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Shell morphometry of seven limpet species from coastal shell middens in southern Africa

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Abstract

Measurements of shell parts and features (elements) of marine limpets can be used to derive morphometric equations for estimating total shell lengths. This is demonstrated for seven limpet species commonly found on the southern African coast. The equations can be used to reconstruct whole shell lengths for highly fragmented limpet samples in prehistoric shell middens. A linear regression model is based on measurements of all shell elements, resulting in high coefficients of determination with excellent predictive power in most cases. These morphometric equations would enable archaeologists to derive more metrical information from fragmentary archaeological material than was previously the case. We also present a case study where morphometric equations of two limpet species are applied to an archaeological sample from the South African west coast for the purpose of investigating possible biases in limpet shell preservation. We conclude that small whole limpet shells survive longer than the bigger ones in this particular case, but that many more such case studies need to be conducted in order to fully understand differential preservation of southern African limpet shells in archaeological sites.

Keywords: Shell middens; Zooarchaeology; Shell analysis; Morphometry; *Cymbula*; *Scutellastra*; Southern Africa; Shell preservation; Shell taphonomy

1. Introduction

Archaeological sites on the south and west coasts of South Africa have received increasing international attention in recent years thanks to discoveries of Middle Stone Age (MSA) components with early remains of anatomically modern humans, as well as elements of material culture that point to early modern human behavior (Erlandson, 2001; Grine et al., 1998; Henshilwood et al., 2001, 2002; Rightmire and Deacon, 2001; Singer and Wymer, 1982). The uppermost levels of these deep, stratified deposits sometimes overlap the bases of several equally deep Later Stone Age coastal sites, and together they now form the very backbone of southern Africa's Stone Age sequence (Deacon and Deacon, 1999; Deacon and Geleinjse, 1988; Fagan, 1960; Goodwin, 1938; Goodwin and Malan, 1935; Inskeep, 1987; Klein, 1972; Marean et al., 2000; Shrire, 1962; Singer and Wymer, 1982; Thackeray, 2000; Volman, 1981; Wurz, 2002). They also provide data from which long-term palaeoenvironmental changes have been inferred (Avery, 1987; Cowling et al., 1999; Klein, 1972; Klein and Cruz-Uribe, 1987, 1996, 2000; Parkington et al., 2000; Shackleton, 1982; van Andel, 1989).

Overall, these sites provide insights into the cultural sequence and environmental background of Upper Pleistocene and Holocene indigenous societies, particularly the changing patterns in procurement of marine resources as sea-level recovered from its lowest mark during the Last Glacial Maximum (Inskeep, 1987; Klein, 1972; Parkington, 1981). Along the South African West Coast, such changes nicely track records of sea-surface temperature and sea-level changes for the southern Atlantic (Cohen et al., 1992; Jerardino, 1993).

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There are parallel increases in the forager population and residential permanence, increased consumption of marine resources, and local depletion of at least three species of gastropods within the last 3500 years (Jerardino, 1996; Jerardino et al., in press). Additional dietary and anatomical patterns have been derived from Holocene human skeletons recovered from the west and south coasts (Lee-Thorp et al., 1989; Pfeiffer and Sealy, 2006; Sealy and Pfeiffer, 2000). Other coastal sites have also provided key evidence that mark the introduction of pastoralism to southernmost Africa (Henshilwood, 1996; Sealy and Yates, 1994; Vogel et al., 1997). Thus, coastal sites have played a major role in the reconstruction of pre-colonial history of southernmost Africa, and continue to do so.

Quantitative and metrical analyses of marine invertebrate remains have provided both central and contextual evidence for the above reconstructions, a task which has often not been easy due to the fragmentary nature of archaeofaunal material. Fortunately, morphometric equations have been established for two species of mussels (Buchanan, 1985; Hall, 1980) and one species of crustacean (Jerardino et al., 2001), which have resulted in productive applications to archaeological case studies (Jerardino et al., in press; Thackeray, 1988).

Typical of the problem are the limpets *Cymbula* and *Scutellastra*, which are known to survive in South African shell middens, but often in statistically inadequate numbers. Archaeologists are thus forced to hugely increase overall sample size and also collect intact shells from material not sampled for marine shells in order to recover enough unbroken shells of these fragile taxa for measurement (Jerardino, in press). But excavations are increasingly faced with time and financial constraints that inhibit the recovery of voluminous shell samples. Planning and budgeting for a sampling strategy that maximizes the recovery of whole limpet shells is made doubly difficult by our inability to predict the degree of shell fragmentation ahead of excavations, let alone shell density, or the extent to which the shells will be cemented in hard matrix as often occurs in MSA components (Klein et al., 2004; Marean et al., 2004; Volman, 1978). Added to these concerns is the uncertainty whether the limpet size record based on whole shells is biased in any way. An argument could be made that larger limpets will survive better in shell midden deposits than smaller ones, thus inflating the mean length of the whole limpets recovered. A counter-argument would hold that small limpets can hide and be protected under larger shells and other spaces, and are thus less likely to fragment *in situ*. Consequently, mean length of whole limpets will distort in favor of smaller overall size. Because morphometric equations yield measurements from fragments, the potential biases introduced by measuring only whole limpets are eliminated.

The best way to overcome these problems is to develop morphometric equations for shells that allow the estimation of shell lengths from easily recognizable shell parts or shell features that survive in the highly fragmented archaeological record. Here, we propose suitable parameters of morphometric equations for seven limpet species commonly found at coastal sites in southern Africa, and apply some of these in a case study involving two of the most dominant limpet species (*C. granatina* and *S. granularis*) found in shell middens along the West Coast of South Africa. This case study is aimed at not only showing how sample sizes of shell measurements are increased with the use of fragmentary material. Here we take it further to check for possible preservational biases.

2. Materials and methods

The control samples used in this study were recently collected limpets in the reference collections of the Departments of Zoology and Archaeology at the University of Cape Town, and of IZIKO: South African Museum, Cape Town. Collection records show that most of the control specimens were collected live. A few with badly eroded apices, probably caused by wave action, were rejected. Table 1 shows the numbers of shells analyzed for seven different species, and the size ranges of each sample. None of the samples represents single localities. Instead, the geographic spread of collected specimens within each sample reflects the overall modern distribution of the species (Branch et al., 1999; Kilburn and Rippey, 1982). The one exception is the *S. granularis* sample, in which most shells came from just two locations on the West Coast, although its natural range extends much farther along south and east coasts where relatively warmer sea surface temperatures prevail (Kilburn and Rippey, 1982). The west/cold to east/warm temperature gradient appears to covary with the mineralogy and crystalline structure of the shell of *S. granularis*, specifically the thicknesses of calcitic and aragonitic layers within the shell (Cohen and Branch, 1992). However, there is no *a priori* reason why this trend should affect external shell morphometry.

The parts of the limpet shell selected for measurement are shown in Fig. 1. The choice of parts was guided by prior knowledge of typical limpet breakage patterns, also which parts were most likely to survive intact. Layout of the measurements was dictated by general shell shape. More measures could be taken on the star-shaped limpets characterized by prominent, long and, protruding ridges (*C. granatina*, *S. oculus* and *S. longicosta*). Fewer measures were possible on those with roughly oval bases and characterized by many thin and/or regularly spaced ridges (*S. granularis*, *S. argenvillei*, *S. barbara*, *S. tabularis*) (Fig. 1). Thanks to the prominent lateral ridges of the star shaped limpets, two additional measurements

Table 1
Numbers of shells analyzed and their size ranges for seven different limpet species

Species	No. of shells	Size range (mm)	
		Min	Max
C. granatina	94	20.8	96.4
C. oculus	112	29.2	120.3
S. argenvillei	97	28.3	95.3
S. barbara	82	26.3	99.1
S. granularis	102	17.3	68.9
S. longicosta	89	29.5	84.5
S. tabularis	63	28.0	135.1

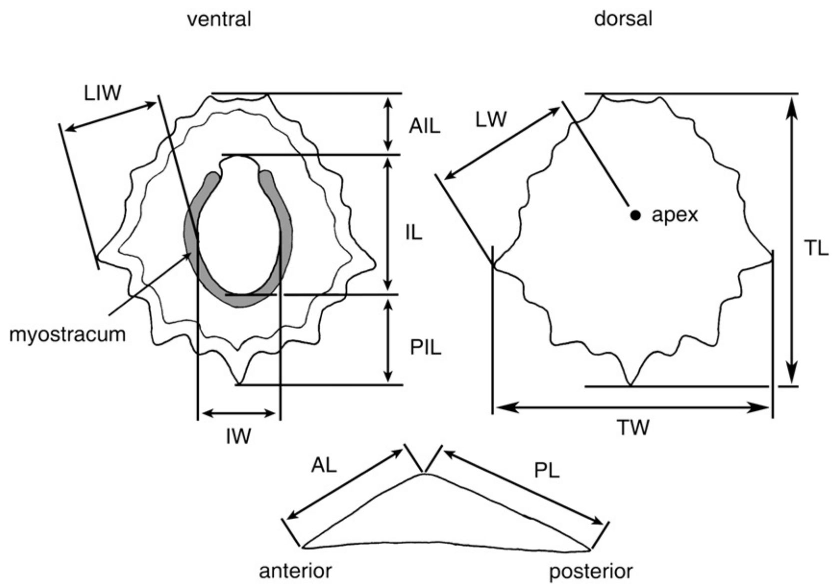

Fig. 1. Measurements obtained from limpet shells on both, ventral and dorsal sides for the purpose of establishing morphometric equations: TL, total length; TW, total width; AL, anterior length; PL, posterior length; LW, lateral width; AIL, anterior inner length; IL, inner length; PIL, posterior inner length; IW, inner width; LIW, lateral inner width. Note that lateral width and lateral inner width were not determined with oval shaped limpet shells.

can be obtained, namely lateral width and lateral inner width. These measurements are more difficult to establish for *C. granatina* shells larger than 60 mm, as lateral ridges are less pronounced when this species reaches full size.

All measurements were obtained with a 0.05 cm precision caliper. Measurements obtained from the ventral side of shells on all species depend on the proper identification of the inner edge of the myostracum (Ridgway et al., 1998), since many of the measurements on this side use this as a starting and/or end point. The inner edge is sharp and unambiguous in fresh specimens of *C. granatina* and *S. granularis* thanks to the brown to red-brown color of shell crystals present in the inner-most area of the shell surrounded by the myostracum. Color contrast in this inner area is not as visually striking in the other five species, although the myostracum (white to pale yellow) nonetheless contrasts with that of the crystals that make up the area contained by it (light blotchy grey to uneven light yellow/ beige and white crystals). Moreover, because the myostracum and the area contained by it in fresh samples have different light refraction properties visible to the naked eye, the inner edge appears sharp throughout with no areas of blending or fuzziness.

Recorded measurements were entered into spreadsheets and from these data Model I regressions were conducted with R statistical software, version 2.2.1 (R Development Core Team, 2005). As noted with previous studies (Jerardino et al., 2001), Model I regressions (Sokal and Rohlf, 1969) work on the assumption that the independent variable, namely shell length, is measured without error. As human and instrumental error are unavoidably present in all such measurements, Model II regressions should be preferred for this and similar cases. However, when the interest is on using these models for predictive rather than descriptive aims, Model I regressions should be employed regardless of the violation of this basic assumption (Legendre and Legendre, 1998).

3. Results

Table 2 presents the parameters (*a* and *b*) and coefficient of determination (r^2) of morphometric equations for the estimation of shell lengths from measurements of the various shell parts for the seven control samples. A linear regression model ($y = a + bx$) fitted the data best for each of the limpet species. The coefficients of determination for all morphometric equations are very high ($\geq$0.75), which shows their good predictive power. The only two exceptions occur with *S. longicosta*. The high r^2 values for inner length, and inner width for all species are most worthy of note, as these shell parts preserve more often than any of the others in archaeological contexts (A.J., personal observation).

3.1. A case study

C. granatina and *S. granularis* shells from a large shell sample weighing nearly 11 kg and excavated from square KK2 of ‘Grootrif G’ shell midden (Jerardino, in press) were chosen for this study. After shells were inspected closely, measurements other than inner length and inner width were also obtained given their relatively high survival and the excellent predictive power of their respective morphometric equations. Also, contrary to the case of fresh specimens, the area contained within the myostracum in these particular archaeological *S. granularis* shells is not always as contrasting, opening the possibility for introducing added error in the measurement of inner length and inner width from these shells. Consequently, measurements of total width and posterior length

Table 2
Parameters of morphometric equations for the estimation of total limpet shell length from measurements on elements of the limpet shells

Species	*X* variable	*a*	*b*	r^2
C. granatina	Total width	2.21	1.05	0.96
	Anterior length	16.05	1.27	0.92
	Posterior length	1.28	1.51	0.97
	Lateral width	7.48	1.48	0.96
	Inner length	12.43	1.38	0.94
	Inner width	18.1	1.75	0.91
	Anterior inner length	4.57	3.48	0.90
	Posterior inner length	2.02	3.39	0.84
	Lateral inner width	0.31	3.05	0.89
C. oculus	Total width	12.69	0.89	0.93
	Anterior length	16.5	1.69	0.94
	Posterior length	−0.66	1.52	0.97
	Lateral width	10.95	1.52	0.94
	Inner length	10.32	1.48	0.95
	Inner width	17.12	2.27	0.93
	Anterior inner length	−0.83	4.36	0.91
	Posterior inner length	−0.19	3.92	0.89
	Lateral inner width	15.43	2.32	0.85
S. longicosta	Total width	6.39	0.90	0.93
	Anterior length	9.20	1.83	0.89
	Posterior length	17.20	1.17	0.84
	Lateral width	7.69	1.46	0.91
	Inner length	20.35	1.25	0.85
	Inner width	22.15	2.04	0.81
	Anterior inner length	9.61	3.25	0.61
	Posterior inner length	18.94	3.05	0.69
	Lateral inner width	5.63	2.34	0.83
S. argenvillei	Total width	3.54	1.27	0.97
	Anterior length	17.66	1.15	0.88
	Posterior length	3.25	1.28	0.95
	Inner length	8.45	1.33	0.96
	Inner width	14.81	2.04	0.88
	Anterior inner length	10.29	3.33	0.88
	Posterior inner length	3.46	3.71	0.93
S. barbara	Total width	5.04	1.11	0.93
	Anterior length	10.59	1.57	0.85
	Posterior length	4.03	1.36	0.94
	Inner length	8.31	1.54	0.94
	Inner width	14.91	2.05	0.87
	Anterior inner length	−0.36	3.77	0.88
	Posterior inner length	2.99	3.55	0.87
S. granularis	Total width	4.31	1.15	0.96
	Anterior length	9.32	1.34	0.88
	Posterior length	2.48	1.28	0.87
	Inner length	3.96	1.35	0.94
	Inner width	7.8	1.9	0.88
	Anterior inner length	7.53	3.32	0.75
	Posterior inner length	4.47	3.54	0.87
S. tabularis	Total width	6.41	1.06	0.97
	Anterior length	10.43	1.89	0.96
	Posterior length	2.71	1.37	0.98
	Inner length	9.68	1.43	0.96
	Inner width	16.03	2.17	0.93
	Anterior inner length	−3.79	4.92	0.95
	Posterior inner length	1.34	4.23	0.91

The model used is that of a linear regression ($y = a + bx$), and measurements are in millimeters. In all cases, $p < 0.001$.

were established for *C. granatina*, and anterior length measurements were also obtained from *S. granularis* shells. In order to test for possible bias in the preservation of limpet shells, the mean sizes based on whole shells were compared against those reconstructed entirely from fragmented shells. The basic tenet in statistical sciences that comparisons are based on independent samples prevents us from comparing mean sizes of whole shells against those based on whole plus broken shells (Sokal and Rohlf, 1969). The statistical significance of any changes in the mean sizes is tested using a *t* test conducted with R statistical software, version 2.2.1 (R Development Core Team, 2005). Boxplots are also employed to present the results graphically.

A total of 486 *C. granatina* shells were identified from this sample consisting of the following: 135 whole shells (27.8%), 232 broken shells (47.7%) from which measurements from shell parts were derived, and a remaining 119 shells (24.5%) for which no metrical observations could be established. In the case of *S. granularis*, a total of 521 shells were recovered from the same sample: 240 were whole shells (46.0%), 172 were broken shells (33.0%) but suitable for obtaining additional metrical data, and 109 shells (21%) for which no metrical data could be established.

Fig. 2 shows the boxplots for *C. granatina* and *S. granularis* shells analyzed for our case study. A *t* test revealed that the mean size of whole *C. granatina* shells (49.5 mm) is significantly smaller ($t = 2.62$, df $= 239.3$, $p < 0.009$) than that established from broken shells (52.7 mm). The overall mean based on whole and broken shells falls, and predictably so, in between these two values at 51.6 mm. Similarly, the mean size of whole *S. granularis* shells (33.3 mm) is also significantly smaller ($t = 3.28$, df $= 370.8$, $p < 0.001$) than that for broken shells (34.5 mm) of the same species, with an overall mean size pooling whole and broken shells together at 33.8 mm.

4. Discussion and conclusions

The most straightforward way to estimate limpet shell sizes from fragmentary material is to obtain measurements on inner length and/or inner width and on two or three other shell parts (total width, anterior and posterior lengths) that have the highest survival rate in archaeological contexts. These are likely to be the most abundant measurable shell parts for both of these limpet species in excavated samples. These measures can be combined with those obtained from any whole limpets that might be recovered in order to calculate overall mean sizes. In very highly fragmented samples with no whole limpets and/or low recovery of inner length and/or inner width, other measures employed in this analysis can also be used to estimate shell lengths (Fig. 1: LW, AL, PL). However, the use of peripheral shell parts based on the ventral side of the shell (Fig. 1: LIW, AIL, PIL) could increase the chances of two or more fragments of the same shell being measured. Careful selection and comparison of such marginal parts will be necessary, including refitting if needed. This will inevitably increase the time and costs of the analysis.

The use of morphometric equations holds three clear advantages. First and foremost they open up possibilities for obtaining shell-size data from severely fragmented samples that are too small to render statistically valid sets of limpet

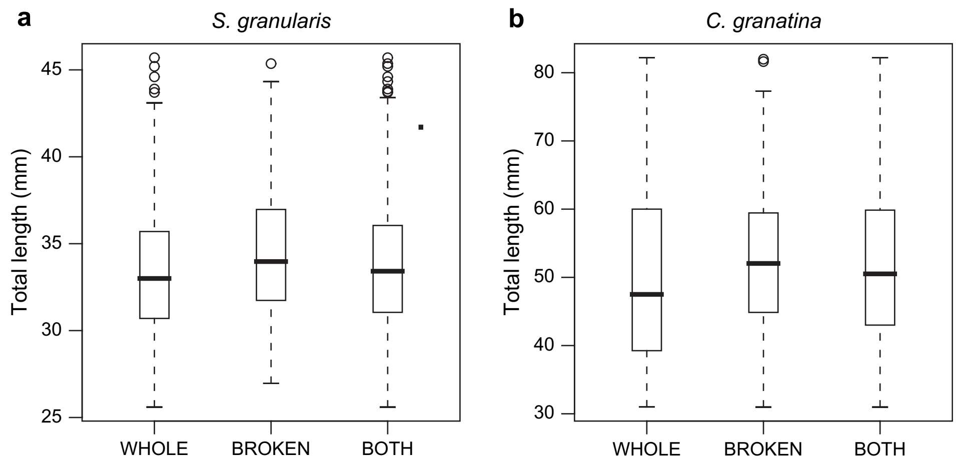

Fig. 2. Box-and-whisker plot of total shell length of *S. granularis* (a) and *C. granatina* (b) in relation to the origin of the sample. Illustrated are lower and upper quartiles (box), the median (line across the box), the range (whiskers) which is 1.57 times the inter-quartile range (Q75–Q25) and extreme values are shown separately (circles).

lengths. This is a pernicious problem for those studying the MSA exploitation of South African marine resources (Klein et al., 2004; Marean et al., 2004; Parkington, 2003; Steele and Klein, 2005). The results of our case study shows that the sample size of shell length measurements can be increased almost three fold for *C. granatina* and nearly two fold for *S. granularis*. These values can vary from case to case and are bound to be much higher where fragmentation, resulting from a combination of taphonomic factors, is more extensive than the one observed here. The second obvious advantage afforded by these equations is that they render it unnecessary to excavate large bulk shell samples in order to obtain enough whole limpets to conduct statistically valid analyses. The savings here are not only in recovery costs but also in transport, processing, storage space, and long-term curation costs.

A third contribution from the use of these equations is the possibility of basing calculations of limpet mean sizes on larger sample sizes and checking for possible preservation biases in the archaeological record. The statistically significant differences between mean sizes based on whole and fragmented shells show that fragmentation has mainly affected the integrity of larger shells and less so that of smaller shells in this specific case. The particular set of taphonomic factors that operated during and after the accumulation of GFG open air shell midden clearly biased the preservation of *C. granatina* and *S. granularis* shells, with smaller shells preserving better than the bigger ones. It is possible that the relatively larger surface area of bigger shells rendered these more susceptible to breakage due to trampling and other attritional factors when compared to smaller ones. Many of the latter were probably protected under larger shells and other gaps. These results of differential preservation may be repeated at other shell middens. However, a different combination of taphonomic factors (e.g., more protection from the elements offered by cave sites, different admixture of archaeological remains, different accumulation rates and varying degrees of burning, acidity and trampling) might well throw other results. These could range from minimum to maximum differential preservation, and/or preservational bias with an opposite trend to the one reported here. Consequently, the analyses and comparisons done here ought to be repeated with shell samples of the same and other limpet species and from an array of depositional contexts before the problem of differential preservation of southern African limpet shells in archaeological sites is properly understood.

The results presented here exemplify the power that morphometric equations have in complementing and enhancing measurements based solely on whole shells. Although the use and strength of morphometric equations has already been recognized and applied to archaeological reconstructions along the southern Pacific coast (Jerardino et al., 1992; Oliva and Castilla, 1992), the generation of these equations for other species elsewhere in the world would be of great benefit given the regular use of metrical observations on whole shells in archaeological reconstructions (Erlandson et al., 2004; Mannino and Thomas, 2002; Milner et al., 2007). Finally, the use of morphometric equations should not be restricted to new research cases only. These ought to be applied to re-evaluate inferred scenarios where whole shells have been the primary source of data.

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References

Avery, D.M., 1987. Late Pleistocene coastal environment of the southern Cape Province of South Africa: micromammals from Klasies River Mouth. Journal of Archaeological Science 14, 405–421.

Branch, G.M., Griffiths, C.L., Branch, M.L., Beckley, L.E., 1999. Two Oceans: a Guide to the Marine Life of Southern Africa. David Phillip, Cape Town.

Buchanan, W.F., 1985. Middens and mussels: an archaeological enquiry. South African Journal of Science 81, 15–16.

Cohen, A.L., Branch, G.M., 1992. Environmentally controlled variation in the structure and mineralogy of *Patella granularis* shells from the coast of southern Africa: implications for palaeotemperature assessments. Palaeogeography, Palaeoclimatology, Palaeoecology 91, 49–57.

Cohen, A., Parkington, J.E., Brundrit, G.B., Van der Merwe, N.J., 1992. A Holocene marine climate record in mollusc shells from the southwest African coast. Quaternary Research 38, 379–385.

Cowling, R.M., Cartwright, C.T., Parkington, J.E., Allsopp, J.C., 1999. Fossil wood charcoal assemblages from Elands Bay Cave, South Africa: implications for Late Quaternary vegetation and climates in the winter-rainfall fynbos biome. Journal of Biogeography 26, 367–378.

Deacon, J.H., Deacon, J., 1999. Human Beginnings in South Africa: Uncovering the Secrets of the Stone Age. David Phillip, Cape Town, Johannesburg.

Deacon, H.J., Geleinjse, V.B., 1988. The stratigraphy and sedimentology of the main site sequence, Klasies River, South Africa. South African Archaeological Bulletin 43, 5–14.

Erlandson, J.M., 2001. The archaeology of aquatic adaptations: paradigms for a new millennium. Journal of Archaeological Research 9, 287–350.

Erlandson, J.M., Rick, T.C., Vellanoweth, R.L., 2004. Human impacts on ancient environments: a case study from California's Northern Channel Islands. In: Fitzpatrick, S.M. (Ed.), Voyages of Discovery: The Archaeology of Islands. Praeger Publishers, Westport, pp. 51–83.

Fagan, B.M., 1960. The Glentyre Shelter and Oakhurst re-examined. South African Archaeological Bulletin 15, 80–94.

Goodwin, A.J.H., 1938. The archaeology of the Oakhurst Shelter, George. Transactions of the Royal Society of South Africa 25, 229–324.

Goodwin, A.J.H., Malan, B.D., 1935. Archaeology of the Cape St. Blaize cave and raised beach, Mossel Bay. Annals of the South African Museum 24, 111–140.

Grine, F.E., Pearson, O.M., Klein, R.G., Rightmire, G.P., 1998. Additional human fossils from Klasies River Mouth, South Africa. Journal of Human Evolution 35, 95–107.

Hall, M., 1980. A method for obtaining metrical data from fragmentary molluscan material found at archaeological sites. South African Journal of Science 76, 280–281.

Henshilwood, C.S., 1996. A revised chronology for the arrival of pastoralism in southernmost Africa: new evidence of sheep at ca. 2000 B.P. from BBC. South Africa. Antiquity 70, 945–949.

Henshilwood, C.S., Sealy, J.C., Yates, R., Cruz-Uribe, K., Goldberg, P., Grine, F., Klein, R.G., Poggenpoel, C., van Niekerk, K., Watts, I., 2001. Blombos Cave, southern Cape, South Africa: preliminary report on the 1992–1999 excavations of the Middle Stone Age levels. Journal of Archaeological Science 28, 421–448.

Henshilwood, C.S., d'Errico, F., Yates, R., Jacobs, Z., Tribolo, C., Duller, G.A.T., Mercier, N., Sealy, J.C., Valladas, H., Watts, I., Wintle, A.G., 2002. Emergence of modern human behaviour: Middle Stone Age engravings from South Africa. Science 294, 1278–1280.

Inskeep, R.R. (Ed.), 1987. Nelson Bay Cave. Cape Province, South Africa: The Holocene Levels. British Archaeological Reports International Series, 357(i)+(ii). Oxford.

Jerardino, A., Castilla, J.C., Ramírez, J.M., Hermosilla, N., 1992. Early coastal subsistence patterns in central Chile: a systematic study of the marine invertebrate fauna from the site of Curaumilla-1. Latin American Antiquity 3, 43–62.

Jerardino, A., 1993. Mid to late Holocene sea level fluctuations: the archaeological evidence at Tortoise Cave, south western Cape, South Africa. South African Journal of Science 89, 481–488.

Jerardino, A., 1996. Changing social landscapes of the western Cape coast of southern Africa over the last 4500 years. PhD thesis, University of Cape Town.

Jerardino, A. Excavations at a hunter-gatherer site known as 'Grootrif G' shell midden, Lamberts Bay, Western Cape Province. South African Archaeological Bulletin 62 (186), in press.

Jerardino, A., Navarro, R., Nilssen, P., 2001. Cape rock lobster (*Jasus lalandii*) exploitation in the past: estimating carapace length from mandible sizes. South African Journal of Science 97, 59–62.

Jerardino, A., Branch, G.M., Navarro, R., in press. Human impact on precolonial West Coast marine environments of South Africa. In: Erlandson, J.M., Rick, T.C. (Eds.), Human Impacts on Marine Environments. University of California Press, Berkeley, CA.

Kilburn, R., Rippey, E., 1982. Sea Shells of Southern Africa. Macmillan, Johannesburg.

Klein, R.G. (Ed.), 1972. Preliminary report on the July through September 1970 excavations at Nelson Bay Cave, Plettenberg Bay (Cape Province, South Africa). Palaeoecology of Africa, vol. 6, pp. 177–208.

Klein, R., Cruz-Uribe, K., 1987. Large mammal and tortoise bones from Eland's Bay Cave and nearby sites, Western Cape Province, South Africa. In: Parkington, J.E., Hall, M. (Eds.), Papers in the Prehistory of the Western Cape, South Africa. British Archaeological Reports International Series, 332(i). Oxford, pp. 132–163.

Klein, R., Cruz-Uribe, K., 1996. Size variation in the Rock Hyrax (*Procavia capensis*) and Late Quaternary climatic change in South Africa. Quaternary Research, 193–207.

Klein, R., Cruz-Uribe, K., 2000. Middle and Later Stone Age large mammal and tortoise remains from Die Kelders Cave 1, Western Cape Province, South Africa. Journal of Human Evolution 38, 169–195.

Klein, R.G., Avery, G., Cruz-Uribe, K., Halkett, D., Parkington, J.E., Steele, T., Volman, T.P., Yates, R., 2004. The Ysterfontein 1 Middle Stone Age site, South Africa, and early human exploitation of coastal resources. Proceedings of the National Academy of Sciences of the USA 101, 5708–5715.

Lee-Thorp, J., Sealy, J.C., Van der Merwe, N., 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. Journal of Archaeological Science 16, 585–599.

Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier, Amsterdam, New York.

Mannino, M.A., Thomas, K.D., 2002. Depletion of a resource? The impact of prehistoric human foraging on intertidal mollusc communities and its significance for human settlement, mobility and dispersal. World Archaeology 33, 452–474.

Marean, C., Goldberg, P., Avery, G., Grine, F.E., Klein, R.G., 2000. Middle Stone Age stratigraphy and excavations at Die Kelders Cave 1 (Western Cape Province, South Africa): the 1992, 1993, and 1995 field seasons. Journal of Human Evolution 38, 7–42.

Marean, C.W., Nilssen, P.J., Brown, K., Jerardino, A., Stynder, D., 2004. Palaeoanthropological investigations of Middle Stone Age sites at Pinnacle Point, Mossel Bay (South Africa): archaeology and hominid remains from the 2000 field season. PalaeoAnthropology 1, 14–83.

Milner, N., Barrett, J., Welsh, J., 2007. Marine resource intensification in Viking Age Europe: the molluscan evidence from Quoygrew, Orkney. Journal of Archaeological Science 34, 1461–1472.

Oliva, D., Castilla, J.C., 1992. Recognition guide and morphometry of ten species of genus Issurella Bruguiere, 1789 (Mollusca: Gastropoda) common in fishery and indigenous shellmidden from central and southern Chile. Gayana Zoologica 56, 77–108.

Parkington, J., 1981. The effects of environmental change on the scheduling of visits to the Elands Bay Cave, Cape Province, SA. In: Hodder, Isaac, G., Hammond, N. (Eds.), Patterns of the Past. Cambridge University Press, Cambridge, pp. 341–359.

Parkington, J., 2003. Middens and moderns: shellfishing and the Middle Stone Age of the Western Cape. South African Journal of Science 99, 242–247.

Parkington, J., Cartwright, C., Cowling, R.M., Baxter, A., Meadows, M., 2000. Palaeovegetation at the last glacial maximum in the western Cape, South Africa: wood charcoal and pollen evidence from Elands Bay Cave. South African Journal of Science 96, 543–546.

Pfeiffer, S., Sealy, J.C., 2006. Body size among Holocene foragers of the Cape ecozone, southern Africa. American Journal of Physical Anthropology 129, 1–11.

R Development Core Team, 2005. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. http://www.R-project.org.

Ridgway, S.A., Reid, D.G., Taylor, J.D., Branch, G.M., Hodgson, A.N., 1998. A cladistic phylogeny of the family Patellidae (Mollusca: Gastropoda). Philosophical Transactions of the Royal Society of London B 353, 1645–1671.

Rightmire, G.P., Deacon, H.J., 2001. New human teeth from Middle Stone Age deposits at Klasies River, South Africa. Journal of Human Evolution 41, 535–544.

Sealy, J.C., Pfeiffer, S., 2000. Diet, body size, and landscape use among Holocene people in the southern Cape, South Africa. Current Anthropology 41, 642–655.

Sealy, J.C., Yates, R., 1994. The chronology of the introduction of pastoralism to the Cape, South Africa. Antiquity 68, 58–67.

Shackleton, N., 1982. Stratigraphy and chronology of the Klasies River Mouth deposits: oxygen isotopic evidence. In: Singer, R., Wymer, J. (Eds.), The Middle Stone Age of Klasies River Mouth in South Africa. University Press, Chicago, IL, pp. 194–199.

Shrire, C., 1962. Oakhurst: a re-examination and vindication. South African Archaeological Bulletin 17, 181–195.

Singer, R., Wymer, J., 1982. The Middle Stone Age of Klasies River Mouth in South Africa. University Press, Chicago, IL.

Steele, T.E., Klein, R.G., 2005. Mollusk and tortoise size as proxies for stone age population density in South Africa: implications for the evolution of human cultural capacity. Munibe 57, 5–21.

Sokal, R.R., Rohlf, F.J., 1969. Biometry. Freeman Press, San Francisco, CA.

Thackeray, A., 2000. Middle Stone Age artefacts from the 1993 and 1995 excavations of Die Kelders Cave 1, South Africa. Journal of Human Evolution 38, 147–168.

Thackeray, J.F., 1988. Molluscan fauna from Klassies River, South Africa. South African Archaeological Bulletin 43, 27–32.

van Andel, T.H., 1989. Late Pleistocene sea levels and the human exploitation of the shore and shelf of southern South Africa. Journal of Field Archaeology, 132–153.

Volman, T., 1978. Early archaeological evidence for shellfish collecting. Science 201, 911–913.

Volman, T., 1981. The Middle Stone Age in the southern Cape. Unpublished PhD thesis, University of Chicago, IL.

Vogel, J.C., Plug, I., Webley, L., 1997. New dates for the introduction of sheep into South Africa: the evidence from Spoegrivier Cave in Namaqualand. South African Journal of Science 93, 246–248.

Wurz, S., 2002. Variability in the Middle Stone Age lithic sequence 115,000–60,000 years ago at Klasies River Mouth, South Africa. Journal of Archaeological Science 29, 1001–1015.