



Australian Tooth-Size Clines and the Death of a Stereotype [and Comments and Reply]
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Australian Tooth-Size Clines and the Death of a Stereotype¹

by C. Loring Brace

There are no races. There are only clines.

[Livingstone 1962:279]

The most important requirement for the analysis of human variation is the appreciation of the selective pressures that have operated to influence the expression of each trait separately.

Human physical variation can best be understood by relating the distributions of specific morphological features to the distribution and history (also the prehistory) of the relevant selective and adaptive forces.

[Brace and Montagu 1977:390-91, italics in the original]

INTRODUCTION

Building upon the insights of E. B. Tylor and Franz Boas, the demonstration that cultural manifestations are entirely independent of aspects of human biology is one of the most impor-

tant lessons taught by the science now known as anthropology. It was not innate biological limitations that kept the inhabitants of the British Isles from discovering the alphabet or the Chinese from devising a steam engine or the Ethiopians from inventing mechanized warfare. Nor are the triumphs of Western civilization or Oriental civilization due to any innate superiority in the germ plasm of Occidentals or Asians. It has been taken to follow, then, that the form and development of human societies can best be understood by the study of cultural dynamics per se with little or no concern for the biology of the peoples in question. One of the consequences of these realizations was the development of ethnology and biological anthropology as completely separate fields. Another was the assumption, by those whose primary concern was in the biological realm, that, in like fashion, the dimensions which constitute their particular province are also to be studied and understood on what are considered to be their own grounds alone. If cultural developments took place completely uninfluenced by phenomena in the realm of human biology, the converse was also generally accepted. By analogy, it was assumed that human biological developments owed nothing to shaping influences in the cultural realm.

In general, this separation has been a good thing, but I suspect that its rigorous enforcement has been carried too far. To be sure, the use of specific cultural traits as indicators for the presence of particular, named racial elements, in the style attributed to the earlier manifestations of the old Viennese cultural-historical school, may have been overdone at one time; but it would seem that a judicious consideration of cultural phenomena which can temper selective forces that would otherwise be expected may well repay our efforts.

As I see it, the most significant contribution that biological

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late Murray Barrett and by Tasman Brown, Frank Ellis, James P. Garlick, Roger Hardley, T. Jacob, the late Stanley Larnach, Peter Lauer, F. P. Lisowski, Mance Lofgren, the late N. W. G. Macintosh, David R. Moore, Graeme Pretty, Michael C. Quinnell, L. J. Ray, George J. Romanes, Alyson Schmidt, Sood Sangvichien, James R. Specht, Peter Stanbury, Robert Stone, Alan G. Thorne, Ronald L. Vanderwal, Alan G. Wallace, Alan West, and Walter B. Wood.

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anthropology can make is right in that area where the socio-cultural and biological realms intersect. The classic example of such an approach put into practice is Livingstone's (1958) splendid demonstration of how West African culture history, ecology, malaria, and the gene frequency for hemoglobin S can all be encompassed within a single interpretive framework. Unfortunately, other biological anthropologists have been a little timid in following up on this brilliant beginning.

If biological anthropologists have been slow to follow up their opportunities, other less qualified writers have not been so reluctant (e.g., Ardrey 1961, Morgan 1972, Morris 1967). Subsequently the realm in which biological anthropologists should properly function has been unaptly rechristened "sociobiology" (Wilson 1975). As Hardin (1977:303) has noted, it really should have been called "*biosociology*," but in any case the extravagant claims of both supporters (e.g., Hamilton 1975, Dawkins 1976) and detractors (Sahlins 1976, Washburn 1977) have effectively deprived the word of the utility it might have had. In response to the thunder of partisan charges, more than one critic has echoed the words of the Bard, "A plague o' both your houses" (Simpson 1977; Brace 1978a: 125).

The principal misfortune that could occur as a result of the dispute over sociobiology is not the resurgence of an unacceptably rigid form of biological determinism, but the possibility that the barrier between the social and the biological sciences may become more formidable than ever. An adequate understanding of the human condition requires not only consideration of the contribution of each realm, but also an appreciation of how matters in each have influenced the state of affairs in the other. For the moment, I am leaving it to others to deal with the general problem (e.g., Alexander 1977, Barash 1978, Barkow 1978). Rather, in the present paper, I hope to show what analysis can do when it builds towards the larger picture by controlling one piece at a time. In this instance, the "larger picture" is the nature of the Australian Aborigines, and the analysis of a single piece of this picture—the teeth—should finally and permanently dispel the widespread assumption that the Australians were a primitive vestige of Pleistocene human form, preserved by isolation in static uniformity until the advent of European settlement in the 19th century. Furthermore, the analysis will suggest how changes in the cultural realm altered the nature of selective forces to produce the remarkable spectrum of physical variation visible in aboriginal Australia. Finally, it will suggest that this biocultural picture was in a state of ongoing evolution fueled in part by regional circumstances within Australia and in part by a long-standing and continuing influx of biological and cultural elements from across the Torres Strait.

MATERIALS

From the biological point of view, the following presentation will be an analysis in one dimension, although there is more than a bit of artifice to this ploy since "the dentition" is a collective phenomenon with a great many dimensions of its own. At the very least there are 32 teeth in the complete normal adult dentition. Each one in turn has crown and root segments, dentine, enamel, cusp and fissure patterns, pulp cavity; and since, in a functioning organism, a tooth is a living structure, each also has a periodontal membrane, innervation, and blood supply. This is just a crude and minimal list, since each of the categories I have mentioned can in turn be broken down still further for study and analysis. Actually, as I have hinted, what I am going to do is the opposite, since I am going to engage in a form of lumping—not of a taxonomic sort, but in the sense of combining histological and morphological components.

From the perspective of evolutionary theory, the justifica-

tion for such a procedure is based on the realization that the forces of selection work on the phenotypic end product and not on its components separately, even if these are under separate genetic control. For all intents and purposes, all the aspects of morphology on which selection acts in a relatively direct manner are polygenic phenomena. This is no less true for teeth than for any other morphological trait. There was once a time when the hope existed that refinements in observation and analysis could lead to the identification of a finite and usable field of dental genetics. For a variety of reasons that have become more obvious with the development of the field of molecular biology, this hope has subsided. The phenomena of pleiotropy and epistasis, introduced by the geneticists of yesteryear as fudge factors to account for their failure to calculate fitness values for individual genes, turn out to be near universals at the level of gross morphology where selection actually operates. A single tooth is a polygenic phenomenon of such complexity that our efforts to determine its precise mode of inheritance can be no more than an exercise in futility. It is enough to know that teeth are under tight genetic control and that change through time represents genuine genetic change.

The following points will serve as a justification for restricting my concern to the teeth:

1. They are durable. As the hardest parts of the human skeleton and the most resistant to chemical degradation, teeth are more likely to survive the ravages of time than any other part of the body. The result is, quite simply, that we have more individuals in the recent and remote past represented by teeth than by anything else.

2. They are easy to measure. Even though techniques of measurement will differ slightly from one observer to another, the differences are small and the phenomena recorded are largely comparable. Quantification lends itself to computer-aided data-processing techniques, and practically limitless amounts of material can be treated and compared.

3. They are under tight genetic control. Even though they are not primary gene products and the genetic background is vastly more complex than we once hoped, the translation from genotype to phenotype is accomplished early in the life-span of an individual, and, of all the aspects of observable adult morphology, teeth are the least subject to environmental modification of genetic intent.

4. The forces of selection act directly upon them. Teeth, as one of my colleagues once put it, are the only parts of the skeleton that come in direct contact with the environment. Some observers still retain a kind of intuitive feeling that because teeth are hard they must therefore be more resistant to change than the softer parts of the body. However, they grow by accretion in the soft and aqueous environment of the immature organism under the influence of countless transient chemical reactions, just like any other tissue, hard or soft. They are in fact extremely responsive to slight changes in the intensity of the selective forces to which they are exposed.

5. They are the one part of the skeleton for which measurements on the living are directly comparable with those on the dead. They are directly accessible to the observer whether the possessor is alive or is a fossil in a collection. The direct assessment of other aspects of the skeleton is hampered in the living by the superimposition of varying amounts of soft tissue, and even with the ingenious use of X-ray techniques the question of comparability tends to remain. Not so with the teeth.

Previous metric studies of the Australian Aboriginal dentition have tended to focus on the teeth of little more than a single local group (Campbell 1925; Hanihara 1976, 1977). The result has been the perpetuation of the belief that the teeth of "the" Australian Aborigine are much the same everywhere they are encountered. Since I suspected that some sort of systematic regional differences might actually exist, I set out to measure samples of specimens from a representative distribu-

tion of the inhabited portions of Australia. Regionally located specimens were made available in museum and anatomy department collections at Brisbane, Sydney, Canberra, Melbourne, Hobart, Adelaide, Perth, and Edinburgh (see fig. 1; Hobart, in Tasmania, and Edinburgh, in Scotland, are not on this map). The results will be discussed later, but at the moment it should be recorded that I did indeed find systematic regional variation and that it was of an order of magnitude that far exceeded anything that has ever been hinted at before.

METHODS

Whatever a tooth is used for, it is only of value to its possessor so long as it retains usable substance. A tooth, of course, is a three-dimensional object, and a full consideration of its wear potential would of necessity include the dimension of crown height as well as those of length and width. In all but the most recent of human populations, however, occlusal wear started right after eruption. In most instances, then, crown-height considerations are restricted to unerupted teeth, and since there are so few of these available for study we have to hope that our assessment of tooth size will be adequate even though we are forced to omit the dimension of height.

As I have noted elsewhere, 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 mesial-distal and buccal-lingual ($MD \times BL$) crown measurements. In previous papers I have compared the dental development of various populations by graphing plots of mean cross-sectional areas (I^1, I^2, \dots, M^3 ; and I_1, I_2, \dots, M_3) as separate maxillary and mandibular tooth-size profiles (Brace 1967a, Brace and Mahler 1973, Brace, Mahler, and Rosen 1973).

The technique is sensitive and successful, but it is also a little cumbersome. To overcome the awkwardness of a multi-

licity 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 $M3$. The result is a composite tooth-size profile (cf. fig. 2).

A still further simplification is the use of the summary tooth-size figure, TS , which can be rendered as $TS = \sum \bar{X}_j$, where $\bar{X} = \sum(MD \times BL)/N_j$, $j = I^1, I^2 \dots M^3, I_1, I_2 \dots M_3$, and N_j = total number of measured teeth in each category. A single figure for tooth size makes it easy to compare a great many groups in a single analysis, but it does have two drawbacks.

First, since it combines figures from both the front and the back of the dental arch, it may obscure real differences between groups that have similar summary tooth-size figures. For example, the figure for European Neanderthals (1,415) is not significantly different from that for Tasmanian Aborigines (1,429), but the Neanderthal total contains an absolutely smaller contribution from the postcanine teeth (1,037 vs. 1,109). The difference in the contribution of the precanine and postcanine teeth can be clearly seen in figure 2. Neanderthal incisors, then, are 18% larger than those in large-toothed Tasmanian Aborigines. This points up an interesting problem, but it actually can be regarded as a refinement of the kind of analysis which is begun in crude form in the present paper.

The second drawback to the use of the summary tooth-size figure is the difficulty in computing a variance for it. This is simple enough where there are sufficient numbers of individuals with measurements for each tooth category. In practice, however, this is the exception rather than the rule when dealing

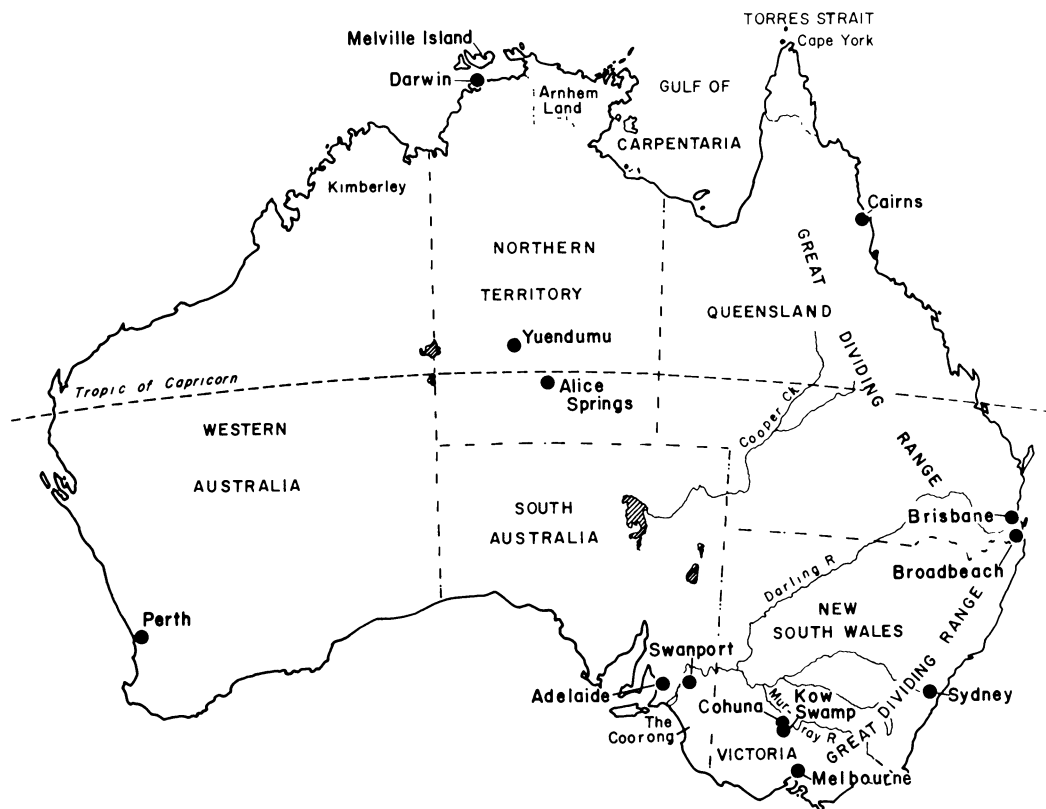


FIG. 1. Australia, with location names used in this paper.

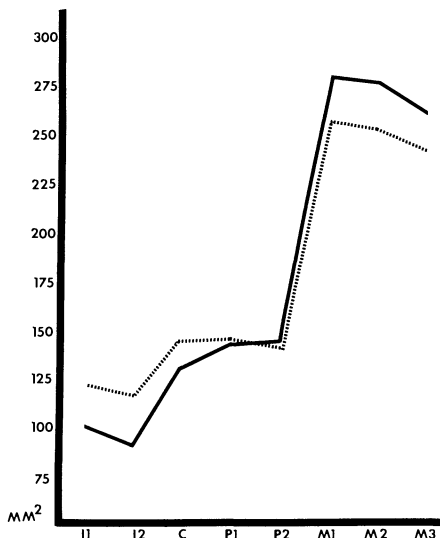


FIG. 2. Composite tooth-size profiles comparing in graphic form the mean cross-sectional areas of Tasmanian Aboriginal (solid line) and Classic Neanderthal (dotted line) teeth. The vertical placement of each labeled point (I1, I2, . . . M3) represents the sum in square millimeters of the upper and the lower means for that tooth category. The Neanderthal figures are from Wolpoff (1971a).

with prehistoric human skeletal material. All too often an incisor or a canine is missing or a molar is too worn to yield a reliable measurement.

For the Australians I measured, however, I was fortunate in getting more than 130 individuals with complete dentitions for two populations—the Walbiri of central Australia and a sample from the Murray River Basin. In both, the standard deviation of the summary tooth-size figure was also over 130, averaging 135, which is what I took for calculating the *t* values when making formal comparisons. This raised still another difficulty, however. In groups that did not have enough complete dentitions to allow the calculation of a measure of variance for the summary tooth-size figure and for which I had to use all of the available teeth to get what I felt was a useful statistic, each tooth category has a different *N*. This can be appreciated by an inspection of the variety of *N*'s in table 1, which lists the mean cross-sectional areas, standard deviations, and summary tooth-size figures for each of 18 groups.

For most groups compared, then, there is no standard deviation for the summary tooth-size figure and the *N* differs from tooth to tooth. If a standard deviation of 135 is used, however, then where *N* is 25 a mean summary tooth-size difference of 100 mm² is significant at the level of .02 > *P* > .01. If *N* is over 60, such a difference is significant at the .001 level. Similarly, a mean difference of 50 mm² is barely significant (.05 > *P* > .02) if *N* is over 60 and significant (*P* > .01) if *N* is over 135. As a kind of informal index, then, a summary tooth-size difference of 50 mm² between groups compared is probably meaningful, and a difference of 100 mm² or more almost certainly has some basic biological meaning.

Using a standard deviation of 135 may be a somewhat arbitrary tactic, but if it errs it does so on the conservative side. For a series of recent and older Chinese and Southeast Asian populations the average standard deviation figure is 79 (Brace 1978b). At the moment, it is not at all clear why variance should drop as one approaches the Asian mainland. To be sure, summary tooth-size figures are significantly smaller—reaching their minimum in modern Chinese (1,157)—but the coefficient of variation, at less than 7, is also smaller than the Australian counterpart, which runs from just below 9 to over 10. Sexual dimorphism is much more marked in Australian tooth measurements, especially in those popula-

tions with the largest average summary tooth-size figure, but even when variance is calculated for each sex separately it is much greater for Australians than for mainland Asians.

Interestingly enough, the summary tooth size for a random group of teeth from the University of Michigan Dental School (1,153) was almost exactly the same as that for the Hong Kong Chinese (1,157), but the standard deviation (32) was less than half the size. This is most curious, since the Dental School figures were compiled from randomly constituted individuals. That is, the teeth were extractions collected over several years, assembled so that there were 50 “pseudo-individuals” with a tooth in each category; the probability that even two teeth in such an assemblage actually came from the same biological individual is practically nil. Given this background, it was a surprise to discover that the variance was smaller than that for any real population for which data exist.

I raise these issues just so the reader will be aware that they exist; a full treatment will have to be deferred for the present.

Finally, there is the always difficult matter of sex determination. In most instances, as with the majority of the fossil record, there is no way to be sure of the sex of the material measured, since recovery and museum records do not indicate which crania are associated with which postcranial remains. We simply have to trust to the probability that the sex ratio in the recovered material is approximately equal. In the two largest samples, however, sexual determinations can be made on the basis of reliable information. In the Walbiri sample, the casts were made on over 70 living male and over 70 living female inhabitants of the Yuendumu settlement. For the Murray Basin material in the Murray Black Collection in Melbourne, I was able to find over 80 sexable females and over 80 sexable males—“sexable” meaning that my estimations based on skull and pelvis were in agreement. In both of these large collections, the sex ratio was very nearly equal on specimens where sex was determined. This supports the assumption that it would also be true for the rest of the material used if we had a means of making the determinations. Hence, for purposes of the present paper, tooth measurements for each group were pooled to give single mean figures for each tooth category in the manner recorded elsewhere (Brace 1967a, Brace and Mahler 1971, Wolpoff 1971a).

TOOTH SIZE

The picture we can build of tooth size in aboriginal Australia is conditioned by the sample of available teeth. In turn, the size and distribution of this sample closely parallels the density and distribution of European-derived settlement in modern Australia. There are two clear-cut reasons for this striking parallel. First, the probability of the discovery of specimens is highest where modern settlement is densest; and, second, the areas which the contemporary inhabitants find most congenial appear to be just those areas that supported the largest aboriginal populations. Consequently we have good representation especially in southeastern Australia and also up the eastern coast but, with a couple of exceptions, sparse coverage elsewhere. The exceptions include Arnhem Land, where anthropological interest in the painted skulls of traditional mortuary ceremonies has resulted in good museum collections, and the central desert, where the University of Adelaide Dental School has been collecting impressions for the last 25 years.

Figure 3 presents a picture of Australasian tooth size, ordered solely by magnitude, compared with half a million years of fossils from the northern hemisphere. Even without the use of statistics it is strikingly apparent that there are major differences in average tooth size within Australia. The difference between the Murray Basin and Cairns averages (1,500 – 1,272 = 228) is greater than the difference between the robust

	Erectus	1578		
S. E. Qnsland.	1530			
Murray R.	1500			
Lower Murray	1442			
Tasmania	1429 = Neanderthal	1415		
Cent. Aust.	1350 = Skhūl	1350		
	Early U.P.	1347		
N. Qnsland.	1272 = Late U.P.	1267		
Java	1240 = Mesolithic	1237		
Thai	1229		Neolithic	1201
China	1157 = Europe	1139		

FIG. 3. Tooth size in contemporary Australasia compared to a northern hemisphere time series. The *erectus* figure is calculated from the data in Weidenreich (1937), the Neanderthal (Western European) figure from the data in Wolpoff (1971a), the Skhūl figure from McCown and Keith (1939), the Early and Late Upper Paleolithic and the Mesolithic (all European) from Frayer (1978), the Neolithic (Wiltshire) from measurements made in the Duckworth Laboratory, Cambridge University, and the modern-Europe figure from the data in Black (1902), Miyabara (1916), and Twisselmann and Brabant (1960).

and gracile australopithecine averages from South Africa (2,250 – 2,095 = 165) and far greater than the difference between the Classic Neanderthals and the Early Upper Paleolithic of Western Europe (1,415 – 1,347 = 68) (Brace 1978b, 1979a, b). Indeed, the average for Cairns is slightly closer to that for Hong Kong Chinese, possessors of the smallest teeth in the Orient, than it is to that for the Murray Basin. From currently available data, it would seem that such a degree of variation exceeds that demonstrable for any other set of modern populations from an area of comparable size.

Not only is the magnitude of difference impressive, but the pattern of the variation clearly is not random. Teeth are smallest in the Cape York Peninsula and display an increase in size roughly but not exactly proportional to geographic distance from the northeast corner of the continent. Maximum size is generally to be found in the upper parts of the Murray Basin, with decreases observable east and south toward the coast, westward downstream, and northwestward toward the central desert.

The largest single summary tooth-size figure is for a coastal group from Broadbeach (Haglund 1968, Wood 1968), just south of Brisbane near the border of Queensland and New South Wales. In its postcranial robustness and its heavy craniofacial reinforcements, the Broadbeach population differs markedly from the configuration generally observable from coastal Aborigines both to the north and to the south, but in these respects it appears to be allied with the poorly documented material inland from Brisbane and with the known center of robustness in the Murray Basin. From this perspective, Broadbeach may represent the northeasternmost extension of the configuration that is best documented along the Murray. Certainly the Broadbeach dentition breaks up in dramatic fashion what is an otherwise gradual cline of north-south tooth-size increase along the east coast of Australia (see fig. 4). Except for Broadbeach, the metric gradient evident in the dental data provides a striking parallel to the gradient of non-metric attributes demonstrated by Macintosh and Larnach (1973).

The other interesting aspect of tooth-size distribution is the fact that the figure for the central desert is smaller than all but the figures for Cape York and the Queensland coast north of Broadbeach. In this case, the figure (1,350) is not only the most reliable of the whole survey, but it is also closer to being a maximum possible figure than that for any other group. The figure was calculated from measurements of casts taken

largely from members of a single group of living Aborigines, the Walbiri of Yuendumu settlement, some 185 miles northwest of Alice Springs. Not only are the teeth those of relatively young individuals, but, because of introduced foods and cooking practices, the average amount of wear is substantially less than that on the teeth from which all the other population figures were derived. The increase in size from the center of Australia to Western Australia, the Kimberleys, and even Arnhem Land, to say nothing of the Murray Basin, must then represent more than just a random phenomenon.

Since I am going to argue that the observable size gradients in Australia are caused by the introduction of genes for smaller teeth from the northeast, I must first deal with the converse possibility, namely, that the gradients are the result of an in situ increase in size emanating from the Murray Basin. While this area appears to be the locus of maximum robustness and concomitant large tooth size in recent Aborigines (fig. 5), there is some evidence (for example, see Pretty 1974:29) to suggest that these were even more exuberantly manifest in the past.

The Cohuna skull, found on the edge of Kow Swamp in 1925 and of evident if unmeasurable antiquity (Mahony et al. 1933), gives substance to the suspicion that at least some prehistoric Aborigines possessed a robustness of facial skeleton and cranial reinforcement not matched in more recent individuals. The existence of similarly “mineralized” skeletal remains has been alluded to from Nacurrie and elsewhere in the Murray Basin (Tindale 1941:141), and further support for this suspicion was provided in 1950 by the late Murray Black in the last of his more than 20 years of collecting along the middle and upper reaches of the Murray (Sunderland and Ray 1959). The burials he recovered at “Doherty’s Hut,” near Coobool Crossing on the Wakool River, a branch of the Murray in New South Wales between Deniliquin and Swan Hill (personal information from L. J. Ray), were heavily permineralized in a manner quite unlike the hundreds of recent burials he had previously excavated. No excavation records were kept, so one cannot claim provenience, stratigraphy, or artifactual associations as evidence for antiquity. A similar degree of permineralization is also visible on some of the Murray Basin skulls sent to the Department of Anatomy in Edinburgh by W. Ramsay Smith of Adelaide early in this century, but these also lack provenience information.

Given the nature of the soil and the climate in that area, however, it is unlikely that such a degree of permineralization could have occurred within the last 2,000 years. (My own informal suspicion, for what it is worth, is that the material is very much older than that.) Both in cranial and in post-

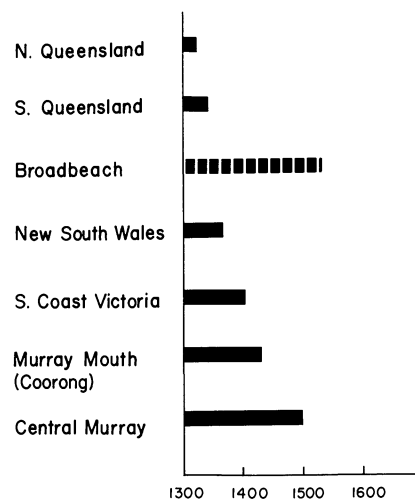


FIG. 4. East Coast Australian tooth-size cline, showing how Broadbeach interrupts the general north-south graded increase.



FIG. 5. One of the robust specimens of the recent Aborigines who inhabited the Murray Basin, excavated by Murray Black in 1947 and now Number 47.55 in the Murray Black Collection at the Department of Anatomy of Melbourne University Medical School.

cranial form, the Coobool Crossing material displays a degree of robustness well beyond that of the most rugged recent Aborigines. One skull, indeed, is nearly indistinguishable from the original Cohuna skull, presenting a pattern that has drawn considerable attention in one of the recently discovered Kow Swamp specimens (Thorne 1971a, b). A summary tooth-size figure for Coobool Crossing can be calculated, and, at 1,544, it is clearly larger than that of any recent Aboriginal group, markedly exceeding that for the Murray Basin and even that for Broadbeach.

Then, of course, there is the Kow Swamp material itself. This was found in the course of proper archaeological excavation and can be dated at 10,000 years B.P., right after the Pleistocene-Holocene boundary (Bowler et al. 1970, Jones 1973). The material I was allowed to measure is much less complete than that from Coobool Crossing, and there are not quite enough unworn teeth to produce a summary tooth-size figure—no measurable lower first molars being present. If, however, one substitutes a lower first molar figure from another robust Australian group—whether it be Murray Basin, Broadbeach, or Coobool Crossing—the resultant summary tooth-size figure is slightly larger than but not significantly different from that of *Homo erectus* from Choukoutien (see fig. 6). From the measurements provided by Thorne (1976:108), using all the material including loose teeth from Kow Swamp, a summary tooth-size figure of 1,561 can be calculated, which is right in between the *erectus* and the Coobool Crossing figures and not significantly different from either one.

I hasten to add that I do *not* subscribe to the view that *H. erectus* was alive and well and living by the Murray River 10,000 years ago. From the available evidence, it would seem that cerebral development was fully sapient. It would appear, however, that the selective forces that maintained a robust dentition and a well-developed postcranial skeleto-muscular system in the Middle Pleistocene continued to operate in Australia right up to the beginning of the Holocene.

Although we know nothing about the appearance of the first Australians, we do know that when they first arrived, perhaps 40,000 years ago, the continent supported a marsupial megafauna that subsequently disappeared. The suspicion has been voiced that this disappearance was caused by human predation (Jones 1968). While the cautious have properly argued that since there is no direct association of human remains, cultural or other, with the megafauna, "it seems therefore unlikely that man had a direct role in the extinction of the large marsupials" (Bowdler 1977:231), it is becoming obvious that human beings coexisted with the megafauna in Australia for many thousand years. At a date of 26,000 B.P. there is evidence for the accumulation of broken bones and partial carcasses of several kinds of giant marsupials in Lancefield Swamp, just north of Melbourne in Victoria (Gillespie et al. 1978). If the one large quartzite flake recovered does not prove that humans were doing the butchering, still the nature of the partial and broken remains suggests to the casual observer that articulated segments had been flung there by some deliberate agency. Perhaps the meat had become "no good" (cf. Meehan 1977: 527). After all, it is not unlikely that the remaining flesh on a dead macropod would have started to spoil before a small group of predators had eaten it all.

Furthermore, although Bowdler argues that the original settlers of Australia had to be coastal people simply to handle the water gaps they had to cross to get there, and this suggests that they were unfamiliar with large-game hunting, yet *something* had to be selecting for the extraordinary robustness and muscularity visible in the Kow Swamp and Coobool Crossing remains and that something had to be more than just collecting the freshwater clams and fish in the waters of the prehistoric Murray River. It seems legitimate to suggest that the physical demands placed upon the hunters of the rhinoceros-sized *Diprotodon* and others of the now-extinct megafauna were greater than those required of hunters of the emu and the grey kangaroo. Whether the original Australians brought their robustness with them or developed it as they concentrated on hunting the megafauna, their skeletons display aspects of reinforcement that recall the skeletal configurations of Middle Pleistocene and early Late Pleistocene hunters elsewhere in the Old World.

Finally, if selective forces maintained robustness in the Late Pleistocene Australian hunters, we would expect to find some evidence for this in the physiques of modern inhabitants of the areas where they existed in greatest numbers. This, I suspect, is the meaning of the great robustness of the recent inhabitants of the Murray Basin and adjacent areas.

Kow Swamp	1581-1588
<i>H. erectus</i>	1578
Coobool Crossing	1544
Broadbeach	1530
Murray Valley	1500
Neanderthal	1415
Walbiri	1350

FIG. 6. Summary tooth-size figures for a series of recent and prehistoric Australian Aborigines with the figures for *Homo erectus* from Choukoutien (from Weidenreich 1937) and Neanderthal of Western Europe (from Wolpoff 1971a). The figure for Kow Swamp is from my own measurements, and its range reflects the use of an M_1 area from recent Murray, Broadbeach, or Coobool Crossing. The figure is slightly smaller if the data used are those provided by Thorne (1976).

In any case, whether it be the result of a relaxation of selective forces in situ, the influx of influences from the outside (perhaps represented, despite the early date, by Mungo [Thorne 1977, Thorne and Wilson 1977]), or a combination of the two, it would seem that the robust recent Murray Basin Aborigines represent a diminution from the even more robust state found in the prehistoric occupants of the area.

CULTURAL DISTRIBUTION

ITEMS OF TECHNOLOGY

If there is some reason to suspect that the gradients of tooth size in Australia represent the influx of outside influences via the northeast corner, then it should be of some interest to see whether this has any parallels in the realm of strictly cultural phenomena. The distribution by trade of technological items over set routes was evidently well established and of long duration. Figure 7 shows the trade route network for aboriginal Australia, which provides a suggestive model for probable directions of precontact gene flow.

The late Daniel S. Davidson devoted years of effort to the demonstration of the distribution of a series of items of Australian material culture (Davidson 1933, 1934, 1936; Davidson and McCarthy 1957; McCarthy 1970). His efforts were deprived of the attention they deserved by the disastrously shortsighted critique of Radcliffe-Brown (1930), which set back major aspects of Australian anthropology by more than a generation (Mulvaney 1975:121). His work, like the present one, was done principally upon museum collections and suffered consequently from similar limitations, namely, large gaps in coverage and the possibility of faulty provenience for given crucial specimens. Even so, some of his distributions are suggestive indeed. Some, to be sure, show the effects of local invention and idiosyncrasies of fixation or absence that remind the biologist of phenomena such as mutation and drift, but some clearly exemplify instances of entrance via the northeast and subsequent dispersion during the course of time.

Edge-ground axes, for example, are unknown in southwestern Australia, the farthest point from the Cape York Peninsula (see fig. 8). To be sure, they were unknown in Tasmania, off the southeast corner of the continent, and they were present in Arnhem Land 20,000 years ago, when Australia and New

Guinea were a single landmass (White 1967). Evidently, then, they had a northern origin, but whether it was northeastern, northwestern, central, or whatever cannot yet be determined.

Davidson's plot of the distribution of netting techniques, however, is much less equivocal (fig. 9). Four types of netting were used on the Cape York Peninsula, three as far south as southern New South Wales, two down into Victoria and South Australia and across to Darwin, and one down to the southwest coast of South Australia and down the continental west coast beyond the Kimberleys. No type of netting was used in the southwestern corner of Australia or in Tasmania. The distribution alone suggests transmission from New Guinea via the Cape York Peninsula after the Torres and Bass Straits were flooded, although there is simply no way, as yet, that we can determine exactly how this occurred.

In this regard, however, there is at least one line of thinking on which it might be profitable to speculate. Netting requires

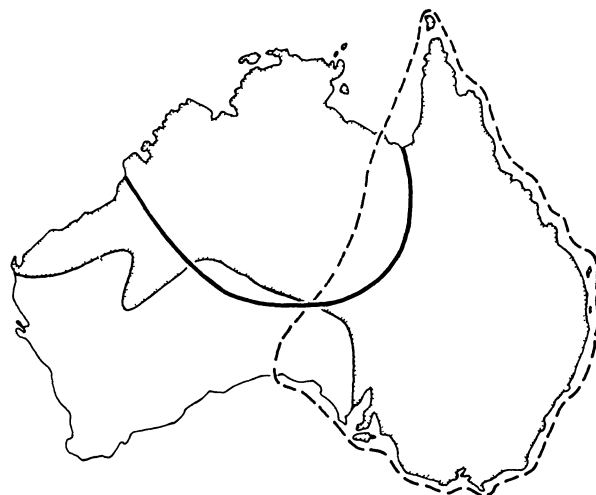


FIG. 8. The distribution of edge-ground stone axes (*shaded area*), boomerangs (*area inside dotted line*), and throwing clubs (*area inside solid line*), drawn after Hayden (1977:90) but essentially the same as Davidson and McCarthy (1957).



FIG. 7. Aboriginal trade routes in precontact Australia, drawn after McCarthy (1939-40).

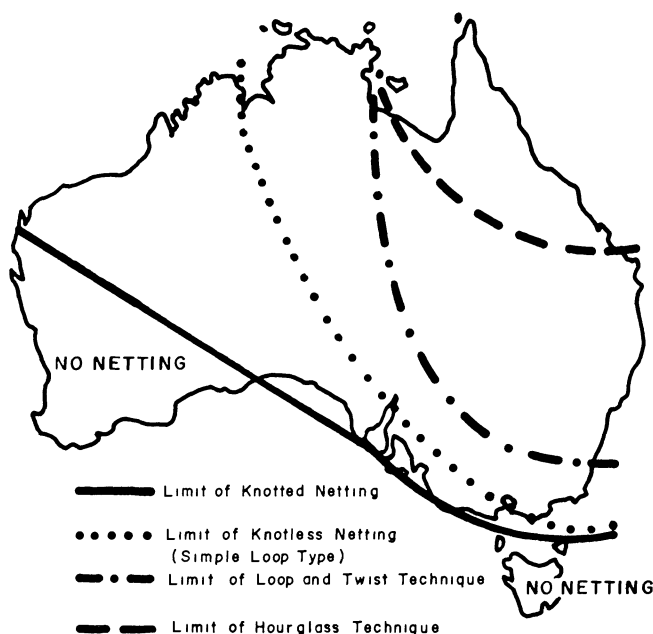


FIG. 9. The distribution of types of netting techniques in Australia, drawn after Davidson (1933).

a knowledge of the manufacture of cordage, and the archaeological record does provide evidence of a definitive *post quem* for the presence of string—namely, fishhooks. The coastal midden at Bass Point, 100 km south of Sydney, contains shell fishhooks and blanks dating back 600 years B.P. but not before. Line fishing clearly was possible from that point on (Bowdler 1976). Once string-making is a part of the technological repertoire, then such otherwise “unobvious” technological steps (Hayden 1977:94) as nets, snares, and dilly bags become much easier to conceive. At the time of contact, the Aborigines of southwestern Australia lacked nets of any kind and engaged in spear fishing only. In the case of Bass Point, the rise in frequency of smaller kinds of fish bones and small shellfish in the midden may just as well reflect the use of nets and dilly bags as it may the impact of line fishing according to Bowdler’s suggestion.

However one looks at it, the use of cordage in the construction of devices for catching small game, birds, and fish profoundly changes the nature of the food quest for a hunting and gathering population. Spearfishing a single small bird or fish or rabbit-sized mammal is a tedious and not greatly rewarding activity, but throwing a net over a flock of birds or drawing one around a school of fish and setting a snare set in a rabbit run can produce edible protein in great quantity. Those who possessed such techniques must surely have had the advantage in sustaining their numbers in a given area over those who lacked them, and the significance of great robustness and muscularity must surely have been reduced.

Also interesting is the distribution of spear types and the use of the woomera or spear-thrower (fig. 10). The spear-thrower was unknown in Tasmania, where the principal weapon was the heavy hand-thrown spear. From the Cape York Peninsula down into the central desert and beyond, the woomera-propelled light spear was in general use. In the southwest corner of Australia, the Kimberleys, the northern edge of Arnhem Land, and the southeast corner of the continent, the Aborigines used the light spear and woomera for hunting, particularly smaller game, and the hand-thrown spear for such occasions as intergroup conflict. The situation in the areas of the Murray and Darling drainage right over to the

coast near Broadbeach and farther north was evidently mixed. Some groups used both kinds of spears, and some only used the hand-thrown spear, apparently lacking the woomera.

In all, the distribution of spear types and woomera usage makes a striking parallel to the distribution of tooth size. By drawing attention to this I do not mean to imply that lack of the woomera per se constitutes a selective force for the maintenance of a larger dentition. Rather, I suspect that items such as nets and spear-throwers were part of a culture complex related to the capture and preparation of the edible portion of the environment that did not enter Australia with the earliest inhabitants. When this complex did get to Australia, presumably after the end of the Pleistocene and possibly symbolized by the small-tool tradition 7,000 years ago (Golson 1974), it would have been particularly useful in those areas that could not be so successfully exploited by the technologically less developed indigenes—namely the desert interior and the littoral margins.

There is another aspect of the Australian physique that may also show an inverse relation to the distribution of the spear-thrower. This is chest and shoulder development. Over a generation ago, Jones (1934:25–26) observed:

The development of the chest and pectoral muscles is always a remarkable feature, so pronounced that the build of the native sometimes appears to us to be top-heavy. Moreover, the chest and shoulders are carried high, so that there seems to be a relative shortness of the neck, which is very apparent when natives wear European clothes. It is this characteristic that enables the outback white man to recognize an aboriginal, clothed in European garments, long before he can distinguish his colour or his features, and this no matter if the native is riding or a-foot.

To be sure, Jones, as did so many, was typologizing about Australia as a whole, but the casual observer, poring over old photographs of Aborigines, gets the distinct impression that chest and shoulder development relative to stature was more robust in those areas where the woomera was absent. Quite the contrary of Brues’s (1959) argument in “The Spearman and the Archer,” chest and shoulder development are far more crucial to the effective propulsion of a spear than to the effort needed to produce a comparable effect with a bow-driven arrow. With good equipment, the average man can shoot an arrow with lethal effect for over 100 m, but hurling a javelin that far is quite another matter. In the absence of technical devices for increasing the velocity and range of projectiles, the burden falls directly on the relevant portions of the human physique. Perhaps it was some of this as well as the adaptive linearity of Birdsell’s Carpentarian “stock” (Birdsell 1948, 1967, 1977) that contributed to what we informally perceive as major regional differences in Australian physique. If this must remain sheer speculation for the moment, it is simply because no one has yet gone to the effort of making a systematic region-by-region study of the functional morphology of the Australian Aboriginal postcranial skeleton. An analysis along the lines of that recently done on Neanderthal shoulder morphology (Trinkaus 1977) might yield interesting results. There is enough material in the various collections that it could be done, and maybe someone who reads this will be stimulated to give it a try.

TECHNIQUES OF FOOD PREPARATION

Body bulk does have a low correlation with tooth size (Garn, Lewis, and Walenga 1968), but it cannot account for the more than 200 mm² average total difference in tooth size that distinguishes the large-toothed from the smaller-toothed Aborigines first encountered by Europeans. Without some further speculative additions, this does not immediately suggest why the teeth of the northern and presumably newer

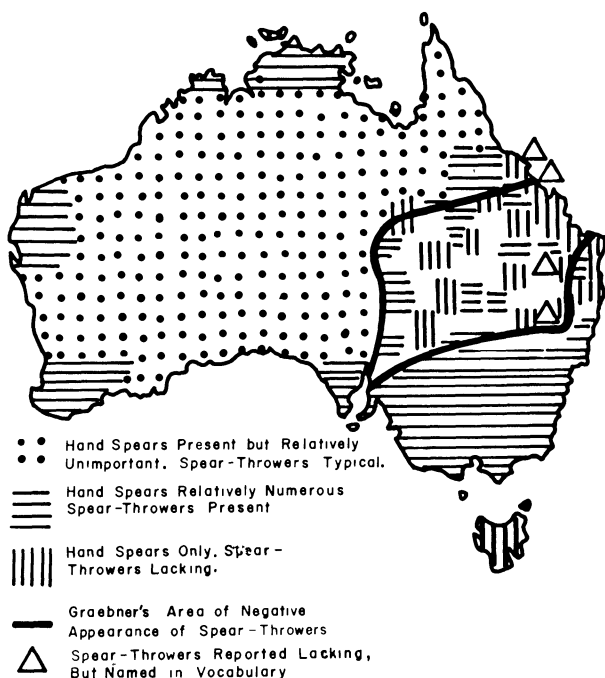


FIG. 10. The distribution of the spear-thrower in Australia, drawn after Davidson (1936).

elements should be smaller than those of their predecessors. I suspect, but I cannot prove, that this may be a reflection of another aspect of the cultural complex that entered Australia after the end of the Pleistocene. In spite of the "Neanderthaloid" image often attributed to aboriginal Australians or the "Mousteroid" parallels invoked in descriptions of their culture, their lifeway could best be characterized as Mesolithic. (I too, only slightly less condescendingly than Tylor [1894], once accepted that derogatory stereotype [Brace 1967b: 105] and have been properly chastised for it [Wright 1976: 268]. The mistake has been corrected in the revised edition [Brace 1979c].) With the possible exception of the Tasmanians, they shared a focus on the utilization of plant food and small game (including fish and fowl) that was typical of post-Pleistocene but nonagricultural people the world around.

Without this focus, in fact, the central desert portions of Australia could not have been inhabited year-round. One can postulate, then, that the first Australians avoided such areas. Their eventual exploitation can be viewed as the result both of indigenous development and the importation of new techniques. One of these involved the utilization of seeds as a major item of diet. As Meggitt (1957: 143) describes it: "Seeds comprise by far the major part of Walbiri vegetable foods. Almost all are collected by women, ground on stones to form a coarse meal which is worked into an unleavened, unsalted paste with the addition of water. In most cases, this is cooked in the ashes to make a heavy, tasteless, evil-looking but nourishing cake." As it happens, Meggitt was describing the vegetable component—comprising more than 80%—of the diet of the Walbiri, whose teeth, as we have seen, are far closer to those of the Aborigines of the Cape York Peninsula than to those of the Murray Basin.

The Mesolithic technique of seed grinding not only made the desert habitable, but slightly reduced the amount of chewing that had hitherto been necessary for survival. As I have suggested elsewhere, a reduction in the selective force maintaining a given trait should be followed by a reduction in the trait itself (Brace 1963, 1967a, 1978b, 1979a, b; Brace and Mahler 1971). On a relative scale, this indeed appears to be the case. Actually this reduction need not simply express change that has occurred in Australia itself as a result of food-processing techniques that have been relatively recently adopted. Whether or not Australian seed grinding represents an extension of Hoabinhian technology (cf. Solheim 1969, Golson 1971), it surely resulted in a reduction in the selective forces affecting the teeth of its first developers. One could predict, then, that the diffusion of such a cultural trait into Australia was also accompanied by gene flow from sources that were already undergoing dental reduction.

At the time of European contact, only the Tasmanians did not make extensive use of grinding stones for the utilization of seeds, although this may just be a function of our ignorance concerning Tasmanian food-preparation techniques (for a discussion of what we do and do not know, see Hiatt 1967-68). It is clear that seed grinding was far more crucial to the survival of the Walbiri than it was to the spear fishermen of Port Jackson and up the east coast, although it would seem that these also represent a kind of intensive resource utilization of an essentially Mesolithic nature that one would not expect for the earliest inhabitants (Lawrence 1971, Bowdler 1976). Unfortunately, there is not yet enough archaeological work for us to check on the antiquity and the extent of utilization of seed grinding in the various regions of Australia. Promising beginnings have been made, however (Jones 1973: 281; Allen 1974; Bowdler 1977), and it should be interesting to see, as the results come in, whether or not the spread of seed grinding in Australia followed a pattern similar to that seen for the spear-thrower and reflected in the gradients of tooth size.

In addition to mechanical techniques of food preparation, cooking can also reduce the amount of compulsory chewing.

Although I have previously suggested that there is a causal relationship between pottery usage and post-Pleistocene dental reduction (Brace and Mahler 1971), it is clear that substantial dental reduction had already been under way in the 20,000 to 30,000 years immediately preceding the end of the Pleistocene in both Europe and China. The depth of so-called hearths at Abri Pataud, in southern France, and the quantity of fire-blackened cobbles have led Movius (1966) to suggest that cooking by means of stone boiling was being carried on early in the European Upper Paleolithic. One could extend this back into the Mousterian and suggest that some form of heated-stone cookery—whether stone boiling or the construction of proper earth ovens—had a currency from the Mousterian on, at least in the northern portions of the Old World (Brace and Montagu 1977: 335-36; Brace 1979c: chap. 11; Brace 1979 a, b).

Earth ovens were in general use in Australia at the time of contact. These ranged from small to large and from rudimentary to complex and sophisticated (Moore 1973: 78). Although food was sometimes reported as being underdone to European taste (McCarthy and McArthur 1960: 119), it could easily be steamed to a very tender consistency. Again, unfortunately, we have little idea about the early use and distribution of the earth oven in Australia. It is reported at Lake Mungo 30,000 years ago (Gill 1974) and at Roonka on the Murray River 18,000 years ago (Pretty 1974), but the examples are small ones and, so far, are only isolated instances. In concluding this section, I should mention that grinding stones appear some 15,000 years ago at Lake Mungo, just east of the lower Darling (Jones 1973), where the people of 10,000 years earlier displayed smallish, slender skeletons distinctly lacking the rugged appurtenances generally visible in both the prehistoric and modern people of the area. It is finds such as these that make interpretive efforts like the current one such risky ventures. One fatal contradiction and the whole carefully erected theoretical edifice collapses in a heap of shattered suppositions. Is it possible that the whole post-Pleistocene seed-utilization complex upon which the food-producing revolution was ultimately based began just northeast of the Murray-Darling juncture in southern Australia, thence to spread north and west, arriving in the Middle East in time to form the basis for the Neolithic early in the Holocene? I doubt it, but I mention this just to indicate the minuscule nature of the substance that underlies even some of the most carefully thought-out speculative schemes.

Actually it would appear that the use of grinding stones was not an important part of the lifeway near the southern Darling drainage area even at 15,000 years ago (Allen 1974). Further, the climate was evidently markedly different from that of the present (CLIMAP 1976, Bowler 1976), and the human adaptive strategy must have differed as well.

LANGUAGE

The linguistic picture can also be interpreted in a manner consistent with the interpretation favored here. What is referred to as Common Australian is best represented by the lexical elements concentrated in the western desert (Capell 1962, Tryon 1971). On glottochronological grounds, this is thought to have an antiquity of between 5,000 and 10,000 years and to have pushed out or supplanted Original Australian, elements of which have been suggested to survive as a substratum in the southeast and other continental margins. Although there is some feeling that Common Australian may have an Australian origin (Wurm 1974), there is also a suggestion of a northern and possibly an extra-Australian source.

The time depth indicated by glottochronology is suggestively similar to that for the antiquity of the entry of the post-Pleistocene small-tool tradition. It is tempting indeed to regard the entry of the linguistic configuration called Common Australian as coinciding with the spread of a technological

manifestation that allowed the exploitation of the resources of the central desert, an area where the biological appearance of the living Aborigines is represented by a degree of relative dental reduction exceeded only, on a regular basis, by the inhabitants of the Cape York Peninsula.

Finally, the phonological similarities and (admittedly weak) genetic ties (Tryon 1971:351-52) between Arandic and some of the Cape York languages have led Wurm (1974:366) to conclude that the Aranda area represents "the point of the farthest penetration of the Papuan influence entering Cape York Peninsula from the North." It would appear, then, that at least two kinds of linguistic evidence can provide some support for the scheme favored here.

AUSTRALIANS, TASMANIANS, AND MELANESIANS

So far my concern has been principally with the question of Australian Aborigines per se. It is now legitimate to enquire, what of their relations to the peoples both to the south and to the north—to the Tasmanians, on the one hand, and to the Papuans and Melanesians, on the other? All sorts of opinions have been voiced since the days of Thomas Henry Huxley and earlier, often without the benefit of adequate samples of the population considered or, indeed, of any quantifiable or testable material at all.

Through it all, and despite evidence to the contrary, there has been a tendency to see something archetypal in Australia. The designation "the Australian Aborigine" occurs repeatedly in both the popular and the professional press, and even where there is manifest care to render "Aborigines" in the plural they are usually chosen to demonstrate the existence of a condition that is considered in the singular. One repeatedly reads that "the dentition is large," "kinship is important," "pottery is unknown," and so on, in "the Australian Aborigine."

Even those few who have examined enough material to realize the extent of the Australian range of variation (Berry and Robertson 1914, Hrdlička 1928, Wagner 1937) tend, when called upon for explanation, to attribute it to separate relatively invariant elements. Berry and his associates, for example, felt that the restricted variation they demonstrated for Tasmanians indicated purity of "type," while the spectrum of difference they documented in Australia could only be accounted for by suggesting that "the Australian is a hybrid" (Berry and Robertson 1914:186), one of its components being the Tasmanian. Wagner (1937) on his part, tried to have it both ways, on one page asserting that "in no other place in the world is there an equally large geographical area with corresponding unity of skull type" (p. 148) and on another noting "an influence coming from north to south with an even gradation between the several regions" (p. 151). Probably the most extreme appraisal of Australian variation was that of Schoetensack (1901:135), who noted that in spite of certain characteristic traces "there is no other race of such variability."² Australia, he claimed, was the Pliocene cradle of humanity, and that extraordinary "variability" was the source from which the various human races later arose.

Subsequent recognitions of Australian variation have discussed it in terms of regional "types" (Fenner 1939) or varying degrees of mixing of similarly conceived elements such as the trihybrid hypothesis (Tindale and Birdsell 1941; Birdsell 1948, 1967, 1977). And then there remain those who feel that there is something basic underlying the whole Australian spectrum that allows it to be described as "homogeneous" (Abbie 1951, 1960, 1968, 1969). As Allbrook (1976) has recently recognized, whether the argument is for the existence of a single essential entity or the hybridization of several such, the motivation is basically typological.

One could say the same thing for Huxley's (1870) claim that

² "giebt es keine andere Rasse von solcher variabilität."

something Australoid could be recognized in the hill tribes of the Deccan in southern India and extending in attenuated form west to Egypt or for the Dravidian or "Pre-Dravidian" migration theories of Giuffrida-Ruggeri (1921) and others who would derive Australians from the Mediterranean via India, Southeast Asia, and Melanesia. One can still see essentially typological expectations in the work of sophisticated users of multivariate statistics (Howells 1976) and students of genetically identifiable variants in serum proteins (Schanfield 1977). Even the brilliant work on the immunological correlates with hepatitis B that earned the investigator a Nobel Prize (Blumberg 1977) began as an attempt to identify an antigen that was hoped to be uniquely Australian (Blumberg 1964, Blumberg, Alter, and Visnich 1965).

For somewhat complicated reasons, Tasmanians have been continually compared to "negritos." Huxley, who first used the word in this context (1870:404), however, meant the dark-skinned and curly-haired people of New Guinea and Melanesia (as distinct from Africa), and no size implications were intended. In fact, the first quantitative studies generally noted the greater cranial capacity and more robust aspect of Tasmanians as compared with Australians (Davis 1874, Jones 1935). Since the term negroito is generally taken to indicate small stature, however, its continuous use in reference to Tasmanians has created an image that has attained a kind of reality in the absence of any direct evidence (Macintosh 1949:139). The fact that the last surviving Tasmanian *was* small may have contributed. Huxley's use of hair form as a sorting criterion led him to put Australians and Tasmanians in completely separate racial categories. The problem then was to explain how they got to Tasmania without leaving traces in Australia. Huxley somewhat offhandedly suggested a direct migration from New Caledonia, possibly by a now-disappeared island chain. A New Caledonian origin has enjoyed intermittent support ever since (Pulleine 1929, Jones 1935, Skinner 1936, Macintosh 1949), but the unlikelihood of this from the cultural point of view has been overwhelmingly demonstrated by Davidson (1937).

Hrdlička (1928), who collected measurements on the crania of the various groups involved, noted that New Caledonians were characteristically Melanesian in form and, as such, were only approached by Australians from the very northernmost part of the continent, a view essentially in agreement with the one offered by Turner (1908) 20 years earlier. The Tasmanians, Hrdlička observed, were substantially removed from the Melanesian configuration and were extremely close to that of southern Australia. He concluded that "the two people are so near . . . that the two strains cannot but be regarded as of fundamentally the same race. The Tasmanians may therefore, it seems, be legitimately considered as merely a subtype of the Australians" (Hrdlička 1928:90-81). More than 40 years later, one of the most recent commentators records his inclination "to regard the Tasmanian aborigines as local variants of a southern Australian population" (Thorne 1971b:317).

The relatively simple approach taken in the present study provides obvious quantitative support for Hrdlička's and Thorne's conclusion. Strictly on the basis of tooth size, Tasmanians at 1,429 fit between the Murray Basin (1,500) and the west coast of South Australia (1,392) figures. Even more precisely, they nearly correspond to the figure for the Coorong (1,422), at the mouth of the Murray. The Cairns figure of 1,272 is obviously closer to the New Caledonian one of 1,259 than to the 1,429 figure for Tasmania, although with the crude tests available and the small sizes of the samples it is hard to attach probability figures. Certainly 1,429 is significantly different from 1,259 ($P < .001$).

From the picture of gradation down the east coast, broken only by what appears to be a spillover from inland at Broad-

beach and on part of the South Victoria coast (fig. 11), one is tempted to postulate southward movement from a source of reduced tooth size in the north. If the first effects of this were felt before the Bass Strait was flooded 10,000 years ago, this would explain why the Tasmanian figure is slightly smaller than that for the Murray Basin. Subsequent continuation of this movement (= gene flow) after the separation of Tasmania would account for the further reduction of teeth intermittently along the coast of Victoria and South Australia. In any case, the explanation that accounts for the Tasmanians will be closely bound to that which makes sense out of the gradient from the Murray Basin south to the coast as well as that down the whole eastern seaboard (fig. 12).

The gradients in Australia down to Tasmania can obviously be turned around and traced north into New Guinea and Melanesia. There also they can be interpreted in terms of selective-force intensity and the history-prehistory of the populations examined. The pattern that emerges has a coherence along the lines of that developed in the present paper, but there are the additional complexities of technological, horticultural, and linguistic traditions of various origins and degrees of contact and independent development. These can be sorted out, but it would take at least as much space again to do so, and it seems best to leave this to another paper (Brace n.d., Brace and Hinton n.d.).

CONCLUSIONS

Admitting that a survey of variation in one biological dimension is a tenuous basis on which to generalize, nevertheless, I feel confident in advancing the claim that the results of this review are in direct conflict with the long-standing feeling that aboriginal Australia was inhabited by representatives of a homogeneous and relatively invariant human "type." That oft-repeated phrase "the Australian Aborigine" owes more to the a priori expectations of the observer than it does to a comparative appraisal of the people who once inhabited Australia. It is, in fact, a manifestation of typological thinking in its best Platonic form, and, as such, it can only impede scientific attempts to understand the situation in the external world.

Tooth size in Australia ran from a minimum in the Cape York Peninsula to a maximum in the Murray Basin. If there

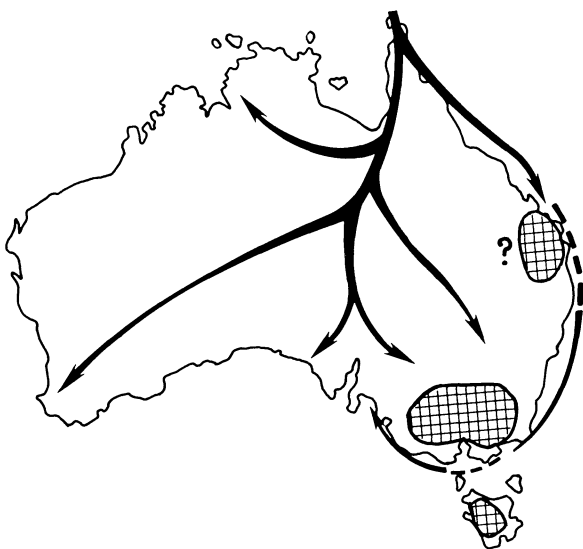


FIG. 11. The hypothetical direction of post-Pleistocene gene flow into and throughout Australia. Tooth size increases roughly in the directions represented by the arrows. Presumed previous pockets with relatively little dental reduction are represented by the cross-hatched patches.

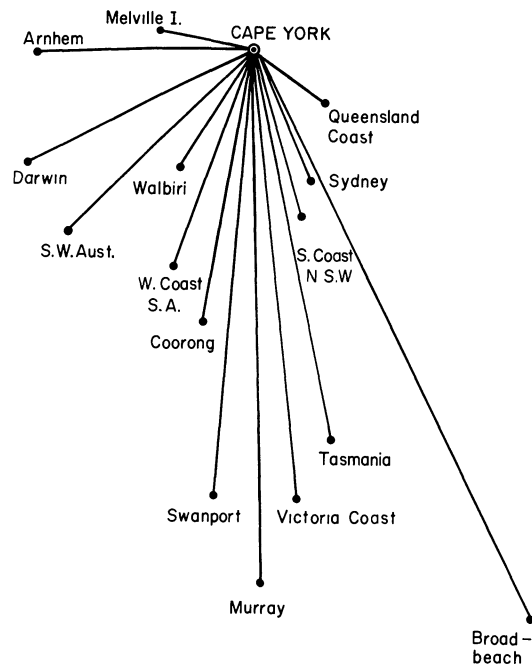


FIG. 12. Schematic representation of tooth-size differences in Australia. The length of each line is directly proportional to the extent to which the tooth-size figure for the named population exceeds the figure for the Aborigines of northern Cape York.

was an earlier gradient representing original entry from either the northwestern Cape area or Arnhem Land, it has been obliterated by subsequent developments and additions. The available data suggest that the earliest Australians possessed large jaws and teeth and that subsequently genes for smaller tooth size entered Australia from the northeast corner, a model which is consistent with the evidence for the spread of a variety of cultural items. While the evidence is tentative at best, it is consistent with the view that more developed food-preparation techniques had occurred outside of Australia, allowing dental reduction to occur. The spread of these elements into Australia may be symbolized by the influx of the small-tool tradition early in the Holocene, and it may have been made possible by associated resource-utilization techniques that promote survival in areas previously sparsely utilized, such as the central desert and the coastal margins. This would account for the tooth-size gradient visible down the east coast and from Cape York to the western desert. The largest teeth in Australia survived in just those areas most favorable to human habitation, where one would expect the genetic contribution of the earliest inhabitants to be most prominently represented.

Tasmanian affinities are clearly with southeastern Australia. Reduction has not proceeded as far as that visible on some parts of the coast of Victoria and South Australia, but it has gone farther than that apparent in the upper Murray Basin. This suggests that the Tasmanians were less unmodified representatives of the initial Australians than were the Darling and Murray Basin inhabitants. Early elements coming down the coast from the north may have affected the early Tasmanians before the sea level rose, accomplishing their isolation, 10,000 years ago. Continued influence from the north subsequently resulted in the further slight reduction of the teeth of Australians living on the coast of southeastern Australia.

If this is a reasonable explanation for the fact that Tasmanian teeth are not as large as Murray Basin teeth, it suggests that dental reduction as a result of northern influence must have begun before the influx of the small-tool tradition in Australia. This in turn suggests that, after initial occupation, Australia was subject to a continuous trickle of cultural-

biological influence from the north rather than having been the receptacle for specific waves, migrations, or invasions.

The model proposed is both more subtle and more logical than many previously favored. Although the data necessary for its confirmation, modification, or rejection have yet to be collected, the first steps are being taken, and we can anticipate that such a test will be possible in the not too distant future. There is one matter about which there can be no doubt. The traditional picture of "the" Australian Aborigine, cogitating upon kinship in pristine invariant purity and splendid isolation, must forever be rejected.

Comments

by T. BROWN and G. C. TOWNSEND

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In spite of numerous studies of the Australian Aboriginal dentition, Brace's work is probably the first attempt to summarize tooth-size variation throughout the continent. Post-Pleistocene changes in hominid dental morphology have attracted considerable interest of late, and this paper is certain to generate controversy and, it is to be hoped, further research. We intend to direct our attention to some of Brace's assumptions and certain aspects of his method.

First, about the assumption that tooth size is under tight genetic control: Genetic studies of tooth diameters in Walbiri families (Townsend and Brown 1978a, b) lead us to support a polygenic mode of inheritance, but they also indicate that the additive genetic component of variance averages about 64%, less than commonly assumed and close to the heritability estimates derived for tooth size in Finns (Alvesalo and Tigerstedt 1974). These values are similar in magnitude to heritabilities reported for a range of general anthropometric characters by Susanne (1977). The inference that teeth are little affected by environment must also be challenged in the light of evidence of developmental interactions during tooth formation conditioned by calcification sequence and space availability (Sofaer et al. 1971). Tooth calcification is certainly affected by a number of environmental conditions, and in this respect it is important to point out that fluoride intake may influence final tooth size (Goose and Roberts 1979). The dental casts of the Walbiri used by Brace were obtained from subjects living in a high-fluoride environment, with up to 1.8 parts per million in the drinking water (Williamson and Barrett 1972). Until the effects of fluoride on tooth size are clarified, measurements from these areas are suspect when used for comparative purposes.

It is a pity that Brace and others have concentrated on tooth size and neglected other extremely important determinants of masticatory efficiency. If there is a phenotypic end product on which selection works, it is surely the mode of tooth occlusion. Optimal functioning occlusion is the key here, and in this sense occlusion means not only the static tooth contacts seen in museum specimens, but also the complex physiological and morphological interactions between masticatory components during formation, growth, and functional adaptation. Tooth-size data have limited significance unless accompanied by observations on occlusal function. For example, we have noted the high incidence of degenerative arthritis in the temporomandibular joints of Australian crania, a condition well documented in other material characterized by heavy attrition and vigorous masticatory function (Richards and Brown 1979). Although the causative factors are not completely understood, the adaptive ability of joint and muscle systems to withstand occlusal stress appears to be an important determinant of reproductive fitness and selection.

Turning now to the methods: We do not agree that teeth are

easy to measure, and we are disappointed that Brace does not include an analysis of measurement error. Our table 1 shows our calculations for summary tooth size in Walbiri males and females using data reported recently (Townsend and Brown 1979). These statistics relate to young individuals with complete dentitions suitable for measurement and with diameters averaged from right and left sides. We were careful to exclude any subjects with partially erupted third molars or anomalous crown morphology, and, as a result, our sample size is somewhat smaller than Brace's for the same group.

Brace's mean values for the Walbiri are considerably lower than ours even when male and female data are pooled. The interobserver difference of about 42 mm² in summary tooth size indicates the extent to which selection, measurement, and recording techniques can bias results. The inclusion of measurements from incompletely erupted third molars, for example, would account for part of this difference. Moreover, Brace does not make it clear if his sample numbers relate to teeth measured or to subjects or if values were averaged from right and left sides.

Our results confirm the extreme variability of tooth size even in one group. In fact, no fewer than 25% of the males showed summary tooth-size values which exceeded Brace's value of 1,530 for the Broadbeach crania. Sex dimorphism is also marked, with a difference in summary tooth size between males and females approaching 100 mm², the level Brace accepts to indicate biological significance between groups. We recognize the great difficulty in obtaining adequate sex-specific tooth-size data from museum material, but the practice of pooling data from males and females leads to problems when formal comparisons are made, particularly when small sample sizes are involved, as is the case with several of Brace's Aboriginal groups.

A further source of possible bias in tooth-size comparisons arises from differences between groups in the extent of attrition. Begg (1954) reported crown diameters for worn and unworn teeth in Aboriginal mandibles. A quick calculation based on these data, excluding third molars, leads to a value of over 50 mm² for the mandible only as a conservative estimate of the reduction in summary tooth size from interproximal attrition alone. This calculation emphasizes the conclusion of Wolpoff (1971b) that "dental comparisons in length and area must include effects of interstitial wear if adaptive information is sought. If, on the other hand, genetic implications are desired, the groups must either have minimal interstitial wear or the same age distribution."

The final matter for comment concerns the statement that seeds are a major item of the Walbiri diet. This gives quite a

TABLE 1
SUMMARY TOOTH-SIZE ESTIMATES FOR WALBIRI
MALES AND FEMALES

	<i>N</i>	MEAN	STAN- DARD DEVI- ATION	CO- EFFI- CIENT OF VARI- ATION	MINI- MUM	MAXI- MUM
Maxilla						
Males.....	46	758	63.9	8.4	625	886
Females.....	54	701	58.6	8.4	576	831
Mandible						
Males.....	50	692	62.1	9.0	579	819
Females.....	67	638	51.0	8.0	539	760
Full dentition						
Males.....	36	1,441	129.1	9.0	1,204	1,705
Females.....	43	1,346	107.4	8.0	1,124	1,588

NOTE: Summary tooth size estimated according to Brace with *N* values relating to individuals with complete dentitions.

misleading impression of the food habits and environment of desert Aboriginals. Several earlier observers have commented at length on the food customs of nomadic people living in the central regions of Australia. Campbell (1939:11), for example, makes it quite clear that "seeds obtained from various grasses and trees provide the native with a significant, though not large, proportion of his diet." Supplies were seasonal, and the effort required in gathering any quantity of seeds was extensive. There is little doubt that desert Aboriginals preferred animal food, and except in seasons or regions of game scarcity meat was their chief item of food. The Central Australian desert is perhaps inappropriately named, because in good seasons the desert blooms with an abundance of plant and animal life, and, as Campbell pointed out (p. 8), "the Australian Aboriginal eats as food anything at all that is safely edible."

In summary, although we do not contest the view that regional and temporal variations in tooth size exist in Australia, we believe that the many sources of bias which can be introduced into analyses of this type, together with the extent of sex dimorphism and intragroup variability, dictate caution when drawing inferences about tooth-size clines and the spread of cultural items as far-reaching as those of Brace.

by EDWARD F. HARRIS

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Brace is to be commended for an insightful synthesis of data on tooth size with material culture trait distributions. These two sorts of data conjointly suggest interpretations of the patterns of human variation which neither suggests in isolation. My comments are essentially twofold:

First, a prime conclusion of the paper—demonstration of a north-to-south cline in eastern Australia—isn't novel, but is an important augmentation of earlier findings. I think the first quantified delineation probably was that based on blood-group gene frequencies by Birdsell and Boyd (1940), and the picture has been elaborated by Graydon and Simmons (1945) and Birdsell (1950). More recent compilations (Mourant 1954, 1976; Simmons and Booth 1971) come to the same conclusion. Isogone maps, particularly those for frequencies of *A*, *B*, and *M*, published by Boyd (1954), Mourant (1954), and Birdsell (1974) are interpretable in either of two complementary frameworks: (1) Climatic parameters involving measures such as temperature, rainfall, and/or humidity can be shown to covary with some gene frequencies (*M* is a good example), so there is the suggestion that natural selection is at least indirectly responsible for contemporary clinal patterning in Australia. (2) Some genes, notably *B*, are distributed with a high in New Guinea (where it is well distributed, suggesting considerable antiquity), across the Torres Strait, and down Cape York Peninsula. This cline is a textbook example of gene flow with increasing isolation by distance. The distribution of *B* coincides with that of the forested region of the peninsula and the southern coastal area of the Gulf of Carpentaria.

In this regard, Brace's gene-flow diagram (fig. 11) appears exaggerated on two counts: The spatial extent of the inroads of gene flow is unsupported by any biochemical (albeit synchronic) data (and Brace certainly would not invoke tooth-size similarities [concordance?] as a demonstration of common origins), and the post-Pleistocene contribution to Australia from New Guinea is, at best, a dab of frosting on a very large, well-baked cake.

A second point: It seems that both biochemical and culture trait distributions emphasize the importance of the earlier Sahul Shelf entry of peoples rather than the subsequent Cape York gateway stressed by Brace. There just aren't enough "data points" (i.e., skeletal series, table 1) available for mapping or otherwise analyzing tooth-size clines to become excited about

the importance of Cape York as a funnel for gene flow from New Guinea revamping tooth size throughout the continent. Although Brace's data are as extensive as is currently possible, they are few enough to fit several models. An approximately north-to-south cline across the whole continent (something akin to that for netting types, fig. 9) seems at least as plausible as figure 11. On a different tack, inspection of the spear-thrower distribution (fig. 10) recalls the centrifugal human migration model championed, say, by Taylor (1927). There are just two samples ("Queensland Coast" and Broadbeach) between Cairns and Sydney. If figure 4 were drawn with the space between groups on the y-axis proportionate to their geographic separation rather than neatly equidistant, the "cline" would deteriorate into a smaller-toothed group in the north (approximating Birdsell's Carpentarian type in location) and a bigger-toothed group in New South Wales. The situation for the bulk of the continent in the middle, and leaving Broadbeach as an isolate, geographically and phenotypically, is at present anyone's guess.

by W. W. HOWELLS

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Brace can be heartily thanked for producing a large amount of primary data and a stimulating essay. While a single summed occlusal-surface-area figure may seem a little too "polygenic," he has nonetheless demonstrated a very considerable variation in tooth size within aboriginal Australia and a degree of patterning in it. He also presents the data in specific and detailed form. They demand explanation, without pointing to one.

The two essential points are the variation itself and its possible causes. With the first, Brace claims to demolish a picture of "the" morphologically uniform Australian Aborigine. I think perhaps he has slain a stereotype already dead and putrefying. Brace seems to see almost all previous writers as typologists. This is fair up to a point: a typological view of Australian uniformity did prevail some time ago, and certainly the hybridists, mixing different parental populations, have been typologists of a higher grade. But with a real framework of prehistory reducing the tendency to depend on typological analysis of the living, there has been a general recognition of regional diversity. This is evident in cranial studies using broader information than teeth alone (e.g., Larnach and Macintosh 1966, 1970; Giles 1976), in studies of general anthropometric characters (Parsons and White 1976), and in blood genetics (e.g., Allbrook 1976 and as outlined in Howells 1973b). What Brace has contributed is copious evidence from tooth size. It is still possible to point to general characteristics of, say, Australian crania without being a typologist of Brace's demonology, and it is easy to confuse the idea of biological uniformity with that of general unity of ancestry or derivation. Birdsell (1967) did attempt to sustain a trihybrid hypothesis by demonstrating statistically significant differences in measurements among different regional groupings, but one can hardly expect samples distributed over a continent to simulate samples drawn at random from a single population. Zoologists since Darwin have recognized the tendency of animal forms to depart from an original, and Australian populations have had perhaps 40,000 years to do so, assuming that there was an original.

In Brace's model, there are large teeth in the southeast, derived from the still larger teeth of the robust original people and those of the early Holocene, with a decrease in size toward Cape York and also the west. These clines reflect a constant trickle of small-tooth genes from Torres Strait, as well as cultural differences imposing demands for large teeth at the other ends. I am not clear as to the relative importance—both seem

to be advertised as primary—but no matter, both might operate. Brace sticks closely to the model, being at pains to try to understand the probable meaning of Tasmanian tooth size in these terms. The problem is that the hypothesis is difficult to test rigorously because various other factors might enter to be considered.

First, immigrant groups, while being of essentially the same major population complex, might not have been homogeneous (Howells 1977). The Niah Deep skull and the later Wadjak skulls provide a contrast in robusticity within the obvious homeland, and my inspection of the fragmentary Tabon Cave postcrania of Palawan suggests to me a range from modest to robust size.

Second, there is the possible influence, phenotypic or selective, of climate and its changes. As Bowler (1976) says, the first immigrants traversed a greater range of climate on penetrating the continent than between their point of origin (in Indonesia) and their landfall. The late Pleistocene brought favorable conditions to the southeast: Lake Mungo was well stocked with fish, and the megafauna was still present. But the earliest human remains, the Lake Mungo skeletons I and III, representing a time of 25,000 to perhaps 30,000 B.P. (Bowler and Thorne 1976), were gracile. This puzzles me as much as Brace, who has the discretion to face the fact. Brace suggests that the megafauna, with the rhino-sized *Diprotodon*, made robusticity in hunters adaptive; but *Diprotodon* was no rhino, only a bloated wombat, which may have been docile and easy to kill. In any case, the available diet might have been expected to nourish large body size, whether under selective stress or not. Granted, the specific food associated with the Mungo skeletons is lake snails, not megamammals. All the same, we must infer that big game did not mean big people. Then the climate deteriorated, with aridity peaking at 15,000 (Bowler 1976). Following this, the human population was, or became, robust. Finally, robustness diminished to the present. This is all a strange set of correlations, at variance with the European situation, except for the most recent part of the story, which is what Brace is dealing with. Of some importance is the newly published (Freedman and Lofgren 1979) skeleton from Cossack, on the shoulder of Western Australia. This is a robust male whose skull length is a mammoth 220 mm. The dentition is almost complete. By substituting values, estimated from the proportional excess of the other teeth over those of Brace's Murray Basin series, for the missing I¹ and the anomalous-looking I² measurements, I get a *TS* for the individual of 1,629, clearly a high value. The find is estimated to date from 2,000 to 6,500 B.P. and would thus be posterior to the Kow Swamp series. It would break the cline of size in the western direction and extend late prehistoric robusticity to the far west, where Brace's samples do not find it in recent material. It would not do to write the find off as an aberration, an explanation which has seldom panned out. In addition, there is the isolated I¹ from Nannup in the very southwestern corner, dated 8,000 to 12,000 B.P.; it is robust, with a cross-sectional area of 84.8—a fairly extreme figure, as Brace's tables show (Davies 1968).

There are other questions: Which is primary, tooth size or general robusticity, especially in terms of the selection/gene-flow model presented here? Does seed grinding for "bread" alleviate selection for large dental areas or foster it (that is, does more grit enter this food than others, making large tooth surfaces adaptive)? Other writers have considered that genetic drift and the founder principle would have been important causes of population differentiation in the Australian cultural situation. Brace does not mention them; but the single character of tooth size is not like blood alleles, and in his model it is fair enough to ignore drift. None of this is meant to denigrate Brace's work and hypothesis, but only to point out how much remains in the way of loose ends and evidence yet to be found.

by JOHN HUIZINGA and TRINETTE S. CONSTANDSE-WESTERMANN
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The title of Brace's paper makes it somewhat top-heavy. In some circles a "stereotype" may once have existed, but nobody with any sense (and certainly no human biologist) today would share the notion of "pristine invariant purity and splendid isolation." Erecting a stereotype and then killing it is not a suitable aim for a paper. Moreover, one cannot suppress the impression that the author has tried to use so much information of such widely divergent origin in the indeed "risky venture" of interpreting Australian biological diversity that he has lost the notion of cause and effect which he seems to be pursuing. This leads to circularity in the reasoning. Phenomena of a cultural nature such as the distribution of certain tools and/or techniques are, on the one hand, brought forward as support for the general hypothesis concerning population spread over the continent, implying gene flow and concomitant genotypic and phenotypic change. On the other hand, however, the same cultural phenomena are introduced as causes of in situ genetic change, since they are supposed to bring about shifts in local selective pressures. Thus it is not clear whether the observed reduction in tooth size is supposed to be a result of (a) the influx of populations with smaller teeth or (b) the diffusion of a certain technology (which does not necessarily imply population displacement), producing environmental change in the broadest sense of the word. This is unfortunate because, generally speaking, a more comprehensive approach than hitherto taken, including both social and biological information and theory, should form a better basis for the understanding of prehistoric population structure and movement than any one-sided approach.

There is also some criticism to be expressed on the more technical aspects of the paper. In our experience teeth are not at all "easy to measure"; intermeasurer differences are not small when expressed as percentages of the measurements themselves. Measuring casts leads to doubtful results (Goose 1963). The objections to the use of the "summary tooth-size figure" are, as stated by the author himself, serious, and as a result the statistics (which, however, are little used here) are weak. Finally, setting a snare in a *rabbit* run may not be the most appropriate example of small-game hunting to be used in the context of Australian prehistory.

by EDWARD E. HUNT, JR.

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For some years, Brace has studied the possible effects of human cultural evolution and diet on the reduction of tooth size. Australia is a key region for this approach because its aboriginal inhabitants were all hunter-gatherers. Even so, sophisticated food processing may have diffused into Australia from the north, along with the immigration of new people. This possible history of the Aborigines seems reasonable to me and yields rather irregular clines toward larger teeth in southern Australia and parts of the east coast.

In my opinion, Brace's work is the most convincing evidence available that human populations have undergone true genetic evolution of the teeth in the past several thousand years.

The most serious gap in this reconstruction is actual pedigrees of tooth size versus reproductive success in human groups undergoing rapid changes in diet. Such work could actually be undertaken in Australia, where some large-toothed communities are living today on European foods.

I doubt whether all dental anthropologists will believe the selective mechanism for dental reduction is as Brace claims until work on the transmission genetics of this trend confirms it.

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Most likely the linearity observed in evolution over generalized time is the result of a multiplicity of movements in all potential directions. Thus the "lumpers" amongst us tend to view most clearly the resultant vector while the "splitters" concentrate upon the contributing vectors. Cultural and biological evolution must occur in some symphonic way. To impute a cause-and-effect relation requires similar time scale and reasonable reaction potential. In the broadest context, cultural change may be a modifier of biologic variation as well as the converse. It is on this level that I am prepared to accept the generalizations of measurement technique and biocultural interrelations suggested by Brace.

The polygenic fields operative in the dentition do in fact produce a resultant vector, the morphologic phenotype. Certainly like dental morphologies are observably familial in clinical dentistry. Additionally, it is clinically observable that mixed dental heredity is inexorably interwoven in sibilings. Variation introduced into populations results in some modification. Net or resultant directionality is phenotypically observable and measurable.

I am not prepared to agree that teeth are "least subject to environmental modification of genetic intent," as protein nutrition beginning in utero is thought to play some role. However, I concur that teeth are extremely responsive to changes in selective forces.

With regard to crown height, it is important to consider that human teeth continually erupt as wear occurs. Thus the occlusal plane may be relatively stable where dental opponents persist, and clinical crown height (that part of the tooth erupted into the oral cavity) is a reasonable measure of original crown height. This must be taken with reservation, subject to intervening periodontal disease and the potential for shortening of the lower third facial dimension secondary to modification of masticatory muscle forces. Nevertheless, at least in the juvenile, some use may be made of the tooth-height variable.

A principal-components analysis would substantiate that combination of upper and lower dental measurements does not result in decreased significance. Thus the derived algorithm, I assume, also meets a similar statistical test. The use of rough categorization to estimate significant differences seems sufficient to advance the general argument that Brace proposes. The question raised about the variance in contemporary extracted dental "sets" compared with that in Australian Aborigines suggests the necessity for analyzing these proposed sets more particularly. They might not pass the principal-components test for combination; chance might have cancelled differences due to overcombination.

I have tested sex determination using skull alone or as little as mandibular fragments (Koritzer 1977). While the accuracy is limited, it is at least stated and probably represents one way to perform a rough check on the estimated ratio of males and females in a population.

The selection of Australian Aborigine populations separated in time for comparison introduces the variable of in-place change, which I cannot evaluate. It would be interesting to see a statistical analysis of the effect of this factor.

If one is to attribute Aboriginal robusticity to macrofauna procurement, one must also assume no sexual division of labor. Conversely, a major sexual dimorphism must exist. If the latter is true, then combination of male and female data may be contraindicated. The grinding of seeds may actually increase tooth wear as grit is incorporated into the diet. Furthermore, any food preparation in a desert environment, outdoors, results in grit incorporation and subsequent tooth wear greater than would otherwise be expected.

To what extent are the living Australian Aborigines inhabiting the central desert as a result of displacement by contact

populations? Do they represent small-toothed coastal types forced into a less hospitable environment?

One must also entertain the possibility that extreme climatological variation in Australia may be the significant cause of parallel cultural and biological climax rather than straight-line change. This effect would be secondary to sequential population displacements. Thus movements over time of a more limited number of founder populations could account for the currently observed variability.

In order to reassess the hypothesis suggested, I have looked at the average values for I¹-C and P¹-M³. The former values may be roughly proportional to facial width and the latter to palatal length. The distribution seems to be bimodal for both values and leads me to suspect the existence of two populations geographically intermingled with expressivity of strong traits subpopulationally. There is a high correlation between anterior and posterior values using a rank-order method; $r = .874$ with $N = 18$ populations and is highly significant.

Generally, I believe Brace has performed a great service in pointing to Australian Aboriginal variation. Speculative "food for thought" is useful and healthy, as it provides a platform for further testing. The dental algorithm employed in this still open question seems adequate to the task.

by A. VINCENT LOMBARDI

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That Brace has applied data taken from the dentition to a problem in anthropology—the nature of population variation in aboriginal Australia—should earn him the gratitude of all anthropologists interested in teeth. With few exceptions, once collected, dental data tend to sink to the bottom of tables, immovable even by their collectors. The key to Brace's success is his use of the simplifying tooth-size summaries for each population. Such data reduction must entail a considerable loss of discriminatory information, but the figures retain validity as a measure of chewing-surface area. In this application, they are weakened further by the small size and uncertain nature of some of the populations considered. Still, Brace has been able to draw from the data a coherent if speculative model of population movements in prehistoric Australia. The synthesis of the dental data with the distribution of material culture and language is less successful: the connections seem selective and strained, perhaps reflecting the meagerness of the cultural data. It is clear, and Brace acknowledges, that his model must be tested where possible against additional and different kinds of biological and cultural evidence.

by CHRISTOPHER MEIKLEJOHN

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Brace has produced an article which is, as his articles usually are, both lucidly written and thought-provoking. We need much more work of this type. I would, however, like to raise the following points in the hope that they will perhaps stimulate the work needed to produce a more comprehensive set of answers to the problems raised.

If I understand the argument correctly, two primary points are being made. Firstly, it is argued that there is a much greater degree of biological variability within the Australian continent than is widely appreciated. The data provided speak for themselves. In this regard the paper must be considered as a valuable piece of work ipso facto. Secondly, it is argued that the variability noted is the product of *both* selective forces mediated through the cultural sphere *and* the introduction of genes from the northeast. The data can in fact be made to fit this model, but I am not convinced that a cause-and-effect relationship is demonstrated. The article appears to skirt the

rather vital issue of what detailed data would be necessary to distinguish the two proposed mechanisms.

As a partial retreat from the possible stridency of the above, I would add that I suspect that much of the problem lies not so much in the approach as in the quality of the data base, especially for the crucial earlier time periods. Not only is the earlier sample of small size and checkered distribution, but there are fundamental problems associated with the apparent presence of early quite gracile material and later very robust material. Until we have some control on the extent of these different modes of variation, we appear to be working in the dark. It seems necessary here, as well as elsewhere, to obtain a proper understanding of the within-population variability before we attempt to interpret any between-group differences. I for one would like to see the dispersion of individual robusticity figures within the samples before I attempted to interpret the between-sample discrimination.

by MICHAEL PIETRUSEWSKY

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Inasmuch as I admire Brace's attempt to relate variation in tooth-crown dimensions of Australian Aborigines to various cultural phenomena, a number of uncertainties surrounding the nature of the material examined, the methodology employed, and the almost total inattention to other biological research in Australia are worth discussing.

Brace himself calls attention to several of the drawbacks associated with the use of tooth-size figures: combining front and back teeth, the problems of statistical variance, etc. Another serious drawback not fully explained is the apparent combining of male and female specimens and the contention that sex ratios for museum material in general should be about equal because two of his samples (Walbiri and Murray Basin) have approximately equal numbers of both sexes. The Walbiri sample consists of casts of teeth made on living populations, where the investigators most assuredly had complete control over the demographic composition of their sample. Additionally, the fact that Brace was able to find over 80 sexable specimens of each sex in the Murray Basin sample can in no way be used to estimate the sex ratio of other museum collections he has included in this study. Unlike most museum collections, the Murray Black Collection was assembled by a single individual who systematically exhumed Aboriginal burials over a considerable time span. My own examination of this material (which is preserved partly in Canberra and partly in Melbourne) has revealed considerable deviation from an even sex ratio and some indications of collector's bias. Aside from these differences of opinion regarding the true sex ratio of this latter sample, inferences about the sex ratio of other collections surveyed by Brace based on two (atypical) collections can only be regarded as misleading and fallacious.

Perhaps my most serious comment concerns the almost complete absence of discussion of the samples utilized. In a rather roundabout way, we learn that some of the samples consist of casts made on living Aborigines, most comprise teeth of near contemporaneous specimens located in various museums and anatomy-department collections, and some may actually represent late Pleistocene specimens mingled with more recent material. Some of the samples apparently represent specimens collected in the environs of a major city (e.g., Sydney), some come from smaller settlements (e.g., Coorong), and a few are from ancient burial sites (e.g., Swanport), while others are derived from arbitrary stretches of river systems or coastal areas of a state (e.g., west coastal South Australia) or from an entire portion of the continent (e.g., southwestern Australia). While sampling of this sort may be unavoidable, some attempt to explain the nature and the extreme diversity of the samples should have been made. Even the identification of the samples

must be surmised from headings in the tables and figures which accompany the text. Certainly, a paper which sets out systematically to examine regional differences in physical variation ought to discuss (and at considerable length) the provenance of the material used. Further, inspection of the sizes of these samples indicates a considerable range—from a single tooth to more than 500. As with any quantitative analysis, sufficient numbers and evenness of sampling are much to be desired.

While this paper is not intended to survey the current state of studies in physical anthropology in Australia, readers (and Brace) might be curious to know if its major findings are supported by other recent work. For example, the view held by Brace (and others) that Tasmanians are related to southern Australian populations is not supported by my recent multivariate craniometric study of many of the same samples utilized by Brace (Pietrusewsky 1979).

While I am happy to see an attempt to synthesize data from a biocultural perspective, the major generalizations advanced in this paper, as Brace himself admits, must remain tenuous.

by C. B. PRESTON

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Tooth size appears to be one of the major mechanisms with which hominids confront their environment (Brace 1962). Traditionally there has been said to be a general tendency toward reduction in tooth size during human evolution (Robinson 1956, Bock and van Wahlert 1965), although this concept is not universally accepted (Garn, Lewis, and Walenga 1969). Two major factors influence the shape and size of the teeth: the genotype of the individual and environmental influences during the formative years of life (van Reenen 1966). Garn (1963) believes that the genes which control tooth morphology are extremely stable and that they have a major control over tooth form, including size, while others (Goose and Lee 1973) believe that genetics may be less important than has been suggested. The heritability of tooth dimensions is better known than that of the nonmetric traits, but the range of variation of tooth size in geographical races appears to be too large to be useful for taxonomic purposes (Alvesalo and Tigerstedt 1974).

Of the environmental factors which affect tooth form, trace elements of the diet have been studied in some detail, and it has been shown that they have an effect on tooth size during the formation of the teeth. Fluorides in the drinking water produce smaller teeth in which cusp height is reduced (Møller 1965) and other morphological changes also take place (Cooper and Ludwig 1965). Boron is said to have the opposite effect, in rats producing bigger teeth (Kruger 1962), while protein has been reported to change tooth form depending on its dietary intake (Malherbe and Ockerse 1944).

Hormones affect tooth morphology (Nobele and Pope 1929), and in this respect shape appears to be more important than size as an expression of sexual dimorphism (Garn, Lewis, and Kerewsky 1967). Differences in tooth size between males and females are known to be usually larger in fossil hominids than in modern man (Hanihara 1978). However, sex-linked differences are rather small in Australian Aborigines, who retain some archaic physical characteristics (Hanihara 1978).

The genetic and environmental factors which influence tooth morphology act on the dentition as a whole and not on the individual teeth (van Reenen 1966). In this respect the teeth are in fact a meristic (Bateson 1894, cited by Butler 1965) series and form a consistent and regular pattern. Butler (1939) viewed the dentition in this light and developed the "field" concept described by Huxley and de Beer (1934) in an attempt to account for gradients in tooth size and shape. Osborn (1978)

argues, in contrast, that morphologic differences are self-generated rather than controlled from outside while believing that a quantum change in environment is matched by a quantum change in response.

Lavelle (1978) states that the mesio-distal and bucco-lingual crown diameters merely provide a sketchy linear profile of a tooth. Factor analysis (Child 1970) performed on the Aboriginal tooth samples may highlight the intergroup differences, and this type of analysis may well support the size gradients which Brace describes.

The distribution of blood-group gene *A* in Aboriginal populations (Mourant 1964) also displays gradients which are in fact clines. The blood-group distribution is an example of a balanced polymorphism in which the relative distribution of the genotypes is held in equilibrium over thousands of years. The zoning of the frequencies reflects movements of peoples during that period of time. The high point for the *A* gene in Australia occurs in the Murray Basin, one of three such areas plotted in the world. This finding indicates that some migration, at least, took place away from the Murray Basin region.

by R. H. ROYDHOUSE

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Brace celebrates yet again Ogden Nash's concept—"Celery raw develops the jaw, whereas celery stewed is more easily chewed." A decline in tooth size due to a lack of need for large teeth—"a decrease in selective forces"—verges on the Lamarckian. Clay pots, animal husbandry, and agriculture have paralleled in development the diminution in size and function of the masticatory apparatus, but does this obvious temporal relationship connect cause and effect? The grand sweep of mammalian evolution shows clearly the predominance of brain over mastication; the skull in form and function becomes a braincase, not the attachment of snout to neck. In the change in humans over 3,000,000 years the trend has accelerated; in addition, by adoption of pedomorphic characteristics and by diversion of sexual dimorphism, humans lose hair and the heavy bone buttresses about the skull, and a decreased jaw size leads to smaller teeth. Teeth become secondary. It is as well to recall that death due to a failing dentition afflicts the elderly, not the young breeders—the folktale of the edentulous Eskimo left to the polar bear describes her as a grandmother. The very existence of teeth as archeological markers and the trouble we have with our own dentition leads us to overvalue their importance to mankind.

This paper contains its own inconsistencies, if not contradictions. Teeth are not part of the skeleton—they are ectodermal in origin and function. No evidence is presented that they are "extremely responsive to selective forces." The adult male gorilla has labored for several million years with the most inadequate dentition for a vegetarian; Brace's hypothesis has passed him by. The factual content of the paper reveals the flaw in the argument—"The largest teeth in Australia survived in just those areas most favorable to human habitation," so the "relaxation of selective forces" did not decrease tooth size.

If one ignores figure 4 and plots on the map of Australia the averages used, one does not find the arrows of figure 11. Rather, the isolation of groups on the large continent separated by an inimical interior is shown. No gradation due to waves of travellers is apparent. Isolation or repeated migratory waves? The data presented themselves argue for isolation within the continent. Melville Island cannot be contiguous in location and time to Perth and South Coast of New South Wales as cause-and-effect relationships imply.

In looking about for support for the theory, one cannot find where the waves of southbound travellers came from, because they seem to have brought only small teeth; it is notable that other external influences are lacking (White and O'Connell

1978). There is a certain fascination in the data. One would rather postulate climatic conditions, concomitant body-size changes, and perhaps the lack of external influence (Darlington 1969) to account for the local persistence of the tooth size. No support, again, is found in overall skull dimensions (Howells 1973*b*) or blood types. The Australian Aborigine remains within an anthropological category, and therefore the supposed stereotype (an unnecessarily emotive word) is not destroyed by tooth sums and divisions.

by L. E. ST. HOYME

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Although I agree with Brace that cultural changes can alter selective pressures and thus affect human biology, I have two reservations regarding this particular case. The first deals with the statistical treatment of the data, the second with theory.

For me, the tooth-size data do not fully support Brace's thesis that technological changes reducing stress led to reduced tooth size. This may be a function of our statistical methods. The tooth areas do indeed vary with culture, but in comparing arch and tooth size I prefer square roots of areas, since a slight change in a side is magnified by a geometric increase in area. Using the sum of square roots of tooth areas, I obtain the same sequence of relative sizes, confirming the cultural associations Brace demonstrates. However, on the question of improved food processing reducing the amount of compulsory chewing and thus reducing tooth size, I interpret Brace's data rather differently. If mastication is primarily a molar function, then molar area ought to be reduced more than incisor area. Using square roots of the data in table 1, I obtained total lengths for the upper half arch, the two incisors and the first and second molars. For the 18 Australian populations, incisor width gave an average of 15.42 mm ($s = .463$) and molar width an average of 23.28 mm ($s = .596$), with $r = .87$. The incisors contributed 19.9–20.9% of arch length and the molars 30.7–31.6%—so little variation as to be nearly constant. When incisor width was expressed as percentage of molar width, all 18 ratios lay within the narrow range 64.1–68.0%. In contrast to the Neanderthal figures cited, it would seem that these Australian molars (and incisors) varied with dental arch size (and body size?) rather than being reduced in size when selective pressure was altered. Alternatively, one may say that selection affected the whole arch, rather than the molar field only.

As for specific theory, I am always disturbed when that which selects for the gander does not also select for the goose. For example, the stresses of hunting megafauna are traditionally listed among the factors maintaining robust (male) body size, with the introduction of light spears and spear-throwers and/or cordage and other physically easier techniques mitigating this selective pressure (on males). There are two problems with this. One is that presumably both sexes were robustly built and that both men and women hunted the big game and dealt with processing the bag. This is quite possible in a small, moving hunting band. It probably takes at least as much muscle to butcher a large animal as it takes to bring it down. On the other hand, introducing techniques which increased the bag while "reducing the significance of robustness" may equally well have allowed its maintenance by relaxing pressures selecting for smaller (i.e., less hungry) body builds. Again, it is possible that both men and women maintained strong shoulders (and hearty appetites) using heavy stones to grind seeds. Seed grinding may have reduced the need for heavy chewing—but at the same time it increased the need for strong backs. In short, a dedicated devil's advocate can counter almost any theory postulating reduction (or increase) with one claiming that the very same factor could have produced the opposite effect. More likely, the truth is that selection is a many-factored thing.

Despite my reservations about the particular statistics and particular theories mentioned, I heartily concur with Brace's thesis that culture can and does affect our physiques, and I respect the skill and thoroughness with which he has marshalled his evidence. For me, at the moment, it seems more likely that tools and tooth size spread together, but further data may change my mind.

by CHRISTY G. TURNER II

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I agree in general with Brace's conclusions that his dental-crown measurement data show (1) that the Australian Aboriginal population is more variable than often characterized and (2) that these data are consistent with a two-migration hypothesis for the peopling of Australia. However, the north coast Cape York sample is too small to suggest, as in figure 11, that this was the place of entry, despite the logic of it due to the narrowness here of the Torres Strait. The Cape York sample of table 1 has at most six individuals and may have as few as three if *N* refers to teeth instead of individuals.

Dental morphology is likely under "tight genetic control" as indicated, but tooth size may not be. Townsend and Brown (1978a) have studied crown-size genetics in Yuendumu Aborigines and found the environmental contribution to be greater than is commonly held. This may be a peculiarity of this Australian group, but since it is one of Brace's samples he needs to speak to this potential problem.

Although data are provided in figure 3 for Asiatic tooth size, there are none for Melanesia—the implied source of the later, smaller-toothed migrants. We are left wondering if any such people actually reside in New Guinea. Swindler's New Britain dental sample suggests that elsewhere in Melanesia they do occur (Turner and Swindler 1978).

Reply

by C. L. BRACE

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The notion of Australian stereotypic uniformity may well have ceased to exist in the minds of the students of the biology of Australian Aborigines, as Howells, Huizinga, and Constandse-Westermann have indicated, but its continuing grasp on life is attested to by comments such as the one by Roydhouse. One could even suggest that the fact that Howells himself chose to represent Australia by only one group in his most recent relevant contribution (Howells 1976) is evidence for the strength of its influence. Recalling the reaction of Mark Twain at the end of the last century, one might note that the reports of its demise are at least somewhat exaggerated.

In general, the commentators agree that there is indeed a considerable range of variation in tooth size represented between the various Australian groups, but their recognition of the nature of the differences is clouded by worries concerning details of technique, the nature of the sample, and the problems of separating the effects of gene flow and selective-force alteration in the generation of the changes observed. Their worries are legitimate and cannot be ignored, but we should not lose sight of the fact that the mean group differences visible in Australia exceed those of any other comparable portion of the world—in fact, they exceed the differences *between* the most divergent of human groups anywhere in the world outside of the southwestern Pacific. They exceed the difference between the "classic" Neanderthals and the European Neolithic (Brace 1979b), they are more than three times as great as the average male-female difference in contemporary human populations, and they are more than twice as great as the sexual differences

observed in the most divergent group in Australia itself (Brace and Ryan n.d.). The magnitude of these differences is too great and the pattern of distribution too consistent to be accounted for by problems of sampling or technique or by invoking isolation and genetic drift.

Speaking of the significance of variation within a given group, Roydhouse could not have been more misleading in his *ex cathedra* and unsupported remarks concerning the gorilla dentition. There are in fact striking regional clines in the size and form of gorilla teeth which clearly correspond to major dietary difference (Groves 1967, 1971). Although gorilla tooth variation is clearly related to diet rather than subsistence strategy and food preparation techniques, it is the best example I can think of to compare with the dramatic gradient visible in Australia.

The comments of both Huizinga and Constandse-Westermann and Brown and Townsend raise questions concerning matters of technique. Brown and Townsend note that I did not state the basis for the establishment of sample number, and it is true that I neglected to mention that I followed the procedure I have previously used (cf. Brace, Mahler, and Rosen 1973). That is, whenever possible I used an average of left and right teeth of the same category, which I counted as a single instance. The logic is based on the assumption that, since the same genetic substrate controls both, an average of the two should be a better approximation of the genetic intent than either taken by itself. Where only one antimere was present, of course, I used that and counted it as a single instance.

Huizinga and Constandse-Westermann are correct in noting that intermeasurer differences can be a factor. In this study, however, all of the measurements reported were done by myself, so the problem should not exist. The puzzle remains, however, concerning the source of the differences between my figures and those of Brown and Townsend on the Walbiri. Their suggestion that the inclusion of measures from incompletely erupted third molars might account for part of the difference does not test out—as one can see if one simply compares the percentage of M3 to M1 from the various groups in table 1. Not only are Brown and Townsend's measurements larger than mine, but those published by Barrett and his colleagues are larger still (Barrett, Brown, and MacDonald 1963, Barrett et al. 1964). I have compared Barrett's measurements with my own, tooth by tooth and dimension by dimension, and his are all 4% larger. I have to confess that I find this baffling, since I can recall noticing, as I measured the Walbiri casts under Brown's benevolent eye in Adelaide, that there was a little scratch on the dental stone cast of each tooth right where I intended to put the tip of my caliper. Eventually it dawned on me that I was following the tracks of the previous measurer. At the time, I was comforted by the thought that we were obviously using exactly the same convention for measurement. The only thing I can suggest is that there may be a slight difference in calibration between my commercially marketed Mitutoyo 15-cm vernier-equipped calipers and the hand-crafted one-of-a-kind set in the Dental School at Adelaide.

Brown and Townsend suggest that I am amongst those who have neglected occlusal function. In fact, I am very much concerned with matters pertaining to occlusion (see Brace 1977), but it is a large and controversial topic that I think should be dealt with one step at a time. My concern here for tooth size is simply one of those steps. Another such step has been taken recently in a study relating population differences in tooth use and wear to changes in the temporomandibular joint (Hinton 1979), and other related studies are currently being pursued as doctoral dissertation projects here at Michigan.

Brown and Townsend also question my treatment of the Walbiri diet. There seems to be no doubt that, like other Aboriginal groups (cf. Worsley 1961:162 and Gould 1969:18), Walbiri *prefer* to eat meat, but there is more than a little doubt

concerning just what percentage of the diet this actually constitutes. Quantification has only been done for one group in Arnhem Land (McArthur 1960, McCarthy and McArthur 1960), and even that effort had to be staged to some extent.

Where the Walbiri are concerned, despite Campbell's claims, their chief ethnographer (Meggitt 1962) has noted, "Flesh foods, although highly prized, are not easily obtained for much of each year in the central desert; and of these, reptiles (especially goannas and lizards) are the most common" (Meggitt 1957:143). Meggitt estimates that vegetable food makes up 70-80% of the diet and that the major part of this is in the form of seeds. The seeds are from many kinds of *Acacia* and from mulga grass. Other accounts of the evidence for diet among groups living in and on the fringes of the desert (for example, Davidson and McCarthy 1957:445 and Birdsell 1979:138) do not support the claim that "meat was their chief item of food."

Both Howells and Koritzer suggest that seed-grinding activity may actually increase the amount of grit in the diet and promote even greater tooth wear. It is certainly true that tooth wear is often pronounced in peoples who rely on processed grain for their subsistence, but I suspect that the amount of visible wear is no longer an indicator of the intensity of the forces of selection. When technology can be used to reduce food to swallowable and digestible form without chewing, then loss of tooth substance or even the teeth themselves is no longer something that can be detected by the forces of selection. At the beginning of the century, Haddon depicted a mallet and pounding block from the Torres Straits "said to be used by toothless persons" (Haddon 1912:124 and fig. 155). In Arnhem Land, the observation was also made that mortars and pestles were used on a wide variety of foods "before almost every meal" for the benefit of infants and old people (Peterson 1968:568). I do not know of similar ethnographic observations for other parts of Australia, but it seems quite clear that the grinding and pounding technology that was nearly ubiquitous at the time of European contact (Davidson and McCarthy 1957:436) represented a substantial reduction of the amount of selection that had maintained tooth size in the Pleistocene. It is this in part that leads me to doubt Birdsell's (1979:119) statement that "the basic tool kit was Upper Paleolithic in character" and suggest that, at contact, the basic Australian adaptation was essentially a Mesolithic one.

Lombardi and especially Pietrusewsky remark on the uncertain nature of my samples. This uncertainty is a perennial problem for those working with museum collections. In rare instances, such as with Broadbeach (Haglund 1968) and Swanport (see the discussion in Howells 1973), the circumstances of discovery are known in some detail. The Walbiri, of course, are known right down to sex, name, and age. The rest of the material, however, cannot in general be treated with such precision. For example, during his first ten years of collecting, Murray Black separated skulls, jaws, and the various long bones, although he did record the name of the district in which particular specimens were excavated. After he severed his ties with the Australian Institute of Anatomy in Canberra and gave his findings to the Medical School in Melbourne, he ceased recording where the material came from, although he left records that allow one to associate the bones of given individuals. In no case did he record information that would allow us to specify the antiquity of his material. Except for that which is obviously permineralized, the best that we can do is to guess that most of the specimens belong to a loose "ethnographic present" extending back from the point of contact about 2,000 years.

Much of the Arnhem Land material can be located according to district and date. In some instances the identity of particular individuals can be specified. Where this was possible, it helped confirm my operating assumption that I was getting a good enough sampling of both sexes to produce a roughly effective

representation of the local population. For the other parts of Australia and Tasmania, however, things are much less secure. Macintosh and Barker (1965) and Howells (1973) have dealt with the problem of the provenience of the Tasmanians, and my measurements were made in the collections utilized by Howells. For western Australia I could not even get enough measurable material to make local clusters comparable to the ones for Sydney, the Victoria coast, and the others in eastern and southern Australia. As a result, my Southwest Australia cluster includes specimens all the way from Shark Bay to the south coast. This clearly is my least satisfactory grouping, but it does not present any unusual aspects of variance and it fits with the picture of the rest of Australia based on more secure data.

As Howells has noted in his comment, the Devil's Lair (Nannup) incisor and the single Cossack site specimen (Freedman and Lofgren 1979) suggest that there had been an earlier manifestation of robustness in the western extreme of Australia that was similar to the Coobool Crossing-Kow Swamp evidence in the southeast. I have suggested that this robustness was the product of selective forces related to the hunting of the Pleistocene megafauna. Howells and St. Hoyme both question whether such activities required any extraordinary muscular effort, but I shall defend my speculative gambit. A slender and lightly muscled person can reduce seeds to flour by repeated pounding or grinding and butcher the largest of animals by repeated blows with a chopping tool, but hunting large game is another matter. Even the most docile of wombats will put up strenuous resistance at repeated spear thrusts from the feeble hunter searching for a vital part, and if it is six feet tall at the shoulders and over twice as long and weighs well over a ton the task becomes even tougher. Since I suspect that the same logic applied to the *Diprotodon* hunters as to those elsewhere in the Middle Pleistocene, it would seem appropriate to quote from my recent treatment of the matter (1979c:70-71):

However much stealth and cunning were used in tracking and stalking, the moment inevitably came when the hand-held spear was thrust into the intended victim. Now the chance that a ton or so of Pleistocene buffalo or whatever [here read *Diprotodon*] will quietly and obligingly expire at the first jab of the hunter's spear are small indeed. In the twitching and thrashing of wounded prey, it is certain that, during the Early and Middle Pleistocene [and I suggest in Late Pleistocene Australia], the hunters regularly got banged around a bit. Torn knee ligaments, broken bones, dislocations or cracked skulls could easily have fatal consequences. Not surprisingly, we see the development of bony and muscular reinforcements in the skeleton of the male hunting hominids.

It is my suggestion that the tooth-size gradation I have documented within Australia and the reduction that can be seen in the southern centers of surviving robustness are due both to a major change of subsistence strategy in situ and to gene flow from outside, where reduction had begun because of the earlier adoption of essentially Mesolithic technological developments. Howells, Huizinga and Constandse-Westermann, and Meiklejohn all ask how one can determine the relative roles of gene flow versus selective-force change. This, of course, is a crucial question, but it cannot be answered just within the context of the present paper. Roydhouse, although he misrepresents my formulation by inventing "waves of southbound travellers," and Turner both realize that this question can only be handled by dealing with events in Melanesia and closer to the Asian mainland. I have actually made a preliminary effort to do just that, and I submitted the manuscript to CURRENT ANTHROPOLOGY as soon as I received notice that the present one had been accepted (Brace and Hinton n.d.). The referees found it controversial, since so much depended on material that was in press, so the Editor decided to postpone a decision on its publishability. Now that the present paper has appeared, perhaps it can be reconsidered. It will not provide a definitive answer to the question raised by Howells et al., but it does represent a step in that direction.

In closing, I would like to quote a couple of items from the unpublished opus of that indefatigable versifier I. Doolittle Wright:

Australian teeth show a grade
From the north where reduction's displayed,
To those in the south
Where the typical mouth
Has a Pleistocene dental arcade.

And finally, as he realized that the spectrum within Australia ran all the way from Neanderthal to Neolithic:

The critics may set up a row
That one shouldn't be doing this now;
But if metrics will fail the
Approach to Australia,
Someone had better say how!

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