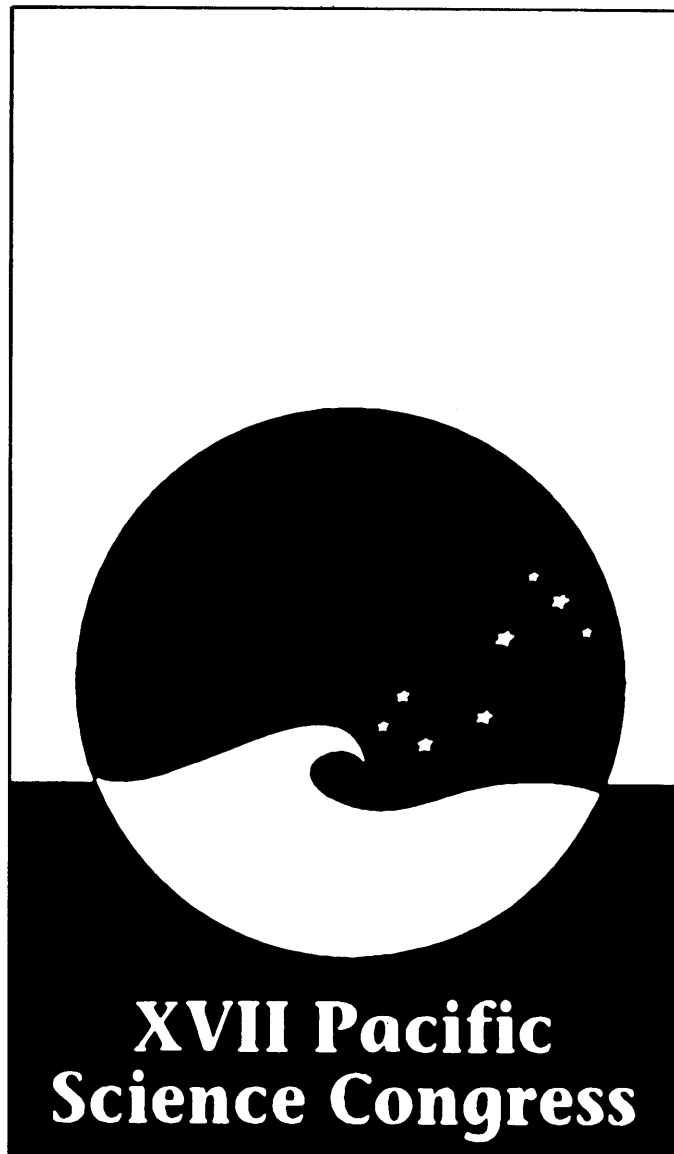


Craniofacial Variation in Pacific Populations

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Post-Pleistocene Change in Australian Aboriginal Tooth Size: Dental Reduction or Relative Expansion?

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ABSTRACT Aboriginal teeth from south-eastern Australia decrease in absolute size during the first three to four thousand years of the Holocene. However, this change in tooth size is not evenly distributed throughout the dental arcade and is more evident in males than in females. Accompanying this reduction in tooth size is a reduction in the size of the cranium, facial skeleton and body. Relative to the reduction in the size of the skeleton the teeth actually increase in size by several percent. Although rates of dental attrition decrease over the same time period it is unlikely that there was any relaxation in the selection for a large and robust masticatory apparatus. Acute dental attrition, with pulp exposure and abscess development, is a feature of both Late-Pleistocene and Holocene Australian Aboriginal populations. Dental reduction in the south-eastern Australian Holocene was probably secondary to a decrease in overall body size. Body size reduction may have been part of a thermoregulatory adaptation to increasing Holocene air temperatures.

There is now a considerable body of data describing an apparently global trend for reduction in the size and robusticity of the human dentition in the post-Pleistocene period. Although there is some variation in the timing and extent of the events involved dental reduction in this period has been recorded from South and East Asia (Brace, 1978; Brace and Nagai, 1982; Brace et al., 1984; Kennedy, 1984; Kennedy et al., 1987; Lukacs, 1984), Europe (Fruyer, 1978; Y'Edynak, 1989), the Mediterranean (Le Blanc and Black, 1974), Africa and the Levant (Calcagno, 1986; Carlson and Van Gervan, 1977; Smith et al., 1986) and Australia (Brace, 1980; Brown, 1987, 1989). Preservational bias has favoured an emphasis on dental data, however, where the orofacial skeleton, cranial vault and other parts of the skeleton are present it appears that there has been a significant reduction in the entire masticatory system and skeletal mass in general (Brown, 1987; Brown, 1989; Carlson, 1976; Kennedy et al., 1987; Smith et al., 1984, 1985, 1986).

Although there is general agreement as to the presence of a post-Pleistocene trend towards reduction of the human masticatory system there is considerable debate as to the evolutionary mechanisms involved. The majority of workers in this area have argued for some connection between cultural development and reduction of the masticatory system. Most of these have focused on the increasing pre-masticatory preparation of food and the greater use of carbohydrate staples which accompanied the

development of agriculture and use of pottery cooking vessels (Brace and Mahler, 1971; Calcagno and Gibson, 1988; Fruyer, 1978; Kennedy et al., 1987; Le Blanc and Black, 1974; Lukacs, 1984; Y'Edynak, 1978). Although there is a general correspondence between these cultural developments and accelerated dental reduction, correlation does not imply causation and there is continued debate over the biological processes involved (Calcagno and Gibson, 1988; Macchiarelli and Bondioli, 1986). It is possible that dental reduction was secondary to skeletal reduction, with selection for smaller body size due to climatic change (Brown, 1987, 1989) or higher population densities and increased competition for resources (Macchiarelli and Bondioli, 1986). Under these conditions it has been proposed that smaller teeth could result from a reduction of the developmental areas available for the teeth (Sofaer, 1973; Sofaer, et al., 1971a), an allometric association with jaw size reduction (Robinson, 1954), or selection favouring a smaller and uncrowded dentition within the reduced facial structure (Brown, 1987; Macchiarelli and Bondioli, 1986).

Skeletal and dental materials recovered from south-eastern Australia provide a useful test of the links between cultural development and post-Pleistocene reduction in tooth size. For most of its human history Australia has been a relatively isolated place. Where undisputed evidence of cultural and genetic contact with smaller toothed populations to the north and north-east is present it is confined to the extreme

north of the continent (Kirk, 1981). At the same time the first Australians were hunter-gatherers 40,000 years ago much as they were at European contact (White and O'Connell, 1982). This is not to imply that an atmosphere of extreme cultural conservatism and minimal technological change prevailed. Developments in stone tool and food preparation technology in prehistoric Australia include the appearance of edge ground tools in the late-Pleistocene (Rosenfeld et al., 1981; Schrire, 1982; Morwood and Trezise, 1989), microlithic backed blades and bifacial points at 4000-5000 years BP (Johnson, 1979; White and O'Connell, 1982) and seed grinding stones in the early to mid-Holocene of the arid region (Smith, 1986). However, neither agriculture or pottery cooking vessels were present before European contact. Moreover traditional diets, and non-masticatory tooth use, in south-eastern Australia required considerable muscular effort and inevitably resulted in acute dental attrition (Kreft, 1862; Beveridge, 1883; Curr, 1889; Campbell, 1939; Barrett, 1977; Brown, 1989). If the dietary models presented in explanation of human dental reduction by Brace (1964, 1967), and others, are correct then you would not expect to find evidence of directional reduction in tooth size in this type of masticatory environment.

Macchiarelli and Bondioli's (1986) suggestion that dental reduction was linked to body size reduction, increasing population densities, disease load and greater stress on resources may be of some relevance to the Australian situation. Lourandos (1983, 1985) and Ross (1985) have argued that a late-Holocene "intensification" in landuse was a feature of south-eastern Australia. The claims for intensification include a greater number of archaeological sites, greater depth of deposit in these sites, the rise of 'villages' and large scale permanent campsites, and greater density of graves in cemeteries (Ross, 1985; Williams, 1987; Pardoe, 1988). However, the archaeological evidence of intensification and the way it should be interpreted has been subject to some criticism (Beaton, 1983, 1985; Brown, 1989; Head, 1990; Bird and Frankel 1991). The chronological basis for the intensification claims are poor and it is not at all clear whether the apparently greater number of younger sites is simply an artifact of preferential preservation and greater site visibility. Whatever the historical reality of the Australian intensification phase population densities and resource pressure did not approach those associated with

the more sedentary lifestyles reported by Macchiarelli and Bondioli (1986).

It has been suggested that a reduction in tooth size may have been secondary to a reduction in the size and prognathism of the orofacial skeleton, or body size in general (Baillit and Friedlaender, 1966; Carlson and Van Gervan, 1977; Smith, 1982). Smaller teeth may then result from a reduction in the developmental areas available for the teeth (Sofaer et al., 1971a, 1971b; Sofaer, 1973), an allometric association with some aspect of body size or facial proportions (Anderson et al., 1975; Glanville, 1969) or selection favouring the maintenance of correct physiological function (Brown, 1987; Calcagno and Gibson, 1988). Comparisons of terminal Pleistocene human skeletons, and crania, from south-eastern Australia have demonstrated that they are considerably larger and more massively constructed than those from the mid to late-Holocene (Thorne and Macumber, 1972; Thorne and Wilson, 1977; Brown, 1987, 1989, 1992). Both cultural and environmental mechanisms have been promoted in explanation of post-Pleistocene reduction in Australian Aboriginal skeletal and dental mass (Brown, 1989; Pardoe, 1991). However, the possibility that diachronic change in the Australian Aboriginal masticatory complex could be directly linked to an altered masticatory environment has not previously been examined in any detail. In part this is because the archaeological record from south-eastern Australia provides little support for this hypothesis. It is also unclear whether the directional change in tooth size reported for the early part of the Australian Holocene is what might be predicted given the reduction in body and skull size over the same time period. The objective of this paper is an examination of post-Pleistocene change in Australian Aboriginal tooth size when placed in this broader perspective.

MATERIALS

The skeletal and dental materials used in this analysis come from the Murray River region of south-eastern Australia. The late-Pleistocene series (L-P) is composed of crania and skeletons from Kow Swamp (Thorne and Macumber, 1972), Cohuna, Coobool Creek and Nacurrie (Brown 1987, 1989, 1992). The sample sizes and dates for each of these sites are listed in Table 1, with Brown (1989) providing additional background information. Each of

TABLE 1. Sample sizes and dates for the Late-Pleistocene, Mid-Holocene and Late-Holocene samples.

Sample	n	Method	Date ¹	Reference
Late-Pleistocene				
Coobool Creek	32	U/Th	14300 ± 1000	Brown 1989
Kow Swamp	9	¹⁴ C	13000 ± 280 - 9590 ± 130	Thorne 1969, 1975, 1976
Nacurrie	2	AMS	11440 ± 160	Brown 1992
Cohuna	1	Morph.	13000 - 9000	Brown 1987, 1989
Mid-Holocene				
Roonka	8	¹⁴ C	7000 - 4000	Pretty 1977; Brown 1989
Barham	6	¹⁴ C	5400 ± 90 - 4670 ± 110	Daley 1986
Keera Station	12	¹⁴ C	5900 ± 550 - 4170 ± 200	Blackwood and Simpson 1973
Late-Holocene				
Swanport	59	Morph.	Recent-European contact	Brown 1989; Pietruszewsky 1990

¹Where more than one date has been reported from a site the range of the published dates are given.

these L-P sites is in close geographic proximity and the skeletons from them share a suite of morphological, metrical and culturally induced traits. In particular, I have argued (Brown, 1981a, 1989) that some of the crania from each of these sites are artificially deformed. To a large degree the dating of the Coobool Creek skeletons is dependent on these morphological characteristics as contamination from modern gelatin, which was used to preserve the skeletons in the 1950's, has precluded meaningful radiocarbon dating. Similarly, the age of the Cohuna cranium is dependent upon morphological and metrical comparison with Kow Swamp and Nacurrie (Brown, 1989, 1992). In compliance with the wishes of Aboriginal communities in the central Murray River region all of the skeletons from these L-P sites were recently reburied.

The mid-Holocene sample (M-H) was drawn from the prehistoric cemeteries at Barham, Roonka and Keera Station. The Roonka site is particularly complex and the stratigraphic relationships and dating of the burials within the site are still being refined. On the basis of Pretty (1977) the skeletons included in the M-H Roonka sample all appear to be older than R48, which has a ¹⁴C date of 3930 ± 120, and younger than 7000 years BP. Poor preservation of much of the M-H sample greatly reduced the numbers available for metric comparison of orofacial development. The Keera Station skeletons were reburied in September 1991. Although undated, morphological and metrical comparisons involving the Swanport crania

have repeatedly associated them with late-Holocene (L-H) Aboriginal series (Pietruszewsky, 1979, 1984; Pardoe 1984; Brown, 1989). The presence of interproximal cervical dental caries, unknown in prehistoric Australian contexts, suggests some contact with European derived carbohydrates and strengthens the argument for a relatively modern date. Swanport formed the largest L-H Aboriginal skeletal population, from southeastern Australia, which remained available for study in 1991.

METHODS

In both the prehistoric past, and European contact period, there was marked regional variation in the mortuary practices employed by Australian Aborigines (Meehan, 1971). Within regions this variation extended to the differential treatment given to particular sexes, particularly males. This appears to be reflected in the apparent sex bias of some museum collections. The potential for cultural bias in sex representation, combined with the pronounced sexual dimorphism recorded for Aboriginal tooth size (Barrett et al., 1963a, 1963b, 1964; Townsend and Brown, 1979; Brown, 1989), required that the sample be subdivided on the basis of sex. The alternative would be to admit the possibility that diachronic trends in tooth size were simply an artifact of the sex distribution of the samples. There was also a possibility that males and females displayed different patterns of diachronic dental change.

Isolated teeth were not included in the analysis and sex was determined through a combination of the morphological and metrical method developed specifically for adult Aboriginal crania by Larnach and Freedman (Larnach and Freedman, 1964; Brown, 1981b), discriminant function analysis of the crania (Brown, 1989) and a morphological comparison of the associated pelvis and sacra (Washburn, 1948; Phenice, 1969). Only 9 of the L-P sample had postcranial skeletons which were complete enough for reliable sex assessment.

Prior to the shift to European derived foods, and methods of food preparation, marked occlusal and interproximal attrition was a feature of Aboriginal dentitions (Campbell and Gray, 1936; Campbell, 1939; Barrett, 1977). For example, in the Murray River region by the time a person had reached 16-17 years of age an average of 3.9% of the occlusal surface of the maxillary first molar was comprised of exposed dentine. At the same age there is considerable reduction of the mesiodistal dimensions, of most teeth, through interproximal attrition. Due to the effects of attrition measures of tooth crown area, or tooth length, tell you something about masticatory function and individual age in these dentitions but convey little in the way of phylogenetic information. For this reason the only measure of tooth size that was recorded for this analysis was the buccolingual crown dimension (Townsend and Brown, 1979), which was recorded to the nearest 0.1 mm. Both Alvesalo and Tigerstadt (1974) and Townsend and Brown (1978) obtain high heritability estimates for this dimension, but the later also found that variance due to common environment was greater with the buccolingual than the mesiodistal dimension. Teeth in which the buccolingual dimension was influenced by attrition were excluded from the analysis.

Student's *t* test is used to assess the significance of differences in mean buccolingual tooth dimensions. This test assumes that variables are normally distributed and there is equality of variance between the groups. Distributions were examined by plotting individual values against corresponding percentage points of a standard normal variable (Gnanadesikan, 1977) and through the use of the Shapiro-Wilk statistic (Shapiro and Wilk, 1965). Homogeneity of variance was examined using the χ^2 test developed by Bartlett (1937). Where a statistically significant difference in variance was indicated by χ^2 , Student's *t* is calculated using the formula based on separate

variance estimates (Snedecor and Cochran, 1967). Graphical comparisons of the distribution of data from different samples are made using the Box plots developed by Tukey (1977). In these plots the box contains the central 50% of the distribution and the horizontal bar passing through the box is the median. The whiskers projecting from the box normally indicate the spread of the upper and lower quartiles, with outliers represented by asterisks (*). Variation in facial size and shape, presence of outliers, distance between group means and group allocation were examined using direct discriminant function analysis (Tabachnick and Fidell, 1989). Variable selection was influenced by preservation, the wish to maximise the number of individuals included in the analysis and the underlying assumptions of distributional normality, and homogeneity of variance and covariance, inherent in discriminant function analysis (Gilbert, 1969; Eisenbeis and Avery, 1972; Huberty, 1984). Missing data decreased the M-H and L-P female samples to such a small size (<7) that there were too few cases to be non-singular, so the females were excluded from the analysis. Linear dimensions and angles follow those used in (Howells, 1973) and Brown (1989). Statistical calculations were performed using SPSS 4.0 (SPSS, 1990), SYSTAT 5.1 (Wilkinson, 1989) and hand calculation.

Several of the arguments developed in explanation of post-Pleistocene human dental reduction concentrate on changes in diet and food preparation technology (Brace and Mahler, 1971; Carlson and Van Gervan, 1977; Calcagno, 1986). The possibility of an association between tooth size and cultural development was examined through a comparison of the relative rates of dental attrition in the L-P and L-H samples. Recent problems concerning access to a large part of the M-H series prevented its inclusion in the attrition analysis. Using the procedures outlined in Richards and Brown (1981) dental attrition was measured as the ratio of the area of exposed dentine to total crown area when viewed from the occlusal. Attrition scores were transformed to logarithms (\log_{10}) to improve the linear relationship between the points prior to principal axis analysis. Age independent rates of wear for the L-P and L-H samples were determined from the attrition scores for the first and second maxillary molars, in combination with the principal axis method advocated by Scott (1979). Plotting of attrition scores did not

reveal sex-based differences in wear rates so male and female data were pooled for the principal axis comparison. Confidence limits and slopes for the principal axes were calculated using formulae in Sokal and Rohlf (1981). The major limitation of this approach is that it excluded juvenile dentitions without dentine exposed on both M1 and M2. Direct comparison was made between the attrition scores for the first maxillary molars in subadults from the L-P and L-H samples. Some control on individual age could be obtained with the subadults through their dental development (Brown et al., 1979) and epiphyseal fusion (Abbie and Adey, 1953; Brown and Grave, 1976).

RESULTS

Tooth size

While the dental materials used in this analysis are all that have been recovered from L-P and M-H sites in the Murray River region of southeastern Australia, the overall sample sizes are nevertheless very small. The sensitivity of dental metric data to sample size effects is highlighted by a comparison of the buccolingual breadth dimensions published in two reports from the long-term growth study of Aborigines at Yuendumu in central Australia. The first of these by Barrett et al. (1964) had sample sizes which, varying by sex and tooth category, ranged between 36 and 81. The second by Townsend and Brown (1979) used a sample which, for most sexed tooth categories, exceeded 140. Comparison of the two sets of data using Student's *t* found significant differences between eight of the means ($.001 < p < .05$), as well as a considerable difference in the sexual dimorphism ranks (Brown, 1989). The differences between these two sets of data are unlikely to be simply the result of intraobserver error. One observer was common to both projects and measurement techniques were consistent throughout. What these data appear to reflect are high levels of intrapopulation variation in tooth size and the need for large samples. While not wishing to totally undermine the results of the analysis to follow I think the results presented here, as well as those in other publications using similarly small samples, need to be interpreted with caution.

Descriptive statistics indicate the relatively large size of the L-P dentitions in comparison to

those from the M-H and L-H groups. However, this is much more apparent in males than in females and is more evident in particular classes of teeth than in others. With one exception, P1 in the M-H sample, the male mean maxillary buccolingual tooth dimensions in the L-P series exceed those in the M-H and L-H groups (Table 2). With two exceptions, P1 and M3 in the L-H group, male mean mandibular buccolingual tooth dimensions in the L-P series also exceed those in the Holocene samples (Table 2). Female mean tooth dimensions in the L-P also tend to be greater than those in the two Holocene groups but to a smaller degree (Table 3). For the maxillary teeth the L-P female means are all greater than those in the L-H group but are below those for M1 and M3 in the M-H series. Only two of the L-P mandibular tooth dimensions, P2 and M3, are greater than those in both of the Holocene groups. Box plots of the buccolingual dimensions clearly show that in males the major period of dental reduction predates the M-H group (Figs. 1 and 2). The average amounts of reduction in males are 4.5% from the L-P to M-H, 3.2% for L-P to L-H, with an increase in average size of 1.2% from the middle to late-Holocene. For some teeth (maxillary I2, P2 and M2 and mandibular I2 and P2) the female box plots show a similar pattern of dental reduction to the males but the overall evidence for directional reduction is less convincing (Figs. 3 and 4). The average amount of dental reduction between the L-P and M-H females is only 1.4%, 1.6% between the L-P and L-H, and 0.9% between the middle and late-Holocene.

The L-P mean dimensions for the male maxillary lateral incisors and first molars are significantly larger than those for both of the Holocene samples, and the L-P mean canine and second molar dimensions are also significantly greater than those in the M-H group. Mean dimensions for the mandibular canine, first and second premolars, and first and third molars in the M-H group are all significantly smaller than in L-P, as are the means for the second premolar and first molar in the L-H series. Mean buccolingual tooth dimensions in the male L-H group are generally greater than, or equal to, those in the earlier M-H group. The M-H mean dimensions are greater than the L-H only for the maxillary premolars and mandibular lateral incisor and first molar. In contrast to the male mean dimensions the only significant difference between the L-P and Holocene female means is for the maxillary lateral incisors, which are

TABLE 2. Buccolingual crown dimensions for the Late-Pleistocene, mid-Holocene, and late-Holocene male maxillary and mandibular dentitions.

	I ¹	I ²	C	P ¹	P ²	M ¹	M ²	M ³
L-P male maxillary								
n	12	14	18	14	17	17	17	20
Mean	8.3	7.8	9.8	10.9	10.7	13.6	13.9	13.2
S.D.	0.24	0.40	0.63	0.37	0.49	0.43	0.73	0.81
Min.	7.9	6.9	8.7	10.6	9.8	12.8	12.7	10.8
Max.	8.7	8.5	11.4	11.8	11.7	14.2	15.3	14.4
M-H male maxillary								
n	8	14	14	13	15	12	16	13
Mean	8.2	7.0**	9.3**	11.1	10.7	13.0**	13.4*	12.8
S.D.	0.41	0.45	0.34	0.34	0.55	0.62	0.67	0.93
Min.	7.3	6.4	8.8	9.9	9.7	12.2	12.4	11.2
Max.	8.5	7.9	9.9	11.1	11.6	14.1	14.9	14.5
L-H male maxillary								
n	9	16	19	18	22	23	26	26
Mean	8.2	7.4*	9.4	10.7	10.5	13.0**	13.6	12.8
S.D.	0.62	0.58	0.65	0.74	0.94	0.75	0.93	0.93
Min.	7.3	6.5	8.0	9.5	8.8	11.5	12.3	10.8
Max.	9.2	8.4	10.6	12.1	12.3	14.5	16.2	14.9
	I ₁	I ₂	C	P ₁	P ₂	M ₁	M ₂	M ₃
L-P male mandibular								
n	3	10	17	18	18	8	11	19
Mean	7.0	7.0	9.1	9.6	9.9	12.9	12.5	11.9
S.D.	0.11	0.45	0.48	0.56	0.57	0.38	0.47	0.69
Min.	6.9	6.4	8.2	8.6	8.9	12.1	11.8	10.2
Max.	7.1	7.6	9.8	10.7	11.0	13.3	13.2	12.8
M-H male mandibular								
n	8	8	13	13	14	11	13	13
Mean	6.7	6.8	8.5**	9.0**	9.2**	12.3*	12.0	11.2**
S.D.	0.34	0.27	0.34	0.30	0.57	0.69	0.82	0.74
Min.	6.3	6.5	7.9	8.5	8.1	11.3	10.9	9.6
Max.	7.4	7.4	9.1	9.4	10.2	13.7	13.5	12.2
L-H male mandibular								
n	7	10	11	13	13	12	13	12
Mean	6.7	6.7	8.8	9.7	9.2**	12.2*	12.1	12.1
S.D.	0.49	0.34	0.67	0.48	0.67	0.64	0.91	0.95
Min.	6.0	6.3	7.8	8.9	7.7	11.0	10.5	10.4
Max.	7.3	7.2	10.0	10.3	10.1	13.6	13.5	13.9

* L-P mean significantly greater than M-H or L-H mean, .01 < p < .05

** L-P mean significantly greater than M-H or L-H mean, .001 < p < .005

significantly larger in the late-Pleistocene. These results support those obtained in earlier studies of prehistoric Australian Aboriginal tooth-size (Brown 1989), particularly in that

post-Pleistocene dental reduction appears to be a male phenomenon as does overall reduction in body size and skeletal mass.

TABLE 3. Buccolingual crown dimensions for the Late-Pleistocene, mid-Holocene, and late-Holocene female maxillary and mandibular dentitions.

	I ¹	I ²	C	P ¹	p ²	M ¹	M ²	M ³
L-P female maxillary								
n	8	10	10	9	11	9	10	7
Mean	8.0	7.4	9.0	10.2	10.2	12.8	13.0	12.2
S.D.	0.49	0.43	0.50	0.46	0.66	0.68	0.73	1.26
Min.	7.5	6.8	8.2	9.2	9.4	12.1	12.0	10.0
Max.	8.8	7.9	9.8	10.7	11.3	13.9	13.8	13.5
M-H female maxillary								
n	7	6	8	9	9	9	10	10
Mean	7.8	6.7**	8.9	9.9	10.0	12.9	12.9	12.3
S.D.	0.24	0.22	0.48	0.55	0.55	0.62	0.67	0.85
Min.	7.5	6.4	8.3	9.3	9.5	12.1	12.0	10.6
Max.	8.2	7.0	9.6	11.1	11.2	13.9	14.1	13.4
L-H female maxillary								
n	10	18	20	16	23	20	24	21
Mean	7.9	6.7**	8.8	10.0	9.8	12.7	12.7	11.8
S.D.	0.46	0.54	0.47	0.49	0.49	0.59	0.66	0.75
Min.	7.3	5.8	8.1	8.7	8.8	11.9	11.7	10.2
Max.	8.7	7.8	9.7	10.5	10.8	14.1	14.0	13.0
	I ₁	I ₂	C	P ₁	P ₂	M ₁	M ₂	M ₃
L-P female mandibular								
n	7	7	10	10	10	6	9	10
Mean	6.3	6.6	8.2	8.8	9.0	11.7	11.6	11.3
S.D.	0.53	0.46	0.48	0.46	0.39	0.54	0.53	0.61
Min.	5.9	6.2	7.6	7.9	8.2	11.1	10.9	9.8
Max.	7.4	7.5	8.9	9.6	9.5	12.5	12.3	11.7
M-H female mandibular								
n	6	8	10	10	9	6	6	8
Mean	6.4	6.7	8.0	8.6	8.8	12.2	11.5	11.1
S.D.	0.29	0.29	0.54	0.57	0.44	0.67	0.80	0.69
Min.	6.0	6.3	6.9	7.7	8.2	11.5	10.6	10.1
Max.	6.8	7.1	8.9	9.4	9.4	13.0	12.7	12.0
L-H female mandibular								
n	7	9	13	12	11	13	16	13
Mean	6.3	6.5	8.2	8.9	8.7	12.0	11.8	11.1
S.D.	0.39	0.35	0.48	0.47	0.52	0.55	0.69	0.92
Min.	5.9	6.1	7.6	8.1	7.9	11.1	10.7	9.9
Max.	6.9	7.2	9.3	9.8	9.6	13.2	13.2	12.6

* L-P mean significantly greater than M-H or L-H mean, .01 < p < .05

** L-P mean significantly greater than M-H or L-H mean, .001 < p < .005

Dental attrition

Prior to calculation of the principal axis equations, and associated 95% confidence limits, attrition data were tested for distributional normality by plotting them against percentage

points of a standard normal variable (Gnanadesikan, 1977). Due to a shortage of individuals with lower levels of attrition each of the distributions had a marked right skew. A variety of transformations were applied but with little effect on the extent of the skew. This

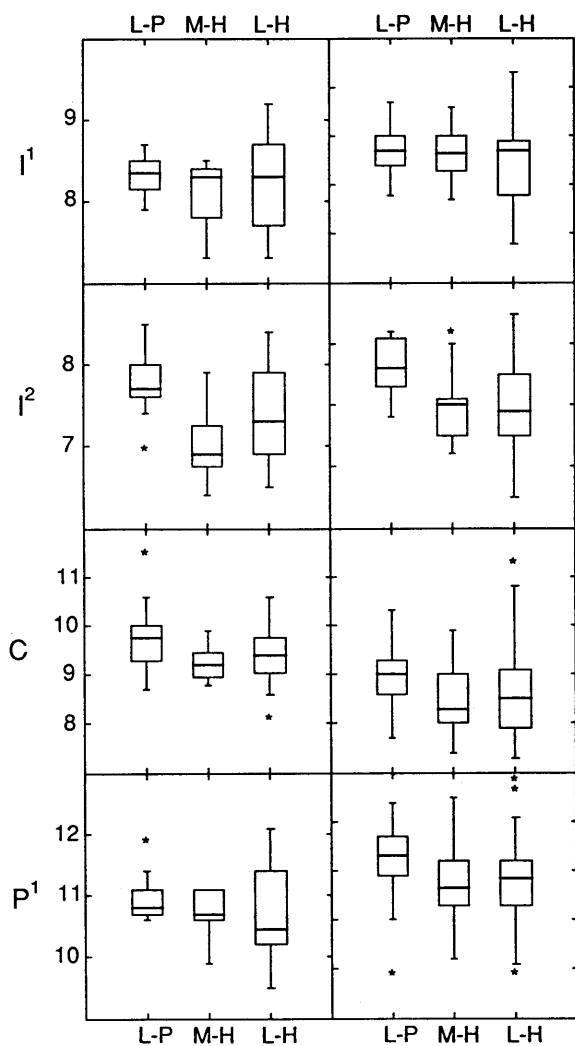


Fig. 1. Box plots of the distributions of the male maxillary buccolingual tooth dimensions for the Late-Pleistocene, Mid-Holocene and Late-Holocene groups (mm).

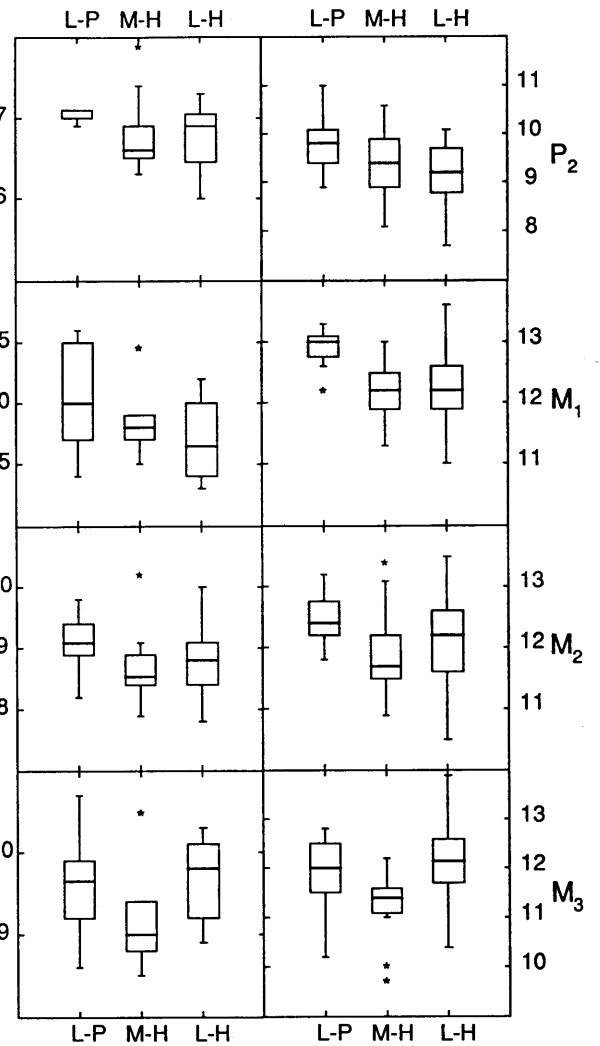


Fig. 2. Box plots of the distributions of the male mandibular buccolingual tooth dimensions for the Late-Pleistocene, Mid-Holocene and Late-Holocene groups (mm).

departure from normality can be expected to reduce the reliability associated with the principal axis confidence limits (Sokal and Rohlf, 1981).

The L-P first and second maxillary molars have greater mean attrition scores (\bar{X} M1 63.33, \bar{X} log10 M1 1.76; \bar{X} M2 35.87, \bar{X} log10 M2 1.26) than those in the L-H group (\bar{X} M1 47.92, \bar{X} log10 M1 1.57; \bar{X} M2 23.68, \bar{X} log10 M2 0.98) and a higher rate of attrition (Figs. 5 and 6). Given the relationship between dental attrition and age in Australian Aborigines

(Richards and Brown, 1981; Richards and Miller, 1991) the differences in mean attrition scores may, at least in part, indicate a difference in the age distribution of the samples. This is supported by plots of the attrition scores in Figs. 5 and 6 where the L-P results show a more marked skew towards individuals with high attrition scores, who presumably represent the older adult population.

Principal axis slopes indicate that rates of attrition for the maxillary first and second molars are greatest in the L-P group (Figs. 5 and 6). However, there are only 17 individuals

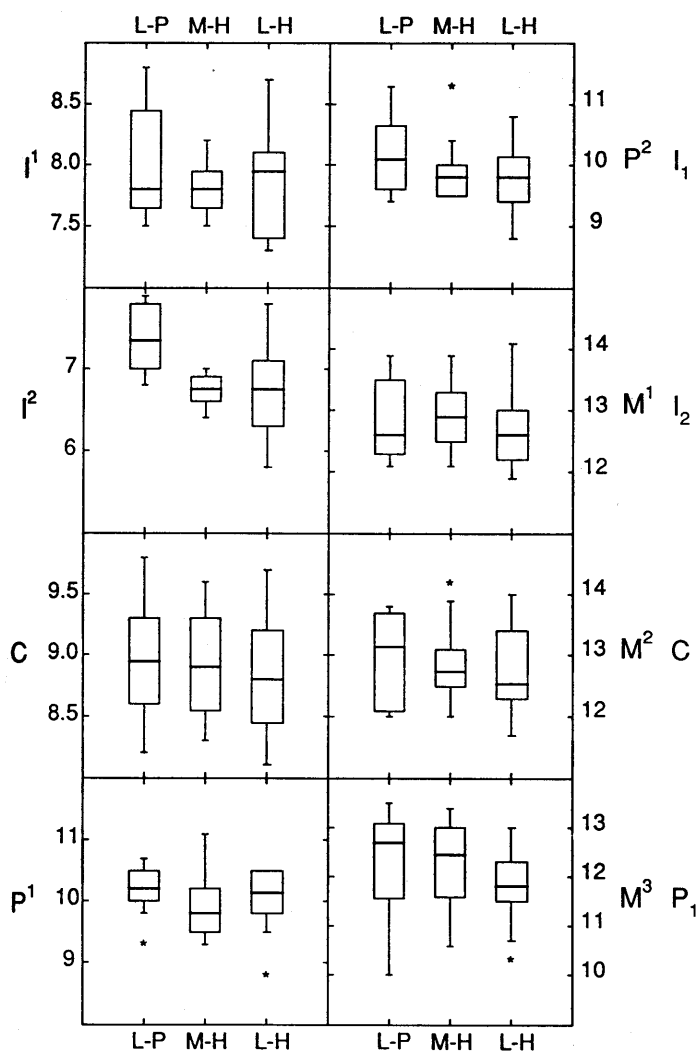


Fig. 3. Box plots of the distributions of the female maxillary buccolingual tooth dimensions for the Late-Pleistocene, Mid-Holocene and Late-Holocene groups (mm).

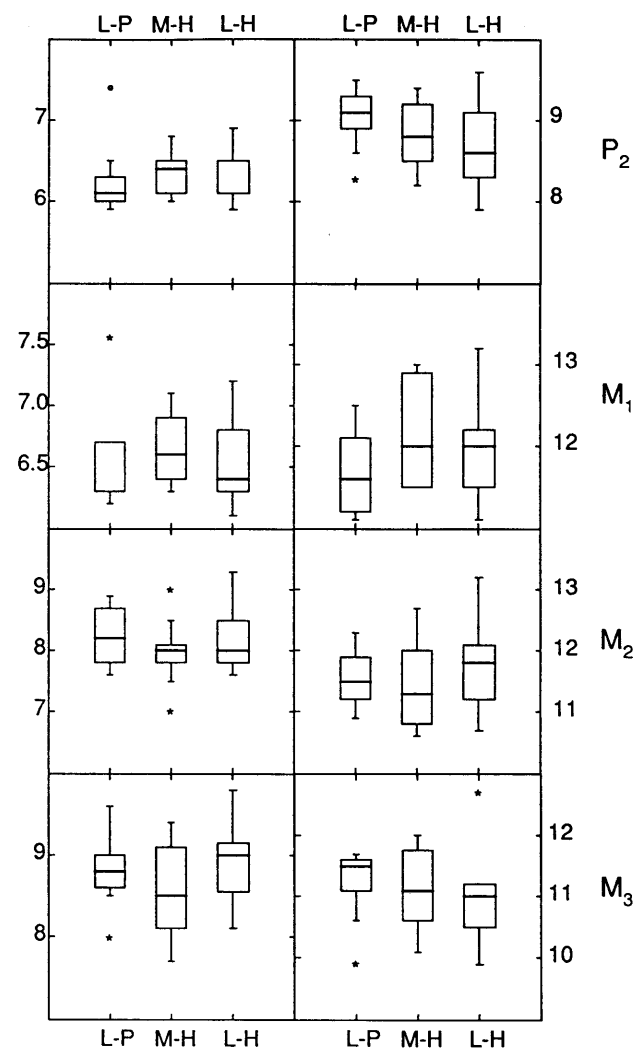


Fig. 4. Box plots of the distributions of the female mandibular buccolingual tooth dimensions for the Late-Pleistocene, Mid-Holocene and Late-Holocene groups (mm).

in the L-P plot and the principal axis equation has been strongly influenced by the two individuals with low attrition scores. Further evidence on relative rates of dental attrition in the L-P and L-H groups was obtained by a comparison of juvenile and young adult teeth (Fig. 7). There is a tendency for the L-P molars to have slightly larger areas of dentine exposure than teeth of similarly aged individuals in the L-H group. If the rates of dental development, and skeletal maturation, were

similar in both groups then these juvenile and young adult L-P teeth provide added support for slightly higher dental attrition rates in the late-Pleistocene. Included within the L-P group is Talgai (Smith, 1918) which was recovered from the Darling Downs, southwest of Brisbane. This is an area with very different environmental conditions to the Murray River Valley and this may be reflected in the relatively high levels of dental attrition in this individual.

Size and shape of the facial skeleton

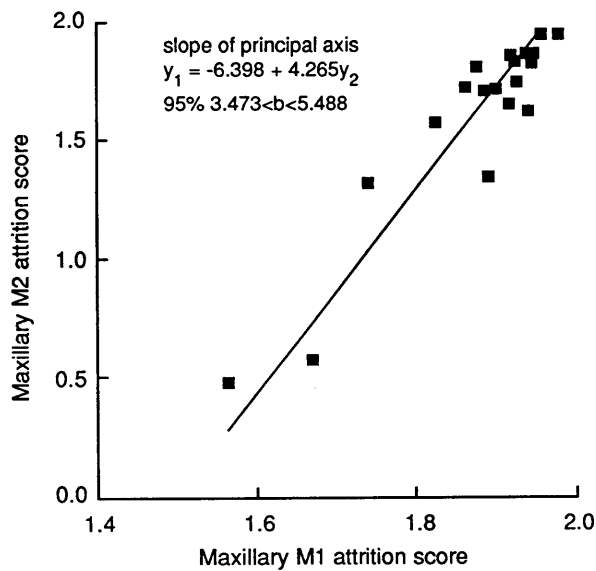


Fig. 5. Principal axis analysis of pooled sex maxillary molar attrition scores in the Late-Pleistocene Australian Aboriginal group.

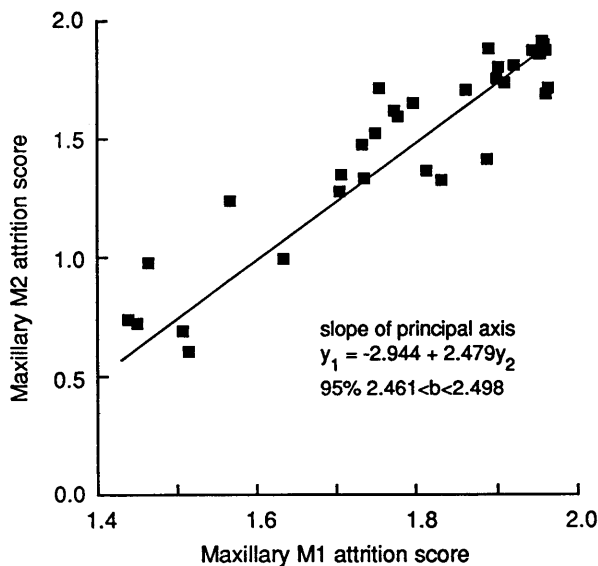


Fig. 6. Principal axis analysis of pooled sex maxillary molar attrition scores in the Late-Holocene Australian Aboriginal group.

The LP orofacial skeletons can be distinguished from the M-H and L-H series by a combination of both size and shape characteristics (Table 4, Fig. 8). Overall the greater size of the LP faces, particularly those of the males, dominates. Most of the mean orofacial dimensions in the L-P group are significantly greater than those in the two Holocene samples (Table 4), with the only exceptions being for the height and breadth of the orbit. For the facial dimensions in Table 4, excluding those for the orbit, modules and mandible, the mean reduction in size between the L-P and M-H groups is 6.7%. For the mandibular dimensions the mean reduction is 7.9% and the palate module 9.8%. The major area of skeletal reduction is in the alveolar segment of the maxilla and mandible, with subnasal height decreasing by 9.6%, symphyseal and mandibular body height 12.8%, and mandibular body thickness 12.9%. Surprisingly although there has been a consistent reduction in the size of the orofacial skeleton between the end of the Pleistocene and middle of the Holocene the orbits increase in size. Post-Pleistocene reduction in overall skull size is indicated by the cranial module results in Table 4, with the L-P cranial vaults 4.6% larger than those in the Holocene. Associated with this is a decrease in endocranial volume from a L-P male mean of 1404.9 ml to 1271.5 ml in the L-H, a reduction of 9.5%. Similarly the L-P females have a mean endocranial volume of 1312.0 ml while the L-H female mean is 1155.5 ml, a reduction of 12%.

In comparison with the Holocene groups the L-P orofacial skeletons are characterised by relatively great supraorbital and postorbital breadths, great facial height and mid-facial breadth, particularly low and rectangular orbits, deep and robust zygomatic bones with a thickened inferior border and column-like frontal process. Inferiorly the subnasal area is elongated and prognathic, with prominent canine eminences and a relatively straight alignment of the canine and incisor roots. Facial prognathism, particularly subnasally, is greater with increased facial height and palate length dimensions influencing the angles of the facial triangle (Fig. 8). The mandibles have bodies which are thickened and particularly high in the symphyseal region. In keeping with a broad cranial base there is great bicondylar and bigonial breadth. The rami are tall and broad

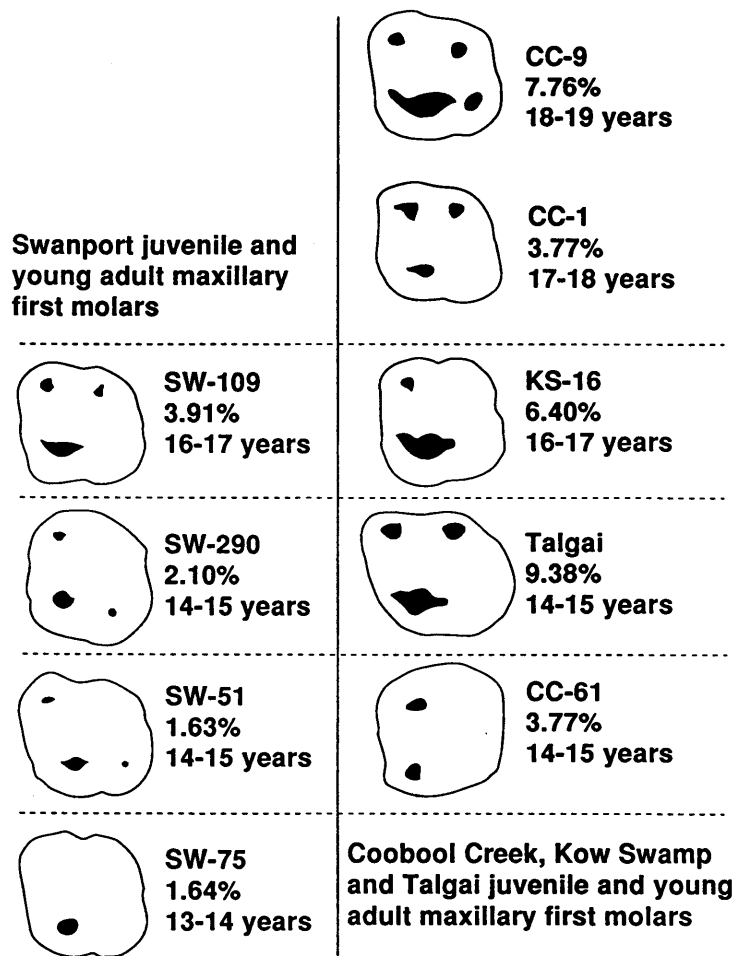


Fig. 7. Comparison of occlusal wear in juvenile and young adult Aboriginal maxillary first molars from Swanport (L-H) with all of the known Late-Pleistocene juvenile and young adult maxillary first molars which have been recovered from Australia.

with robust elongated coronoid processes and massive condyles. Areas of masticatory muscle attachment in the L-P series are both larger and more rugose than in the Holocene groups but it is not clear if this is related to increased masticatory load or allometrically linked to greater body size.

Direct discriminant function analysis was performed using seven orofacial variables as predictors of membership in the three male groups. Predictors were supraorbital breadth, post-orbital constriction, nasion-nasospinale, nasospinale-prosthion, nasal breadth, orbital height and alveolar length. Variable selection was influenced by preservation and an

examination of the univariate results (Table 4). Of the original 84 cases 33 were excluded from the analysis due to missing data. Missing data was concentrated in the older LP and MH groups, particularly in the more fragile areas of the maxilla and mandible. Alveolar damage, due to the abscess development associated with acute dental attrition, frequently prevented the measurement of palate dimensions and the location of prosthion. Graphical and statistical evaluation of homogeneity of variance-covariance, linearity and normality indicated that the analysis complied with the assumptions of discriminant function analysis.

Two discriminant functions were calculated,

TABLE 4. Comparison of orofacial and cranial dimensions in the late Pleistocene Australian Aboriginal male sample with those in the two Holocene male Aboriginal groups using Student's *t* test (mm)

Variable	Late-Pleistocene			Mid-Holocene			Late-Holocene		
	n	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.
Supraorbital breadth	31	117.2	4.98	9	107.8**	2.48	29	110.2**	2.94
Postorbital breadth	33	99.8	5.92	10	92.9**	3.07	29	96.6*	4.17
Nasion-nasospinale	22	54.5	3.18	10	50.8**	2.65	29	51.7**	2.56
Nasospinale-prosthion	23	20.8	3.40	10	18.8	3.36	28	16.5**	2.42
Nasal breadth	26	29.3	1.82	11	27.9*	2.25	25	26.4**	1.35
Orbital height	26	31.2	2.49	10	33.3†	2.86	29	34.1†	2.33
Orbital breadth	26	43.4	3.46	9	44.4	2.65	25	43.9	1.18
Alveolar length	22	64.9	2.42	10	61.8*	4.31	29	61.5**	3.15
Alveolar breadth	22	72.6	3.25	8	68.2**	4.65	28	66.6**	2.72
Palate module ¹	20	47.1	3.31	8	42.5*	5.71	28	40.9**	2.87
Gnathic index ²	17	104.7	3.38	8	102.0	3.07	27	103.5	3.63
Nasal angle	17	74.1	3.55	8	69.0**	3.12	27	74.1	3.97
Prosthion angle	17	66.1	2.35	8	72.1**	2.50	27	67.8*	2.93
Basion angle	17	40.4	1.94	8	38.9	2.65	27	38.4**	2.39
Cranial module ³	24	158.1	4.54	8	150.9**	3.18	28	150.2**	3.44
Endocranial volume (ml)	19	1404.9	96.96	-	-	-	23	1271.5**	92.95
Symphyseal height	25	39.2	2.94	8	34.2**	4.16	15	32.3**	2.87
Symphyseal thickness	30	16.4	1.46	11	15.8	1.32	16	14.4**	1.09
Body height	22	33.8	2.39	7	29.5**	3.30	16	27.5**	2.65
Body thickness	29	15.6	1.86	9	13.6**	1.26	16	14.2*	1.61
Bicondylar breadth	11	128.1	8.75	8	121.5	7.48	13	120.6*	3.81
Bigonial breadth	20	110.7	7.13	8	102.1*	9.67	13	101.1**	3.95
Ramus height	18	62.4	4.46	9	59.1	5.71	15	61.8	3.42
Ramus minimum breadth	27	36.5	3.54	9	35.5	3.71	15	36.4	3.18

¹ Palate module = alveolar length x breadth / 100 (Larnach, 1964).

² Gnathic index = basion-nasion / (basion-prosthion x 100) (Krogman, 1962).

³ Cranial module = cranial length + breadth + height / 3 (Bass, 1971).

* Mean value significantly less than LP mean, .01 < p < .05.

** Mean value significantly less than LP mean, .001 < p < .005.

† Mean value which is significantly greater than LP mean, .01 < p < .05.

with a combined $\chi^2 = 80.00$, $p < .001$. After removal of the first function there was still a significant association between groups and predictors, $\chi^2 = 12.77$, $p < .05$. The two discriminant functions accounted for 91.3% and 8.7%, respectively, of the between-group variability. Fig. 9 demonstrates how the first discriminant function maximally separates the L-P series from the two Holocene groups, with the loading matrix correlations between predictors and discriminant functions (Table 5) indicating that this is due to greater nasal breadth, supraorbital breadth and subnasal

height (nasospinale-prosthion) in the late-Pleistocene males. The second discriminate function discriminates the M-H group from the L-P and L-H samples, with discrimination on this function resulting from the lower supraorbital and postorbital dimensions in the mid-Holocene sample (Tables 4 and 5).

Of the three groups included in the analysis the L-P males displayed the highest levels of variation, with greater dispersion around the group centroid than in the two Holocene groups (Fig. 9). However, the classification probabilities did not indicate that any of the L-P

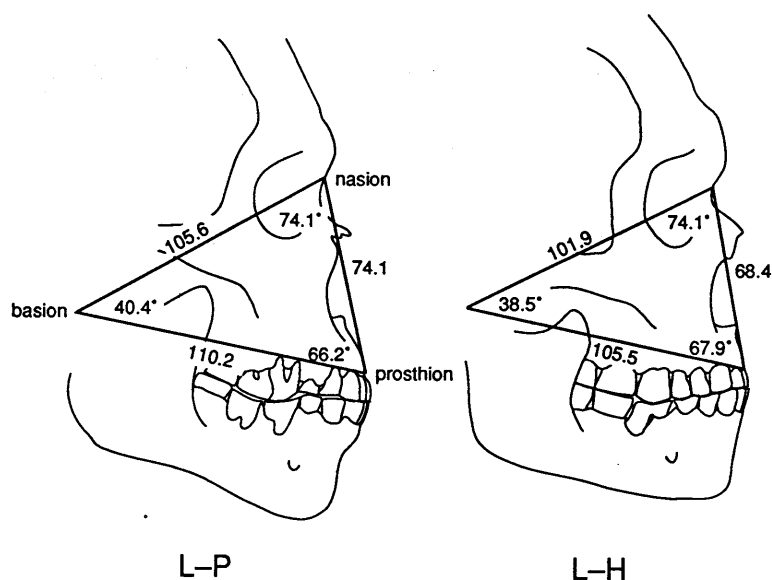


Fig. 8. Comparison of male mean facial shape and size for Late-Pleistocene and Late-Holocene south-eastern Australian Aborigines.

TABLE 5. Loading matrix of correlations between predictors and discriminant functions for the analysis of the Late-Pleistocene, Mid-Holocene and Late-Holocene male groups

Variable	Function 1	Function 2
Nasal breadth	0.457	0.290
Orbital height	-0.277	-0.048
Alveolar length	0.276	-0.033
Supraorbital breadth	0.424	-0.720
Postorbital breadth	0.049	-0.612
Nasion-nasospinale	0.241	-0.385
Nasospinale-prosthion	0.331	0.369

cases should be considered multivariate outliers with $p < .001$. Group classification results revealed that none of the Holocene orofacial skeletons had been allocated to the L-P group, and only one of the L-P cases (Coobool Creek 65) had been allocated to the mid-Holocene due to its relatively reduced supraorbital and subnasal dimensions. There was greater overlap between the two Holocene samples with 22.2% of the M-H group being classified as L-H and 20.8% of the L-H group classified as M-H. The classification results are supported by the Mahalanobis distances (D^2) between group means which indicate that the L-P series is the

most distinctive in the analysis, with a D^2 of 4.26 between the L-P and M-H, 4.64 between L-P and L-H and 2.91 between the two Holocene groups. The overlap in the distributions of the Holocene groups, combined with their similar distances from the L-P series, suggests that the major period of change in orofacial dimensions in south-eastern Australia was in the early Holocene, with little change between 5000 years BP and the present.

DISCUSSION

Comparison of dental dimensions from late-Pleistocene, mid-Holocene and late-Holocene Aboriginal skeletons from south-eastern Australia indicates that there has been a reduction in tooth size during the first 5000 years of the Holocene. The rate at which the teeth reduce in size varies according to sex and tooth category. Dental reduction is considerably greater in males, which has the effect of reducing levels of sexual dimorphism in the Holocene. However, the L-P and M-H female samples are small and these results may change when a larger sample becomes available. Average amounts of dental reduction in males are 4.5% from the L-P to M-H, with a slight

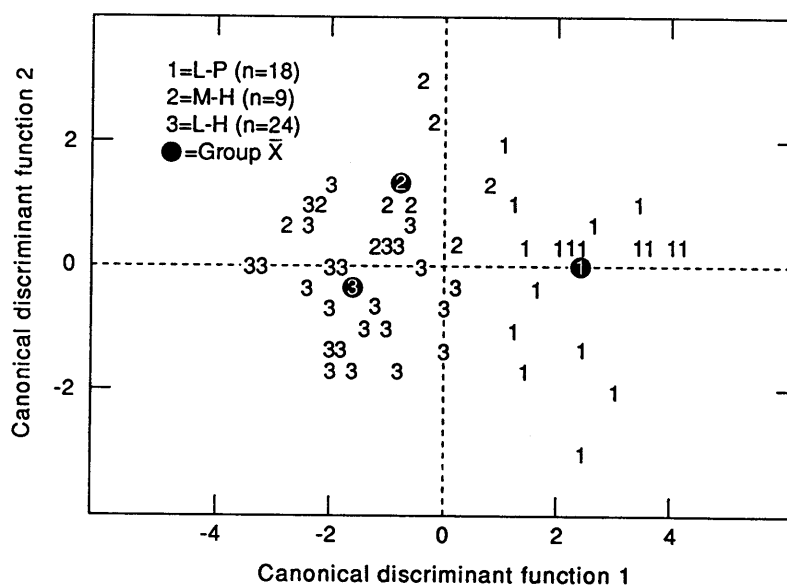


Fig. 9. Direct discriminant analysis of 7 oro-facial skeletal dimensions for the 3 male groups. Loading matrix correlations indicate that the major separation on function 1 is due to greater nasal breadth, supraorbital breadth and mid-facial height dimensions in group 1. Separation on function 2 results from lower supraorbital and postorbital dimensions in group 2.

increase of 1.2% from the middle to late-Holocene. Female average tooth size decreases 1.4% from the L-P to the M-H, with a further decrease of 0.9% over the second half of the Holocene. Reduction in tooth size during the first 5000 years of the Holocene is considerably less than that which occurred for the facial skeleton and cranial vault over the same time period. Most male facial dimensions in the L-P group are 6-12% larger than those in mid-Holocene. Relative to the average decrease in male craniofacial dimensions of 7.3% (combined face and mandible) the teeth have actually increased in size. Similarly tooth size has increased relative to the reduction in endocranial volume of 9.5%, and if the male stature estimates in Brown (1987, 1989, 1992) for L-P (181 cm) and L-H (166 cm) are correct this extends to body size as well.

The teeth which decrease most in size between the L-P and M-H are the maxillary lateral incisors and first molars, and the mandibular second premolars and first molars. If there is a developmental interaction, involving dental field theory and allometric relationships, between decreasing size in the facial skeleton and the developmental areas of the teeth (Sofaer et al., 1971; Anderson et al., 1975; Gould, 1975) then you would expect the later developing teeth in each category to

preferentially reduce rather than the first molars. It is also unlikely that this dental reduction is a straight forward allometric response to decreasing skull and body size (Pilbeam and Gould, 1974; Wolpoff, 1985). In Australian Aboriginal skeletons the maxillary lateral incisors and first molars, and mandibular second premolars and first molars, have lower levels of shared variance with craniofacial size and stature than most other teeth. For example the r^2 values between these teeth and endocranial volume in a sample of 153 modern Aboriginal crania varies between 0.09 and 0.18 while the canines and second molars vary between 0.25 and 0.27. If tooth dimensions were reducing allometrically with the size of the facial skeleton or cranium then this should be most apparent in the teeth whose size covaries most closely with these skeletal features. This would mean that maximum reduction occurs in the canines and second molars which is not what happens, at least for the buccolingual crown dimension.

There are also differences in the rates of dental attrition between the late-Pleistocene and late-Holocene groups, with the principal axis results indicating a higher rate of dental attrition in the Pleistocene. This is a surprising result as there is nothing in the archaeological record of south-eastern Australia to indicate either a

change in food preparation technology or diet over this time period (White and O'Connell, 1982). Before developing causal links between this parallel change in attrition and tooth size it should be noted that both the L-P and L-H groups are hunters and gathers with typically acute levels of dental attrition. The dentitions of both groups are characterised by occlusal dentine exposure at an early age and baring of the pulp cavity, followed by apical abscess development and tooth loss, in early middle age. Differences in rates of attrition between the L-P and L-H are probably only sufficient to allow for pulp exposure 2 to 5 years earlier in life, in the Pleistocene, than in the late-Holocene. Higher rates of dental attrition in the Australian Pleistocene could as readily be the result of the greater use of the teeth in functions unrelated to mastication (Barrett, 1977), for example the prolonged chewing of fibre to make twine (Beveridge, 1883; Curr, 1889), or higher levels of airborne and waterborne grit as minimal pre-masticatory preparation of food.

Dental and skeletal data agree in placing the major period of size reduction in south-eastern Australia between 10,000 and 5,000 years BP, with little or no change over the last 5000 years. Morphological and metrical comparison of the mid-Holocene crania from Keera Station and Barham place them within the modern range of variation and distinct from the late-Pleistocene materials from Coobool Creek, Nacurrie and Kow Swamp (Brown, 1989; Daley, 1986). It has also not been possible to distinguish the mid-Holocene crania and dentitions from Roonka from recent South Australian samples (Pietruszewsky, 1979; Smith et al., 1988). In combination these data suggest that in south-eastern Australia diachronic change in the size of the skeleton and dentition was primarily an early Holocene, 8000 to 6000 years BP, phenomenon. This falls within the period of structural reduction of the facial skeleton and dentition reported for the Mediterranean (Le Blanc and Black, 1974), Nubia and the Levant (Carlson and Van Gervan, 1977; Calcagno, 1986; Smith et al., 1986), where similarly there is no apparent change after 6000-4000 years BP.

Although there are chronological differences of the order of ± 1500 years, the timing of these events are in general concordance with those reported for dental reduction in South and East Asia (Brace, 1978; Brace and Nagai, 1982; Brace et al., 1984; Kennedy, 1984; Lukacs, 1984; Kennedy et al., 1987), and Europe (Fraye, 1978; Y'Edynak, 1989). Explanations

of dental reduction in the Old World almost invariably focus on the chronological associations with the Neolithic, development of agriculture, advances in food preparation technology and more sedentary lifestyles. While these models may indeed have some explanative power in the Old World it is unlikely that cultural developments played a major role in Australia. Technological change, at least in a form which can significantly alter the structure of the food bolus, decrease dental attrition and reduce the selection for a large and robust masticatory apparatus, did not happen in south-eastern Australia. Although there is some reduction in the rate of maxillary molar attrition, relative to the size of the face, head and body the teeth actually increase in size in the mid to late-Holocene. This may be because the factors selecting for large teeth take precedence over whatever is selecting for smaller body size.

It is also unlikely that Macchiarelli and Bondioli's (1986) suggestion that dental reduction followed selection for smaller body size under conditions of high population density, increased competition for resources and greater disease load is of relevance to the Australian situation. Claims for an intensification phase in the south-eastern Australian Holocene with increased sedentism, higher population densities, forced use of marginal environments and the development of more complex social networks (Lourandos 1983, 1985; Ross, 1985; Williams, 1987; Pardoe, 1988) have been severely criticised. It is becoming increasingly clear that the evidence for intensification was largely an artifact of site selection, site preservation and dating strategy (Beaton, 1983, 1985; Brown, 1989; Head, 1990; Bird and Frankel 1991). More importantly if the intensification phase did not begin until 4,000 years BP (Lourandos 1983, 1985; Ross 1985), with a peak at 2000-2500 years BP (Ross 1985), then this postdates by several thousand years the period of body size and dental reduction.

I have previously argued that a more reasonable explanation of Holocene size reduction was climatic change during the first half of the Holocene (Brown 1987, 1989). This explanation relies on three separate groups of observations. Firstly, in conformity with the bioclimatic predictions of (Bergmann, 1847) and (Allen, 1877) many species with extensive geographic distributions display an inverse relationship for both body size and limb proportions with environmental temperature and humidity (Mayr, 1963; Peters, 1983; Yom-Tov

and Nix, 1986). Similar surveys of body size, limb proportions and head form in humans have confirmed that global variation in human body form correlates with climate (Hiernaux, 1968; Schreider, 1975; Roberts, 1978; Macho, 1987). The generally accepted explanation of this relationship relies on the observation that larger animals, with their smaller surface-to-volume ratios, lose less heat per gram of body weight to the environment than smaller conspecifics (Gordon et al., 1976).

Secondly palaeoclimatic data (Shackelton and Opdyke, 1973; Singh and Geissler, 1985; COHMAP, 1988) indicate that during the period 8000-6000 years BP in south-eastern Australia sea levels rose to their current position, there was a gradual increase in average air temperatures with less seasonal variation and cool, temperate plant taxa disappeared from all but upland regions. Finally, the post-Pleistocene reduction in Aboriginal stature, muscle bulk and endocranial volume, combined with alterations in head size and shape, correspond with what would be predicted for a human population living in a hotter climate (Roberts, 1953; Beals, 1972; Roberts, 1978; Guglielmino-Matessi et al., 1979; Crognier, 1981; Beals et al., 1983). If selection is favouring a reduction in skeletal and muscle mass some reduction in tooth size could be expected as well due to the allometric associations with head and body size (Wolpoff, 1985). If the dentition remained too large, with associated displacement and malocclusion of teeth, selection may have favoured continued reduction in tooth size until a balanced occlusion was obtained (Brown 1987).

It is unclear how relevant the post-Pleistocene reduction in dental and skeletal mass in south-eastern Australia is to arguments for structural reduction of dental dimensions in other parts of the world. Most studies of structural reduction in human tooth size have not extended to include other aspects of the masticatory system, or cranial and body size in general. Where a wider range of data have been obtained, most notably by Smith and her co-workers for the Levant (Smith et al., 1984, 1985, 1986), it appears that the Australian situation is repeated with a reduction of both skeletal and dental elements. Perhaps if the extensive body of data on post-Pleistocene dental reduction collected by Brace (1964, 1967, 1978, 1980; Brace and Mahler 1971; Brace and Nagai 1982; Brace et al., 1984), and others who have been stimulated by his work, were examined relative to skeletal and cranial size then relative dental expansion may be a

feature of these areas as well. Whatever the situation in Europe and Asia it appears clear that relative to body size human teeth increased, rather than decreased, in size during the Australian Holocene.

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