human origins has more in common with the "special creation" in the "scientific" creationist approach of Christian fundamentalism (Morris, 1974: 104, 133) than with anything resembling the expectations of evolutionary biology. Finally, the invocation of support from mtDNA work relies on evidence that is passed on via the female line without male input and suggests a genesis that must have been the result of what could only be referred to as a form of immaculate conception.

What we are seeing is a reversion to the typological essentialism of Medieval scholasticism (Brace, 1988a)—a "great leap backwards" as it has been called (Brace, 1989:444). The same "logic" by which such specimens as Kabwe, Petralona, and Steinheim are removed from *Homo erectus* works just as well to deny that modern Asians or Australians can be called *Homo sapiens*. Although the possible consequences are almost certainly unintended, there is a very real chance that this movement could be used to strengthen the racist advocacy evident in the works of Arthur Jensen (Jensen, 1969; 1980; Neary, 1970), and, more recently, J. Philippe Rushton (Rushton and Bogaert, 1987, 1988).

It is not our purpose to use the present occasion to frame a definitive rebuttal. What we hope to do, however, is to add a bit more perspective to the use of dental data, and to suggest that, if other aspects of past and present human biology were treated in similar fashion, this might just point the way to a more productive approach to the study of human evolution. Specifically, we shall argue that differences in tooth size between living human populations are strictly in proportion to the length of time that specific food preparation techniques have been a part of the cultural repertoire of each particular population in question, and that this can be tested by the use of both skeletal and archaeological data.

THE STUDY OF HUMAN TOOTH SIZE

Previous work has clearly shown that there are major differences in tooth size between the living populations of the world (Brace, 1980; Brace and Ryan, 1980; Brace and Hinton, 1981). Furthermore, it is apparent that human tooth size underwent a clearcut reduction during the Late Pleistocene and, even more rapidly, in the Holocene (Brace, 1967, 1979b; Brace and Mahler, 1971; Brace et al., 1987). In addition, this picture of recent reduction is valid in all of the major geographic regions so far studied (Brace and Mahler, 1971; Brace, 1979b, 1980; Hinton et al., 1980; Brace and Nagai, 1982; Brace et al., 1984; Brace and Vitzthum, 1984; Lukacs, 1984, 1985; Calcagno, 1986).

Sexual Dimorphism

Although the larger picture provided by this research is beyond challenge, there are a host of problems that remains concerning the details and the interpretations. We would like to mention some of the more prominent of these here. First, there is the question of sexual identification. Specification of sex is especially important in populations where sexual dimorphism is great or even unknown. Of course, as Oxnard has pointed out, teeth "do not bear recognizable gonads" (Oxnard, 1987:65). Consequently it is virtually impossible to separate loose teeth by sex. The result is that our assessment of tooth size in populations at the level of antiquity of the Neanderthals and earlier can be made only on the basis of pooled samples of males and females, and we have to hope that both sexes are well enough represented to make our picture generally appropriate for the group in question. Whenever possible, however, we have used the mid-sex mean for the various metric dimensions treated, that is

$$(\Sigma \bar{X}M + \bar{X}F)/2$$

(Brace et al., 1987; Brace and Hunt, 1990). All the between-population comparisons presented here use data that have been compiled in this fashion (see Tables 2 and 4).

Tooth Size in Relationship to Body Size

It is widely accepted that there is a low but positive correlation between tooth size and body size within any given human population (Garn et al., 1966, 1968; Brace et al., 1987). Consequently, it is legitimate to ask whether the change in tooth size through time is simply a reflection of a change in body size. It is also legitimate to consider the related question of whether the differences in tooth size between the various living human groups can be accounted for by differences in body size.

Most of our data on tooth size in both recently living and prehistoric populations come from specimens that lack associated postcranial elements. On the other hand, particularly where it is a matter of data on recently living human groups, most of the teeth we have been able to measure are still implanted in the facial skeletons in which they had grown. It is on the basis of these craniofacial remains that we have been able to make our assessments of sex.

Furthermore, we can also use cranial dimensions to give us some idea of the size of the individuals involved. Although cranial size does not have a one-to-one correspondence to body size, we can argue that the main differences in brain size between the individuals and populations of the world are almost entirely the allometric expression of differences in body bulk. The measurements of the portion of the cranium that houses the brain should therefore give us the most readily acquired access to an assessment of brain size, and we would suggest that this in turn can provide us with the only indication of body size that we are ever likely to have (Martin, 1983; B.H. Smith, 1989).

In the past, Karl Pearson and his disciples produced various formulae designed to give estimates of actual cranial capacity (Pearson, 1926; Hooke, 1926). Measurements of maximum cranial length, width and height were used in conjunction with carefully worked out constants where the results were checked against the figures derived from direct measurements of volume. The approximation of true capacity from the use of only three measurements made on the exterior of the cranial vault is most impressive, but the use of a constant can add nothing to our understanding of variation in cranial size. This can be gained only by the treatment of the actual measure-

ments used. For this reason, we have avoided the use of the various formulae previously suggested and have treated the three measurements as though they were the axes of an ellipsoid. We suggest that this amounts to treating the individuals and populations of the world in fair and equivalent fashion.

To represent tooth size, we have used a product of the mesial-distal and buccal-lingual dimensions of the tooth crowns. These have been referred to as "cross-sectional areas," and the issues surrounding their uses have been discussed previously (Brace, 1980; Brace et al., 1987). A great deal of information on tooth size is available as has been noted, and, while there is also a great deal of information available for cranial dimensions (see, for example, Howells, 1973), it is much less easy to assemble information on the covariation of tooth size and cranial size from data gathered on the same individuals in a series of populations. And, if we were to attempt a comparison of individuals where we had metric representations of each tooth plus the cranial variables, then our sample sizes for each group would be too small to allow us to get any reliable results.

For these reasons, we have restricted our within-population tooth-size/body-size appraisal to a consideration of the cross-sectional areas of M^1 and M^2 and the three principal cranial dimensions. Since this amounts to comparing areas with volumes, we have converted our data into comparable units by using the square roots of the former and the cube roots of the latter.

The within-population correlation between tooth size (TS) and the brain size indicator of body size (BS) is positive, but it ranges from low (0.12) to moderate (0.60) (Brace et al., 1987). When calculated across a series of 21 groups ranging from Japan to Australia, the correlation is clearly negative (-0.384) (Brace and Hunt, 1990). And when we calculate the coefficient using 23 representatives of the 8 major geographic clusters of human populations (Brace et al., in press b, and see Tables 1 and 2), the correlation is nearly 0 (0.034) and it is not significant ($p = 0.879$). In any case, where the issue is modern *Homo sapiens* as a species, it is obvious that tooth size has become decoupled from body size during the recent evolutionary past (Brace et al., 1987).

Variance

Mean BS figures were calculated from individuals with all three measurements present. Standard deviations were produced for the mean of each. For our population comparisons, we used mid-sex means, but there is no acceptable way to produce standard

TABLE 1. Names, Ns, and Collection Location for Samples Used in Constructing Figure 2

Population	F	M	Total
Ainu ^{a,b}	46	59	105
N. Australia ^c	6	12	18
S. Australia ^c	12	10	22
Breton ^d	10	21	31
S. Afr. Bushman ^e	41	49	90
N. California ^f	15	9	24
Chengdu ^g	40	46	86
N. China ^h	1	42	43
Dahomey ⁱ	16	17	33
England ^j	12	25	37
Eskimo ^k	24	24	48
France ^l	18	21	39
Gabon ^m	19	19	38
Germany ⁿ	10	30	40
Hong Kong ^o	36	78	114
India, Bengal ^p	10	18	28
Italy ^q	16	26	42
Japan ^{r,s}	71	126	197
Michigan ^m	27	34	61
Norway ^t	18	26	44
Peru ^u	11	7	18
Shanghai ^v	61	86	147
Tanzania ^w	18	18	36

^aUniversity Museum, University of Tokyo.

^bDepartment of Anatomy II, Sapporo Medical College.

^cDepartment of Anatomy, School of Medicine, Edinburgh University.

^dMusée de l'Homme, Paris.

^eHowells, 1973.

^fLowie Museum, University of California, Berkeley.

^gDepartment of Anatomy, Chengdu College of Traditional Chinese Medicine, Chengdu, Sichuan, People's Republic of China.

^hBritish Museum (Natural History), London.

ⁱDuckworth Laboratory, Cambridge University.

^jAmerican Museum of Natural History, New York.

^kPrince Philip Dental Hospital, University of Hong Kong.

^lPeabody Museum, Harvard University.

^mMuseum of Anthropology, University of Michigan.

ⁿAnatomical Institute, University of Oslo.

^oFudan University, Shanghai, People's Republic of China.

^pBritish Museum (Natural History), London.

^qDuckworth Laboratory, Cambridge University.

^rAmerican Museum of Natural History, New York.

^sPrince Philip Dental Hospital, University of Hong Kong.

^tPeabody Museum, Harvard University.

^uMuseum of Anthropology, University of Michigan.

^vAnatomical Institute, University of Oslo.

^wFudan University, Shanghai, People's Republic of China.

deviations for these. A figure produced by adding the male and female standard deviations and dividing by two would not be legitimate, but it is little better to merge the male and female data to produce a single estimate of variance. The larger male dimensions have a weighting effect that cannot be corrected. This is the reason we have left the separate male and female standard deviations as columns in Table 2.

The problem with generating something of an equivalent to variance for TS is even greater, since

the N figure for each tooth category in most of our groups is different as we have indicated in Table 3. In the few instances in which enough complete dentitions were available so that a σ could be produced for a single group, the figures ranged from 79 for Hong Kong Chinese to 141 for South Australian Aborigines (Brace, 1980:144). The Australian data produced the largest coefficients of variation for modern human odonometrics, either by individual tooth or TS.

Oddly, the smallest σ and the smallest coefficient of variation we have encountered is from a series of isolated teeth collected at the clinic in the University of Michigan Dental School. These were arbitrarily grouped into 50 "pseudo-individual" dentitions possessing a tooth in each category. Since the teeth all came from different real individuals of unknown sex and represented an uncontrolled sampling of European, Asian, and African ancestry, those pseudo-individuals cannot reflect any real population in the world. Yet, with a TS of 1,153 and a σ of 32, this curious group has a lower coefficient of variation than any real population for which we have data.

To be on the safe side, we suggest that the variance figures derived from the South Australian data are least likely to overestimate real differences. On the basis of these data, it has been shown that a TS difference of 50 mm² has a probable significance of 0.05 > 0.02 when N is > 60, and > 0.01 when N is > 135. When TS differs by 100 mm², the p value is 0.001 when N is > 60. This is the basis for the suggestion that a TS difference of 50 mm² is probably significant, and that a difference of 100 mm² is almost certainly has some basic biological meaning (Brace, 1980:144).

Geographic Distribution of Tooth Size

On the basis of Euclidean Distance analysis using 18 craniofacial variables (Brace et al., 1989) from samples representing all the major geographic and ethnic human populations of the world, we can show that the biological spectrum of modern *Homo sapiens* is reasonably well represented by eight relatively distinct population clusters: African, Amerindian, Australo-Melanesian, Eskimo, European, Indian, Jomon-Pacific, and Mainland Asian (Brace et al., in press a,b). These clusters emerged from the comparative analysis of more than 2,000 individual crania, and they are even more clearly delimited when the measurement battery was expanded first to 21 and then to 24 variables (Brace and Hunt, 1990).

We realized somewhat belatedly that our clusters would be even more clearly separated if our measurement battery had concentrated more on trivial

TABLE 2. Mean TS and BS Figures Plus Male and Female BS Standard Deviation Values for the Samples Displayed in Figures 2 and 3

Population	TS	BS	σM	σF
Ainu	1,141	1,812	140.1	145.6
N. Australia	1,272	1,532	175.4	136.4
S. Australia	1,429	1,682	153.3	176.9
Breton	1,126	1,633	119.5	125.5
S. Afr. Bushman ^a	1,139	1,453	—	—
N. California	1,238	1,789	131.2	136.5
Chengdu	1,203	1,662	183.1	143.7
N. China ^b	1,261	1,715	137.6	—
Dahomey	1,120	1,656	115.1	121.5
England	1,280	1,672	116.2	134.3
Eskimo	1,130	1,761	137.2	103.2
France	1,130	1,663	93.7	97.5
Gabon	1,335	1,623	123.8	119.6
Germany	1,141	1,666	168.1	103.6
Hong Kong	1,154	1,714	121.7	111.9
India, Bengal	1,144	1,522	159.9	137.8
Italy	1,149	1,675	147.4	134.9
Japan	1,222	1,712	141.9	130.5
Michigan	1,260	1,705	168.5	114.6
Norway	1,103	1,712	136.7	119.9
Peru	1,297	1,638	201.0	122.2
Shanghai	1,197	1,708	145.0	114.4
Tanzania	1,362	1,633	119.5	125.5

^aHowells (1973) prints male and female σ figures for individual dimensions, but no variance can be calculated for their products.

^bA female N of 1 does not permit calculation of a variance.

rather than adaptively important dimensions, but this did not occur to us until after the analysis of data that had taken several years to collect (Brace, in press; Brace and Hunt, 1990). The clusters are consistent, however, and we use representatives of them here to display the relative tooth-size/body-size proportions found in the spectrum of living human groups.

When the simple means of tooth size and brain size for representatives of each of eight major clusters of modern human populations are plotted, it is interesting to note that Europeans fall right in the middle of the modern human range of variation when the ordering is ranked according to brain size as in Figure 2. When the ordering is ranked by decreasing amounts of tooth size as in Figure 3, Europeans are at the bottom of the modern human range of variation.

When the ordering is by relative tooth size as in Figure 4, Europeans are once again near the lower end of the range of variation along with the Hong Kong Chinese. Only the Ainu from the Jomon-Pacific cluster show relatively even smaller teeth. Members of the latter cluster, interestingly enough,

have among the largest cranial dimensions and presumably are the bulkiest of the groups represented. At the opposite end of the scale, some of the members of the Australo-Melanesian cluster have the largest teeth—both absolutely and relatively—of all the peoples of the world, followed in both regards by the representatives of sub-Saharan Africa.

Tooth Size Reduction and Time

If one looks at tooth size through time, it is clear that there has been a major reduction since the beginning of the Late Pleistocene. Figure 5 shows that both tooth size and body size have decreased in Europe over the last 50,000 years. We have added data from the modern Ainu, Chinese and southern Australian aborigines to the right hand end of the graph. Whereas the Ainu and the Chinese show the same kinds of dental reduction visible in Europe, the Australians clearly do not (Table 4).

When tooth size is considered in proportion to the figure we have taken to represent body size, as is

TABLE 3. Average and Range of N for the TS/BS (Cranial Volume) Index

Population	TS N		
	BS N	Range	Average
Neanderthal ^a	6	5 - 20	13
Late U.P. ^{b,c}	2	12 - 33	25
Mesolithic ^{d,e}	10	46 - 116	80
Neolithic ^{f,g}	49	17 - 57	39
Modern Europe ^{h-i}	291	86 - 271	187
Ainu ^{m,n}	106	91 - 196	137
China ^o	227	25 - 234	108
S. Australia ^{p,q}	21	164 - 338	209

^aCranial Measurements: La Chapelle-aux-Saints (Boule, 1913); La Ferrassie (Heim, 1976); Shanidar (Trinkaus, 1983); Monie Circeo (Sergi, 1939); Amud (Suzuki, 1970); Tabun (McCown and Keith, 1939); Dental Measurements: Brace, 1979.

^bCranial Measurements: Obercassel (Verworm, Bonnet, and Steinmann, 1919).

^cDental Measurements: Frayer, 1978.

^dInstitute de Paléontologie Humaine, Paris.

^eModern Europe consists of Anglo-Irish, Cornish, Denmark, England, Finland, France, Germany, Ireland, Italy, Lapp, Norway, Scotland, and Sweden.

^fDuckworth Laboratory, Cambridge University.

^gMusée de l'Homme, Paris.

^hAmerican Museum of Natural History, New York.

ⁱPanum Institute, Copenhagen.

^mPeabody Museum, Harvard.

ⁿAnatomical Institute, University of Oslo.

^oDepartment of Anatomy II, Sapporo Medical College.

^pFudan University, Shanghai.

^qDepartment of Anatomy, School of Medicine, Edinburgh University.

^rMurray Black Collection, School of Medicine, University of Melbourne.

shown in Figure 6, it is apparent that the reduction in the dentition is more dramatic than that in bodily bulk. Australian aborigines have not followed an identical path, however, for even though Australian tooth size has been decreasing since the late Pleistocene, it has remained larger in proportion to body size than was true even for the "classic" Neanderthals of western Europe.

It is clear that relative tooth sizes change dramatically during the Late Pleistocene in the northern portions of the Old World. These changes evidently produced the major north-south differences now obvious in the living populations of *Homo sapiens*. If, then, tooth size relative to body size was maintained at a constant level by the forces of selection throughout much of the duration of the genus *Homo*, then the

relative differences that can be seen between the various modern human populations should be proportional to the differences in the time at which the onset of change began to influence those formerly given levels of selection. Finally, the agencies that produced the Late Pleistocene reductions must have had something to do with survival in the northern areas inhabited by the human species during that time.

REDUCTION RATIONALES

Selection Scenarios

Whereas there can be no doubt that tooth size in the various living populations of *Homo sapiens* is smaller, although by differing amounts, than it had been in their Pleistocene ancestors, there is no agreement on the process by which reduction was accomplished. The conventional wisdom deriving from the neo-Darwinian synthesis is to regard all change as the result, by definition, of natural selection (Fisher, 1930). The obvious sticking point in this instance is to discover just what advantage there would be in having smaller, weaker, and more friable teeth.

Where dental reduction is manifest in a simplification of crown fissure patterns, as it is in many documented instances (Turner, 1976, 1979, 1986, 1989), the argument can be put forward that the greater resistance to carries offered by small and simple tooth crowns would have significant survival value (see Chapter 5, *Illis volume*). We could offer the objection that 90% of the reduction and crown simplification had already occurred before carries achieved a level that could count as a selective force, but data simply do not exist in sufficient quantities to settle the matter in either direction. These questions they are not completely unrelated to the issues, we have followed the strategy of confining our work to the simple metric matter of tooth size.

One of the selectionist arguments offered is that dental reduction is simply a consequence of facial reduction (Sofaer, 1973; Sofaer et al., 1971). The disadvantage caused by the crowding of unreduced teeth in small mandibles and maxillae would presumably lead to a selective advantage in the possession of smaller teeth. Of course, this just puts the real problem off yet another step by introducing the question of what advantage there would be in having smaller faces in the first place. Furthermore, it reverses the usual view that the forces of selection act directly on the teeth themselves (cf. Eckhardt, 1971), and that the supporting facial skeleton develops secondarily to accommodate the size of the teeth thus determined.

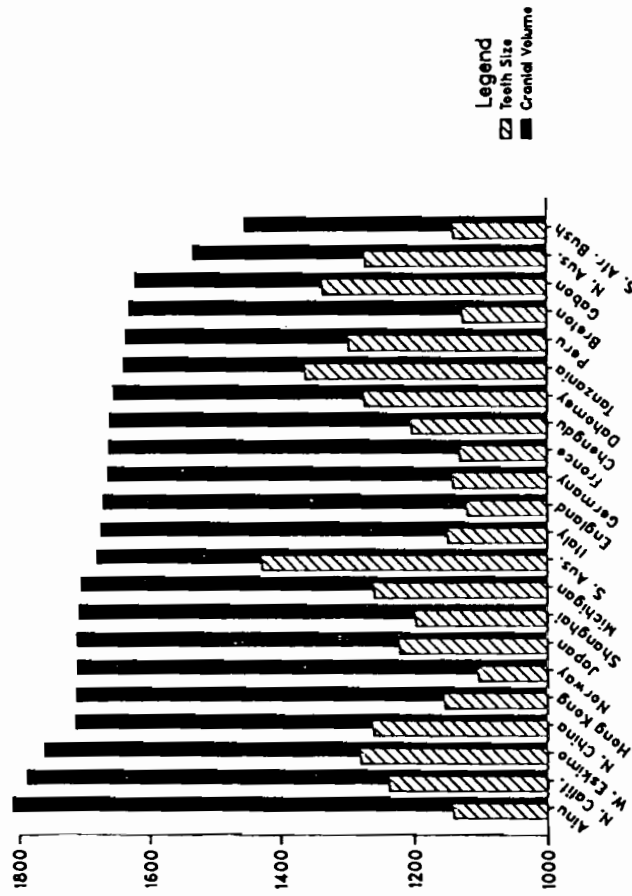


Fig. 2. Mean cranial volume in cm^3 (BS) and mean total tooth size in mm^2 (TS) figures plotted for 23 groups representing the eight major regional clusters of modern human populations. The order from left to right is determined by decreasing cranial volume. The collections from which these data were derived are recorded in Table 1, and the data used are recorded in Table 2.

Also, as with the caries argument, the evident effects of tooth crowding did not become apparent until after the end of the Pleistocene by which time 90% of tooth size reduction had already taken place.

Another selectionist argument that has been invoked to account for tooth size reduction is the "stomatobudget effect" (Jolly, 1970). In this scenario, the energy saved by growing smaller teeth would increase the survival potential of their possessors. In reply to this, we are skeptical that the minuscule amount of energy saved would be enough to represent any kind of competitive edge. Between the end of the Pleistocene and the present in France, TS reduced by a total of 107 mm^2 (Brace, 1979b). If one considers that there have been approximately 500 generations in that time, then the average amount of energy per generation is 0.21 mm^2 . We doubt that the energy required to grow two-tenths of a millimeter of tooth area could amount to a discernible nutritional differential.

After looking at the various presentations, we doubt that a selectionist argument can suffice to account for the evidence we present that human tooth size has undergone differing but in some instances substantial reduction in the recent past. We are led instead to consider what has erroneously been called a "non-Darwinian" alternative. Darwin himself recognized that reduction follows when selective forces no longer require the use of a particular trait (Darwin, 1859:134,454), although he was not in a position to discuss in detail the mechanism by which this was accomplished.

The Probable Mutation Effect

To date, the somewhat tortured attempts to use selectionist arguments to account for the observable reductions in tooth size would appear to be examples of the hyperselectionist views characterized as the "Panglossian paradigm" (Gould and Lewontin, 1979), that "favourite parlor game" in which the attempt is made to explain "everything in terms of largely hypothetical selective advantages" (Rusc,

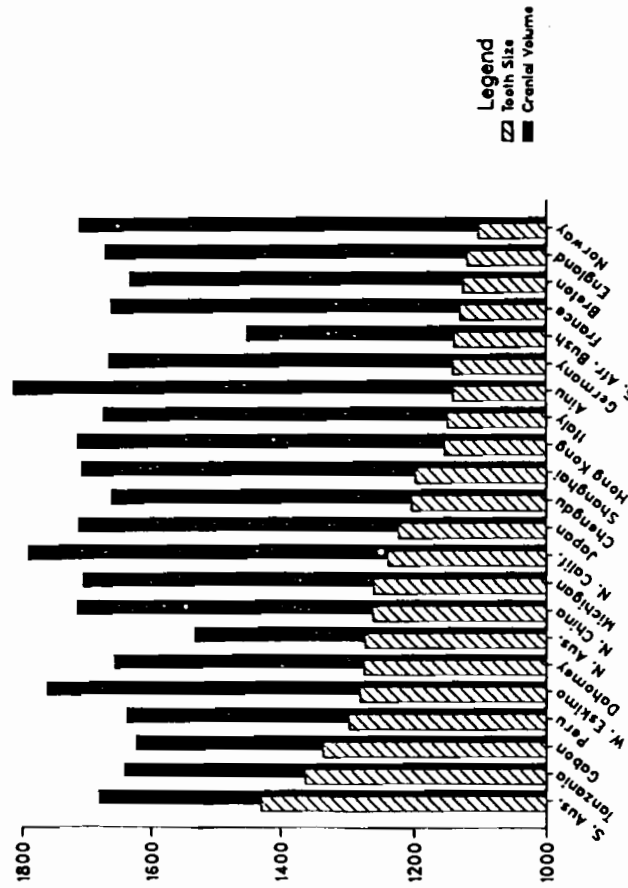


Fig. 3. Mean total tooth size in mm^3 (TS) and mean cranial volume in cm^3 (BS) figures for representative samples of the eight major regional clusters of modern human populations. The order from left to right is determined by decreasing tooth size.

1982:134). This is based on the assumption that everything in the biological world owes its particular manifestation exclusively to natural selection even if we are unable to see how this could be. The parallel has been noted to the "scientific vision of the myth of natural harmony—all structures well designed for a definite purpose. It is, indeed, the vision of the foolish Dr. Pangloss so vividly satirized by Voltaire in *Candide*" (Gould, 1980:40) where "all is for the best in this the best of all possible worlds." If we are unable to understand how that can be so, presumably it is because our finite intellect cannot comprehend the workings of a Divinely created world. Traditional Christianity would constrain us to believe even though we cannot understand. So too would those who insist that selection is the only agency that can produce evolutionary change.

The view to which Gould and Lewontin were referring was a late nineteenth century view, and perhaps it was as succinctly stated by Alfred Russel Wallace as it was by anyone: "The assertion of 'inutility' in the case of any organ . . . is not, and can

never be, the statement of a fact, but merely an expression of our ignorance of its purpose or origin" (Gould, 1980:32). This in essence was the stance taken by one of the creators of the neo-Darwinian synthesis, R.A. Fisher (Fisher, 1930; Fisher and Ford, 1950), and it has become a part of the dogma of the synthetic theory of evolution.

As molecular biology has matured, however, it has become increasingly difficult to maintain the blanket credibility of that stance, particularly since it is now evident that more than 90% of the molecular stuff of heredity itself, DNA, is not transcribed (Ohno, 1970, 1972; Britten, 1986; Luximon and Gilpin, 1987). In a series of chemical, behavioral, and morphological features, it can be shown that reductions are proportional to the time elapsed since they were last needed for survival. In fruit flies where reproduction is limited to parthenogenesis, female mating behavior disappears over the course of a couple of decades (Carson et al., 1982). In ground squirrels in the Lake Tahoe basin in Nevada and adjacent California, "the coordinated system of behavioral and physiological

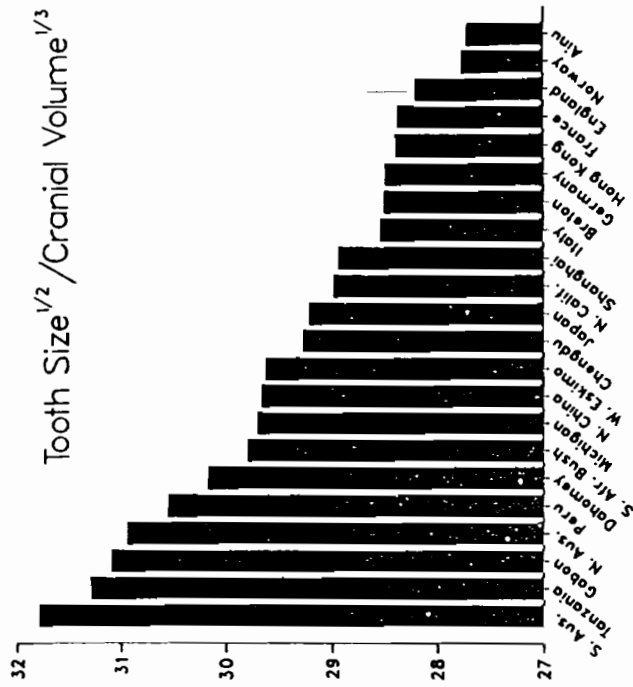


Fig. 4. Relative tooth size for representatives of the eight major regional clusters of modern human populations used in Figure 2. Tooth size-to-brain size proportions are determined by dividing the square root of TS by the cube root of BS. For purposes of plotting, the proportion was multiplied by 10.

defenses against rattlesnakes is lost . . . after prolonged (i.e., about 60,000 years) absence of predation" (Coss and Owings, 1989:34). And in Mexican fishes of the genus *Astyanax*, and in other cave-dwelling organisms, the reduction of structures related to the perception of and the protection from light is directly proportional to the length of time that the species in question has inhabited a particular cave system (Wilkins, 1971, 1973). Even better, the structure of the protein α -crystallin in the lens of the blind mole rat, *Spalax ehrenbergi*, which has been subterranean for some 25 million years, shows an amino acid replacement rate more than four times that of the normal mammalian rate of change in the α A chain. Furthermore, when compared with six other rodents where normal vision has been maintained, that particular polypeptide chain shows nine amino acid replacements in *Spalax* as opposed to none in the other rodents (Hendriks et al., 1987:5321).

In each of these cases, the changes documented are just those predicted by the logic inherent in the Prob-

able Mutation Effect (PME) (Brace, 1963). According to this, the most likely result of the most likely mutation will be a reduction in the phenotypic manifestation of the trait under the control of that particular locus. If the trait is subject to the forces of natural selection, most mutations affecting it by chance will be weeded out. However, if selection is reduced or suspended in reference to that particular trait, then selection will not weed out the recurrent chance mutations. Since most of these tend to interfere with the development of the trait to its full original manifestation, the trait will undergo a reduction in proportion to the length of time that selection influencing its maintenance has been reduced or suspended.

At its most basic, it is a matter of entropy which can be described by the phrase, "if anything can go wrong, it will." At least one physicist has referred to it as the 4th law of thermodynamics, although it is probably better known as "Murphy's Law" (Roe, 1952:46). One of its corollaries that applies specifically to the molecular workings of the PME is that, "left to themselves, things always go from bad to

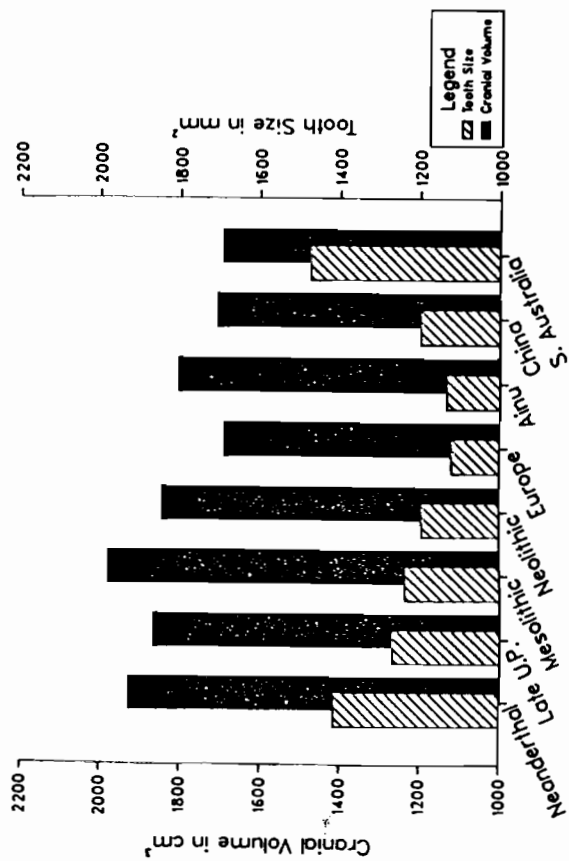


Fig. 5. Tooth size (mm²) and body size (indicated by cranial volume in cm³) changes in Europe over the last 50,000 years compared with tooth size and body size in China, among the Ainu, and in southern Australia. Neanderthal, 50,000; Upper Paleolithic, 20,000; Mesolithic, 10,000; Neolithic, 5,000; the rest are all "modern." Sources and Ns are indicated in Table 2 and the figures used are listed in Table 4.

TABLE 4. Total Tooth Size (TS) and Cranial Volume (BS) for a Time Series of European Samples and Representations of the Three Main Asian and Pacific Clusters Identified in This and Previous Studies^a

Population	TS	BS
Neanderthal	1415.0	1926.1
Late Upper Paleolithic	1267.0	1865.7
Mesolithic	1237.0	1979.9
Neolithic	1196.0	1845.9
Modern Europe	1127.0	1691.9
Ainu	1132.3	1805.4
China	1197.3	1708.3
South Australia	1429.8	1694.2

^aSee Table 2.

worse," although that is putting a selectionist interpretation on the results. Where selection is suspended, the structure simply deteriorates to a lesser version of its original condition, but this is neither bad nor worse—nor, for that matter, good.

A simple quantitative model was published five years ago (McKee, 1984) demonstrating that the

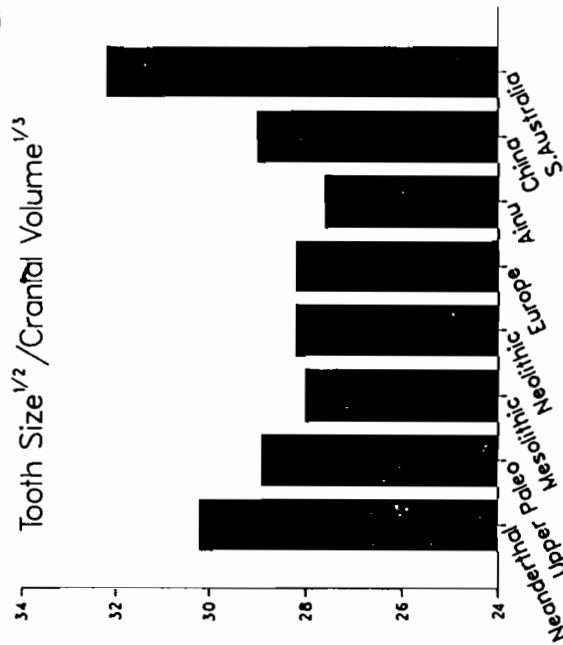


Fig. 6. BS/TS proportions plotted over the last 50,000 years in Europe plus for representatives of three of the regional clusters from Asia and Oceania. The data used are from Table 4.

In contrast, we would argue that the process by which a tooth develops is along the lines of what is described in the "morphoregulator hypothesis" (Edelman, 1988). From this point of view, a tooth is an epigenetic phenomenon that emerges as the result of a substantial morphogenetic process not unlike the process by which feathers, also structures of epidermal origin, differentiate in the skin of the developing chick (Edelman et al., 1985:213-216). At the very least, such a process is controlled by more than one enzyme and at least one polypeptide cell-adhesion molecule. Each regulator enzyme in turn is made up of some hundreds of amino acid residues and each, as is also true for the amino acid residues in the cell-adhesion molecules, is specified by the three nucleotides of a codon, any one of which can be regarded as a single gene. The number of genes controlling a single enzyme then can be as much as three times the number of its constituent amino acid residues. Where the development of a single morphological entity such as a tooth is regulated by a number of enzymes and other molecules during the course of its development, the number of relevant genes runs into the thousands. The probable influence of any one, however, is far smaller than the phenomena noted by Calciagno and Gibson (1988) as the results of single

gene changes. Nor is the likelihood of increase anywhere near so great as the likelihood of decrease in any of the processes mediated by a random change in the vast majority of the individual nucleotides involved. If the average mutation produces a random change of a single amino acid residue in an enzyme, the average consequence is that the enzyme will not work as well as previously if indeed it works at all. In the matter of morphogenesis, the most likely result of such a random change is that the aspect mediated by the molecule in question will be inhibited to a greater or lesser extent. A randomly occurring change, then, will have distinctly nonrandom consequences.

Finally, the complaint has also been voiced that the PME is unstable (Calciagno and Gibson, 1988:514). As the number of examples mentioned above will indicate, this is simply not true. On the other hand, this is not a matter to be dismissed lightly, and the challenge to produce credible tests must be kept clearly in mind. At the same time, the demonstration of how selection operates to produce the changes observed faces similar problems. As Ernst Mayr has cogently reminded us, "it is methodologically very difficult to prove the selective value of many characters" (Mayr, 1982:172). With all of this in mind, we suggest that, from the perspective of molecular

and developmental biology, there is no reason a priori why the PME should not work under conditions of relaxed selection. This should have been obvious from an appraisal of the initial efforts to view evolutionary dynamics from the perspective of molecular biology (Antfinsen, 1959; and see the more recent work that has built upon this perspective, e.g. Ohia, 1974, 1980; Nei, 1975, 1987; Kimura, 1983), and this should be even more apparent when ongoing work in morphogenesis is taken into account (Edelman et al., 1985; Edelman, 1988).

TECHNOLOGY AND TOOTH SIZE CHANGE

The conditions that result in the relaxation of those selective forces that previously maintained tooth size have been discussed repeatedly over the past several years (Brace, 1977, 1980, 1988b; Brace and Nagai, 1982; Brace et al., 1984, 1987; Brace and Vitzthum, 1984) and do not need to be repeated here. Instead, we present a brief summary.

Although the use of the anterior teeth as ancillary tools may have led to the increase of incisor size in some human populations at the end of the Middle Pleistocene and the beginning of the last glaciation (Brace, 1962, 1988b:119-120), the principal function of the dentition has always remained the processing of food (Hrdlička, 1911; Brace, 1977, 1979a; Brace and Hinton, 1981; Brace et al., 1987). As one earnest commentator has expressed it, "But primarily, teeth are for feeding with" (Hillison, 1986:5). Contrary to the usual expectations that aspects of diet should be the focus of our concern, however, we repeat the observation that, "The important thing to look to is not so much the food itself but what was done to it before it was eaten" (Brace, 1977:199). If that can be accepted, it should follow that the introduction of nondental food processing techniques should lead to changes in the forces of selection that had previously maintained the dentition. At that point, we should expect the probable mutation effect would begin to demonstrate its consequences. This leads to the prediction that the Late Pleistocene and post-Pleistocene dental reductions we document should follow immediately after the introduction of specific elements of food processing technology.

Earth Ovens and the Use of Frozen Foods
Throughout most of the Pleistocene, hominids could make only intermittent use of the north temperate zone. Although we have recorded our skepticism about a recent African origin for "anatomically modern" *Homo sapiens*, there is no debate about the

fact that hominid beginnings were ultimately both African and tropical. Until the latter part of the Middle Pleistocene, occupation of the more northerly portions of the Old World was only intermittent. To this day, humans retain the physiological characteristics of tropical mammals and cannot survive in the north without altering, by cultural means, the impact of environmentally imposed selective forces. The use of clothing, artificial shelter, and fire were prerequisites for permanent habitation in the north, and it is no surprise to find that all of these cultural features first make their documented appearance in the cultural complex associated with the first permanent occupation of the area extending from the Middle East to western Europe and including southern Russia. This is the cultural complex called the Mousterian.

The control of fire during the Mousterian played a crucial role in more than one respect. The possibility that fire was used earlier cannot be ruled out, although there has been much discussion and debate (Perles, 1975; Cowlett et al., 1981; Binford and Ho, 1985), but there can be no doubt that it is consistently associated with occupation sites beginning with the Mousterian, as early as Riss II well over 200,000 years ago, and continuing without break from that point on (Bordes, 1953, 1955, 1961, 1968, 1977; Mellars, 1965, 1986; de Lumley, 1976; Straus, 1989). Not only can we assume that it was used for warmth to fend off the chill as the last glaciation began to assert its influence, but we can see evidence to the effect that it was used for the purposes of cooking food for the first time. Mousterian "hearths" consistently contain fragments of burned bone, and these are not demonstrable from earlier time levels.

The Mousterian "hearth," however, is not the residue of the kind of open-air camp fire that typically comes to mind when that term is used. Instead, it characteristically retains a substantial depth even after the passage of more than 50,000 years. When seen in the vertical face of an archaeological trench, it often presents the kind of pattern that one sees in the photograph of a nebula in an astronomy book. There is the swirl of traces of charcoal apparent in the trench wall, accompanied by fist-sized fire-blackened rocks and fragments of burnt animal bone. For those who have participated in or attended the preparation of a Polynesian luau where a pig is baked in an earth oven, the pattern presented by the "hearths" displays a very familiar configuration. In fact, the pattern is essentially identical—a nebula-like swirl of charcoal, fire-blackened fist-sized rocks, and occa-

small pieces of charred animal bone, pig in the case of the residues of a luau.

It seems abundantly clear that the Neanderthals of the Mousterian were cooking their food in the same way that the Polynesians still do (Grachner, 1913; Brace, 1977, 1979a,b, 1988b; Brace et al., 1987; Green, 1979; Straus, 1989). We can suggest that the Neanderthals did this for reasons of basic practicality faced by those pursuing a hunting and gathering way of life in an area that was becoming increasingly influenced by the onset of glacial conditions was the simple matter of dealing with food that had become frozen. Whether the Neanderthals were regularly preying on things the size of a mammoth or a woolly rhinoceros, even an animal such as a pig or a deer cannot always be entirely consumed at a single sitting. A day later, it would be frozen solid during the winter months in a periglacial setting. The technique of making a fire in an excavated pit and heating a quantity of rocks to be raked over the packet of food after the fuel is exhausted, the whole being then sealed in with dirt, was standard for earth-oven cooking in many parts of the world right up to the present time.

In the tropics, earth ovens can be used to counter the effects of the onset of spoilage of meat acquired by hunting a day or so earlier (McArthur, 1960:112; Moore, 1973). In the case of the Neanderthals, the efficient use of fuel for the purposes of thawing is an obvious impetus for the development of earth-oven cooking techniques. Large animals can be butchered into packets appropriate for thawing later in the earth oven. Small animals can be stored frozen for later use and then thawed whole.

Although we can suggest that the appearance of the earth oven during the Mousterian was probably associated with the advantages of being able to thaw meat that had become frozen, it also had an unintended consequence. Meat cooked in such a fashion can become quite tender indeed, and in such condition it requires less chewing to render it swallowable than would be the case if it remained uncooked. In turn, this should represent the relaxation of selection for maintaining teeth at the size level that can be seen throughout the Middle Pleistocene. The appearance of the earth oven in the archaeological record, then, should mark the time at which the dental reduction manifest in the Late Pleistocene had its beginning.

From this point on, individuals should have been able to survive despite the loss of a significant number although not all of their teeth. The fact that the famous Neanderthal from La Chapelle-aux-Sains

had survived for years after the loss of his molars has been cited as evidence of the reduction of selection for maintaining Middle Pleistocene levels of chewing capacity that followed the development of earth oven-cooking (Brace, 1977, 1979a,b, 1988b). The subsequent picture of tooth-size reduction proceeding at the rate of 1% every 2,000 years has been offered as the ongoing consequence of that reduction of selection for maintaining tooth size. That rate by itself was sufficient to convert a Neanderthal-sized dentition into one of "anatomically modern" size and form by the end of the Pleistocene, and we can suggest that the reduction in the supporting facial architecture that followed the reduction of the dentition itself was what accounted for the emergence of modern human face form from a Neanderthal ancestral condition (Brace, 1979; Brace et al., 1987). Not all heated-stone cookery was of the earth-oven variety. The argument has been offered that, while earth ovens are plausible in the Mousterian, the distribution of fire-cracked rock in the subsequent Perigordian and even more recent Magdalenian was more consistent with their use in stone boiling (Movius, 1966:320-322; Leroi-Gourhan and Brézillon, 1966; Frayer, 1976:43). In any case, the consequences for the human dentition are the same.

Pottery and the Increase in the Rate of Dental Reduction

Obviously, if the development of the earth oven produced a reduction in the forces of selection that influence the maintenance of tooth size, the technological innovation represented by the invention of pottery must have had an even greater effect. Once a population has acquired the use of pottery, it possesses the capability to convert its food into drinkable consistency which would drastically decrease the necessity of having teeth at all. The point of time coinciding with the adoption of pottery should mark the onset of an even more rapid rate of dental reduction, and, as we shall show, this indeed seems to be the case.

Long after the development of the earth oven, but well before the invention of pottery, there was another development in the realm of food processing technology that also has to be considered. This is the discovery of pounding and grinding techniques and tools to assist in these practices. While these made possible the use of food items such as pulses and grains that had previously been unavailable, it did not in and of itself reduce the amount of mandatory mastication. Flat breads and cakes, incorporating both the powdered grinding stone from the flour-making

process and the grit of the ashes in which they were cooked, may even have increased the amount of wear normally encountered. Certainly, there was an obvious change in the angles of wear on the occlusal planes of the molar teeth of the beneficiaries (B.H. Smith, 1984). In addition, there is some suggestion that molar wear did increase with the increase in the use of grain as a source of food (P. Smith, 1977, 1982; P. Smith et al., 1984).

With the addition of pottery to the food-processing armamentarium of the Neolithic approximately 9,000 years ago in the Middle East and at similar levels of antiquity in East Asia going back to several thousand years earlier in Japan (Chang, 1987; Nissen, 1988; Pearson, 1986), a major relaxation of the selective forces maintaining tooth substance had taken place. Thenceforth, the "beneficiaries" could survive in the complete absence of any teeth at all. There are essentially no pre-Neolithic burials of individuals who had been completely edentulous at the time of death, but, from the Neolithic on, the presence of edentulous skeletons in cemeteries is not unusual. In many cases, the extensive record of alveolar resorption in such individuals attests to the fact that they had lived for many years in a state of complete toothlessness.

In all of the parts of the world where the use of pottery has been continuous for at least 7,000 years—namely Europe, the Middle East, China, Japan and Southeast Asia—the rate of dental reduction is effectively the same (Brace et al., 1987). Furthermore, it is effectively double the rate where it can be tested for the Late Pleistocene. This post-Pleistocene rate amounts to approximately one percent per thousand years.

Genesis of Modern Differences in Tooth Size

From the available skeletal and archaeological evidence, it is evident that the hominids of the Middle Pleistocene pursued the same survival strategy virtually throughout their entire range of occupation. The generally accepted view is that this entailed a mixture of hunting and gathering, although some doubts have been expressed concerning just how much large animal hunting was actually involved (Binford, 1987). Whatever they were doing, it required a level of physical exertion that maintained a degree of muscularity and skeletal robustness that was well beyond what we would describe as "anatomically modern," and that characterized the appearance of *Homo erectus* wherever that hominid is found.

Since brain size in *Homo erectus* had not reached

modern levels, it cannot be used as an index for body size in the same fashion that we have done for the representatives of *Homo sapiens*. We can only argue by analogy that the selective forces imposed by their hunting and gathering mode of subsistence produced a degree of robustness and bulk comparable to that found in the earliest representatives of *Homo sapiens*, the "classic" Neanderthals.

The robustness of the jaws and teeth appears to have been the same both throughout the areal extent of *Homo erectus* and also through time, although the quantity of information on which that claim is based is so small that this view must be regarded as tentative at best. In general, however, it would appear that similar hunting and gathering activities led to the use of food stuffs that put the same pressures on the jaws and teeth of all Middle Pleistocene hominids. Certainly there is no evidence or reason to suspect that there was a spectrum of jaw and tooth size differences that was in any way comparable to what we can see in the representatives of *Homo sapiens* alive in the world today. A basic summary of the changes in hominid tooth size through time and the spectrum visible today can be seen in Figure 7.

Although the $>1,600 \text{ mm}^2$ TS in *Homo erectus* was smaller than the $2,000 \text{ mm}^2$ TS found in the preceding australopithecines (Brace et al., 1973), it was larger on the average than it is in any living human population where the spectrum runs from a maximum of just under $1,500 \text{ mm}^2$ down to $\sim 1,100 \text{ mm}^2$ (Brace, 1979a,b). The emergence of "modern" human form was uniformly associated with dental reduction. The differences in tooth size that can be seen between the various living human populations, then, were the consequences of different amounts of reduction from the Middle Pleistocene condition. These in turn can be associated with the differing lengths of time that the forces of selection maintaining tooth size have been modified in the different parts of the world inhabited by "modern" *Homo sapiens*.

We should note that the right-to-left scale in Figure 7 is more "logarithmic" than linear which means that the spread at the right hand end is really far more sudden and dramatic than it would appear from the uncorrected nature of the plot. Because of the nature of the scaling, a certain degree of compression is inevitably represented. For example, the slight change in the line that leads from the Neanderthals of 100,000 years ago to the modern European condition that occurs at 50,000 is represented by the "classic" Neanderthals with a TS of $1,415 \text{ mm}^2$, but the change in direction of the line that leads from "Ne-

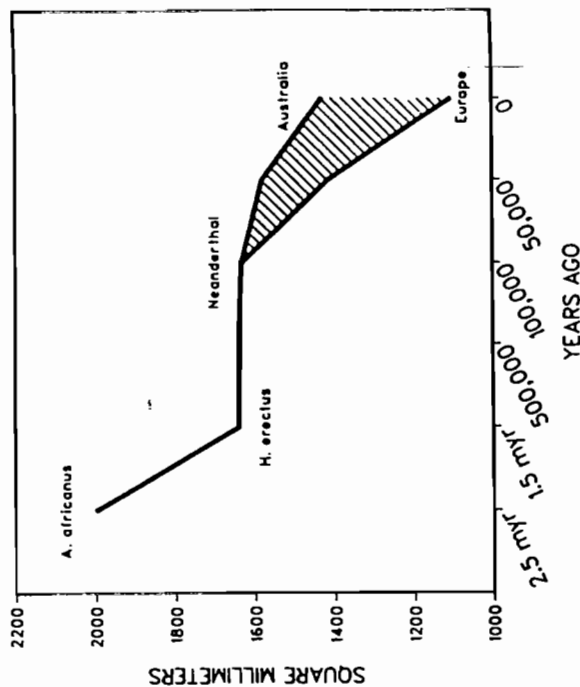


Fig. 7. Hominid tooth size from the australopithecines to the spectrum visible in the living populations of *Homo sapiens*. The australopithecine (*A. africanus*) and *erectus* data are from Brace et al. (1973), the Neanderthal (Krapina, 100,000 years ago, and late Neanderthal, 50,000 years ago) data are from Brace (1979b), and the modern spectrum is recorded here in Table 2.

anderthal" to "Australia" also is located at 50,000 years ago. The point in question is represented by the Kiwi Swamp material from the Murray River Basin with a TS of at least $1,581 \text{ mm}^2$ (Brace, 1980:147). The date, however, is less than 20,000 years (A. Thorne, personal communication) rather than the 50,000 years of the Neanderthal-to-Europe line, but this does not change the fact that similar dynamics are represented in both cases.

The most important of these modifications are reductions caused by specific cultural developments. The first of these, as we have noted above, is the development of earth oven cookery. While this had become a universal cultural feature by the dawn of written history, it had an antiquity in the area occupied by the Mousterian tradition that predates its appearance elsewhere. Recently, Mousterian dates of between 80,000 and 115,000 years ago have been produced for sites in Israel (Schwarz et al., 1988; Valladas et al., 1988; Stringer et al., 1989). Although these dates seem awkwardly early when compared with the dates of sites with typologically similar Mousterian tools elsewhere (O. Bar-Yosef, personal communication), the Mousterian cultural

tradition with which the earliest earth ovens are associated goes back more than 200,000 years (Straus, 1989) and clearly predates any other cultural tradition with which they can be associated. Earth ovens, we have argued, represent a cultural adaptation to survival in the north temperate zone back at the beginning of the Late Pleistocene. In line with the argument developed above, we suggest that the onset of those dentofacial reductions by which "modern" face form was produced began earliest in the areas in which the Mousterian culture originally flourished. The cultural adaptation that made survival possible at comparable latitudes in Asia appears to have been considerably later (Jia and Huang, 1985), and, presumably, the path toward dental reduction therefore did not begin quite so early in Asia as it did throughout the northwestern extent of Late Pleistocene human occupation.

In any case, modern populations that can trace their ancestry to the north temperate zone should exhibit the effects of having begun to undergo dental reduction earlier than is true for those whose Late Pleistocene forebears were located in latitudes that are farther south. The earth oven reached Australia

some 30,000 years ago (Bowler et al., 1970; Mulvaney, 1975:152), and we would predict that the Australian aborigines were the last to begin the Late Pleistocene trajectory of dental reduction.

Whereas the different time level associated with the adoption of the earth oven marks the difference in the time of the onset of dental reduction, the picture is complicated slightly by the adoption of pottery at different times in different parts of the world. Pottery never did reach aboriginal Australia, and, with the late adoption of the earth oven there, we would predict that the Australian aborigines should have the largest—that is, the most unreduced—teeth of the living populations of the world today, and of course they do.

Dental reduction in sub-Saharan Africa has proceeded somewhat farther than is evident in Australia. So far, there is no archaeological evidence showing that earth ovens were ever used in Africa, but this could just be because the question has never been investigated. The extent to which tooth size reduction has occurred in sub-Saharan Africa may then be the result of the spread of pottery use without an earth oven precursor. We know altogether too little about the antiquity of cooking in Africa, and it remains a question that deserves systematic investigation. The sporadic occurrence of pottery predates agriculture (Robbins, 1972), but its wholesale usage clearly accompanies the agricultural extension into West Africa in the second millennium B.C. (Coursey and Alexander, 1968). The subsequent postpottery rate of reduction applied over the next four thousand years may have been sufficient to produce the difference in relative tooth size in Africa as opposed to Australia.

The similar relative sizes of teeth in India, eastern Asia and the Americas may reflect the fact that, although the postpottery trajectory had roughly the same time of onset and effect that it did in Europe, previously there had been a shorter earth oven-associated period of reduction. On the other hand, the earliest pottery tradition in the world, the Jōmon pottery of Japan, could be the reason why the groups that constitute the Jōmon-Pacific cluster, the probable descendants of the makers of the Jōmon pottery, display the greatest amount of dental reduction of any of the populations in the world today.

If our Middle Pleistocene ancestor, that putative African "Eve," was decidedly macrotodont by the standards of today, it was not a dietary change that led to the reductions that produced the modern condition. Instead, it was the development of the first culinary technology that reduced the burdens of food processing that had formerly been performed by the

teeth alone. It is ironic to think that, in the cultivation of the culinary arts, our gain has also led to our loss. The very traditions that culminate in the delights savored by the gourmet have led to the reductions in those parts of our anatomy that have allowed us to enjoy masticating the products of that emergent cuisine.

CONCLUSIONS

The foregoing leads us to offer the following points as working generalizations. These should not be taken as "proven" or even definitive. Rather, they should be regarded as representations of the current state of our knowledge, and, as such, they are more in the nature of tentative offerings that can serve as the basis for revision as more information becomes available and as our theoretical perspective becomes refined.

1. Middle Pleistocene hominids before the expansion in brain size that produced our own species are best classified as *Homo erectus*. Total tooth size, at about 1,600 mm², was about 25% smaller than it had been in the ancestral australopithecine stage, but it was larger than that found in any living population of *Homo sapiens*. Because of the similar foraging strategies used during the Middle Pleistocene throughout the areas occupied by *Homo erectus*, a similar mix of plant and animal matter was present in the diet of all hominid populations. This means that the processing burden placed on the dentition was similar, which in turn leads us to expect that tooth size remained the same until something occurred to change that balance between selection and morphological response.

2. Modern human tooth size represents a reduction from the common Middle Pleistocene condition, although that reduction has proceeded to different extents in different parts of the world. The reductions that produced the various manifestations of the "modern" condition began after the onset of the Late Pleistocene approximately 100,000 years ago.
3. Reductions in tooth size during the Late Pleistocene and comparisons of tooth size between the various modern human populations as well as between modern and prehistoric humans can be assessed in meaningful fashion only when differences in body size are taken into account. If we make the operational assumption that brain size has not changed in proportion to body bulk since the emergence of *Homo sapiens* by the beginning of the Late Pleistocene, then we can use measurements of cranial capacity to serve as an indicator of body size in the

various groups compared. The summary tooth size (TS) to brain size (BS) index enables us to compare tooth size between past and present populations of *Homo sapiens*, where the differences observed are not simply proportional to differences in average bodily bulk.

4. Late Pleistocene dental reductions began long before there was any indication of a change in the nature of the food used since the Middle Pleistocene. Dental reduction correlates with the adoption of new food preparation techniques rather than with a change in the nature of foods used. The most important of the new food preparation techniques was the use of earth ovens for cooking, initially as a means of thawing frozen foods throughout the northern extent of occupation during the Late Pleistocene. The incidental reduction in the previously necessary amount of mastication represented a relaxation of the forces of selection that had formerly maintained Middle Pleistocene amounts of tooth substance. The ensuing dental reduction was the result of the Probable Mutation Effect.

5. After the end of the Pleistocene, the adoption of pottery further relaxed the forces of selection that had previously maintained usable tooth substance. The ensuing dental reduction produced by the Probable Mutation Effect doubled among the beneficiaries of pottery usage to a rate of 1% per 1,000 years.
6. The maximum degree of dental reduction among the living peoples of the world occurs along the northern edge of human habitation in a band running from the western to the eastern extremity. The modern inhabitants of this stretch are the descendants of the first people to use cooking in the preparation of their food. Within this band, the regions where dental reduction has proceeded furthest are those areas in which pottery has been in use for the longest time.

7. South of the area of the greatest antiquity of nonidental means of food preparation, tooth size increases in proportion to the recency of culinary technology. Although earth ovens were in general use in Australia at the time of first European contact, pottery had not yet been adopted. Consequently, dental reduction has proceeded to a lesser extent among aboriginal Australians than in any of the other living representatives of *Homo sapiens*.

EPITAPH

As has happened so often in the past, we find that our hard-won insights have been anticipated by some rather unlikely people. For example, the importance of both earth ovens and pottery and the contexts

within which they developed were clearly appreciated by that ethnogastronomic enthusiast, Earl E. Eaton in his most celebrated work, *The Quick and Dirty Cookbook*. Remarkably, he extolled these events in verse, although it is obvious that the crudeness so apparent in his culinary accounts also pervades his efforts at so-called "poetry." He has called this offering:

Archaeogastronomy

Mammoth was tough on the jaw,
And could easily stick in the craw,
Unless chewed enough,
Which was hard when the stuff
Was eaten all bloody and raw.

Then after one had one's fill,
Of a late autumn mammoth kill,
It froze in a block,
That was hard as a rock.

'Til next spring put an end to the chill.

So fuel for a fire was lit,
Over rocks in a shallow pit;
And the heat from the stones
Thawed the meat on the bones
Interred in the ashes and grit.

We suspect that this primeval scene,
And the taste that emerged from between
The rocks in the ground
And the food heaped around,
Gave rise to the first true cuisine.

This manifestation of gain,
Didn't lead to the usage of grain;
Just takes it toll,
Which, swallowed whole,
As gastrointestinal pain.

Whether put in a kettle and stewed,
Or merely fermented and brewed;
The invention of crockery
Improved upon rockery.
For what could be counted as food.

Sherds can serve as a clue,
That a graminiferous brew;
Prepared in a pot,
Fermented or not,
Could be drunk without having to chew.

Commentators on matters gastronomical rarely consider the consequences that the subject of their enthusiasms might have had on human physical form. The latter task has been left to those more directly concerned, and one of these, the unfrocked orthodontist, Carey S. Moeller, had produced just such a reflection which he originally intended as a part of his "Orthodontophobia" (printed in Brace, 1977:204). It seems appropriate to include it here:

We're living on lime that we borrow;
For the sweets that we love, to our sorrow;
Produce the decay,
That will hasten the day,
Of the toothless jaws of tomorrow.

Somehow it seems inevitable that the last word on dental reduction was the one gloomily penned by that inept producer of doggerel, I. Doolittle Wright (quoted in part by Brace, 1979b:548). It seems most fitting to use the full original version to close our discussion:

We used to use teeth as a tool;
And before the invention of gruel,
The audible crunch
Of the things they would munch
Made abrasion the general rule.

Now dental reduction is fast,
And Man shall be toothless at last;
He eschews his chews
And will choose to lose
The teeth that he had in the past.

Our grip gets progressively limper,
Our defiance of Fate but a whimper;
Bald, blind and toothless,
Our end shall be ruthless;
And not with a fang, but a simper.
Sic Transit gloria oris

ACKNOWLEDGMENTS

The research on which this project is based was supported in part by Faculty Research Grants from the Horace H. Rackham School of Graduate Studies at the University of Michigan (1977, 1980, 1983), by the Committee on Scholarly Communication With The People's Republic of China (1980, 1985), by the University of Michigan Museum of Anthropology Research Fund (1984, 1985, 1986), by the LSB Leakey Foundation (1986), by the National Science Foundation (BNS-8616298), and by Diana Blaban

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