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Peer review history for:

Oster S, Reynard JP, Cawthra HC, Esteban I, Pargeter J, Fisher EC. Late Pleistocene and Holocene fauna from Waterfall Bluff Rock Shelter, Mpondoland, South Africa. *S Afr J Sci.* 2024;120(11/12), Art. #17449. <https://doi.org/10.17159/sajs.2024/17449>

HOW TO CITE:

Late Pleistocene and Holocene fauna from Waterfall Bluff Rock Shelter, Mpondoland, South Africa [peer review history]. *S Afr J Sci.* 2024;120(11/12), Art. #17449. <https://doi.org/10.17159/sajs.2024/17449/peerreview>

Reviewer A: Round 1

Date completed: 25 April 2024

Recommendation: Accept / **Revisions required** / Resubmit for review / Decline

Conflicts of interest: None

Does the manuscript fall within the scope of SAJS?

Yes/No

Is the manuscript written in a style suitable for a non-specialist and is it of wider interest than to specialists alone?

Yes/No

Does the manuscript contain sufficient novel and significant information to justify publication?

Yes/No

Do the Title and Abstract clearly and accurately reflect the content of the manuscript?

Yes/No

Is the research problem significant and concisely stated?

Yes/No

Are the methods described comprehensively?

Yes/No

Is the statistical treatment appropriate?

Yes/No/**Not applicable**/Not qualified to judge

Are the interpretations and conclusions justified by the research results?

Yes/Partly/No

Please rate the manuscript on overall contribution to the field

Excellent/**Good**/Average/Below average/Poor

Please rate the manuscript on language, grammar and tone

Excellent/Good/Average/Below average/Poor

Is the manuscript succinct and free of repetition and redundancies?

Yes/No

Are the results and discussion confined to relevance to the objective(s)?

Yes/No

The number of tables in the manuscript is

Too few/**Adequate**/Too many/Not applicable

The number of figures in the manuscript is

Too few/Adequate/Too many/Not applicable

Is the supplementary material relevant and separated appropriately from the main document?

Yes/No/**Not applicable**

Please rate the manuscript on overall quality

Excellent/**Good**/Average/Below average/Poor

Is appropriate and adequate reference made to other work in the field?

Yes/No

Is it stated that ethical approval was granted by an institutional ethics committee for studies involving human subjects and non-human vertebrates?

Yes/No/**Not applicable**

If accepted, would you recommend that the article receives priority publication?

Yes/**No**

Are you willing to review a revision of this manuscript?

Yes/No

Select a recommendation:

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Yes/No

Comments to the Author:

This is a nicely written and clear manuscript that I enjoyed reading. I have made small comments and suggestions directly into the PDF.

My main concern with the paper is the size of the sample presented here. It is extremely small and I feel that the manuscript would be better suited for a short report (research letter) rather than a research article. I appreciate the fact that you remain cautious in your interpretations but, still, the sample described here, 59 remains, cover several thousands of years, and some critical phases in terms of climatic change. The LBCS layers cover a period of possible 20 000 years and are represented by 13 remains only, while most faunal analyses, sometimes for a single chrono-stratigraphic phase, tend to include complete faunal samples (identifiable and non-identifiable material) of hundreds or thousands of specimens.

I would recommend adding some information on the following aspects:

- The non-identifiable fraction of the faunal assemblage: it is ok to focus on identifiable material first, and it provides a first overview of species present. However, to understand several taphonomic aspects of the faunal assemblage, it is important to provide the reader with an estimate of which percentage of the total faunal assemblage the identifiable material represents. I would encourage including a few pieces of information on number and/or weight of non-identifiable faunal material from SRCS and LBCS. What is the proportion that is identifiable?
- Is the material presented all piece-plotted? What about sieving and sorting? Was the sorted material considered? In my experience, for a number of small prey items, a significant portion ends up in the sieve (e.g. bones of monitor lizard, mole rats, etc.). What is the size-cut for the piece-plotted material?
- Add pictures of some of the faunal remains. It's already very preliminary with only 59 remains presented here, and no microscopic analysis of bone surface modifications. At least, I would include pictures of the most diagnostic remains, some teeth, the bones with the cut-marks, etc. It could be just one figure showing several diagnostic bones and a couple of cut-marked bones. Surely you have information on the burning stage (this does not require the use of a microscope) and you could also consider adding this to the manuscript.
- Provide information on skeletal elements. You could for instance add a table or a SOM with the anatomical identifications for each of the 59 specimens.
- If you want the paper stand-alone, I would encourage you to add a map of the region with the location of the site.

[See Appendix 1 for Reviewer A's comments made directly on the manuscript]

Author response to Reviewer A: Round 1

L11 - Does the fauna come from the entire sequence - MIS3 to the mid-Holocene? I would make this clearer in the abstract.

AUTHOR: No, it does not; the oldest fauna comes from the MIS3, while the youngest dates to the Early Holocene (10750-10720). This has been made clearer in the abstract.

L48 - Same comment as in the abstract - from which layers does this preliminary sample come from? I understand that the detail of the stratigraphic provenance of the material belongs to the material and methods section but it should be clearer from the introduction which time period you are dealing with (or whether the sample covers the entire sequence of WB).

AUTHOR: The timeframe from which the fauna comes has been made clearer (L29)

L79 - This feels a little bit out of place here, inside a paragraph on carnivores. It feels like you should either have an entire section on the small rodents occurring in the area (probably beyond the scope of this paper), or simply remove it.

AUTHOR: The sentence has been removed entirely as a detailed section on small rodents would be beyond the scope of this paper.

L132 - was

AUTHOR: Changed to 'was'. "The fauna documented in this report was recovered..." (L69).

L161 - % missing

AUTHOR: RESPONSE: The % has been added (L83-91).

L163 - In italics

AUTHOR: The words *Procavia capensis* have been put in italics (L90).

Table 1 - Check that the "cf.", "sp." and "indet." are not in italics.

AUTHOR: Italics have been removed from "cf." "sp." and "indet."

Table 1 - Same comment - should not be in italics.

AUTHOR: Italics have been removed from "indet."

Table 1 - Not in italics

AUTHOR: "Aves" is no longer in italics

Reviewer B: Round 1

Date completed: 03 May 2024

Recommendation: Accept / Revisions required / Resubmit for review / **Resubmit elsewhere** / Decline

Conflicts of interest: None

Does the manuscript fall within the scope of SAJS?

Yes/**No**

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Yes/**No**

Are the methods described comprehensively?

Yes/**No**

Is the statistical treatment appropriate?

Yes/**No/Not applicable**/Not qualified to judge

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Yes/**No**

Are you willing to review a revision of this manuscript?

Yes/**No**

Select a recommendation:

Accept / Revisions required / Resubmit for review / **Resubmit elsewhere** / Decline

With regard to our policy on '[Publishing peer review reports](#)', do you give us permission to publish your anonymised peer review report alongside the authors' response, as a supplementary file to the published article? Publication is voluntary and only with permission from both yourself and the author.

Yes/No

Comments to the Author:

This article uses an archaeozoological approach to explore Late-Pleistocene to mid-Holocene paleoenvironment and paleoecological conditions along the Eastern Cape coast. Archaeological sites that date to the LGM are rare and publication of research results is an important contribution to our understanding of this period. Although the results are promising, the small dataset does not support the paleoenvironmental and -ecological interpretations presented. Preliminary results warrant publication, but in this case the article would be better suited as a technical report in an archaeology-focused journal until a more comprehensive analysis of the faunal assemblage has been completed.

The identification of leopard seal remains is significant and the first direct evidence of this species from Pleistocene and Holocene contexts along the southern African coast. The publication of this finding could be reworked as a Research Letter in the SAJS.

Comments

- Check Rutherford 2006 – there are multiple authors of this chapter.
- Jackal genus has changed to *Lupulella*. *Felis sylvestris* is the European wildcat, do you mean *Felis lybica* (African wildcat)?

- L72 – *Tragelaphus oryx* not onyx.
- L93 – add teeth as identifiable material.
- L118 – Issue with Table 3 and 4. They are not included in manuscript, but do not correspond to those in the preceding reference either.
- Add total assemblage size for this study by weight or NISP/NSP for SRCS and LBCS to better evaluate the data presented. If information on the complete assemblage size for SRCS and LBCS, excavated to date, is available, please include this as well.
- Methods – taphonomic identification methods should briefly be explained in the methods section. Although not really discussed in the paper, mention of taphonomic results does require some methodological context.
- L169 – reference on distribution range needed.
- Table 1 – Monitor should be Monitor lizard.
- L161 – % missing. L163 – *Procavia capensis* – italics. L179 – mole rats, not rates. Check that all references are formatted in the same way in the text. Table 1 – Testudinidae, Bovidae, Aves – not italicised.
- L226 – Provide brief information, position or affiliation for Kevin Cole.
- The authors use different ways of referring to indeterminate bovid remains throughout the text, (e.g., size 2, size two, Bovid 2, Bov 2, 'Bovid 2') – “medium sized bovid” might be more appropriate for a non-specialist audience; whichever term is preferred should be used consistently (in the text and tables).
- The sample size for the LBCS assemblage is very small (n=13), with interpretations about paleoecology and environment based on seven ungulate bones/teeth. The sample size for SRCS is larger (n=59), but again inferences linked to ungulate diet are based on 19 bones/teeth (not individuals). These samples are so small that statements about the presence/absence of grazers/browsers cannot reliably be supported (e.g., “The absence of exclusive grazers ... (L200), “The generally even mix of grazers and browsers ...” (L259)). Although there are issues with quantification methods, there should be some clarification on the number of individuals represented here. Could the six mixed-feeder bones/teeth from one taxon (Table 2) be the same individual? If that were the case, the authors are relying on one mixed feeder and one browser to draw inferences about the entire LBCS deposit. Expanding the sample for this important stratigraphic unit would allow for a more convincing argument.
- Regarding the use of *Syncerus africanus* instead of *S. caffer* – I understand the sentiment, and this is a global issue. However, reference to another publication that simply uses *S. africanus*, without context, is not appropriate. Consider referencing the wider issue or published arguments (e.g., Roksandic et al. 2023; Smith & Figueiredo 2021). Informal changes to scientific names have wide-ranging impacts (Ceríaco et al. 2023; but see Bae et al. 2023).

Bae, C.J. et al. 2023. Placing taxonomic nomenclatural stability above ethical concerns ignores societal norms, *Zoological Journal of the Linnean Society*, Volume 199, Issue 1, Pages 5–6,

Ceríaco, L.M. et al. 2023. Renaming taxa on ethical grounds threatens nomenclatural stability and scientific communication: Communication from the International Commission on Zoological Nomenclature, *Zoological Journal of the Linnean Society*, Volume 197, Issue 2, Pages 283–286.

Roksandic, M. et al. 2023. Change in biological nomenclature is overdue and possible. *Nat Ecol Evol* 7, 1166–1167

Smith, G.F. & Figueiredo, E. 2021. Proposal to add a new Article 61.6 to permanently and retroactively eliminate epithets with the root *caf[e]r-* or *caff[e]r-* from the nomenclature of algae, fungi and plants. *Taxon* 70: 1395-1396

Author response to Reviewer B: Round 1

Check Rutherford 2006 – there are multiple authors of this chapter.

AUTHOR: The reference has been corrected to reflect all the authors of the chapter, Savannah Biome

L74/75 - Jackal genus has changed to *Lupulella*. *Felis sylvestris* is the European wildcat, do you mean *Felis lybica* (African wildcat)?

AUTHOR: Naming was done according to Skinner & Chimimba 2006, where the African wild cat is still called *Felis sylvestris*. We have had to remove the section on carnivores due to word-length constraints, but we thank the reviewer for highlighting those changes.

L72 – *Tragelaphus oryx* not *onyx*.

AUTHOR: misspelling has been corrected

L93 – add teeth as identifiable material

AUTHOR: We have now cut the manuscript down to 2000 words to reformat it to a Research Letter. Given this, we have had to remove the discussion on faunal preservation.

L118 – Issue with Table 3 and 4. They are not included in manuscript, but do not correspond to those in the preceding reference either.

AUTHOR: Additional tables were supposed to be added; however, due to oversight, they were not. These should be included now.

Add total assemblage size for this study by weight or NISP/NSP for SRCS and LBCS to better evaluate the data presented. If information on the complete assemblage size for SRCS and LBCS, excavated to date, is available, please include this as well.

AUTHOR: Most of the collection for the SRCS and LBCS remains unanalysed, and therefore, no total assemblage NISP/NSP or weight can be provided as these numbers cannot be generated until the entire assemblage has been analysed.

Methods – taphonomic identification methods should briefly be explained in the methods section. Although not really discussed in the paper, mention of taphonomic results does require some methodological context

AUTHOR: A sentence describing the taphonomic analysis undertaken has been added (L80).

L169 – reference on distribution range needed.

AUTHOR: Unfortunately, because we had to cut the ms to a Research Letter format, all information on *Raphicerus* was removed.

Table 1 – Monitor should be Monitor lizard

AUTHOR: Monitor has been changed to Monitor Lizard

L161 – % missing. L163 – *Procavia capensis* – italics. L179 – mole rats, not rates. Check that all references are formatted in the same way in the text. Table 1 – Testudinidae, Bovidae, Aves – not italicised.

AUTHOR: The missing % has been added. *Procavia capensis* has been written in italics, mole rates in L197 has been changed to mole rats. Italics were removed from Testudinidae, Bovidae, Aves. References were double checked.

L226 – Provide brief information, position or affiliation for Kevin Cole

AUTHOR: Information on who Kevin Cole is has been added “Principal Scientist at the East London Museum” (L120).

The authors use different ways of referring to indeterminate bovid remains throughout the text, (e.g., size 2, size two, Bovid 2, Bov 2, ‘Bovid 2’) – “medium sized bovid” might be more appropriate for a non-specialist audience; whichever term is preferred should be used consistently (in the text and tables).

AUTHOR: Bov 1 and size 1 are not referring to the same thing. In L75 & 76 we note that bovids are referred to as Bov 1-4, while indet. mammal remains are referred to as size 1-4. However, to ensure no future confusion will arise, we restrict the use of either of these terms throughout.

The sample size for the LBCS assemblage is very small (n=13), with interpretations about paleoecology and

environment based on seven ungulate bones/teeth. The sample size for SRCS is larger (n=59), but again inferences linked to ungulate diet are based on 19 bones/teeth (not individuals). These samples are so small that statements about the presence/absence of grazers/browsers cannot reliably be supported (e.g., “The absence of exclusive grazers ... (L200), “The generally even mix of grazers and browsers ...” (L259)). Although there are issues with quantification methods, there should be some clarification on the number of individuals represented here. Could the six mixed-feeder bones/teeth from one taxon (Table 2) be the same individual? If that were the case, the authors are relying on one mixed feeder and one browser to draw inferences about the entire LBCS deposit. Expanding the sample for this important stratigraphic unit would allow for a more convincing argument.

AUTHOR: The reviewer makes a good point, and we acknowledge that our sample size is too small to make any significant interpretations on palaeoecology (L. However, for the LBCS deposit, the mixed feeder bones (eland) come from different stratigraphic units with very different radiocarbon dates. Of the 4 eland remains, one is from LGIT and dated to 15,050 - 14,380 cal. BP, two are from the LGM but have different dates (20,190 - 19,340 cal. BP and belongs to a juvenile and the other 24,050 - 23,160 cal. BP). The last is from the MIS3 dated to 31,000 - 30,100 cal. BP. It is thus highly unlikely that all four of the mixed feeder bones belong to the same individual, given the dates and the age range of the specimen. For the other specimen similar discrepancies occur where they have been retrieved from different SubAggs correlating to different age ranges. Even accounting for bones of the same species that are recovered from the same SubAgg, the generally even mix of browsers and grazers is maintained. The sample size will be expanded in future papers, but we feel that, for now, a short report highlighting the important seal remains is warranted.

Regarding the use of *Syncerus africanus* instead of *S. caffer* – I understand the sentiment, and this is a global issue. However, reference to another publication that simply uses *S. africanus*, without context, is not appropriate. Consider referencing the wider issue or published arguments (e.g., Roksandic et al. 2023; Smith & Figueiredo 2021). Informal changes to scientific names have wide-ranging impacts (Ceríaco et al. 2023; but see Bae et al. 2023).

AUTHOR: We thank the reviewer for the references, and for their understanding, as this epithet is particularly offensive to South African researchers of colour. We have been guided by the references suggested and have included them to support the use of a different name.

Late Pleistocene and Holocene fauna from Waterfall Bluff Rock Shelter, Mpondoland, South Africa

Abstract

Archaeological deposits from Waterfall Bluff Rock Shelter on the coast of Mpondoland occur across a broad period – from Marine Isotope Stage 3 (~39-29 ka) to the mid-Holocene (~8 ka) – and show persistent human occupations across this timeframe. Because the site's position remained consistent throughout millennia, with the shoreline never migrating further than 8 km from the site, data from Waterfall Bluff is key to exploring human settlement patterns along relatively stable coastlines. This study explores the palaeoenvironment of Waterfall Bluff through an analysis of identifiable fauna. The results indicate that the area around Waterfall Bluff was host to grazing and browsing herbivores during the Pleistocene-Holocene transition. The identified species suggest a mosaic environment of grasslands and bushy and forested environments. The remains of the leopard seal were also recovered in layers dating to the Last Glacial Maximum. Leopard seal remains are rare in archaeological sites, and this is the first direct evidence of leopard seal recovered from Pleistocene and Holocene archaeo-faunal assemblages along the southern African coast. Palaeoenvironmental, palaeobotanical, and archaeozoological data suggest the site was an important hub for numerous habitats and resources that prehistoric hunter-gatherers exploited.

Significance

Archaeological sites that date to the Last Glacial Maximum (LGM) are rare in southern Africa. The recently excavated site of Waterfall Bluff off the coast of Mpondoland in the Eastern Cape shows that human occupation persisted there from Marine Isotope Stage 3 to the mid-Holocene. A leopard seal tooth was identified in the LGM layers, making it the first evidence of a leopard seal recovered off the coast of South Africa. This may suggest significantly cooler temperatures off the Eastern Cape coast during this period.

Keywords

Palaeoenvironment, Archaeozoology, Pleistocene-Holocene transition, Marine Isotope Stage 3, Last Glacial Maximum, Mpondoland, Eastern Cape Province

Introduction

Coastal archaeological records are scarce across southern Africa during the Terminal Pleistocene due to climatic and environmental variability¹. Coastal records from this period are even rarer because of sea-level fluctuations, which bias currently exposed archaeological records to interglacial periods. Waterfall Bluff (WB), located next to the Mlambomkulu waterfall in the Lambasi district of Mpondoland in the Eastern Cape Province, provides an important benchmark on hunter-gatherer adaptations in a persistent coastal environment during the Late Pleistocene and across the Pleistocene-Holocene transition.

40 The Mpondoland Paleoclimate, Paleoenvironment, Paleoecology, and Palaeoanthropology
41 Project (P5) has excavated at WB since 2015 ^{1,2,3}. These excavations have documented
42 repetitive occupations of the rock shelter by hunter-gatherers during late Marine Isotope
43 Stage (MIS) 3 (~39 ka - 29 ka), MIS 2 (~29 - 14 ka), the early Holocene (~11.7 – 8 ka), and
44 the middle Holocene (~8 to 5 ka), including during the Last Glacial Maximum (LGM) and the
45 glacial/interglacial transition ¹. The abundant remains of marine shellfish, fish, mammals, and
46 charcoal from coastal taxa demonstrate that Late Pleistocene hunter-gatherers routinely
47 collected various resources from coastal zones ^{1,3,4}. Here, we describe a preliminary sample
48 of **WB fauna** to better understand the local paleoenvironmental and paleoecological
49 conditions and the implications for hunter-gatherer subsistence during the Late Pleistocene
50 and Early Holocene.

51

52 **Regional Ecology**

53 Eastern Mpondoland is known for its diverse landscapes, including deeply dissected
54 plateaus extending from the Mthatha River mouth to the Umtamvuna River mouth. The area
55 is currently dominated by sourveld grassland, forest vegetation, and bushveld, including the
56 Southern Coastal Forest, Southern Mistbelt Forest, and Scarp Forest. The Pondoland-Ugu
57 Sandstone Coastal Sourveld occurs in the neocoastal peneplain on the Msikaba formation
58 sandstones. At the same time, the Savanna biome and Eastern Valley Bushveld are
59 restricted to fire-resistant areas such as rocky outcrops and small ravines ^{3,5,6}. Rainfall is
60 concentrated during the austral summer, with coastal rain less seasonally dictated and frost
61 occurring infrequently ^{3,5,7}.

62 The Eastern Mpondoland region is home to various animal species in different
63 environments. Browsers such as bushbuck (*Tragelaphus scriptus*), blue duiker (*Philantomba*
64 *monticola*), common duiker (*Sylvicapra grimmia*), and grey rhebok (*Pelea capreolus*) are
65 primarily found in environments that provide underbrush, including riverine underbrush,
66 woodlands, forests, and coastal bush ^{8,9}. The grey rhebok prefers habitats with rocky
67 mountain slopes or rocky riverine valleys ⁸, while the vervet monkey (*Ceropithecus*
68 *pygerythrus*), though not a browser, prefers riverine woodlands with adequate fruit-bearing
69 trees ⁸ **Error! Bookmark not defined.**. Grazers such as the southern reedbuck (*Redunca*
70 *arundinum*), oribi (*Ourebia ourebi*), and bontebok (*Damaliscus pygargus*) prefer grassland
71 environments with short grass for grazing and longer grass for cover ^{8,9}. Mixed feeders like
72 the eland (*Tragelaphus onyx*) are versatile in their environmental needs, occurring in
73 grassland biomes to woodlands ^{8,9}.

74 Carnivores in the area include leopards (*Panthera pardus*), African wild cats (*Felis silvestris*),
75 caracals (*Caracal caracal*), and black-backed jackals (*Canis mesomelas*), which are mainly
76 versatile in their environmental needs ⁸. Leopards and African wild cats occur in rocky
77 hillsides with underbrush and woodland biomes. At the same time, caracals and black-
78 backed jackals prefer more arid conditions and occur in savanna biomes and open
79 grasslands ⁸. Frugivores like the woodland thicket rat (*Grammomys dolichurus*) occur in
80 riverine forests and woodland thickets ⁸.

81

82 **Site Background**

83 Waterfall Bluff (31°26'01, 1" S, 29°49'19.2" E) is located ~24 m above the modern coastline
84 next to the Mlambomkulu River waterfall. The site is best known for preserving rare evidence
85 of coastal occupation and foraging during the Late Pleistocene, including across glacial
86 periods and glacial/interglacial transitions. The high-resolution records recovered from the
87 site include multi-proxy paleoclimate and paleoenvironment data as well as marine and
88 terrestrial fauna (shellfish, marine fish, and marine mammals). The marine fauna dating to
89 the LGM is unique across southern Africa, and it can be attributed to the persistent location
90 of the coastline within the foraging range from the site across glacial and interglacial periods
91 ¹. Toolmakers made the site's lithics assemblage predominantly on hornfels, and the site's
92 deposits preserve abundant and well-preserved faunal remains. Preservation of stratigraphy,
93 bones, and shells generally follows a north-south gradient from the shelter mouth and
94 dripline (poorer preservation) to the more protected inner sanctum of the shelter (better
95 preservation) ¹.

96 Abundant and well-preserved botanic remains have also provided detailed insights into local
97 paleoenvironments and plant use by prehistoric hunter-gatherers ³. Multi-proxy
98 paleoenvironmental data, for example, show varying but sustained soil moisture across the
99 Late Pleistocene. These records also show the presence of all major vegetation types found
100 in the region today from the end of the Pleistocene to the Holocene ³. These findings imply a
101 complex mosaic of environments that would have supported varying plant and animal
102 resources for prehistoric people.

103 All excavated data have been mapped in 3D with total stations to millimetric accuracy using
104 total stations tied into the Universal Transverse Mercator (UTM) grid system. More than
105 17,000 artefacts, faunal (terrestrial and marine), and plant remains have been plotted in 3D
106 to date. Additional specialist samples for micromorphology, OSL dating, charcoal, etc., have
107 been similarly mapped in 3D.

108 The site's stratigraphic sequence follows natural layers consolidated into "Stratigraphic
109 Aggregates" (StratAggs). As defined by Karkanas et al. ¹⁰, StratAggs are laterally continuous
110 layers of sediments. StratAggs can be subdivided into sub-Stratigraphic Aggregates
111 (SubAggs), representing identifiable and discrete anthropogenic, biogenic, or geologic
112 events. At Waterfall Bluff, the Light Brown Coarse Sands (LBCS) are the earliest StratAgg,
113 composed of loosely compacted and moist coarse sands interspersed by archaeologically-
114 rich dark lenses. The oldest deposits (LBCS Colton) have been dated via single-grain
115 optically stimulated luminescence (OSL) to 37.6 ± 4.2 ka. The youngest LBCS deposits have
116 been dated via OSL to 12.5 ± 1.2 ka (minimum age of sediment deposition), and a Bayesian
117 ¹⁴C accelerator mass spectrometry model from 13,520-12,830 cal yr BP to 14,070-13,570
118 cal yr BP ¹ (Table 3 and 4).

119 The Shell Rich Clayey Sands (SRCS) StratAgg overlays the LBCS. SRCS deposits have
120 been dated using Bayesian ¹⁴C accelerator mass spectrometry model from 11,000 cal yr BP
121 to ca. 10,500 cal yr BP ¹. The SRCS comprises a dark, clay-rich sedimentological matrix with
122 low roof spall abundance. It is archaeologically rich, and shell-supported matrices are
123 common. Evidence of prehistoric and recent sediment disturbances truncating older deposits
124 is visible in the SRCS, creating an exceptionally complex stratigraphy. The ages and
125 locations of each SubAgg are provided in Figure 1.

126 For more detailed information about the excavation sequence, chronology, and
127 archaeological remains, readers can refer to Fisher et al. ¹ and Esteban et al.¹⁰. Additionally,

128 Esteban et al.³ describe multi-proxy paleoenvironmental proxies, while Oertle et al.⁴ provide
129 in-depth shellfish preservation information.

130

131 **Method and materials**

132 The fauna documented in this report were recovered from the early Holocene SRCS and the
133 Late Pleistocene LBCS deposits during the 2016 and 2019 excavations. Excavations at
134 Waterfall Bluff were conducted under the auspices of the Eastern Cape Provincial Heritage
135 Resources Authority, permit #[anonymised]. The remains were analysed following Klein and
136 Cruz-Uribe¹¹ and Driver¹², where specimens are first identified to element before they can
137 be assigned to taxa. Fauna was compared to reference specimens in the comparative faunal
138 collections at the Ditsong National Museum of Natural History, Pretoria. Bovidae (bovids) not
139 assigned to a Linnaean Family were categorised according to size classes based on Brain¹³
140 (1974). Size class 1 (Bovid 1) is the approximate size of a steenbok (*Raphicerus*
141 *campestris*), Bovid 2 is the size of a grey rhebuck, Bovid 3 is equivalent to a wildebeest
142 (*Connochaetes* spp.) and Bovid 4 to an eland. Only specimens identified to taxa are reported
143 here, and identified fauna was presented according to the number of identified specimens
144 (NISP). Ungulates were categorized as grazers, browsers, and mixed feeders, following
145 Skinner and Chimimba⁸. Table 1 presents the identified faunal taxa.

146

147 **Results**

148 Most specimens (NISP=59; 81.9% of all identified specimens) were recovered from the
149 SRCS deposits, with only a small portion (NISP=13; 18.1%) coming from the LBCS layers.
150 Most of the recovered specimens were poorly preserved, with extensive charring and signs
151 of water damage, likely due to the excavation's proximity to the drip line. Additionally, the
152 assemblage was extensively fragmented, with most specimens being less than 2 cm long.

153 Only a rudimentary, macroscopic assessment of bone surface modification was undertaken.
154 Approximately 10% of the identifiable assemblage consisted of bones that showed evidence
155 of anthropogenic modification, such as cut marks and percussion marks. None of these
156 bones could be assigned to a particular species, though the size classes ranged from size 1
157 to size 2. A charred astragalus with cut marks from the SRCS Jess deposits was identified
158 as belonging to a blue duiker (CN004835, Lot 221). Percussion marks were only evident on
159 bones from the Bov 1 and Bov 2 size classes.

160 Taxonomic identification of the specimens was primarily based on teeth, with phalanges
161 being the second most frequently used element for identification (11 phalanges; 15.3 of
162 identifiable bones). Of the bones that could be sorted into a size class, the 'Bovid 2' size
163 class was the most prevalent (NISP=10), while rock hyrax (*Procavia capensis*) was the most
164 identifiable species (NISP=8). Among bovids, eland (NISP=6), *Raphicerus* spp. (NISP=5)
165 and common bushbuck (NISP=4) were the most prevalent. *Raphicerus* remains could not be
166 definitively identified as either Cape grysbok (*Raphicerus melanotis*) or steenbok
167 (*Raphicerus campestris*) without considering the geographic distribution of the two species.
168 While Cape Grysbok is found in the Western and Eastern Cape, steenbok has a much
169 broader distribution, making it more likely that the *Raphicerus* remains belonged to
170 steenbok.

171 A seal tooth (CN47208, Lot 303) was recovered from the LBCS SubAgg Lily (Table 1)
172 (Fig.2). The crown has three distinct cusps and is unlike those of the more common fur seal
173 (*Arctocephalus* spp.), which are smooth with less pronounced lateral cusps. The trident-
174 shaped postcanine tooth corresponds to the earless seal (Phocidae), of which four species
175 occur along the southern African coast: the crabeater seal (*Lobodon carcinophaga*), the
176 leopard seal (*Hydrurga leptonyx*), the elephant seal (*Mirounga leonina*) and the Weddell seal
177 (*Leptonychotes weddellii*)⁸. Although worn, the tooth matches the prominent, triple-cusped
178 crown of leopard seals, which are used to sieve krill. Based on our assessment, the tooth
179 does not resemble the other three Phocidae species and is most likely that of a leopard seal.
180 Notably, at least three other bone fragments (a vertebrae and two unidentified bone
181 specimens) recovered from the LBCS and SRCS layers may also belong to seal. Seal bone
182 has a relatively distinct internal morphology, so it is likely these are indeed seal. However,
183 following our method (i.e., Driver¹²), only specimens identified to element can be assigned
184 to a genus/species, and ribs and vertebrae are not used to identify taxa beyond size class.
185 Thus, per our identification protocol, these specimens were not included in our taxa list.

186

187 **Discussion**

188 Given the small faunal sample, making detailed inferences regarding local
189 palaeoenvironments is problematic. Nevertheless, the sample is large enough to suggest
190 broader palaeoecological conditions.

191 **Late Pleistocene environment**

192 The LBCS yields a particularly small faunal sample with only two identified bovid species.
193 Interestingly, none of these species are exclusive grazers (Table 2). Eland are mixed-feeders
194 adaptable to various environmental conditions and would have thrived equally in a bushy or
195 grassy environment. The common duiker (an obligatory browser) provides evidence for a
196 bushy environment since this species requires bushes and trees for shelter, shade, and
197 forage. African mole rates are not a good proxy for environments because they occur in
198 various habitats. However, because they commonly occupy sandy riverine areas, their
199 occurrence suggests the presence of sandy substrates¹⁴. In sum, although the sample size
200 is limited, the absence of exclusive grazers and the presence of at least one exclusive
201 browser suggest a more forested and bushier environment in the LBCS layers at WB.
202 Furthermore, other lines of palaeoenvironmental evidence at the site suggest the presence
203 of afrotemperate forests and other woodland landscapes along the ~8 km of exposed
204 continental shelf in front of WB³.

205 The recovery of marine taxa from the site presents intriguing ecological implications. The
206 presence of fish and seal remains in the LBCS layers indicate that the site was within
207 foraging distance of the coast¹ (Table 1). The neocoastal site's location is adjacent to the
208 narrow continental shelf meant it was within foraging range of the coast throughout glacial
209 times. However, sandy areas may have been present too, such as along the modern coast¹.
210 The identification of several possible barnacle remains in the sample, along with previous
211 finds of marine shellfish, also shows that WB hunter-gatherers were systematically exploiting
212 coastal resources even when the coast was ~8 km away^{1,3,4}. Furthermore, slightly elevated
213 levels of *Typha* and *Cyperaceae* pollen and phytoliths support the presence of freshwater
214 nearby, suggesting possible wetland habitats during the LBCS Lily³.

215 The leopard seal tooth (Fig. 2) is from SubAgg Lily in LBCS, one of several SubAggs from
216 the LGM, with a modelled age range of 22,560-19,340 cal. BP ¹. This could suggest that
217 leopard seals occurred further north than their usual home ranges, closer to WB, during the
218 peak of the LGM. This extended northward range could also lead to leopard seal bodies
219 being washed up on the coasts near WB more frequently. Leopard seals are apex predators
220 whose habitats are restricted to pack ice around the Antarctic and with a maximum range to
221 the sub-Antarctic islands (Siniff 1991; Rogers 2009). Their primary source of food is krill
222 (50%), followed by penguins (20%), pinnipeds (15%), fish (9%), and cephalopods (6%)
223 (Bonillas-Monge 2018). To the best of our knowledge, this is the first occurrence of leopard
224 seal recovered from an archaeological site off the southern African coast. The only modern
225 records of leopard seals in South Africa were in East London in 1946, Hout Bay in 1969 ⁸,
226 and a dead leopard seal reported to the East London museum in 1994. More recently, Kevin
227 Cole spotted a living individual near Cove Rock in 2014 (Fig. 3) (K. Cole, pers. comm.).
228 Another living specimen was sighted in 2021 at Kommetjie beach in Cape Town, and the
229 same seal was sighted again in Yzerfontein on the West Coast ¹⁵.

230 The presence of leopard seal in LBCS at WB may suggest that their colonies occurred in
231 territories beyond the Antarctic and sub-Antarctic oceans. It is also possible that this was an
232 isolated instance of a leopard seal straying too far from its home range, or it may be the
233 remains of a leopard seal body that was washed up on the shore from the closer northern
234 ranges of its habitat. However, the colder climatic conditions during the LGM, characterised
235 by local sea surface temperatures approximately 3°C lower than current levels (as indicated
236 by core MD96-2048 ¹⁶), may have provided suitable environments for leopard seal colonies
237 to have spread north. Leopard seals are known to favour cooler waters ¹⁷, and it is plausible
238 that their hunting ranges extended further north than those observed today ¹⁸. Extended
239 periods of sea ice persistence may have facilitated increased leopard seal populations
240 during the LBCS. In line with this cold theory, more Antarctic ice may have cut off specific
241 krill distribution ranges and spawning grounds around the east Antarctic and Antarctic
242 Peninsula. This would have compelled the krill to expand their distributive range northwards
243 for breeding purposes and forced leopard seals to roam further north outside their usual
244 ranges (Southern Ocean) in search of enough food to survive ^{18,19}. Furthermore, WB is close
245 to a river mouth that would have washed inland nutrients into the ocean, thus maintaining a
246 constant level of ocean nutrients that would have supported and propagated the marine
247 animals upon which leopard seals preyed.

248 **Early Holocene environment**

249 The faunal sample recovered from the SRCS layers provides insights into the broader early
250 Holocene environment between ~11 and 8 ka. The relative prevalence of bushbuck and
251 reedbuck suggests that the abundance of size two bovids here likely represents these
252 species. Bushbuck suggests a bushy, riverine environment ⁸. Although browsers dominate in
253 terms of NISP (Table 2), the relative abundance of reedbuck at WB indicates a grassy
254 environment and the likely presence of permanent water nearby. The presence of other
255 water-dependent species, such as African buffalo and bontebok/blesbok, supports this ^{8,9}.
256 Esteban et al. ³ found that summer rainfall increased during the Early Holocene period,
257 promoting moister environments that the southern reedbuck would have favoured. This
258 accords with the mouth of the Mlambomkulu River near WB, which currently provides a
259 constant fresh water supply ¹. The generally even mix of grazers and browsers suggests the
260 pervasiveness of browse and grasses during the Early Holocene. Indeed, the relatively equal

261 distribution of grazers and browsers suggests a mosaic environment of interdigitated
262 habitats in the Eastern Mpondoland region throughout the Pleistocene-Holocene transition
263 period (Table 2).

264 Within the SRCS layers, mountain reedbuck and grey rhebok indicate rocky, steep-sloped
265 habitats near WB ^{8,9}. Modern analogues for these kinds of habitats are found along the
266 numerous major river drainages in the region, characterised by rocky and steep slopes and
267 bushveld vegetation. Blue duiker and vervet monkey remains from the SRCS (Table 1)
268 indicate the presence of forests or thickets, which they require for cover and food ^{8,20,21}. Blue
269 duikers often exploit monkeys' feeding habits and eat the fallen foliage and fruits that the
270 monkeys drop while scavenging in the treetops ⁸. Furthermore, cut marks on the blue duiker
271 specimen indicate that hunter-gatherers, rather than carnivores, were the primary
272 accumulator of these small bovids at WB.

273 The most common animal remains found at the site – eland (a mixed-feeder), bushbuck (a
274 browser), and reedbuck (a wetland-linked grazer) – suggest that WB was a mosaic of both
275 open and closed environments. Additionally, the remains of water-dependant species, such
276 as African buffalo, and riverine-adapted species, such as bushbuck and vervet monkeys ⁸,
277 indicate the presence of freshwater. This suggests that the water flow of the nearby
278 Mlambomkulu River may have persisted from the LGM, and incisions of palaeo-rivers on the
279 now-submerged continental shelf indicate active riverine run-off during this time ³.

280 A detailed taphonomic analysis has not been conducted on the sample. Yet, given our
281 observations of anthropogenic modification, we can assume that most of this assemblage
282 was accumulated by people. Along with marine resources ¹, bovids were likely key food
283 sources for WB people. Our preliminary analysis shows that a range of herbivores, including
284 the very large eland and the smaller bushbuck and reedbuck, were likely targeted by
285 hunters. Given their relative abundance in our sample, these species were probably
286 common in and around WB.

287

288 **Conclusion**

289 WB is a significant site in the Mpondoland region of the Eastern Cape Province in South
290 Africa due to its persistent human occupation from the MIS3 to the mid-Holocene. Facilitated
291 by a narrow continental shelf, near continuous occupations over glacial periods resulted from
292 a relatively stable shoreline, with the distance to the coastline during the LGM estimated at
293 only ~8 km from the modern coast ¹. The palaeoenvironmental, palaeobotanical, and
294 archaeozoological data indicate that WB was a crucial hub for numerous habitats and
295 resources, which prehistoric hunter-gatherers used. This study's preliminary analysis of
296 identifiable fauna shows that WB was host to grazing and browsing herbivores. The remains
297 of water-dependent herbivores indicate a consistent source of fresh water nearby. The fauna
298 suggests that WB maintained a relatively grassy and bushy environment, with a mix of
299 grasslands, bushy, and forested habitats. Although tentative, the data suggest mixed,
300 possibly bushier, landscapes during the LGM, becoming more open with typical bushveld
301 vegetation in the Early Holocene.

302 The identification of leopard seal remains at WB is significant as it is the first direct evidence
303 of this species recovered from Pleistocene and Holocene archaeo-faunal assemblages

304 along the southern African coast. This and other faunal and palaeobotanical data may
305 indicate a substantial ecological shift in the coastal environment during the LGM. Although
306 the faunal sample analysed in this study is relatively small, it provides valuable insight into
307 the palaeoecology of the region. Excavations at WB are ongoing, and future analyses of
308 larger faunal samples would better contextualise the site's palaeoecology. Overall, WB
309 provides a unique opportunity to study human-environment interactions in southern Africa
310 during the Pleistocene-Holocene transition, a period that has been poorly recorded in
311 southern African coastal sites.

312

313 **Data availability**

314 The data supporting the results of this study are available upon request to the corresponding
315 author.

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374

375 Table 1. Number of identified specimens (NISP) from Waterfall Bluff

Taxa	Common name	SRCS	LBCS	Total
<i>Hydrurga leptonyx</i>	Leopard seal		1	1
<i>Ceropithecus pygerythrus</i>	Vervet Monkey	1		1
<i>Procavia capensis</i>	Rock Hyrax	4	4	8
<i>Sylvicapra grimmia</i>	Common Duiker		1	1
<i>Tragelaphus oryx</i>	Eland		6	6
<i>Syncerus africanus</i> *	African Buffalo	1		1
<i>Redunca fulvorufula</i>	Mountain Reedbuck	1		1
<i>Redunca arundinum</i>	Southern Reedbuck	1		1
<i>Redunca</i> sp.	Reedbuck	3		3
<i>Philantomba monticola</i>	Blue Duiker	1		1
<i>Ourebia ourebi</i>	Oribi	1		1
<i>Damaliscus pygargus</i>	Bontebok/blesbok	1		1
<i>Pelea capreolus</i>	Grey Rhebok	2		2
<i>Tragelaphus scriptus</i>	Bushbuck	4		4
<i>Raphicerus cf. campestris</i>	Steenbok	5		5
Bovidae: Indet.	Bov 1	7		7
	Bov 2	10		10
	Bov 3	2		2
	Bov 4	4		4
<i>Bathyergidae</i> sp.	African Mole Rat		1	1
<i>Hystrix africaeaustralis</i>	Porcupine	1		1
<i>Testudinidae</i>	Tortoise	7		7
<i>Varanus</i> sp.	Monitor	1		1
Aves	Bird - small	2		2
Total		59	13	72

376 *Given the racial offensiveness of the original species name *Syncerus caffer*, we use *Syncerus*
 377 *africanus* following Dusseldorp & Reynard²²

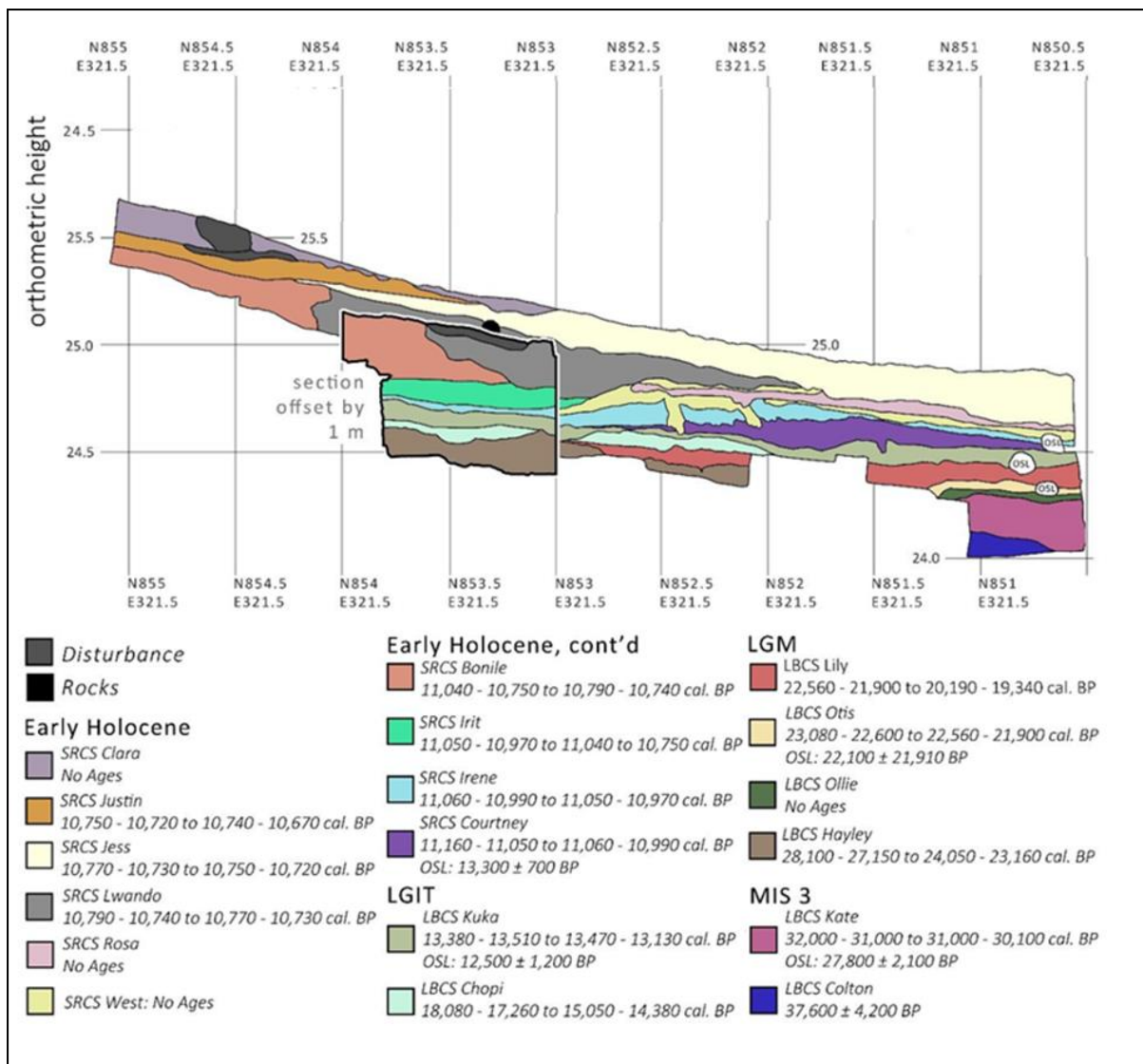
378

379 *Table 2. Ungulate dietary categories at Waterfall Bluff. Data is based on the number of*
380 *identified specimens. NTAXA = number of taxa*

Dietary preference	SRCS	LBCS	Total	NTAXA
Grazers	8	0	8	5
Mixed-feeders	0	6	6	1
Browsers	11	1	12	4

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382



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 384
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Figure 1. The ages and locations of SubAggs at Waterfall Bluff (Adapted from Esteban et al.¹).



388

389 *Figure 2. Leopard Seal Tooth (#CN47208, Lot 303)*

390



391

392 *Figure 3. [anonymised] and a leopard Seal at Cove Rock, 2014. Credit: [anonymised]*

393

394