

Early to mid-Holocene South African Later Stone Age human crania exhibit a distinctly Khoesan morphological pattern

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The sample of South African early to mid-Holocene Later Stone Age (LSA) human crania is small and quite fragmentary, limiting our knowledge of human craniofacial morphology for this period. Previous limited analyses have described the morphology displayed by these early crania as a combination of Khoesan and non-Khoesan traits. Although essentially Khoesan-like in terms of facial morphology, their overall large size and robust neurocranial structure were regarded as atypical of Khoesan craniofacial morphology, leading to questions about the role of these early populations in the ancestry of recent Khoesan populations. Here we provide a quantitative analysis in which we compare five well-preserved pre-5000 BP LSA crania with (i) a large sample of post-5000 BP LSA Khoesan crania; and (ii) a sample of crania from recent South African Bantu-speakers. We show that these pre-5000 BP crania fall comfortably within the range of variation observed for the post-5000 BP Khoesan sample, in terms of both size and shape, suggesting that distinctive Khoesan craniofacial morphology was already present in South African LSA populations by the first half of the Holocene.

Introduction

Khoesan is a term used to identify a large cluster of southern African peoples who share a number of linguistic, cultural and biological traits which distinguish them from neighbouring Bantu-speakers.^{1,2} Although linguistically diverse, all Khoesan

groups speak click languages.^{3,4} Similarities in territorial organization, gender relations, kinship, ritual and cosmology are also shared across all Khoesan groups.² Biologically, the Khoesan exhibit a number of morphological characteristics such as light yellow-brown skin, epicanthic eye folds and female steatopygia, that are unique among southern African populations.^{2,5}

The Khoesan possess some of the deepest genetic roots of all recent humans, possibly reaching as far back as the early Late Pleistocene.^{6,7} In contrast, their distinctive phenotype appears to have had a much more recent origin. Late Pleistocene South African fossils, such as the c. 110 000–90 000-year-old Klasies River specimens and the c. 80 000–55 000-year-old Border Cave specimens, cannot be securely assigned to any contemporary African population, let alone to the Khoesan, on the basis of craniofacial traits.^{8–12} The more recent Hofmeyr cranium (ELM 24; c. 36 000 years old) also does not resemble the craniofacial pattern of recent Khoesan peoples.¹³

On current evidence, the earliest appearance of Khoesan-like craniofacial traits in South African human populations likely dates back to the terminal Pleistocene or early Holocene. Analyses of the 'Fish Hoek Man' cranium (SAM-AP 4692), reportedly dated to c. 12 000 BP, indicate a close resemblance to recent Khoesan peoples.^{14–19} However, a secure date for SAM-AP 4692 is not yet available, and therefore this specimen cannot at this stage provide firm support for a terminal Pleistocene age for the appearance of characteristic Khoesan craniofacial traits.

The earliest securely dated cranium which displays close morphological affinities to Khoesan crania is the terminal Pleistocene/early Holocene 'Albany Man' cranium (UCT 378) from Elands Bay Cave on the Cape southwest coast (Table 1).^{18,20} In addition to UCT 378, systematic excavations in 1978 produced a second fragmentary, early Holocene cranium, UCT 374 (Table 1).^{18,20} Bräuer and Rösing¹⁸ note that UCT 378 combines large overall size and robusticity with typical Khoesan facial morphology. UCT 374 has thus far not been described in the literature.

The site of Matjes River Rock Shelter in the southern Cape has also produced several fragmentary human crania from its terminal Pleistocene/early Holocene Layer D.^{21,22} Unfortunately, only one individual from this layer, NMB 1342 (also designated MR 1), has been securely dated to the terminal Pleistocene/early Holocene (Table 1).^{22,23,27} Like UCT 378, NMB 1342 is a large, robust cranium which displays characteristic Khoesan facial

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Table 1. Securely dated terminal Pleistocene/early Holocene South African human crania.

Accession no.	Locality/Region	Date (BP)	Dating lab. no.	Reference
UCT 378	Elands Bay Cave, S.W. Cape	10 860 ± 180	OxA-478	18, 20, 27
NMB 1342	Matjes River Cave, S. Cape	10 120 ± 200	UCLA-1746A	22, 27
"	"	9688 ± 36	OxA-V-2064-56	23
UCT156*	Knysna Heads, S. Cape	10 110 ± 80	GrA-23223	19, 31
UCT 374	Elands Bay Cave, S.W. Cape	9750 ± 100	Pta-3086	18, 20, 27
ALB 119	Wilton Large Rock Shelter, E. Cape	8260 ± 720	GaK-1541	24, 25, 27
SAM5055*	Robberg Peninsula, S. Cape	6995 ± 50	OxA-V-2065-42	19, 31
SAM4182*	Drury's Cave, S. Cape	6811 ± 36	OxA-V-2056-26	19, 31
UCT180*	Oakhurst Rock Shelter, S. Cape	6180 ± 70	Pta-3718	26, 27
SAM6272*	Darling district, S.W. Cape	5830 ± 80	Pta-9082	19, 31

*Crania marked with an asterisk were used in the current analysis.

morphology. The other fragmentary crania from Layer D display similar robust Khoesan-like morphology.¹⁸

Wilton Large Rock Shelter in the Eastern Cape and Oakhurst Cave in the southern Cape produced securely dated crania from the first half of the Holocene (Table 1).²⁴⁻²⁷ Although belonging to a sub-adult, ALB 119 from Wilton Large Rock Shelter, resembles crania from Elands Bay Cave and Matjes River Layer D in terms of combining Khoesan facial form with overall large size and robusticity.¹⁸ Unfortunately, the crania from Oakhurst have not previously been analysed from a morphological perspective. We include one cranium from this site, UCT 180, in our analysis.

Braüer and Rösing¹⁸ have argued that although many of these early crania display Khoesan-like facial morphology, their large overall size and robusticity apparently distinguishes them from more recent Khoesan crania. It has even been suggested that their greater size and robusticity may align them with Bantu-speakers rather than with the Khoesan.^{18,28} There has, however, never been an adequate investigation of the purported distinctiveness of early to mid-Holocene South African crania. The fragmentary nature of this cranial sample and the absence of a comparative cranial sample which adequately represents the range of morphological variation present in Khoesan populations stifled previous attempts to address this issue. It is in this context that we present a metrical comparison between five, well-preserved, pre-5000 BP LSA crania (four of which have recently been directly dated for the first time), a sample of post-5000 BP LSA Khoesan crania, and a cranial sample from recent Bantu-speakers.

Materials and methods

Adult status and sex were determined on the basis of a combination of cranial and, when available, postcranial morphological characteristics.^{29,30} The five pre-5000 BP crania analysed all belong to males. Accession numbers, localities, dates and dating laboratory numbers for these crania are provided in Table 1. The crania which made up the post-5000 BP LSA Khoesan sample ($n = 100$) was composed of individually dated male crania from the western, southwestern, southern and southeastern coasts and coastal forelands of South Africa.^{19,31} A comparative Bantu-speaker cranial sample ($n = 50$) was composed of recent cadaver-derived male crania from the Raymond A. Dart Collection of Human Skeletons, University of the Witwatersrand, Johannesburg.

Three-dimensional coordinates of 20 cranial landmarks were recorded on the left side of each cranium (Table 2) using a Microscribe™ 3-D digitizer and *InScribe-32* software (Immersion Corp., San Jose, CA). Most landmarks were of homology type I, according to the criteria of Bookstein.³² Four were of type II (P, O, BA, MXT) and two were of type III (1/2BN, 1/2BL). Homology type I concerns discrete juxtapositions of tissues (points in space where two or three structures meet, such as cranial sutures) and have the highest rates of reproducibility; homology type II

Table 2. Cranial landmarks used in this study and their descriptions.

Landmark no.	Landmark	Landmark description
1	B	Bregma
2	1/2BN	Halfway along bregma to nasion arc
3	N	Nasion
4	NS	Nasospinale
5	PR	Prosthion
6	D	Dacryon
7	ZYO	Zygoorbitale
8	FMO	Frontomolare orbitale
9	ZYM	Zygomaxillare
10	PTP	Pterion posterior
11	P	Porion
12	1/2BL	Halfway along lambda to bregma arc
13	AST	Asterion
14	L	Lambda
15	O	Opisthion
16	BA	Basion
17	BOC	Basioccipital-sphenoid synchondrosis
18	H	Hormion
19	TSP	Temporal-sphenoid junction at petrous
20	MXT	Maxillary tuberosity

concerns maxima of curvatures of morphogenetic processes (e.g. the glabella); and homology type III concerns constructed landmarks (e.g. midpoints between two landmarks). Prior to analysis, coordinate data were transformed into linear data, and a subset of 48 variables was selected to represent overall cranial morphology without redundancy (Table 3).

Principal components analysis (PCA)^{33,34} was used to investigate the morphological affinities of the pre-5000 BP sample and also to characterize their primary morphological traits. All analyses were carried out on untransformed data (preserving size). The computation of the principal components (PCs) was done via the correlation matrix. PCA has the advantage of being able to reduce a large data set of (possibly) correlated variables into a (smaller) number of uncorrelated variables, the PCs. Analysing the PCs makes it easier to identify meaningful underlying variables that distinguish crania from one another. PCs may be plotted against each other, to visualize morphological relationships. Specimens that are morphologically similar occupy similar multivariate space. PCA is particularly useful in the context of this study in that it allows for the evaluation of size and size-related shape variation within the study sample. In biological studies, the first principal component commonly reflects variation in size and size-related shape. One can determine whether the crania of pre-5000 BP people were significantly larger than those of later Khoesan people by analysing the first principal component.

Results

Table 4 presents the eigenvectors for the first three PCs (see supplementary material online). The component loadings on the first PC are all positive, confirming that this reflects size-related variation. In Figs 1a and 1b, the component scores

Table 3. Subset of linear distances selected for further analyses.

No.	Distance	No.	Distance	No.	Distance
1	B-1/2BN	17	PR-MXT	33	P-MXT
2	B-N	18	D-ZYO	34	1/2BL-L
3	B-PTP	19	D-FMO	35	AST-L
4	B-1/2BL	20	ZYO-FMO	36	AST-O
5	1/2BN-N	21	ZYO-ZYM	37	AST-BA
6	1/2BN-PTP	22	FMO-ZYM	38	AST-TSP
7	N-NS	23	FMO-PTP	39	L-O
8	N-D	24	ZYM-PTP	40	O-BA
9	N-ZYO	25	ZYM-P	41	BA-BOC
10	N-FMO	26	ZYM-MXT	42	BA-H
11	N-PTP	27	PTP-P	43	BA-TSP
12	NS-PR	28	PTP-1/2BL	44	BOC-H
13	NS-ZYO	29	PTP-AST	45	BOC-TSP
14	NS-ZYM	30	PTP-L	46	BOC-MXT
15	PR-ZYM	31	P-AST	47	H-MXT
16	PR-H	32	P-TSP	48	TSP-MXT

for the first three PCs are plotted against each other. In both plots, 95% confidence ellipses are constructed around the post-5000 BP and Bantu-speaker samples. PC 1 represents size and size-related shape variation. The most positive values along PC 1 represent large crania characterized by long/broad faces and prognathic maxillary regions. The most negative values represent small crania, characterized by short/narrow faces and orthognathic maxillary regions. The most positive values along PC 2 represent crania characterized by reduced frontal heights, lengths and breadths, and retracted upper-facial regions. The most negative values represent crania characterized by increased frontal heights, lengths and breadths, and projecting upper-facial regions. The most positive values along PC 3 represent crania characterized by increased frontal heights, lengths and breadths, reduced facial heights, and increased neurocranial lengths and posterior neurocranial heights. The most negative values represent crania characterized by reduced frontal heights, lengths and breadths, increased facial heights and reduced neurocranial lengths and posterior neurocranial heights. Although there are overlaps along both PCs in Fig. 1a, it is evident that crania in the post-5000 BP sample are generally smaller than crania in the Bantu-speaker sample, and are characterized by shorter/narrower faces and less prognathic maxillary regions (PC 1). Post-5000 BP crania are also characterized by increased frontal heights, lengths and breadths, and more projecting upper-facial regions, while crania in the Bantu-speaker sample display the opposite trend. All five pre-5000 BP crania fall well within the 95% confidence ellipse of the post-5000 BP cranial sample, while three (UCT 180, SAM-AP 5055, UCT 156) fall outside the range of variation of the Bantu-speaker sample. Their positions along PC 1 indicate that they are relatively large and possess relatively longer/broader faces and more prognathic maxillary regions than the majority of post-5000 BP crania. They are indistinguishable from the Bantu-speaker comparative sample along this PC. Their positions along PC 2 indicate that they are characterized by increased frontal heights, lengths and breadths and projecting upper-facial regions. These traits distinguish them from the majority of the Bantu-speaker sample and align them with the post-5000 BP LSA sample. In Fig. 1b, all five pre-5000 BP crania again fall within the range of variation of the post-5000 BP sample, with four (UCT 180, SAM-AP 4182, SAM-AP 5055, UCT 156) falling outside the range of variation of the Bantu-speaker sample. The earliest cranium in the pre-5000 BP sample, UCT 156, falls on the edge of the 95% confidence ellipse of the post-5000 BP sample, reflecting a combination of large frontal region, projecting upper-facial region, reduced facial height and increased neurocranial length.

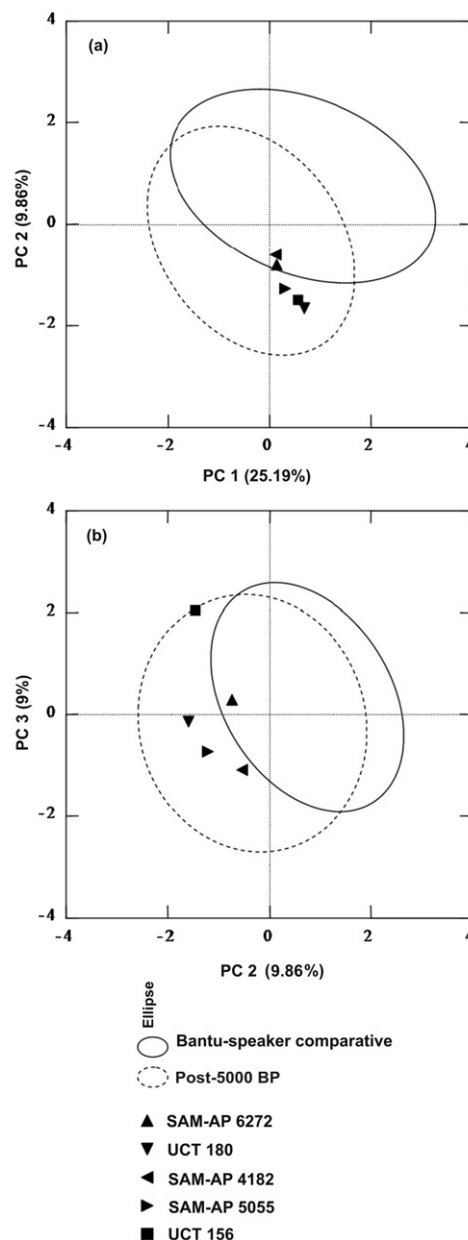


Fig. 1. Plot of (a) PC 1 and PC 2 and (b) PC 2 and PC 3 of a principal components analysis based on the five pre-5000 BP LSA crania, a sample of post-5000 BP LSA crania and a sample of crania from recent South African Bantu-speakers

Discussion and conclusion

With only five pre-5000 BP LSA crania available, sample size is an obvious problem when it comes to interpreting the results of this study. A larger sample would be desirable because it would better reflect the original variation of this early population. However, it is very rare that Pleistocene and early Holocene human skeletal material is found in adequate quantities to be truly representative of the original variation of an ancient population. The results should be taken with caution, bearing this limitation in mind. Nevertheless, the available sample does allow for certain preliminary deductions.

The current study confirms previous observations that early to mid-Holocene South African human crania resemble those of more recent Khoesan populations in terms of facial shape.¹⁸ Although these early crania are relatively large, they fall well within the range of variation of late Holocene LSA Khoesan crania, in terms of both size and primary shape variation. This contradicts an earlier assertion that early to mid-Holocene

populations possessed significantly larger crania than recent Khoesan.¹⁸ The individuals studied here also fall outside or on the edge of the range of variation of a recent Bantu-speaker comparative sample, further confirming their Khoesan affinities.

It has been suggested that early to mid-Holocene South Africans differed from later Khoesan people in terms of possessing more robust crania.¹⁸ Although the current study does not specifically investigate robusticity, it is known that robusticity is strongly correlated with cranial size.³⁵ Since cranial size during the South African early to mid-Holocene appears to have been quite large, it comes as no surprise that early crania were also quite robust. Some late Holocene LSA crania also display a combination of large overall size and high levels of robusticity.^{19,31} High levels of robusticity are thus also not unique to the early sample.

The contradiction between the results of this study and the observations of Bräuer and Rösing¹⁸ can be explained. When Bräuer and Rösing¹⁸ performed their study, very little was known about craniofacial variation in Khoesan populations during the Holocene. This was primarily due to the poorly dated LSA skeletal sample.^{18,36} Today, we have access to a large, well-dated South African LSA cranial sample which extends across most of the Holocene.^{19,31} We are thus in a better position to analyse cranial morphology at specific times during the Holocene.³¹

This study showed that early to mid-Holocene South African populations already possessed distinctly Khoesan craniofacial morphology. Although results indicate that the Khoesan phenotype was already present at the start of the Holocene, we are currently not in a position to determine when it actually originated. As has been stated, the c. 36 000-year-old Hofmeyr cranium does not display Khoesan morphology. The Khoesan phenotype must thus have originated sometime after c. 36 000 years ago, during the terminal Pleistocene, a hypothesis previously suggested by Morris.^{37,38} Unfortunately, there is no securely dated, complete cranium from this period currently available to confirm this hypothesis. Nevertheless, a probable terminal Pleistocene origin for the Khoesan phenotype marks them as one of the few contemporary human populations whose morphological origins pre-date the advent of the Holocene. On current evidence, the craniofacial traits which characterize contemporary Chinese, European and Native American populations only appeared to have developed during the course of the Holocene.³⁹⁻⁴¹

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- Schultze L. (1928). *Zur Kenntnis des Körpers der Hottentotten und Buschmänner*. G. Fischer, Jena.
- Barnard A. (1992). *Hunters and Herders of Southern Africa*. Cambridge University Press, Cambridge.
- Westphal E.O.J. (1963). The linguistic prehistory of southern Africa: Bush, Kwadi, Hottentot, and Bantu linguistic relationships. *Africa* **33**, 237–265.
- Westphal E.O.J. (1971). The click languages of southern and eastern Africa. In *Current Trends in Linguistics*, vol. 7. Linguistics in Sub-Saharan Africa, ed. T.A. Sebeok, pp. 367–420. Mouton, The Hague.
- Tobias P.V. (1978). The San: an evolutionary perspective. In *The Bushmen*, ed. P.V. Tobias, pp. 16–32. Human and Rousseau, Cape Town.
- Soodyall H. and Jenkins T. (1992). Mitochondrial DNA polymorphisms in Khoisan populations from southern Africa. *Ann. Hum. Genet.* **56**, 315–324.
- Knight A., Underhill P.A., Mortensen H.M., Zhivotovsky L.A., Lin A.A., Henn B.M., Louis D., Ruhlen M. and Mountain J.L. (2003). African Y chromosome and mtDNA divergence provides insight into the history of click

- languages. *Curr. Biol.* **13**, 464–473.
- Singer R. and Wymer J.J. (1982). *The Middle Stone Age at Klasies River Mouth in South Africa*. University of Chicago Press, Chicago.
- Grün R., Shackleton N.J. and Deacon H.J. (1990). Electron-spin-resonance dating of tooth enamel from Klasies River Mouth cave. *Curr. Anthropol.* **31**, 427–432.
- Beaumont P.B. (1980). On the age of Border Cave hominids 1–5. *Palaeontologia afr.* **23**, 21–33.
- Morris A.G. (1992). Biological relationships between Upper Pleistocene and Holocene populations in southern Africa. In *Continuity or Replacement: Controversies in Homo sapiens evolution*, eds. G. Bräuer and F.H. Smith, pp. 131–143. A.A. Balkema, Rotterdam.
- Wolpoff M.H. (1996). *Human Evolution*. McGraw-Hill, New York.
- Grine F.E., Bailey R.M., Harvati K., Nathan R.P., Morris A.G., Henderson G.M., Ribot I. and Pike A.W.G. (2007). Late Pleistocene human skull from Hofmeyr, South Africa and modern human origins. *Science* **315**, 226–229.
- Peers B. and Goodwin A.J.H. (1953). Two caves at Kalk Bay, Cape Peninsula. Part II: Peer's Shelter B/102. *S. Afr. Archaeol. Bull.* **8**, 67–77.
- Deacon J. and Wilson M. (1992). Peers Cave: The 'Cave the World Forgot'. *The Digging Stick* **9**, 2–5.
- Rightmire P.G. (1974). *The Later Pleistocene and recent evolution of man in Africa*. MSS Modular Publications, Module 27, 1–38.
- Rightmire P.G. (1978). Human skeletal remains from the southern Cape Province and their bearing on the Stone Age prehistory of South Africa. *Quat. Res.* **9**, 219–230.
- Bräuer G. and Rösing F.W. (1989). Human biological history in southern Africa. *Rassengeschichte der Menschheit* **13**, 6–137.
- Stynder D.D. (2006). *A quantitative assessment of variation in Holocene Khoesan crania from South Africa's western, south-western, southern and south-eastern coasts and coastal forelands*. Ph.D. thesis, University of Cape Town, South Africa.
- Parkington J.E. (1981). The effects of environmental change on the scheduling of visits to the Elands Bay Cave, Cape Province, S.A. In *Pattern of the Past: Studies in honour of David Clarke*, eds I. Hodder, G. Isaac and N. Hammond, pp. 341–359. Cambridge University Press, Cambridge.
- Protsch R.H. and Oberholzer J.I. (1975). Paleoanthropology, chronology, and archaeology of the Matjes River Rock Shelter. *Z. Morphol. Anthropol.* **67**(1), 32–43.
- Döckel W. (1998). *Re-investigation of the Matjes River Rock Shelter*. M.A. thesis, University of Stellenbosch, South Africa.
- Sealy J.C., Ludwig B. and Henderson Z. (2006). New radiocarbon dates for Matjes River Rock Shelter. *S. Afr. Archaeol. Bull.* **61**, 98–101.
- Deacon J. (1969). *Re-excavation and description of the Wilton type site, Albany District, eastern Cape*. M.A. thesis, University of Cape Town, South Africa.
- Deacon J. (1972). Wilton: an assessment after 50 years. *S. Afr. Archaeol. Bull.* **27**, 10–45.
- Patrick M. K. (1989). *An archaeological and anthropological study of the human skeletal remains from Oakhurst Rockshelter, George, Cape Province, southern Africa*. M.A. thesis, University of Cape Town, South Africa.
- Morris A.G. (1992). *A Master Catalogue: Holocene human skeletons from South Africa*. Witwatersrand University Press, Johannesburg.
- de Villiers H. and Fatti L. (1982). The antiquity of the Negro. *S. Afr. J. Sci.* **78**, 212–215.
- Buikstra J.E. and Ubelaker D.H. (1994). *Standards for Data Collection from Human Skeletal Remains. Research Series*, no. 44. Arkansas Archaeological Survey, Fayetteville.
- White T.D. and Folkens P.A. (2000). *Human Osteology*. Academic Press, San Diego.
- Stynder D.D., Ackermann, R.R. and Sealy, J.C. (in press). Craniofacial variation and population continuity during the South African Holocene. *Am. J. Phys. Anthropol.*
- Bookstein F.L. (1991). *Morphometric Tools for Landmark Data: Geometry and biology*. Cambridge University Press, Cambridge.
- Jolliffe I. (1986). *Principal Component Analysis*. Springer-Verlag, New York.
- Duntzman G.H. (1989). *Principal Components Analysis*. Sage Publications, California.
- Lahr M.M. and Wright R.V.S. (1996). The question of robusticity and the relationship between cranial size and shape in *Homo sapiens*. *J. Hum. Evol.* **31**, 157–191.
- Hausman A.J. (1980). *Holocene human evolution in southern Africa: the biocultural development of the Khoisan*. Ph.D. thesis, State University of New York, Binghamton, NY.
- Morris A.G. (2002). Isolation and the origin of the Khoisan: Late Pleistocene and early Holocene human evolution at the southern end of Africa. *Hum. Evol.* **17**, 105–114.
- Morris A.G. (2003). The myth of the East African 'Bushmen'. *S. Afr. Archaeol. Bull.* **58**, 85–90.
- Cunningham D.L. and Jantz R.L. (2003). The morphometric relationship of Upper Cave 101 and 103 to modern *Homo sapiens*. *J. Hum. Evol.* **45**, 1–8.
- Van Vark G.N., Kuizenga D. and L'Engle Williams F. (2003). Kennewick and Luzia: lessons from the European Upper Paleolithic. *Am. J. Phys. Anthropol.* **121**, 181–184.
- Powell J.F. and Neves W.A. (1999). Craniofacial morphology of the first Americans: Pattern and process in the peopling of the New World. *Yrbk Phys. Anthropol.* **42**, 153–188.

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Supplementary material to:

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Table 4. Eigenvectors for the first three principal components.

Variable*	PC1	PC2	PC3
B-1/2BN	0.058	-0.329	0.198
B-N	0.115	-0.324	0.180
B-PTP	0.087	-0.212	0.297
B-1/2BL	0.089	0.001	0.124
1/2BN-N	0.029	-0.372	0.147
1/2BN-PTP	0.051	-0.371	-0.013
N-NS	0.207	0.049	-0.059
N-D	0.141	0.005	0.024
N-ZYO	0.155	0.015	-0.146
N-FMO	0.192	-0.022	-0.079
N-PTP	0.098	-0.309	-0.252
NS-PR	0.129	0.004	-0.022
NS-ZYO	0.167	0.014	-0.178
NS-ZYM	0.185	-0.002	-0.157
PR-ZYM	0.202	0.027	-0.143
PR-H	0.203	0.043	-0.072
PR-MXT	0.148	0.075	-0.057
D-ZYO	0.057	0.002	-0.180
D-FMO	0.162	0.016	-0.099
ZYO-FMO	0.174	0.094	0.036
ZYO-ZYM	0.156	-0.101	-0.051
FMO-ZYM	0.215	-0.013	-0.078
FMO-PTP	0.040	-0.295	-0.267
ZYM-PTP	0.136	-0.159	-0.227
ZYM-P	0.158	0.084	0.038
ZYM-MXT	0.053	-0.010	-0.050
PTP-P	0.110	0.142	0.133
PTP-1/2BL	0.113	-0.024	0.396
PTP-AST	0.138	0.204	0.224
PTP-L	0.136	0.067	0.376
P-AST	0.153	0.071	0.040
P-TSP	0.115	0.026	0.009
P-MXT	0.228	0.077	0.003
1/2BL-L	0.119	-0.004	0.118
AST-L	0.031	-0.202	0.147
AST-O	0.100	-0.155	-0.033
AST-BA	0.184	-0.057	0.027
AST-TSP	0.187	0.027	0.031
L-O	0.127	-0.084	0.148
O-BA	0.066	0.070	0.050
BA-BOC	0.173	0.127	-0.016
BA-H	0.130	0.161	0.036
BA-TSP	0.156	0.059	0.024
BOC-H	0.063	0.090	0.012
BOC-TSP	0.079	-0.048	0.095
BOC-MXT	0.199	0.024	-0.022
H-MXT	0.213	-0.006	-0.035
TSP-MXT	0.197	0.065	-0.023

*See Table 2 for definitions.