C. Loring Brace

Museum of Anthropology, University of Michigan, Ann Arbor, Michigan, U.S.A.

Received 13 October 1978 and accepted 25 April 1979

Keywords: Neanderthals, tooth size reduction

Krapina, "Classic" Neanderthals, and the Evolution of the European Face

Except for the front end of the dental arch, tooth size remained at approximately the same level throughout the Middle Pleistocene. The Krapina Neanderthals at the end of the last interglacial differed from *Homo erectus* only in having larger front teeth. From that time on, tooth size in populations at the northern edge of the area of human occupation in the Old World has reduced approximately in proportion to the time elapsed. The "Classic" Neanderthals of western Europe, in fact, have teeth that are 15% smaller than those of the earlier Krapina Neanderthals and only 5% larger than the early Upper Palaeolithic. Reduction since the early Upper Palaeolithic has proceeded another full 20%. It is suggested that the development of heated stone cooking in the Mousterian, originally for the purpose of thawing frozen food, reduced the forces of selection that had previously maintained tooth size during the Middle Pleistocene. The operation of the Probable Mutation Effect, then produced the observed reductions.

1. Introduction

In previous works, I have argued that there was no reason not to regard the European Neanderthals as directly in the line of evolution of modern Europeans, in fact being their ancestors (Brace, 1962, 1964, 1967*a*,*b*; Brace & Montagu, 1965, 1977; Brace, Nelson & Korn, 1971). The reluctance to view the fossil and recent evidence in such a straightforward way, it seemed to me, was principally a survival of the reluctance to apply the model of Darwinian evolution to attempts to understand the genesis of the human condition.

The original Neanderthal skeleton was discovered (1856) before the publication of Darwin's *Origin of Species* (1859), and was subsequently pronounced "Pathological" by Rudolf Virchow (1871) the most distinguished pathologist of his day and the person credited with actually founding the field of cellular pathology (Ackerknecht, 1953). Later the most complete and authoritatively described Neanderthal was discovered in France at La Chapelle-aux-Saints in 1908, and interpreted (Boule, 1911–1913) in the context of an intellectual tradition that had previously rejected a Darwinian approach (Stebbins, 1974). The strength of an interpretive tradition that has become established is a remarkable thing. Opinions ventured, even on the basis of inadequate evidence, will tend to be perpetuated without change even though factual material that is quite at variance with them may have been available for years. The generally accepted interpretation of the place of the "Classic" Neanderthals is a case in point. Following Boule, most students have regarded them as an aberrant and "specialized" group that may have developed its peculiar traits in partial isolation in western Europe and whose contribution to the ancestry of modern Europeans was either non-existent, or, at best, minor. In the sense of Thomas Kuhn, this could be called the paradigm of normal science (Kuhn, 1962). And even though, as some pointed out (Schwalbe, 1906, 1913; Hrdlička, 1927, 1930; Weinert, 1932), the data to support such a position were far from compelling even when it was first articulated and certainly are not so today (Frayer, 1977, 1978), it nonetheless remains in various guises the dominant view at the present time (Poirier, 1977; Constable, 1973; Kennedy, 1975; Howells, 1974, 1975, 1976; to list only a few). Neanderthal form, so the feeling goes, is just too "different" from modern and the time period between the two simply too short to allow the one to give rise to the other.

Journal of Human Evolution **8**, 527–550

0047–2484/79/050527+24 $02.00/0

Initially the question of where moderns had come from was put off by suggesting that they had developed somewhere in "the East" following which they came to western Europe as invaders, displacing or extinguishing—in any case, supplanting—the "Classic" Neanderthals. When this was first offered it was a classic example of *ignotus per igontius*, explaining the unknown by invoking the yet more unknown. It did have the effect of heightening interest in the pursuit of prehistoric research in what was then "the mysterious Orient". In the 1930's, these efforts were repaid by the discovery of human remains at Mount Carmel in what then was Palestine.

These were promptly and excellently described (McCown & Keith, 1939) and, whatever interpretive rationale was offered, it was obvious to all that the skeletons, especially those from Mugharet es-Skhūl, were intermediate in form between "Classic" Neanderthals and full moderns. But if the form showed how Neanderthal morphology could be converted into modern, the possibility that Skhūl represented a genuine evolutionary intermediary was apparently contradicted by the supposed "fact" that it had a last interglacial date (Garrod & Bate, 1937). With the materials from Mount Carmel as a guide, it was evident that what some even referred to as "primitive" modern form existed well before the "Classic" Neanderthals of western Europe. This seemed to confirm the earlier view that the Neanderthals were too recent and too different to have been possible ancestors of modern Europeans.

The Mount Carmel remains were also the most complete and best preserved of what was thought to be the last interglacial human skeletal material, and consequently they were used as a guide for interpreting the much more fragmentary remains from other sites. This, plus the fact that Weindenreich used a reconstruction technique that erroneously elevated and expanded the Ehringsdorf cranial vault (Kleinschmidt, 1931, p. 109–115) and that the Krapina fragments were preponderantly immature and/or female (F. Smith, 1976), led to the generally held assumption that eastern and early remains were more modern in form than later western European finds (McCown & Keith, 1939; Hooton, 1946; Howell, 1951, 1952, 1957; Howells, 1944, 1976; Kennedy, 1975). The result of these accidents of history was the creation of that now widely held conceptual entity, the "early" or "progressive" Neanderthals.

Ironically the "progressive" Neanderthals are not early and the "early" Neanderthals are not progressive. The supposed third interglacial date of the Mount Carmel sites was the result of procedural and analytical errors (Higgs, 1961*a*,*b*; Jelinek *et al*., 1973). In fact, the Tabūn skeleton is the equivalent in both morphology as well as date of the "Classic" Neanderthals of western Europe, and the Skhūl remains are halfway between Neanderthals and moderns in date as well as form. Mount Carmel, then, is not early, and its specifically progressive component is, in fact, late. On the other hand, the genuinely early (last interglacial) material, if fragmentary, is distinctly non-modern. Ehringsdorf, for example, if properly reconstructed, would present a low-vaulted–projecting-occiput appearance that is far more Neanderthal than modern, and Krapina, for reasons I shall treat subsequently, has aspects that are clearly less modern than even the "Classic" Neanderthals.

2. The Importance of Tooth Size

More than a dozen years ago, I suggested that not only were the Classic Neanderthals the direct lineal ancestors of modern Europeans, but that the transformation was accomplished basically by a reduction of the large Middle Pleistocene face and various related cranial appurtenances (Barce, 1964, 1967*a*). Further, I suggested that the key to face size was mainly in the size of the teeth, and that changes in tooth size could be related to specific changes in the operation of the forces of selection. If the reader can accept these assertions, then, happily, the task of analyzing the evolution of human face form over the last 100,000 years is greatly simplified. Teeth are more durable and hence more readily preserved than any other parts of the skeleton. They calcify at a relatively early age in the life of an individual and are therefore less influenced by the vicissitudes of the long course of maturation, being a closer representation of the genotype. They come in direct contact with the environment and consequently are sensitive indicators of adaptive change. And, finally, they are easy to measure with accuracy and replicability. For these reasons, the rest of this paper will focus on the dentition of various prehistoric and modern groups in an effort to put the changes of the last 100,000 years in some kind of perspective.

3. The Summary Tooth Size Statistic

For practical purposes, the best indicator of tooth size—and hence the actual trait on which selection operates—is the cross-sectional area, a product of the medial-distal and buccal-lingual (MD × BL) crown measurements (Brace, 1967*a*; Brace & Mahler, 1971; and see Figure 1).

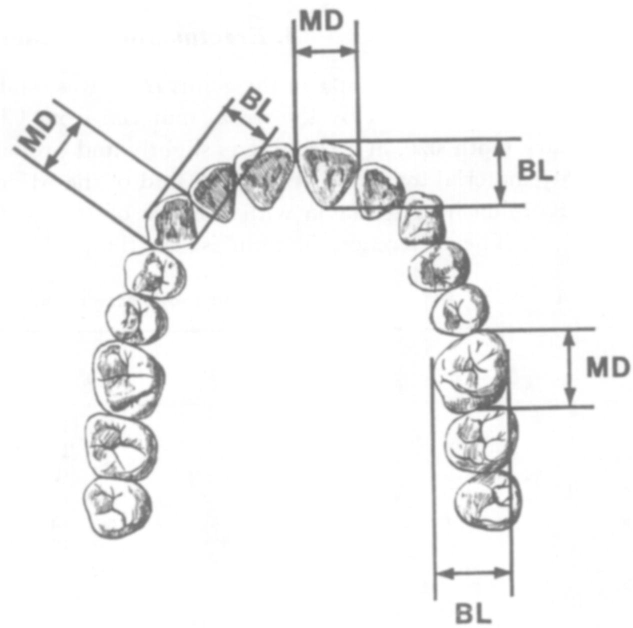


Figure 1. Schematic representation of how the mesial-distal (MD) and buccal-lingual (BL) measurements are taken. MD measurements are made from contact surface to contact surface in the midline of each tooth. BL measurements are perpendicular to the MD measurement for each tooth.

In previous papers I have compared the dental development of various populations by graphing plots of mean cross-section areas (I, I^2, ... M^3; and I_1, I_2 . . . . . M_3) as separate maxillary and mandibular tooth-size profiles. The technique is sensitive and successful, but it is also a little cumbersome. To overcome the awkwardness of a multiplicity of graphs, we can make the assumption that the various regions of the dental arch are just as well represented by combining upper and lower tooth size means to form a single composite tooth-size profile to represent each population. In this, the mean area of the upper central incisor is simply added to that of the lower central incisor to form a single I1 area; the mean area of the upper lateral incisor is added to that of the lower lateral incisor to form a single I2 area; and so on through M3. This was the procedure used in constructing the graphs that illustrate the points that will be made in the subsequent portion of this paper.

A still further simplification is the use of the summary tooth size figure, *TS*, which is simply the sum of the means of the cross-sectional areas for each tooth category, $I^1 + I^2 + \ldots\ldots M^3 + I_1 + I_2 + \ldots\ldots M_3$, which can be written:

$$TS = \Sigma X_j$$

$$\text{where } \bar{X} = \frac{\Sigma(MD \times BL)}{N_j}$$

and $j = I^1, I^2 \ldots\ldots M^3, I_1, I_2, \ldots\ldots M_3$

and N_j = total number of measured teeth in each category.

Examples of the treatment and use of this statistic can be found in Brace (in press *b*, *c*, and submitted for publication). Such a procedure reduces the size of the dentition of a given population to a single figure and allows the simultaneous comparison of a great many dentitions. By the judicious use of both summary tooth sizes and composite profiles, we should be able to develop a clear idea of the course of hominid dental evolution.

4. *Erectus* and Neanderthal Tooth Size Comparison

Base condition for tooth size in the genus *Homo* was established by the Middle Pleistocene and is best exemplified by the *erectus* material from Choukoutien (Weidenreich, 1937). Summary tooth size, at 1578, differs slightly and probably not significantly from that of the only material available at the very end of the Middle Pleistocene, the Neanderthals from Krapina in Yugoslavia with a figure of 1631 (the Krapina data are recorded in Table 1). The difference, 53 mm, is less than the difference (78 mm) between the

Table 1 **Krapina tooth size data. *N* is indicated in parentheses**

	MD	BL	Area (MD × BL
I^1	10·3 (15)	9·0 (15)	92·4
I^2	8·5 (17)	9·0 (16)	76·1
C	9·1 (18)	10·2 (17)	92·9
P^1	8·5 (11)	11·4 (10)	96·9
P^2	8·0 (15)	10·8 (14)	86·8
M^1	12·3 (13)	12·6 (12)	156·7
M^2	11·2 (12)	12·5 (13)	138·8
M^3	10·7 (10)	11·8 (9)	126·1
I_1	5·9 (9)	7·9 (9)	46·6
I_2	7·0 (11)	8·1 (11)	57·3
C	8·3 (9)	9·6 (10)	80·2
P_1	8·4 (12)	9·2 (11)	77·6
P_2	7·9 (13)	9·8 (13)	78·1
M_1	12·2 (11)	11·6 (10)	141·6
M_2	12·8 (12)	11·8 (12)	150·7
M_3	12·1 (18)	10·9 (16)	131·7
			TS = 1631

Aurignacian and Magdalenian of western Europe. From an inspection of summary tooth size alone, one could conclude that the selective forces maintaining tooth sizes had undergone little change throughout the Middle Pleistocene.

If in fact there is any meaningful difference between the dentitions of the Choukoutien Pithecanthropines and the Krapina Neanderthals, it is at the front end of the dental arch. As the composite tooth size profile shows (Figure 2) the larger sizes of the Krapina summary tooth size is almost entirely due to the contribution of the incisors and canines.

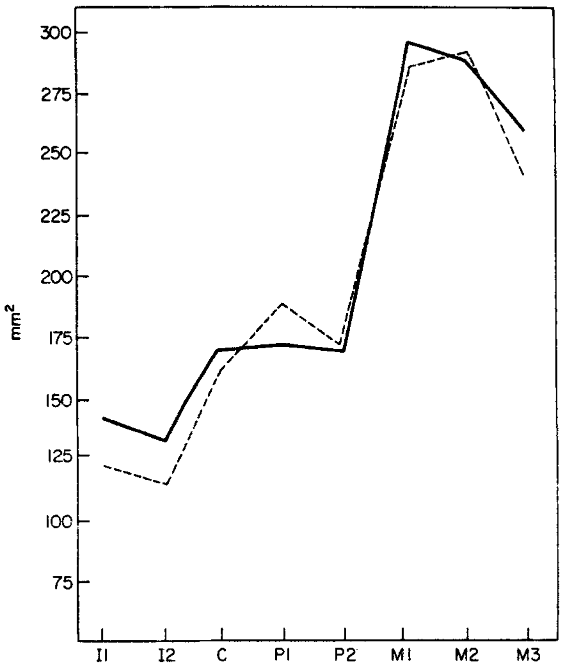


Figure 2. Composite tooth size profiles comparing *Homo erectus* from Choukoutien with the Krapina Neanderthals. Each point on the vertical scale represents the sum in square millimeters of the cross sectional areas of the upper and lower tooth labelled at the bottom of the graph. The *Homo erectus* measurements are from Weidenreich (1937), and the Krapina measurements were done by myself on the material made available to me through the generosity of Dr Ivan Crnolatac and the late Dr Josip Poljak in the National Museum of Geology and Paleontology in Zagreb, 1959. —, Krapina; · · · ·, *Homo erectus*.

What difference there was in the selective forces influencing the maintenance of tooth size relates especially to the front teeth. By a substantial margin, Krapina incisors are the largest observable in human evolution, both earlier and later. Surely this must indicate that the forces of selection had acted with particular effect on the anterior part of the human dentition just before the last glaciation, at least for those populations living towards the northwestern extreme of the area of human habitation.

While the dentition as a whole is primarily a food processing machine, the various regions of the dental arch play somewhat different roles. The principal and obvious function of the molars is the crushing of food. The incisors, however, are not such an obvious grist mill. Although they are sometimes referred to as "cutting teeth", the flat wear and edge-to-edge occlusion that was the general human condition prior to the Industrial Revolution in Europe (and only slightly earlier in China) meant that they were generally quite unable to cut in the shearing sense implied. At best they could deliver a focussed pinch after which separation of the portion of the object within the mouth from that remaining outside was accomplished by a manual tug on the outer portion. In such an instance, the front teeth actually served as a clamp, and separation was produced not by cutting but by tearing, with the force being applied by pulling with the hands (cf. Brace, 1977).

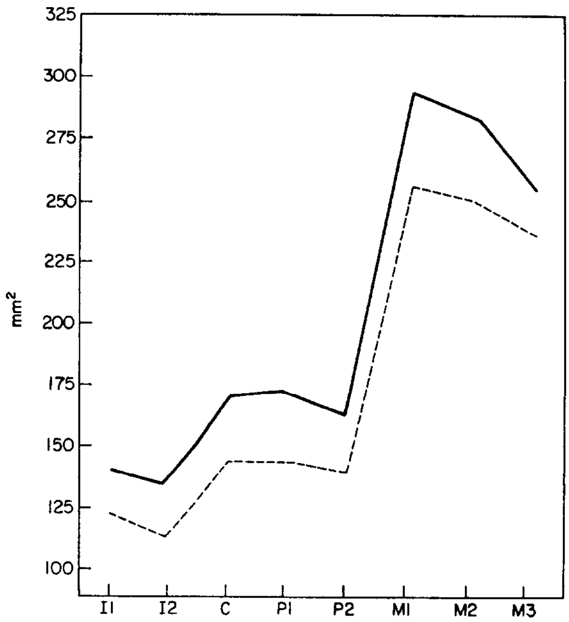
From this, I think we can conclude that the principal function of the anterior dentition was to hold objects that were then manipulated by the hands. Where this kind of activity was principally a gustatory adjunct and the foodstuffs involved remained essentially the same—which was generally true from the advent of *Homo* until the Mesolithic—there should have been little observable dental change.

When we actually do see changes, as with the increase in anterior tooth size in the Krapina remains, we are justified in suspecting that the anterior teeth were being used for more than just the processing of food. It would seem to be a reasonable suggestion that their function as clamp had been extended to non-edible objects whose manipulation was important for human survival. While it is difficult to know just what these objects were, it is perhaps significant that this maximum development of the anterior dentition occurs just at the beginning of the cultural efflorescence that allowed people to continue to occupy an area that became climatically less and less hospitable. To an increasing extent, survival came to depend on the development of clothing and shelter, and it would not seem unreasonable to suggest that the appearance of the largest of anterior teeth was directly related to their manufacture.

Then as special tools were developed to take over the tasks formerly performed by the teeth, we should expect the latter to manifest the changes normally associated with conditions of relaxed selection (Post, 1962, 1963, 1965, 1966). Indeed, as cutting and scraping tools proliferate in the Mousterian and the ensuing Upper Palaeolithic the anterior teeth do undergo the expected reduction. But reduction is not confined to the anterior teeth alone. As can be seen in Figure 3, the dentition of the "Classic" Neanderthals of western Europe shows a substantial reduction in each tooth category when compared with the Krapina Neanderthals of some 40,000 years earlier.

Evidently P. Smith (1976, 1977*a,b*) is quite right in insisting that my earlier (1964) lumping of the two as a single stage was incorrect. My error had been caused by using the only geological evidence available at the time. The subsequent reassessment of the

Figure 3. Composite tooth size profiles comparing Krapina (based on the data in Table 1) of western Europe (based on the data in Wolpoff, 1971). —, Krapina; · · · ·, "Classic" Neanderthals.



dating of Krapina (Malez, 1970) has made clear that the site was not contemporary with the Würm Mousterian of western Europe. Separate treatment is obviously warranted on the basis of date alone, and, as the measurements show, major differences in tooth size are clearly apparent.

Summary tooth size for the early Würm Neanderthals of western Europe, at 1415 mm, is a good 215 mm smaller than the 1631 mm figure that is largely derived from the last interglacial Neanderthals from Krapina. This is substantially greater than the 155 mm difference between the robust and gracile South African Australopithecines, and surely indicates a major change in the intensity of the selective forces maintaining human tooth size. Evidently the late Pleistocene reduction in tooth size which, I claim, ultimately produced the "modern" face had already made a substantial beginning by the time of the "Classic" Neanderthals of western Europe (cf. the similar realization by Sheets & Gavan, 1977). If, as I once claimed, "Neanderthal man is the man of the Mousterian culture prior to the reduction in form and dimension of the Middle Pleistocene face", then perhaps the Krapina remains qualify as Neanderthals, but, ironically, the "Classic" Neanderthals of western Europe clearly do not.

The question of whether a given fossil is or is not a Neanderthal, or, indeed, of what the formal definition of Neanderthal should be is essentially a typological matter, and, since the category has no acceptable taxonomic status, is of no great evolutionary significance. Its importance, such as it is, lies principally in the realm of the history of the discovery of the evidence for human evolution. This is interesting and not without significance in its own right, but it has no bearing on our present concern. My continued use of the term, then, will necessarily only be in the loosest colloquial sense.

As we have seen, the western European Neanderthal teeth are not only markedly reduced when compared with those of the late third interglacial Neanderthals, but the reduction has occurred to a comparable extent in each tooth category. The lines in the composite tooth-size profiles are remarkably parallel when the two groups are plotted on the same graph. When the erectus profile is added to the graph with the two Neanderthal groups (Figure 4), it is apparent that the late Neanderthal group had *erectus* sized incisors but distinctly smaller post-canine teeth, while the early Neanderthals had *erectus*-sized molars but larger incisors. Put another way by *erectus* standards, both Neanderthal groups had relatively large front teeth, even though the later ones are smaller in every way than the earlier ones.

5. Neanderthal and Megadont "Modern" Tooth Size Comparisons

This relative enlargement at the anterior end of the Neanderthal dental arch is even more evident when megadont modern populations are brought into comparison (see Table 2). For example the Australian aborigines of the Murray Basin had fully *erectus*-sized molars but their front teeth were distinctly smaller (Figure 5). And when the Murray Basin aborigines, with a summary tooth-size figure of 1497 mm are compared with the classic Neanderthals with a figure of 1415, the composite profile shows markedly smaller incisors, yet the molars are absolutely larger (Figure 6). And when the "Classic" Neanderthals are compared to the extinct Tasmanians who had a summary tooth size (1429) that was not significantly different, the same pattern of larger Neanderthal incisors and smaller molars was again visible (Figure 7). The total summary tooth-size difference

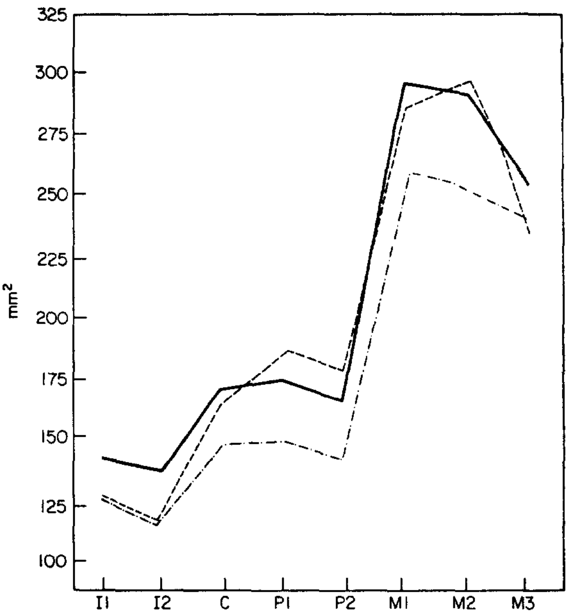


Figure 4. Composite tooth size profiles of *Homo erectus* (data from Weidenreich, 1937), Krapina (data from Table 1) and "Classic' Neanderthals (data from Wolpoff, 1971). —, Krapina; · · · ·, *Homo erectus;* — - —, "Classic" Neanderthals.

Table 2 **Tooth size data for Murray River aborigines, Tasmanians, and the Walbiri of Yuendumu settlement, in the desert heart of Australia. *N* is indicated in parentheses**

	Murray Basin MD RL	Tasmania MD BL	Walbiri MD BL
I^1	9·5 × 8·0 (332)	9·2 × 7·3 (7)	9·0 × 7·5 (151)
I^2	7·6 × 7·0 (421)	7·4 × 6·7 (18)	7·3 × 6·5 (150)
C	8·4 × 9·2 (455)	8·0 × 9·1 (23)	8·0 × 8·6 (153)
P^1	7·6 × 10·4 (473)	7·6 × 10·3 (40)	7·4 × 10·0 (155)
P^2	7·2 × 10·3 (210)	7·4 × 10·4 (40)	6·9 × 10·0 (155)
M^1	11·2 × 13·0 (210)	11·1 × 12·7 (60)	10·8 × 12·1 (156)
M^2	11·0 × 13·3 (210)	10·8 × 13·0 (56)	10·5 × 12·3 (156)
M^3	10·0 × 12·5 (204)	10·2 × 12·5 (39)	9·8 × 11·7 (150)
I_1	5·8 × 6·6 (295)	5·4 × 6·1 (11)	5·6 × 6·3 (152)
I_2	6·5 × 6·8 (348)	6·1 × 6·3 (15)	6·4 × 6·5 (153)
C	7·5 × 8·4 (388)	7·1 × 8·1 (19)	7·1 × 7·8 (153)
P_1	7·5 × 8·9 (389)	7·1 × 8·1 (19)	7·2 × 8·5 (153)
P_2	7·6 × 9·1 (384)	7·3 × 9·1 (24)	7·2 × 8·8 (153)
M_1	12·0 × 12·2 (385)	11·9 × 11·8 (31)	11·6 × 11·4 (153)
M_2	12·3 × 12·0 (399)	12·0 × 11·4 (33)	11·3 × 11·2 (153)
M_3	11·9 × 11·4 (397)	12·0 × 11·2 (28)	11·6 × 11·2 (146)
TS	1497	1429	1350

between the largest and smallest toothed Australian groups was almost exactly the same as the difference between the Krapina and western European Neanderthals.

In like fashion, the molar to incisor proportions were the same in the large *v* the small Australian group (Figure 8) and in the early *v* the late Neanderthal groups (cf. Figure 3), although, as should be obvious, the Neanderthals showed relatively and absolutely

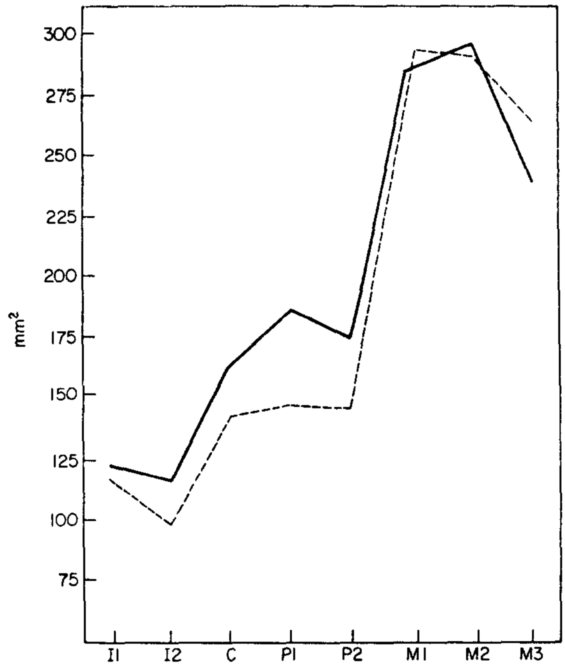


Figure 5. Composite tooth size profiles of Murray Basin Australians (data from Table 2) compared with *Homo erectus*. —, *Homo erectus*; · · · ·, Murray Valley.

larger incissors when compared to the Australians. Evidently the profile lines remained parallel when total tooth size was reduced between the last interglacial and the Würm glaciation in Europe. Likewise the profile lines of large and small-toothed Australians

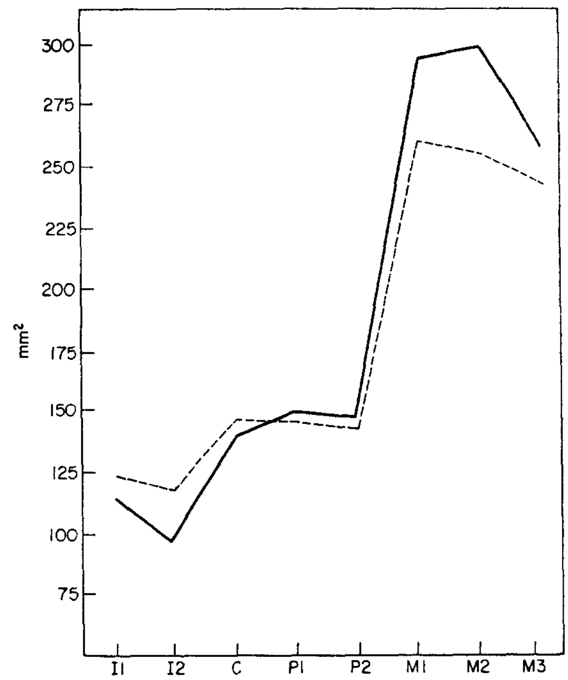
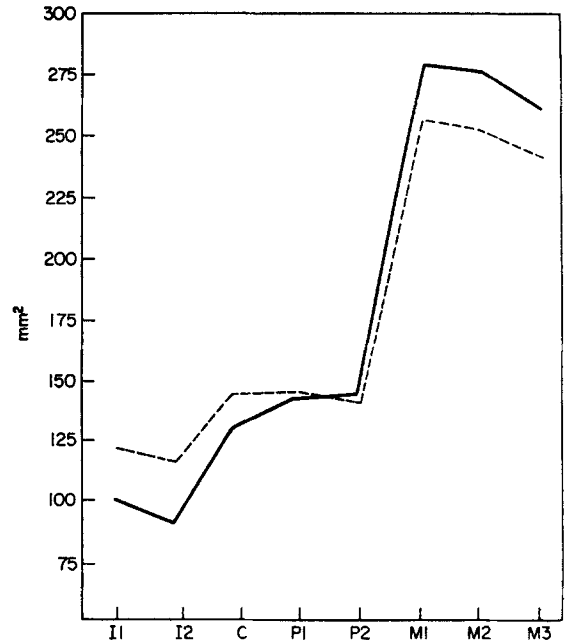


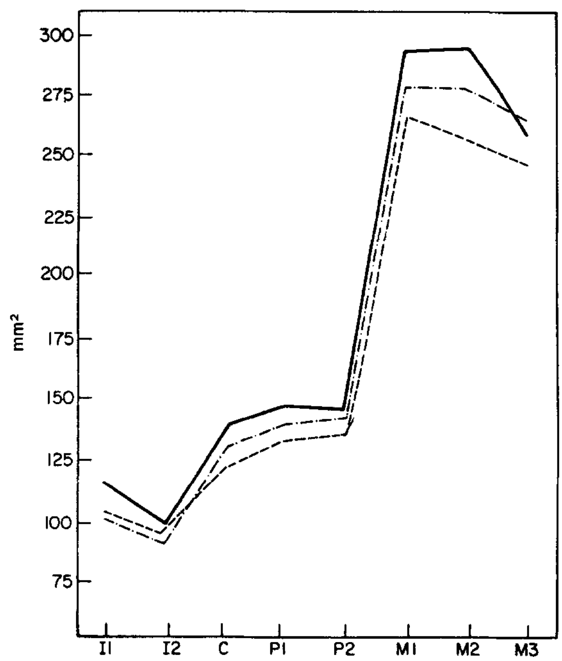
Figure 6. Composite tooth size profile comparing Murray Basin Australians with "Classic" Neanderthals. —, Murray Valley; · · · ·, "Classic" Neanderthals.

Figure 7. Composite tooth size profile comparing Tasmanian aborigines (data from Table 2) with "Classic" Neanderthals. —, Tasmania; . . . ., "Classic" Neanderthals.



were parallel. But the profile lines of Neanderthals and Australians differed. Apparently there was something in the selective forces relating to the dentition in the European Mousterian that kept the front teeth relatively large even when the dentition as a whole was undergoing reduction.

Figure 8. Parallelism in the decrease from larger to smaller toothed Australians as shown in composite tooth size profiles (from the data in Table 2). —, Murray Valley; — · —, Tasmania; · · · ·, Walbiri.



This difference in pattern between Palaeolithic Europeans and living Australian aborigines decreases as tooth size reduces. In Europe, or, more properly, Eurasia, reduction is clearly visible through time (Brace, in press, *b*). In Australia it is a matter of area, although, as I have argued elsewhere, this really is a reflection of the different lengths of time that particular selective forces have been suspended (Brace, in press *a*). For example, the Walbiri of Yuendumu settlement some 185 miles northwest of Alice Springs in the desert heart of Australia, with a summary tooth size of 1350, are close to the small end of the Australian range of variation markedly down from the 1497 mm of the Murray Basin aborigines. If my reconstruction, based on linguistics, technology and cultural adaptation, is correct, they should represent the near maximum response to the post-Pleistocene influx of an essentially Mesolithic life-way in what had up to that time been an essentially Palaeolithic Australia.

Walbiri tooth size, at 1350, is also smaller than that for the "Classic" Neanderthals of western Europe with 1415 mm. And, as the composite tooth-size profiles show, the difference is almost entirely in the forward part of the dental arch (Figure 9). The molars are very nearly identical—both groups being substantially reduced from the Middle Pleistocene values of Krapina and the Murray Basin aborigines.

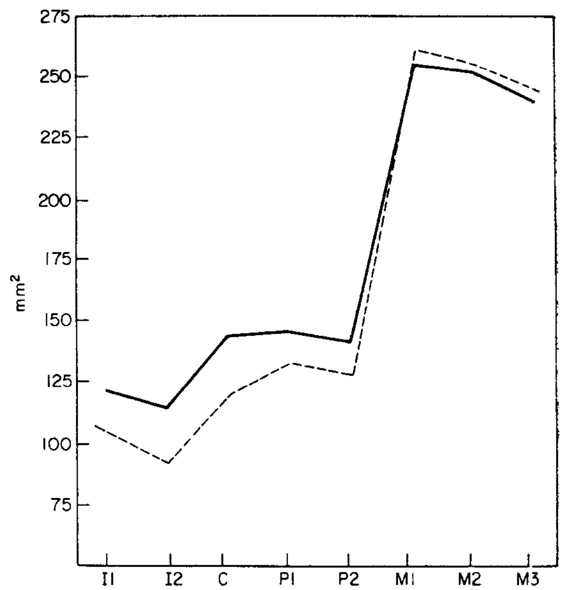


Figure 9. Walbiri (Central Australia) and "Classic" Neanderthals compared by means of composite tooth size profiles. —, "Classic" Neanderthals; · · · ·, Walbiri.

When the Walbiri are compared with a late Mousterian and an early Upper Palaeolithic group, the evident convergence is striking (Figures 10 and 11). With summary tooth size figures respectively of 1350, 1353 and 1352 mm, there is virtually no overall difference. The late Mousterian group is actually from the Middle East, being the Skhūl Neanderthaloids from Mount Carmel, Israel, of about 35,000 B.C. The earlier Neanderthal pattern of slightly larger front teeth compared to molars is still present at Skhūl but not nearly so marked. Sample size is actually extremely small so that the comparison can be no more than tentatively suggestive at best.

When the Walbiri are compared with a sampling of teeth from the early Upper Palaeolithic of about 30,000 B.C., again with an identical total tooth size, the convergance

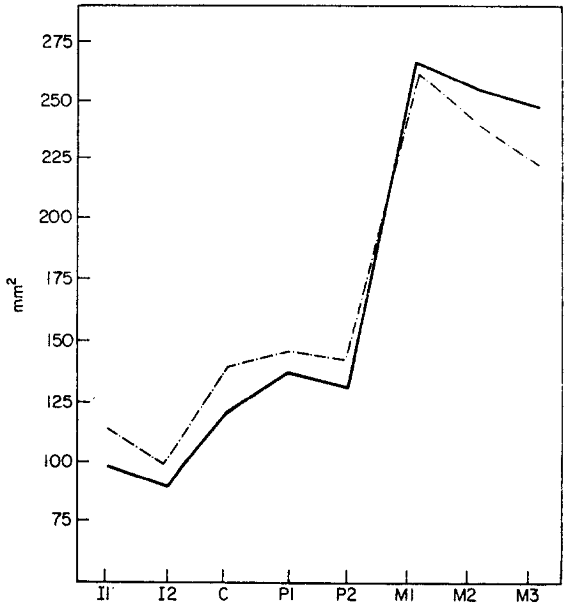


Figure 10. Walbiri (data in Table 2) and late Mousterian Neanderthaloids from Skhūl (data from McCown & Keith, 1939) compared by means of composite tooth size profiles. —, Walbiri; — - —, Skhūl.

is even closer (Figure 11). Aurignacian incisors are just slightly larger and molars a shade smaller, but neither difference is even close to being significant. I suggest that the development of a manipulative technology in the Mousterian had reduced the adaptive significance of large-sized front teeth to such an extent that by the beginning of the Upper Palaeolithic only traces remained of their former relatively robust development.

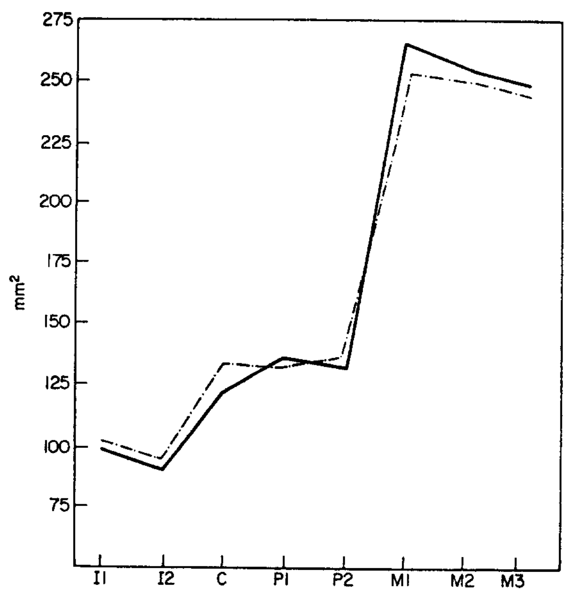


Figure 11. Walbiri and early Upper Palaeolithic (data from Frayer, 1978) compared by means of composite tooth size profiles. —, Walbiri; — - —, Aurignacian.

6. Tooth Size in the Greater Mousterian Culture Area

In my treatment so far, I have used last interglacial Neanderthals from the Balkans, early Würm and beginning Upper Palaeolithic material from western Europe, and late Mousterian remains from the eastern Mediterranean as though they could all stand as temporal representatives of the sequence of a single combined area. This is somewhat at variance with the traditional view where western Europe has been regarded as a kind of cul-de-sac where the "Classic" western Neanderthals were cut off by the Würm glaciation from contacts with human populations to the east and either preserved their supposed archaic features or possibly even regressed—stagnating in cold and wretched isolation.

I suspect, however, that this expectation of "isolation" is more a reflection of the national provincialism of modern scholarship than a product of the actual data. Certainly the climate in the early Würm failed to produce any evidence for isolation and speciation in creatures as diverse as the mammoth or the mouse—or any of the other Pleistocene mammals that have been studied, all of which maintained an unbroken distribution that ran from western Europe south of the Alps via Italy and the Balkan Peninsula to the Middle East. Zoogeography, then, provides no evidence for an environmentally imposed discontinuity. And if mammals were not restricted, there is even less reason to expect that humans had been so.

The best indications for the extent of human habitation are the imperishable products of human manufacture, stone tools, and it is noteworthy that a complex of typogically similar stone tools recognized as the Mousterian runs without break all the way from the Zagros Mountains of Iraq to the Atlantic coast of western Europe. Surely this distribution means that the same cultural solutions to environmentally posed problems were being utilized throughout this area and that biological consequences for the shaping of human form should also have been the same. Finally, of course, where cultural elements are distributed genes are sure to accompany them.

Previously I have tried to give this recognition in what I called the greater Mousterian Culture Area, a zone encircling the Mediterranean Basin and including western and eastern Europe, the Balkans, southern Russia, Crimea, the Caucasus, Turkey and the adjacent Middle East. This construct has not been challenged, but it has not been accepted either, and, in practice, it has in effect been ignored. Its proof ultimately will have to be by archaeological comparison and analysis, but an appraisal of available human skeletal material, however rare, incomplete and tentatively dated, should also be of some help. The only skeletal populations in the Middle East that are temporally comparable to the early to mid-Würm "Classic" Neanderthals of western Europe are the remains from Shanidar Cave in the Zagros Mountains of Iraq.

Only preliminary reports are available and no full interpretive treatment has been offered, although there has been a kind of tacit assumption that since it is from the Middle East, the legendary source of "true modern" form, it is somehow less "extreme" or "aberrant" than the European Neanderthals. Presumably the occiput is less "bun-shaped", the forehead less sloping, the alveolae less prognathic and the chin more pronounced. But this view, which I like to refer to as the palaeoanthropological equivalent of the Garden of Eden hypothesis, seems to have reified the western European Neanderthals as invariant duplicates of La Chapelle-aux-Saints and dispensed with any attempts at quantification at all. Admittedly, given the rudimentary nature of the preliminary publications, quantification would involve the use of scaled photographs or casts, but even this is better than not doing it at all. For the tooth-size figures in my comparison, then, I am relying on unpublished measurements kindly provided by Dr Erik Trinkaus. The comparison of composite profiles (Figure 12) shows that Shanidar is very close to being a mean representative of its western European contemporaries. From what is available to us, it would appear that, as with cultural traditions, there was no real difference in human form in the early to mid-Würm between western Europe and the Middle East. The "pecularities" of the late western European Neanderthals are more a matter of enduring myth than of demonstrable reality.

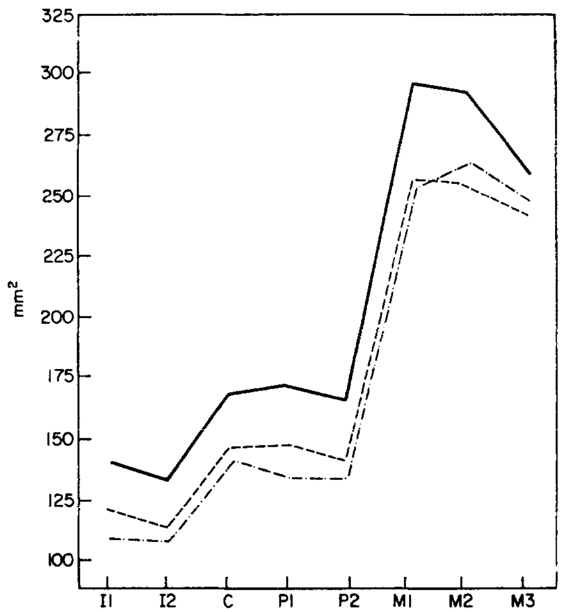


Figure 12. The similarity of Shanidar and the "Classic" Neanderthals of western Europe—and their reduction from the condition seen at Krapina—shown by composite tooth size profiles. The Shanidar plot is based upon measurements taken by Dr Erik Trinkaus on the material housed in Baghdad. —, Krapina; · · · ·, "Classic" Neanderthal; — · —, Shanidar.

And, dentally, at least, their supposed "conservative" appearance has been greatly overemphasized. As Figure 13 clearly shows, the supposedly wide gap between the "Classic" Neanderthals and early moderns is actually an extremely narrow one. The difference between the summary tooth size figures is only 63 which is less than the difference between the early (Aurignacian) and late (Magdalenian) Upper Palaeolithic modern groups (at 78 mm) (Figure 14) and it is absolutely dwarfed by the 200 mm gap between the Aurignacian and twentieth century people of European extraction (1153 mm for the extractions I collected from the University of Michigan Dental School).

If western Europe and the Middle East are culturally and biologically similar early in the Würm, one would expect a comparable degree of resemblance to be visible at the end of the Mousterian and the beginning of the Upper Palaeolithic. In western Europe, the only skeletal material that can be located at the end of the Mousterian is from Hortus in southern France (de Lumley-Woodyear, 1973). There are not enough teeth to make a complete profile, but the figures from C to M3, even though based on only between one and five individuals, fall midway between the European early Upper Palaeolithic and "Classic" Neanderthal means. Unfortunately there are no early Upper Palaeolithic skeletons from the Middle East. But when the Skhūl Neanderthaloids from Mount Carmel are compared with the Aurignacian material in the west—groups that are probably no more than 4000 years apart in time—there is virtually no difference in their summary tooth sizes, and, as can be seen (Figure 13) the composite tooth-size profiles

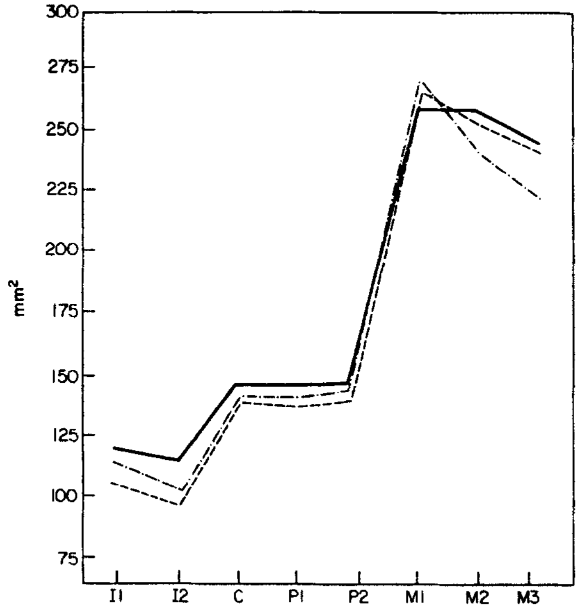


Figure 13. "Classic" Neanderthals, Neanderthaloids and early Upper Palaeolithic composite tooth size profiles showing the gradual transition from Neanderthal to early modern status. —, "Classic" Neanderthals; — - —, Skhūl; · · · ·, Aurignacian.

are also extremely similar. This just provides further confirmation for the expectation that the cultural and biological developments in both Europe and the Middle East—and presumably the entire connecting area—moved in parallel fashion from the last

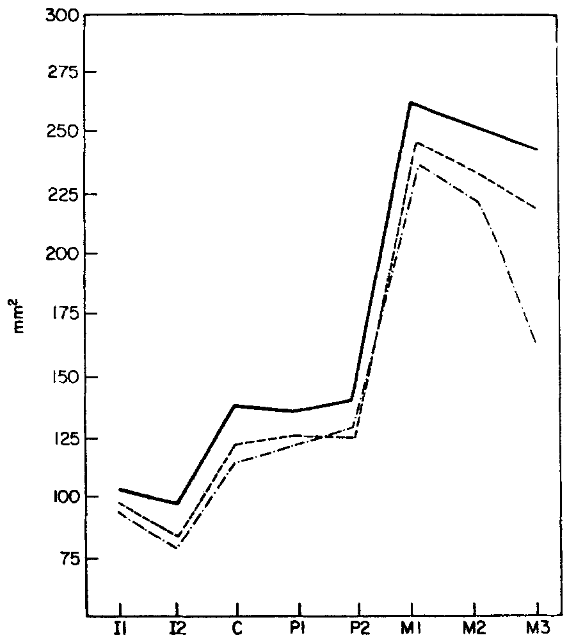


Figure 14. Early and late Upper Palaeolithic composite tooth size profiles (from data in Frayer, 1978), compared with extractions at the University of Michigan Dental School (from data in Brace, in press, *b*). —, Aurignacian; · · · ·, Magdalenian; — - —, Dental School.

interglacial on towards the end of the Pleistocene. If, as I claim, cultural developments have altered the nature of selective forces, then we should have been able to predict parallel biological changes from the archaeological evidence alone. It is nice, however, to have the confirmation that we get from the spotty but reassuring skeletal remains.

7. Dental Reduction after the End of the Mousterian

There was a tendency on the part of an earlier generation of anthropologists, and still to an extent evident today, to regard the story of human evolution as having been completed with the arrival of what was somewhat prematurely regarded as "modern" form. It was a wondrously teleological and self-congratulatory view. Covertly, it seemed to assume that "modern man" (I use the term advisedly) was the object and end of evolution. Once this exalted state had been reached, *we* had "arrived", evolution ceased, and it was our destiny to live happily ever after in changeless splendor, world without end, amen. The consequence of this is that practically nobody has paid any attention to prehistoric human skeletons of less than 30,000 years antiquity, and the few who have done so have generally been ignored. As is evident in Figure 15, the teeth of western

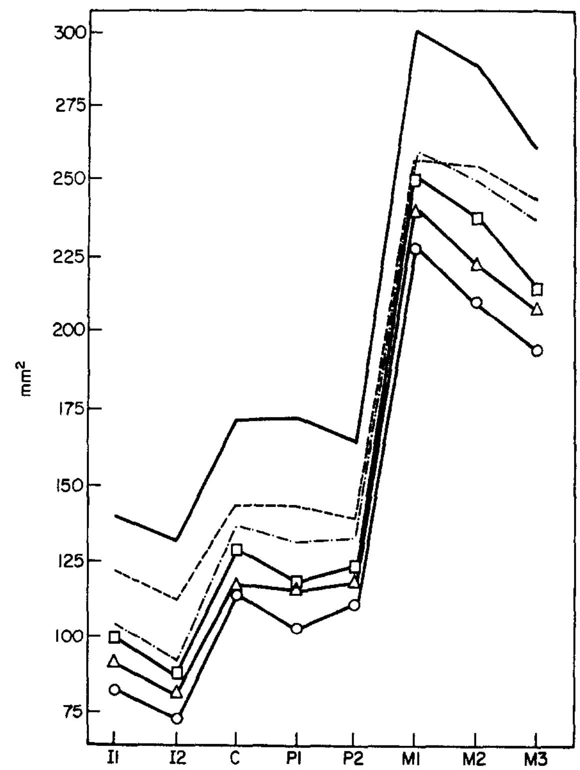


Figure 15. 100,000 years of European dental reduction demonstrated by changes in composite tooth size profiles that are roughly proportional to the time between the groups represented. [Data from Tables 1 and 3, Wolpoff (1971) and Frayer (1978)]. —, Krapina; — — —, "Classic" Neanderthal; —.—, Aurignacian; □—□, Mesolithic; △—△, England-Neolithic; ○—○ 17th Century London.

Europeans continued to reduce after the end of the Pleistocene. Neolithic English Teeth are clearly smaller than Mesolithic teeth, and 17th century Londoners clearly had smaller teeth than those from the Neolithic of Wiltshire, and if I had inserted a line representing British teeth at the time of the Roman occupation, it would have neatly split the difference between the Neolithic and modern positions on the graph.

Table 3 **Neolithic and Romano–British and 17th century London tooth size data. *N* is indicated in parentheses**

	Neolithic MD BL	Romano-British MD BL	17th century London MD BL
I^1	8·4 × 7·2 (18)	8·3 × 7·2 (29)	7·8 × 6·6 (15)
I^2	6·5 × 6·4 (27)	6·5 × 6·3 (32)	6·2 × 6·0 (17)
C	7·6 × 8·6 (39)	7·5 × 8·3 (43)	7·4 × 8·2 (34)
P^1	6·8 × 9·1 (45)	6·6 × 8·9 (47)	6·4 × 8·6 (41)
P^2	6·5 × 9·3 (41)	6·4 × 9·0 (44)	6·3 × 8·9 (42)
M^1	10·7 × 11·6 (56)	10·1 × 11·4 (42)	10·1 × 11·3 (44)
M^2	9·6 × 11·5 (52)	9·3 × 11·3 (47)	9·2 × 11·2 (40)
M^3	8·9 × 11·2 (32)	8·4 × 10·7 (38)	8·5 × 10·5 (24)
I_1	5·1 × 6·2 (17)	5·3 × 6·1 (28)	5·1 × 5·8 (12)
I_2	5·8 × 6·5 (28)	5·9 × 6·4 (33)	5·8 × 6·2 (21)
C	6·7 × 8·0 (34)	6·8 × 7·8 (41)	6·8 × 8·0 (33)
P_1	6·9 × 7·9 (43)	6·8 × 7·8 (37)	6·6 × 7·4 (42)
P_2	7·0 × 8·3 (38)	6·8 × 8·2 (42)	6·8 × 8·1 (33)
M_1	11·1 × 10·7 (50)	11·1 × 10·6 (45)	10·9 × 10·5 (43)
M_2	10·8 × 10·3 (52)	10·5 × 10·2 (43)	10·6 × 10·0 (44)
M_3	10·6 × 10·1 (40)	10·3 × 9·8 (33)	10·7 × 9·8 (33)
TS	1201	1151	1120

Figure 15, then, displays a good picture of the changes that have taken place in human tooth size over the last 100,000 years. None of the steps is particularly large, but the difference between the last interglacial and modern group is over 40%. And if I had chosen another of the several modern groups available, including one from the Center for Human Growth at the University of Michigan, the difference would have been well over 50%. By any standards, this is an impressive evolutionary change to have occurred in just 100,000 years and it contrasts markedly with the relative stability of the previous million years of hominid existence—at least where the dentition is the focus of our concern.

8. Selective Force Change and Tooth Size Reduction

I have dealt with my views on change at the front end of the dental arch, but, aside from noting that the primary role of the molars is in reducing food to digestible size and consistency, I have not yet mentioned why there should have been such a marked reduction in molar size. Previous studies, including earlier ones by myself, have tended to focus on diet. But there is no evidence for a major dietary shift until very near the end of the Pleistocene. At that time, the growing focus on plant foods and techniques for processing them, including grinding tools and pottery, paves the way for the food producing revolution. This certainly had its effect, and there is incomplete but suggestive evidence that this superimposed a gradient of differential tooth size on what had been relative biocultural uniformity throughout the region that I had earlier designated the greater Mousterian culture area. This, however, is clearly a later refinement on the gross picture that had been developing for nearly the previous 100,000 years and does not account for the major changes that had already occurred.

Since, except for the last minor alterations, all the changes that produced modern face form out of a Middle Pleistocene precursor took place in the absence of any discernible dietary change, then we are forced to the conclusion that the people during this period must have been doing something other than chewing to alter the composition of their food. In pondering this problem, I have generated a little aphorism to guide us in approaching the nature of the selective forces that have acted to maintain the functional capacity of the molars, "It is not so much what is eaten, but what is done to it beforehand" (cf. Brace, 1977, p. 199). Whether that doing is by thermal or mechanical action, anything that alters the amount of necessary chewing perforce changes the adaptive value of the food-processing part of the dentition. And the alterations with which we are most familiar—cutting, pounding, grinding and, above all, cooking—all serve to reduce the amount of previously compulsory chewing. It is my contention that this constitutes selection relaxation and, following the predictions inherent in the Probable Mutation Effect (Brace, 1963), the consequences should be visible in the reductions of the structures so affected.

Certainly human molars, the primary anatomical food processing machinery, undergo a dramatic reduction during the late Pleistocene. Just as certainly there no obvious reason why such a reduction should be advantageous, although a number of attempts have been made to explain it on such grounds. One such suggested that a reduction in jaw and tooth weight significantly lessened the angular momentum to be overcome when swivelling the head around to see if something from behind might be threatening the person in question (Brues, 1966).

For my part, I find it impossible to believe that the reduction in a tenth of a millimeter of tooth enamel played any role that selection could have detected in altering the significant rate of head-swivelling speed. Another such effort is the tentative suggestion that smaller teeth provide less surface to be attacked by carious lesions (Greene, 1970). This too is a dubious explanation at best. Except for the unique instance of the rotten dentition of the famous "Rhodesian" skull, caries are practically non-existent during the Pleistocene. As a significant phenomenon they post-date the development of intensive agriculture long after the late Pleistocene dental reduction had already taken place.

Other similar attempts have been made but they are equally unconvincing. The repeated efforts to offer some positive reason for what clearly appears to be a change which was of no discernable value to the possessor is obviously the result of adherence to the ruling orthodoxy of modern evolutionary theory, namely, evolutionary change *must* be guided by natural selection, and if we have failed to discover how this works in a given instance, this is only because of the limitations of our less-than-infinite intellects.

For my part, however, I cannot bring myself to the point of substituting faith for reason just because it is the fashionable thing to do. I find it quite sufficient and satisfying to use the entropy-based model of the Probable Mutation Effect to explain those late Pleistocene reductions that all seem to occur when human ingenuity has interposed a barrier between the previously operating forces of selection and the human physique. Our best evidence for these reductions is dental, and if the proliferation of a manipulative technology is sufficient to account for a relaxation of the selective forces relating to the front end of the dental arch, then evidence for the development of a culinary technology should do the same for the back end of the dental arch.

9. Food Preparation Techniques and Selective Force Change

Now if manipulatory tools are obvious, what is the evidence for food-processing? Some of this surely is in the presence of the manipulative tools themselves. It is only reasonable to assume that food was amongst the items to which the growing numbers of cutting tools were applied. Undoubtedly this had some effect in reducing the involvement of the teeth, but this hardly can account for a dental reduction of up to 50%. And at the very end of the Pleistocene, the sudden and extensive proliferation of pounding and grinding tools indicates not only a significant expansion in the items that could be used as food but the capacity of reducing hitherto obdurate items to the consistency of paste or flour. This, and the subsequent development of pottery which enabled the further reduction of the edible to the drinkable, obviously signalled a dramatic reduction in the necessary involvement of the dentition.

But again, these developments only occurred after dental reduction had already proceeded to very nearly its current extent. One could guess that some other major form of food preparation had been in regular use going right back to the last interglacial. It is my contention that this guess is correct and that the evidence has been there all along only we have simply failed to recognize it. For years, archaeological site reports dealing with the Mousterian and the Upper Palaeolithic have recorded what they call "hearths" with quantities of associated fire-cracked and blackened cobbles or "river pebbles" of about the size of a human fist or a little larger. Occasionally in the literature and often in informal discussion, archaeologists have speculated on what these collections signify. Perhaps, some have suggested, they were Palaeolithic bed warmers periodically raked out of the fire to help relieve the glacial chill of a long winter's night in a European cave.

More relevant to my present concern—and possibly why I think it may be closer to the truth—is the suggestion that, during the Perigordian in France, the heat-fractured stones may indicate the practice of cookery by means of stone boiling (Movius, 1966). I do not mean to discount this because they may very well have been doing just that, but to any archaeologist who has worked in Oceania, the form of these Palaeolithic "hearths" and the quantities of fire-altered stone they contain can mean only one major thing—the people of the European late Pleistocene were making extensive use of earth oven cookery (Brace, in press, *b*). In many instances, even after 50,000 years, the "hearth" has a depth of a foot or two below the level with which it is culturally linked; charcoal, burnt bone and blackened rocks swirl together in a streaked and spherical fashion; and it is quite clear that the feature was derived from more than the open campfire which the usual description calls to mind. On the other hand, it is quite consistent with an interpretation which regards these as the traces of prehistoric earth ovens.

One can easily duplicate the observed features by scooping out a pit in the earth, spreading rocks on the bottom, building a fire over them, and then, when it has died down, placing a wrapped bundle of food in the middle, raking the rocks around it, and burying the whole with dirt for a few hours and then pulling the food bundle out. The residue is a fine duplicate of a late Pleistocene "hearth" and you also have a packet of food, the flavor held in, steamed to soft and succulent perfection.

Such a technique can greatly reduce the previously necessary amount of chewing, and I venture the suggestion that it was something like this that allowed the "Old Man" of La Chapelle-aux-Saints to live so long after the loss of his molars that his cheekbones became altered from lack of masseter use and the angles of his mandible resorbed to produce what a whole misguided generation of anthropologists came to regard as "typical" Neanderthal form. It may have been no less than the first clear evidence for the consequences of what I would like to call the "culinary revolution".

10. The Significance of Cooking

In passing, we should consider a common misconception concerning cooking. We commonly hear how the principal purpose of cooking is to improve the taste of food, but this like other attempts at rationalization, may very well be an after the fact justification that masks the true significance of the phenomenon. Again, I suspect that we like the taste of the food that we cook as opposed to the situation of cooking the food to the taste we like.

Cooking does more than simply make food easier to chew and alter its taste both of which I suspect were secondary to its original significance. Cooking makes it possible to use as food something that would be inedible or positively poisonous when eaten untreated.

Consider the small group of Australian aborigines and a large kangaroo. Recorded commentary observes that it is eaten rather underdone to European tastes, but this commentary was only made at the first eating (McCarthy & McArthur, 1960). The creature served as food for several days, and that in a land infested with flies, subject to tropical heat and devoid of refrigeration. Before each subsequent eating, the flies were brushed off, the rotten parts discarded, and the salvageable portion wrapped and re-cooked in proper earth oven fashion. By the time the last of the kangaroo was gone, the final portions must have been well-cooked indeed—but the significant fact is that cooking allowed the people to go on using it as food for days longer than could have been the case if they had been forced to use it only once.

In glacial Europe, of course, cooking also had the effect of allowing people to utilize food that had been frozen after an earlier kill. In fact, this may very well have been the circumstance which directly led to the first systematic utilization of the techniques of cookery for which the Palaeolithic earth ovens provide evidence. After all, a small band of Palaeolithic hunters could scarcely consume an entire mammoth at a single sitting. A day later, of course, the thing would be solid block of ice. Obviously it was only worth the effort and hazards of hunting the Pleistocene megafauna if techniques were known that allowed them to thaw and eat the frozen leftovers.

The logic of the rationale seems inescapable, and the archaeological evidence provides some support for the view that cooking was one of the keys to human survival as the onset of the last glaciation put a chill on the northern areas of human habitation throughout the Old World. Although it would be stretching matters a bit to claim that the heights of culinary sophistication reached by France and China represent the matured consequences of techniques that their Neanderthal ancestors had invented simply in order to survive, yet it *is* my view that the maximum degree of dental reduction in the world today runs in a band from west to east in just that area where the amount of required mastication has longest been reduced because of the application of culinary ingenuity.

11. Conclusion

From the perspective of tooth size alone, it is clear that the "Classic" Neanderthals of western Europe are not the extreme and aberrant phenomenon that we have been led to believe. Nor are they characterized by the retention in unreduced form of Middle Pleistocene faces and teeth, Instead, it is the early Neanderthals from Krapina that represent the last of that Middle Pleistocene configuration of dento-facial robustness that had remained relatively constant for perhaps as much as a million years, starting with the emergence of *Homo erectus* late in the Lower Pleistocene.

The late Neanderthals of western Europe had already taken a substantiated step in the direction of modern form with teeth that were a good 15% smaller than those of their predecessors late in the last interglacial. Ironically the major gap is *not* between the "Classic" Neanderthals and the earliest "Moderns" since the tooth size difference involved was only 5%. If we do not balk at allowing both the Krapina remains and the Mousterian skeletons of western Europe to be called "Neanderthals", and we accept the early Upper Palaeolithic people as ancestral to modern western Europeans even though modern European teeth are a full 20% smaller, then there is no good reason for us to deny the possibility that it was just that 5% reduction that converted the late Neanderthals into the early "Moderns". In fact, in the graphic representation of tooth size in Figure 15, the height of each line on the graph is almost exactly proportional to the antiquity of the population represented.

Clearly some change in the nature of the forces of selection had taken place approximately 100,000 years ago that allowed these relatively rapid reductions to occur. I have suggested, after considering the evidence from archaeology and from the ethnographic record, that the development of culinary technology relaxed the selective forces that had maintained tooth and face sizes throughout the Middle Pleistocene. The quantities of fire-blackened rocks in Mousterian and Upper Palaeolithic hearths may indicate that some form of heated stone cookery was regularly employed. The stimulus for the development of such techniques may have been provided by the onset of the last glaciation when, to an increasing extent, foodstuffs froze before they could be consumed. The original purpose of cooking may simply have been to thaw frozen food so that it could be eaten but the unintended by-product was a significant reduction in the amount of previously necessary chewing.

Under these conditions, then, mutations alone, accumulating unopposed, accomplished the reductions that produced the modern face from a Middle Pleistocene ancestral condition via a late and transient Neanderthal stage. In parallel with reductions in skeletal robustness and muscularity, tooth and face size continued to decrease in the late Pleistocene and the post Pleistocene, and the trend has continued right up to the present. There is no reason not to expect that it will continue on into the future. As a requirement for survival, the dentition is now superfluous. Given this situation, it is not an unwarranted extrapolation to predict that that culmination of the trend I have documented will be the appearance of an edentulous species if in fact the human line manages to survive another hundred thousand years. Our current facial configuration, then, like that of our Neanderthal ancestors, is simply an arbitrary and transient point in a spectrum of rapid and continuing evolutionary change.

12. Postscript

It is too late to realize that our self-declared wisdom is insufficient grounds for taxonomic assessment and to rechristen ourselves *Homo "gastronomicus"*, but it is not too late to recognize the role played by culinary traditions in literally shaping the face of humanity.

By the end of the Pleistocene at both the Far Eastern and the northwestern extent of human occupation, the residents displayed a degree of dento-facial reduction which only a few of the rest of the world's peoples have subsequently come to approach. Reduction has gone even further in those areas that have served as the loci for food-producing revolutions, but these are relatively minor modifications on the form that evolved across the northern portions of the Old World by those people who first developed a frozen food technology.

In closing I append two limericks from the pen of that deservedly obscure observer of the human scene, I. Doolittle Wright. These are from the volume *Inverse*, whose editor, A. Nonny Mussleigh, has been unable to get support for publication principally because the contents are generally as trivial as they are inept. Here, however, one might make the case that, even though Wright has shamelessly perverted the perceptive artistry of T. S. Eliot, in fact he has anticipated some of the points made in this paper:

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 will be ruthless;
And not with a fang but a simper.

The research on which this paper is based was accomplished in spite of refusals of support from the National Science Foundation. Partial funding was provided by the Horace H. Rackham School of Graduate Studies at the University of Michigan, by the University of Auckland, and unwittingly, by the Wenner Gren Foundation for Anthropological Research. For access to original materials, I am indebted to the cooperation of the late Murray Barrett, to Tasman Brown, Ivan Crnolatac, Frank Ellis, J. P. Garlick, Mirko Malez, the late Josip Poljak, to Graeme Pretty, L. J. Ray, Robert Stone, C. B. Stringer, R. L. Vanderwal and A. G. Wallace. Portions of this paper were delivered at the First Congress of European Anthropologists, Zagreb, Yugoslavia, September 3, 1977.

References

Ackernecht, E. H. (1953). *Rudolf Virchow: Doctor, Statesman, Anthropologist.* Madison, Wisconsin: University of Wisconsin Press.

Brace, C. L. (1962). Refocussing on the Neanderthal problem. *American Anthropologist* **64**, 729–741.

Brace, C. L. (1963). Structural reduction in evolution. *The American Naturalist* **97**, 39–49.

Brace, C. L. (1964). The fate of the "Classic" Neanderthals: A consideration of hominid catastrophism. *Current Anthropology* **5**, 3–43.

Brace, C. L. (1967*a*). Environment, tooth form, and size in the Pleistocene. *Journal of Dental Research* **46** (supplement to Number 5), 809–816.
Brace, C. L. (1967*b*). *The Stages of Human Evolution: Human and Cultural Origins.* Englewood Cliffs, New Jersey: Prentice-Hall.
Brace, C. L. (1977). Occlusion to the anthropological eye. In (J. A. McNamara, Jr., Ed.) *The Biology of Occlusal Development,* pp. 179–209. Ann Arbor, Michigan: Center for Human Growth and Development, Craniofacial Growth Series Monograph **7.**
Brace, C. L. (in press, *a*). Australian tooth size clines and the death of a stereotype. *Current Anthropology.*
Brace, C. L. (in press, *b*). Biological parameters and Pleistocene hominid life-ways. In (I. S. Bernstein, Ed.) *Biological Influences on Social Organization: Evolution and Adaption.* London: Academic Press.
Brace, C. L. (in press, *c*). Tooth reduction in the Orient. *Asian Perspectives* **19,** 203–219.
Brace, C. L. (in press, *d*). Tooth size and Austronesian origins. In (P. B. Naylor, Ed.) *Proceedings of the Second Eastern Conference on Austronesian Languages.* Ann Arbor, Michigan: Michigan Series in South and Southeast Asian Languages and Linguistics.
Brace, C. L. & Mahler, P. E. (1971). Post Pleistocene changes in the human dentition. *American Journal of Physical Anthropology* **34,** 191–204.
Brace, C. L. & Montagu, M. F. A. (1965). *Man's Evolution: An Introduction to Physical Anthropology.* New York: Macmillan.
Brace, C. L. & Montagu, A. (1977). *Human Evolution: An Introduction to Biological Anthropology,* 2nd Edn. New York: Macmillan.
Brace, C. L., Nelson, H. & Korn, N. (1971). *Atlas of Fossil Man.* New York: Holt, Rinehart and Winston.
Brues, A. M. (1966). "Probable mutation effect" and the evolution of hominid teeth and jaws. *American Journal of Physical Anthropology* **25,** 169–170.
Constable, G. & the Editors of Time-Life Books (1973). *The Neanderthals.* New York: Time-Life Books.
Frayer, D. W. (1977). Metric dental change in the European Upper Palaeolithic and Mesolithic. *American Journal of Physical Anthropology* **46,** 109–120.
Frayer, D. W. (1978). *Evolution of the Dentition in Upper Palaeolithic and Mesolithic Europe.* Lawrence, Kansas: University of Kansas Publications in Anthropology **10.**
Garrod, D. A. E. & Bate, D. M. A. (1937). *The Stone Age of Mount Carmel, Volume 1: Excavations at the Wady el-Mughara.* Oxford: Clarendon Press.
Greene, D. L. (1970). Environmental influences on Pleistocene hominid dental evolution. *BioScience* **20,** 276–279.
Higgs, E. S. (1961*a*). North Africa and Mount Carmel: recent developments. Some Pleistocene fauna of the Mediterranean coastal areas. *Man* **61,** 138–139.
Higgs, E. S. (1961*b*). Some Pleistocene faunas of the Mediterranean coastal areas. *Proceedings of the Prehistoric Society* **27,** 144–154.
Hooton, E. A. (1946). *Up From the Ape,* 2nd Edn. New York: Macmillan.
Howell, F. C. (1951). The place Neanderthal man in human evolution. *American Journal of Physical Anthropology* **9,** 379–416.
Howell, F. C. (1952). Pleistocene glacial ecology and the evolution of "Classic Neandertal" Man. *Southwestern Journal of Anthropology* **8,** 377–410.
Howell, F. C. (1957). The evolutionary significance of variation and varieties of "Neanderthal" man. *Quarterly Journal of Biology* **32,** 330–347.
Howells, W. W. (1944). *Mankind So Far.* Garden City, New York: Doubleday.
Howells, W. W. (1974). Neanderthals: names, hypotheses, and the scientific method. *American Anthropologist* **76,** 24–38.
Howells, W. W. (1975). Neanderthal Man: facts and figures. In (R. H. Tuttle, Ed.) *Paleoanthropology: Morphology and Paleoecology,* pp. 389–407. The Hague: Mouton.
Howells, W. W. (1976). Explaining modern man: evolutionists *versus* migrationists. *Journal of Human Evolution* **5,** 477–495.
Hrdlička, A. (1927). The Neanderthal Phase of Man. *Journal of the Royal Anthropological Institute* **57,** 249–269.
Hrdlička, A. (1930). *The Skeletal Remains of Early Man.* Washington D. C.: Smithsonian Miscellaneous Collections **83.**
Jelinek, A. J., Farrand, W. R., Haas, G., Horowitz, A. & Goldberg, P. (1973). New excavations at the Tabun cave, Mount Carmel, Israel, 1967–1972: a preliminary report. *Paleorient* **1,** 151–183.
Kennedy, K. A. R. (1975). *Neanderthal Man.* Minneapolis, Minnesota: Burgess.
Kleinschmidt, O. (1931). *Der Urmensch.* Leipzig: Quelle & Meyer.
Kuhn, T. S. (1962). *The Structure of Scientific Revolutions.* Chicago: University of Chicago Press.
McCarthy, F. D. & McArthur, M. (1960). The food quest and the time factor in aboriginal economic life. In (C. P. Mountford, Ed.) *Records of the American-Australian Scientific Expedition to Arnhemland, Volume 2: Anthropology and Nutrition,* pp. 145–194. Melbourne: University of Melbourne Press.

McCown, T. D. & Keith, A. (1939). *The Stone Age of Mount Carmel, Volume 2: The Fossil Human Remains from the Levalloiso-Mousterian.* Oxford: Clarendon.

Malez, M., Ed. (1970). *Krapina 1899–1969.* Zagreb: Jugoslavenske Akademije Znanosti: Umjetnosti.

Movius, H. L., Jr. (1966). The hearths of the Upper Perigordian and Aurignacian horizons at the Abri Pataud, Les Eyzies (Dordogne), and their possible significance. In (J. D. Clark & F. C. Howell, Eds) Recent studies in paleoanthropology. *American Anthropologist* **68** (Special Publication, Part 2), 296–325.

Poirier, F. E. (1977). *Fossil Evidence: The Human Evolutionary Journey,* 2nd Edn. St. Louis, Missouri: Mosby.

Post, R. H. (1962). Population differences in red and green color vision deficiency: a review and a query on selection relaxation. *Eugenics Quarterly* **9,** 131–146.

Post, R. H. (1963). "Colorblindness" distribution in Britain, France and Japan: a review with notes on selection relaxation. *Eugenics Quarterly* **10,** 110–118.

Post, R. H. (1965). Notes on relaxed selection. *Anthropologischer Anzeiger* **29,** 186–195.

Post, R. H. (1966). Deformed nasal septa and relaxed selection. *Eugenics Quarterly* **13,** 101–112.

Schwalbe, G. (1906). *Studien zur Vorgeschichte des Menschen.* Stuttgart: Scheizerbart.

Schwalbe, G. (1913). Kritische Besprechung von Boule's Werk: "L'homme fossile de la Chapelle-aux-Saints" mit eigenen Untersuchungen. *Zeitschrift für Morphologie und Anthropologie* **16,** 527–610.

Sheets, J. W. & Gavan, J. A. (1977). Dental reduction from *Homo erectus* to Neanderthal. *Current Anthropology* **18,** 587–588.

Smith, F. H. (1976). *The Neanderthal Remains from Krapina: A Descriptive and Comparative Study.* Knoxville, Tennessee: Department of Anthropology, University of Tennessee, Report **15.**

Smith, P. (1976). Dental pathology in fossil hominids: What did Neanderthals do with their teeth? *Current Anthropology* **17,** 149–151.

Smith, P. (1977*a*). Selective pressures and dental evolution in hominids. *American Journal of Physical Anthropology* **47,** 453–458.

Smith, P. (1977*b*). Regional variation in tooth size and pathology in fossil hominids. *American Journal of Physical Anthropology* **47,** 459–466.

Stebbins, R. E. (1974). France. In (T. F. Glick, Ed.) *The Comparative Reception of Darwinism,* pp. 117–163. Austin, Texas: University of Texas Press.

Weidenreich, F. (1937). The dentition of *Sinanthropus pekinensis. Palaeontologia Sinica,* New Series D, No. 1, Whole Series No. 101, 1–180.

Weinert, H. (1932). *Ursprung der Menschheit.* Stuttgart: Enke.

Wolpoff, M. H. (1971). *Metric Trends in Hominid Dental Evolution.* Cleveland: Case Western Reserve University Press, Case Western Reserve Studies in Anthropology **2.**