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International Journal of Paleopathology

journal homepage: www.elsevier.com/locate/ijpp

The people behind the samples: Biographical features of Past Hunter-Gatherers from KwaZulu-Natal who yielded aDNA

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ARTICLE INFO

Keywords:

Later Stone age
Khoe-San
Hookworm
Malaria
Schistosomiasis
Cribra orbitalia
Child growth

ABSTRACT

Purpose: Skeletons sampled for ancient human DNA analysis are sometimes complete enough to provide information about the lives of the people they represent. We focus on three Later Stone Age skeletons, ca. 2000 B.P., from coastal KwaZulu-Natal, South Africa, whose ancient genomes have been sequenced (Schlebusch et al., 2017).

Methods: Bioarchaeological approaches are integrated with aDNA information.

Results: All skeletons are male. Dental development shows that the boy, with prominent cribra orbitalia, died at age 6–7 years. Two men show cranial and spinal trauma, extensive tooth wear, plus mild cribra orbitalia in one. **Conclusions:** Dental wear and trauma of the adults are consistent with hunter-gatherer lives. Even partial aDNA evidence contributes to sex determination. Parasitic infection such as schistosomiasis is the best-fit cause for the child's anemia in this case.

Contribution to knowledge: The convergence of genomic and bioarchaeological approaches expands our knowledge of the past lives of a boy and two men whose lives as hunter-gatherers included episodes of trauma and disease.

Limitations: The skeletons are incomplete, in variable condition, and from poorly characterized local cultural contexts.

Suggestions for further research: Thorough osteobiographic analysis should accompany paleogenomic investigations. Such disciplinary collaboration enriches our understanding of the human past.

1. Introduction

The bones and teeth from past peoples can provide information at both population and individual scales. To the extent that skeletal size and shape reflect genetic inputs, the analysis of human remains provides information about population relationships - a topic now enhanced greatly by the study of extracted fragments of ancient DNA. In addition to population studies, both forensic anthropology and bioarchaeology have demonstrated the value of outlining the features of individual lives in ways that DNA studies cannot address. Evidence of past diets, diseases and habitual behaviours reminds us of the challenges and complexities of past lives. It also contributes to the heritage knowledge of contemporary peoples represented through inadequate or biased written histories.

Human evolutionary genomics is a rapidly expanding field of

scholarship (Schlebusch et al., 2017). While initial discoveries focused on past events in the northern hemisphere, technological innovations have recently supported the study of the human past in Africa. Exploration of the Khoe-San genome, identified by studies of contemporary descendants as one of the world's oldest extant human genomes (Nielsen et al., 2017), has been especially intense. Estimates of the time of divergence and population size of the Khoe-San lineage (Schlebusch et al., 2013, 2012) are dependent on the richness of the genomic information, as defined by both the completeness of individual genomes and the number of individuals sampled (Kim et al., 2014). While the calibration continues, and new patterns emerge, it is important that the genomic evidence is integrated into the broader context of the human past, reinforced by archaeological and bioarchaeological evidence (Lombard et al., 2018).

Recently, the full genomes of seven southern African individuals

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<https://doi.org/10.1016/j.ijpp.2018.10.008>

Received 27 March 2018; Received in revised form 18 October 2018; Accepted 25 October 2018

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who lived in KwaZulu-Natal were characterized in detail (Schlebusch et al., 2017). Three of these were hunter-gatherers found in humid, subtropical, coastal dune contexts. Two (Ballito Bay A and B) are from 40 km north, and one (Doonside) from a few kilometers south of the city of Durban, South Africa (29°53'S 31°03'E). With this study we aim to further explore the past lives of these three individuals, focusing on their behaviors and environmental challenges. By doing so, we extend the narratives revealed by their bones and teeth beyond their population affinities to details about their individual lives. The genomic research (Schlebusch et al., 2017) also includes study of skeletal remains of ancestral Bantu-speakers, which will not be explored further here.

The antiquity and isolation of southern African peoples provides the context for quantification of the timing of the deepest population splits among modern humans, that being between San-ancestral and other groups - estimated by Schlebusch and colleagues (2017) to have occurred between 350,000 and 260,000 years ago. Their genomic research demonstrates that the three hunter-gatherers from the KwaZulu-Natal Province of South Africa, who died about 2000 years ago, were ancestral to the southern Khoe-San. The study identifies their sexes, their skin and eye pigmentation, their non-lactase persistence, and the absence of genetic variants protecting them against *Plasmodium vivax* (one of five parasites that cause malaria in humans) and sleeping sickness. Our intent is to combine these observations with those from the fragmentary skeletons, to build a more complete picture of each of their lives.

1.1. The archaeological and environmental context

The three individuals under discussion here, all from coastal locales, were not obtained from formally excavated archaeological sites. Yet, based on their age and location, we can provide their broad context within the South African cultural sequence. Socio-economies that lack evidence for herding and that occur between about 4000 and 100 years ago in South Africa are associated with the final Later Stone Age (see Lombard et al., 2012 for the South African cultural sequence). Features of this Holocene material culture include hunting with bows and arrows, the use of composite poisoned bone arrowheads, relatively short and light spears, digging sticks weighted with bored stones, and the presence of standardized ostrich eggshell beads that were prepared using grooved stones (Scheinfeldt et al., 2010; Skoglund et al., 2017). Two thousand years ago was shortly before herding communities from East Africa arrived on the southern African landscape with their sheep, goats, and cattle (e.g., Lander and Russell, 2018). Bantu-language-speaking, or Iron Age, farming communities migrating from West Africa did not arrive in KwaZulu-Natal until about AD 300–400 (Maggs, 1980).

The three individuals discussed here followed a lifeway sustained by game hunting, fishing, gathering wild plant foods and foraging for shellfish along the KwaZulu-Natal coastline. All three individuals yielded dietary isotope values consistent with diets that included a sizable proportion of sea food (Ribot et al., 2010), so we may assume that they spent much of their time close to the coast. Curation documents indicate that both of the Ballito Bay individuals were associated with Later Stone Age shell middens. This is consistent with their putative subsistence activities. Some of the oldest evidence for shellfish exploitation in KwaZulu-Natal comes from the Middle Stone Age occupation layers at Sibudu Cave located approximately 15 km inland from the Indian Ocean and 40 km north of Durban (Plug, 2006), dating between about 77,000 and 40,000 years ago (Wadley et al., 2011; Wadley, 2015).

Where systematic survey and excavation projects have been conducted in the province, it is evident that the region was occupied during the last four millennia. For example, work in the Thukela Basin identified numerous sites (summarized in Mazel, 1989, and Lombard et al., 2012), mostly located on mixed grassland/woodland inland regions between the coastal plain and the mountains of the uKhahlamba-

Drakensberg. More than 1900 site records are lodged at the KwaZulu-Natal Museum for Later Stone Age sites distributed across province (Gavin Whitelaw pers. comm. January 2018). Sixty-one of the above-mentioned Later Stone Age sites are associated with coastal shell middens similar to the ones where the individuals from Ballito Bay and presumably Doonside were discovered. Such middens are often reported as part of cultural heritage surveys (e.g., Anderson and Anderson, 2016), but dated midden sites in KwaZulu-Natal are scarce. The dating of the human remains, together with their DNA, have now confirmed that the Ballito Bay middens and the Doonside locale were used by Khoe-San people during the Later Stone Age, before the arrival of farming communities.

The Kwa-Zulu Natal province is often called “the garden province.” Coastal regions of the province typically have subtropical thickets and deeper ravines; steep slopes host some Afromontane Forest. These landscapes would have held various small-to-medium sized mammals, tortoise and ostrich that could be hunted and trapped (Wadley and Jacobs, 2004). Available plant foods include roots and corms that provide carbohydrates as well as leafy greens and fruits (van Wyk and Gericke, 2000). Plant bedding preserved at Sibudu Cave shows utilization of sedge and other monocotyledons topped with aromatic leaves containing natural insecticidal and larvicidal chemicals that function as protection against pests, including mosquitoes. The presence of these plant materials and others suggest the production of herbal medicines (van Wyk et al., 1997; Wadley et al., 2011). Coastal resources included a variety of shellfish species, which provide iron-rich, nutrient-dense protein (Venugopal and Gopakumar, 2017), as well as washed-up fish and other collectable foods.

2. Material and methods

Curated skeletal remains from KwaZulu-Natal that are available for research are scarce (Ribot et al., 2010). Some features of the three skeletons chosen for genomic study were previously reported by Ribot and colleagues in a study that focused on chronology, craniometrics and dietary stable isotopes of all the region’s curated skeletons (2010). They demonstrated that the seven skeletons that pre-date immigration of Bantu-speakers (older than 1000 A.D.) are craniometrically distinct from Iron Age crania. Evidence from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses of bone collagen show that they were dietarily more reliant on marine foods than the later agriculturists. The values from the juvenile (Ballito Bay A) clustered with those of the adults, indicating an age post-weaning. In this population, weaning appears to have been completed by age four (Clayton et al., 2006). The Later Stone Age high $\delta^{15}\text{N}$ values cluster tightly, showing that they “ate appreciable quantities of marine foods, as might be expected for coastal Later Stone Age hunter-gatherers” (Ribot et al., 2010:108). These characteristics are fully consistent with the skeletons being ancestral Khoe-San. Two adults and one child from this sample were subsequently chosen for genomic study (Table 1). The immature skeleton (Ballito Bay A) had not been included in the craniometric aspect of the 2010 study.

The skeletal remains of all seven ancestral Khoe-San individuals were studied in 2007. Measurements and observations of the bones and teeth followed standard procedures (Buikstra and Ubelaker, 1994). Special attention was given to the teeth, which are helpful for estimation of juvenile age at death (AlQahtani et al., 2010), population affiliation (Black et al., 2009) and diet as reflected in occlusal wear (Lukacs, 2017; Perez-Perez et al., 2017). Interpretations were made within the context of distinctive features of Khoe-San ancestral populations (Dewar and Pfeiffer, 2004; Harrington and Pfeiffer, 2008; Kurki et al., 2008; Pfeiffer and Sealy, 2006). A description of the healed cranial trauma of Ballito Bay B was subsequently published (Pfeiffer, 2012, 2016). During the 2007 study, other behavioural and palaeopathological features were noted but have not been previously reported. We report on some of those observations here.

Table 1
Summary of previously published characteristics of the Ballito Bay and Doonside human remains from KwaZulu-Natal.

Ribot (2010)					Schlebusch (2017)			
	Sex &/or Age	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	^{14}C date BP	CAL. date BP (2 σ) ^a	Samples	DNA coverage	Sex
Ballito Bay A	Child	-14.4	11.8	1980 +/-20 (Pta-5796)	1986-1831	L&R petrous, PM tooth	12.94	XY
Ballito Bay B	Adult M	-13.6	13.3	2940 +/- 50 (Pta-5803)	2149-1932 ^a	L petrous, PM teeth	1.25	XY
Doonside (DBN 3062)	Adult F	-13.8	14.2	2110 +/-50 (Pta 5800)	2296-1910	Femur Humerus Femur Foot/hand	0.01	—

^a A duplicate date was generated for Ballito Bay B by Schlebusch and colleagues: 2110 +/- 30 BP (Beta 398217). The calibrated date is based on this. Calibrations were modeled using OxCal v.4.2 and SHCal 13 calibration curves, with no adjustment for marine-origin dietary carbon. Hence, all dates may be slightly biased toward greater antiquity.

3. Results: Osteobiographic details of the skeletal remains

3.1. Ballito Bay A

The catalogued unit at the KwaZulu-Natal Museum included only a skull, mandible and relatively complete dentition. Perhaps the missing basi-occiput was used for the radiocarbon date, as no other sampling was apparent in 2007. On loan to the University of Cape Town and studied there were a complete left humerus shaft and a left clavicle, the color and preservation of which are consistent with that of the skull. The bone tissue is in excellent condition, and curatorial reconstruction is minimal, with shellac-like coating limited to areas where skull bones have been joined. Both deciduous and permanent teeth are present. The deciduous molars are significantly worn, a pattern consistent with chewing tough or sandy foods (Fig. 1). The four permanent M1s are fully erupted and show very slight wear. The maxillary incisors are deciduous, but the central mandibular permanent incisors are partially erupted with prominent unworn mamelons. The deciduous anterior teeth are glued in place, and radiography was not employed to evaluate root development. Dental eruption is consistent with an age at death of 6–7 years (AlQahtani et al., 2010). There is no evidence of caries, nor of enamel hypoplastic defects that can be observed using the unaided eye.

The occipital bone shows complete fusion of the squamous portion to the partes laterales, but open sutures with the basi-occiput. The latter normally fuses to the pars lateralis between 5 and 7 years (Schaefer et al., 2009). The two well-preserved long bones (Fig. 2) provide measures of linear growth. The maximum lengths of the clavicle and humerus can be compared to values for other Later Stone Age children with ages at death determined from dental development. Based on comparison to previously studied Later Stone Age juvenile skeletons with long bone lengths similar to Ballito Bay A, he is within the expected size range for his dental age (Tables 2 and S1).

A noteworthy feature of the cranium is the presence of pronounced, bilateral porotic lesions on the roof of the orbits, which appear to have been active at the time of death. It can be characterized as Stage 4 cribra orbitalia (Buikstra and Ubelaker, 1994; 1992a), with coalescence of foramina and some thickening (Fig. 3). There is no porotic



Fig. 2. Ballito Bay A humerus and clavicle. Credit: S.Pfeiffer.

Table 2
Measurements (in mm) of Later Stone Age juveniles with similar long bone lengths to that of Ballito Bay A. Dental ages are based on AlQahtani et al., 2010 and represent the midpoint of 1-year intervals. For a key to catalogue codes, see (Morris, 1992a).

Catalogue designation	Dental Age (yrs.)	Clavicle length	Humerus length
MMK 214	2.5	73	134
ALB 137	3.5	72	146
MMK 238	3.5	80	
S5 Proto	4.5		136
SAM-AP 6052	4.5	75	138
UCT 437	5.5	74	137
SAM-AP 4207	5.5	72	148
SAM-AP 6054B	6.5	81	145
Ballito Bay A	6.5	75	146
ALB 132	7.5	82	164
Skel #4	7.5	88	172
ALB 133	8.5	79	157



Fig. 1. Ballito Bay A dentition, maxillary and mandibular. Credit: S.Pfeiffer.

hyperostosis of the parietals, nor is there notable porosity on the alveolar bone or the somewhat damaged hard palate (Fig. 1). In the areas where the frontal bones meet the greater wings of sphenoid, there is some porosity. Interpretation of what constitutes abnormal porosity in bones that were growing at the time of death is a subject of discussion



Fig. 3. Ballito Bay A frontal bone showing cribra orbitalia. Credit: S.Pfeiffer.

(Brickley, 2018; Buikstra and Ubelaker, 1994; Lewis, 2007). While the latter porosity may or may not reflect areas of normal, rapid growth, the presence of cribra orbitalia is an indicator of compromised health.

3.2. Ballito Bay B

This skeleton is represented by a well-preserved cranium and mandible missing only the right condyle, both coated with a shellac-like preservative. The dentition shows wear to the point of cusp obliteration and the development of secondary dentine (Fig. 4). There is bilateral evidence of mild, “healed” (Klaus, 2017; Zuckerman et al., 2014) cribra orbitalia.

The postcranial skeleton is represented by well-preserved long bones of the arm and forearm, scapulae, clavicles, patellae and first ribs. The pelvis is represented by fragmentary os coxae, a partial fifth lumbar vertebra, and sacral vertebrae S1 through S3. The femora are missing their distal portions, and the lower leg bones are absent. There is a small number of hand and foot bones.

The pelvic remains are consistent with the morphology of the skull and mandible, all indicating male sex. Although pubic symphyses are absent, the sciatic notches are narrow and the extant left auricular surface is not raised. The palate is high, mastoid processes are large (Buikstra and Ubelaker, 1994), although there is little brow ridge development, as is characteristic of ancestral Khoe-San crania of both sexes (Morris, 1992b). Age at death is at least middle adulthood, as indicated by complete fusion of all late-maturing epiphyses, sharp edges and shallow pits on sternal rib ends (Işcan and Loth, 1986) and a left auricular surface showing a morphology consistent with an age at death of 40–50 years (Buckberry and Chamberlain, 2002). There is ectocranial suture obliteration along much of the coronal suture. Maximum femoral head diameter is 40.3 mm, consistent with values for Khoe-San ancestral populations (Kurki et al., 2012).

This man survived a superficial cranial wound, as shown by a stone flake embedded in the right parietal (Fig. 5). It is surrounded by some reactive bone tissue changes but does not involve the inner table of the diploë. Other indicators of a physically challenging life include evidence of anterior endplate sclerosis with some remodeling of superior S1. The posterior vertebral body surface retains the appearance typical for a young to middle adult, but the anterior surface is compressed, with slight osteophytic development (Fig. 6). No comparable damage was noted on the inferior L5. There is bilateral osteoarthritic lipping on both proximal ulnae and indications of ulnar hyperflexion on both distal humeri. The humeri show relatively balanced use of the arms, as



Fig. 4. Ballito Bay B maxilla showing dental wear. Credit: S. Pfeiffer.



Fig. 5. Ballito Bay B cranial wound showing stone embedded Credit: S. Pfeiffer (see also Pfeiffer, 2012, 2016).



Fig. 6. Ballito Bay B trauma damage to S1. Credit: S.Pfeiffer.

reflected by midshaft diameters (Table S2).

3.3. Doonside (DBN 3062)

The bone tissue of this curated unit is in poorer condition than the two previously described. Extensive plastic and shellac-like products were used in the reconstruction of the skull. There are some maxillary teeth, but the mandible is absent. Postcranially, preservation is variable, with considerable breakage. Complete long bones include the right humerus, left femur, left tibia and both fibulae (see Table S3 for measurements). Most tarsal bones are in excellent condition, but the scapulae, vertebrae, ribs and hip bones are represented by fragments. Based on the extended zygomatic root, wide and high palate (Bass, 2005), narrow sciatic notches and low carrying angle indicated by the distal humerus (Rogers, 1999), the skeleton is adult male.

While the teeth show heavy wear, other skeletal indicators suggest an age at death younger than that of Ballito B. The two extant auricular surfaces show morphology consistent with late 30's to early 40's (Buckberry and Chamberlain, 2002). Most synovial joints show little or no osteoarthritis (except the mandibular fossae, which show pitting). The tarsal bones show evidence of well-developed facet extensions, consistent with deep squatting as a relaxed habitual posture (Dewar and Pfeiffer, 2004). Using the maximum femur length of 367 mm to estimate stature (Feldesman and Fountain, 1996), he was about 1.42 m tall.

The maxillary dentition shows evidence of heavy wear as the result of vigorous chewing, with some abnormal wear planes, likely resulting from the absence or misalignment of mandibular anteriors. The second molars are heavily worn and the first molars are absent, with periapical resorption evident on both palatal and buccal sides of the right first molar, the buccal side of the left first molar, and the right second premolar alveolae. Periapical inflammation likely resulted from tooth pulp cavity exposure caused by wear that was too rapid for secondary dentine to develop, or by tooth breakage (Hillson, 1996). While such abscesses can be circumscribed within the oral cavity, they can also lead to blood-borne infections (Waldron, 2009).

4. Discussion

Three skeletons discovered along the South African east coast have now been characterized in several ways, producing a picture of who

they were and how they lived. About 2000 years ago, these ancestors of the southern Khoe-San lineage exploited coastal food resources and led a physically vigorous life. It seems highly probable that the spondylolisthesis suffered by one of the men would have caused back pain (Pye et al., 2004; Raastad et al., 2015). Previously identified as distinctive craniometrically (Ribot et al., 2010) and genomically (Schlebusch et al., 2017), we can add that they were small-bodied and had dental wear consistent with the isotopic evidence for reliance on sandy coastal foods. The helicoidal wear pattern seen clearly in one of the men is caused by habitual mastication of abrasive foodstuffs (Hillson, 1996), like shellfish with sand adhering. The teeth of the other man are worn and/or damaged to the point of abscess and loss.

The sex of the Doonside skeleton illustrates ways that the different research approaches complement and self-correct each other. Focusing on the skull alone, Ribot and colleagues identified this skeleton as female. While they do not specify their criteria, the authors are familiar with ancestral Khoe-San cranial morphology. They may have been influenced by an early assessment (Galloway, 1936), which may have been based on a less reconstructed skull. Genomic research found evidence “consistent with XY [male] but not XX [female]” (2017, Table S2). Study of the full set of fragmentary remains indicates that male sex is most probable. This is consistent with the genomic results. Also of potential value is the association of ancient DNA yield with patterns of post-mortem diagenesis. The skeleton providing the highest yield (Ballito Bay A) is of well-preserved, unmodified bone, and was the least exposed to any form of curatorial preservative, while that which provided the lowest yield (Doonside) was the most friable and the most modified. This may be a spurious correlation, since different skeletal elements were sampled in each case. Nevertheless, it is important that these patterns be monitored, to minimize non-productive destructive testing in future. In this case, the better yields are associated with sampling the petrous portion of the temporal bone and the weaker results are from samples of long bone. The tissue density and low cell turnover within the petrous pyramid appears to make it particularly attractive for ancient cell retrieval (Hansen et al. 2017; Jørkov et al., 2009).

4.1. Differential diagnosis of cribra orbitalia

The skeletal remains of the child, now known to be a little boy, provide biographical features that are inaccessible through the other approaches. The examination of his nuclear genome suggests the probable absence of any genetic variant that would have been protective against malaria. He was experiencing an active bone marrow response at the time he died, consistent with the presence of anemia (Brickley, 2018). Cribra orbitalia of the type seen here is a symptom of marrow expansion caused by a number of haemopoietic factors (Brickley, 2018; Walker et al., 2009). Its frequency is highest among children, followed by adult women; the trait is very rare in adult men (Steyn et al., 2016). A survey of ancestral Khoe-San children observed cribra orbitalia in 13 of 43 crania, all cases being slight to moderate (Pfeiffer, 2007). All previously documented instances among ancestral Khoe-San children are less extensive than that of Ballito Bay A.

Megaloblastic anemia is commonly associated with scurvy (dietary deficiency in vitamin C) or dietary deficiencies of components including folic acid, the B vitamins, and critical minerals like iron (Klaus, 2017, Lewis 2018). Given the isotopic and ecological evidence for a probable diet high in plant-sourced vitamins and proteinaceous shell fish that are high in iron, megaloblastic anemia is unlikely in this case. Non-dietary causes for anemia need to be explored.

The presence of cribra orbitalia in two of the three skeletons suggests an environmental cause for anemia. Bilateral cribra orbitalia was also observed on the skull of another male skeleton from the same region and antiquity, which was studied by Ribot and colleagues (2010), but was not chosen for genome study (catalogued as PMB 91/54 from Tinley Manor, S.Pfeiffer, pers. obs.). The most common environmental

factor associated with anemia leading to cribra orbitalia is malaria. Destruction of parasitized red blood cells, failure to produce sufficient red blood cells and sequestration of red blood cells in the spleen are all associated with this parasitic disease (Gunn and Pitt, 2012).

In their genomic study, Schlebusch and colleagues found that the Iron Age individuals in their sample from KwaZulu-Natal carried an allele (Duffy) that confers resistance against one endemic form of malaria, *Plasmodium vivax*. The Khoe-San skeletons did not carry this allele. The acute form of malaria, *P. falciparum*, is thought to leave little trace on the skeletons, but low grade recurring infections by *P. vivax* could lead to skeletal indicators of anemia (Setzer, 2014). Mosquitoes through which the pathogen is transmitted could have been present in the humid, warm coastal environment in which these foragers lived. From regional archaeological evidence like that at Sibudu (Wadley et al., 2011) plus modern practices (van Wyk et al., 1997), it is reasonable to assume that they had knowledge of medicinally useful plants, including some with insecticidal properties.

There is skeletal evidence against the argument that malaria is the cause of their cribra orbitalia. In addition to cribra orbitalia, malarial infection is associated with other skeletal changes, including porotic hyperostosis, spinal porosity, and porosity in areas immediately inferior to the humeral and femoral heads (cribra humeralis and cribra femoralis) (Smith-Guzmán, 2015). None of those features are present on the skeletal remains of the three Stone Age foragers in our sample. We deem it unlikely that ancestral Khoe-San peoples co-existed with *P. vivax* for many millennia, without evidence of a genetic response. Nevertheless, the possibility of malaria cannot be discounted.

There are other environmental factors that are more plausible causes than malaria. Other conditions associated with anemia severe enough to cause skeletal changes are hookworm and schistosomiasis (Garcia, 2009; Mitchell, 2016). Both of these parasitic infections are public health problems in the region today (Manyasgadze et al., 2016; Saathoff et al., 2005).

Hookworms that infect humans include the *Ancylostoma duodenale* and *Necator americanus* species, which are known to cause hemorrhage of red blood cells (Gunn and Pitt, 2012). It has been suggested that infestation by *Necator americanus* (the dominant genus in KwaZulu-Natal today) is associated with cribra orbitalia in a Canadian coastal archaeological context (Bathurst 2005). While the symptoms of infection with this intestinal parasite are less severe than those of schistosomiasis, it cannot be ruled out in this case.

Schistosomiasis is considered more severe than hookworm in its health effects. Also known as snail fever and Bilharzia, it is a disease caused by parasitic flatworms called schistosomes. The urinary tract or the intestines may be infected. Symptoms include abdominal pain, diarrhea, bloody stool, or blood in the urine. It is known to affect child growth and contribute to poor cognitive function. In addition to haemolytic anemia, it is linked to malnutrition, liver malfunction and susceptibility to other diseases (Mduluzi and Mutapi, 2017). The intermediate snail hosts associated with *Schistosoma haematobium* are endemic in much of KwaZulu-Natal and the Eastern Cape, but not in other parts of South Africa (Magaisa et al., 2015). The limited distribution of the disease is consistent with the rarity of skeletal signs of anemia among the Khoe-San ancestral skeletons from the South African coast to the south and west of KwaZulu-Natal.

5. Conclusions

This bioarchaeological exploration of the human remains that were used in a recent genomic study demonstrates the diverse perspectives that can be brought to our study of the human past. Tooth wear in the juvenile and the adults corroborates the prior results from dietary stable isotopes, that the diet included gritty foods, like shellfish. The adult postcranial dimensions provide evidence for small adult body size, joint surfaces and trauma are evidence of vigorous physical activity, and, as explored in prior reports, use of weaponry consistent with the Later

Stone Age. All these features are consistent with other Later Stone Age skeletal remains of the southern and western coasts. Unique to this east coast sample is the presence of notable haemopoietic marrow expansion linked to active bone remodeling in the child, and evidence of cribra orbitalia in men. We suggest that the most probable cause is schistosomiasis, a parasitic disease known to cause anemia, which is limited in its extent and is endemic in this region today.

In the context of best practices for studying the African past, the integration of bioarchaeological evidence into paleogenomic research has been vigorously advocated (Morris, 2017; Prendergast and Sawchuk, 2018). Bioarchaeology and palaeopathology have the potential to contribute substantially to the broader goal of seeing genomics benefit contemporary Africans (Nordling, 2017). The linkage of genomic evidence to environmental factors that would have challenged the health and survival of past populations is especially interesting, as in this case where endemic parasitic diseases were present.

It is noteworthy that the bones and teeth of a little boy who lived two millennia ago have provided new insights into the origin and diversification of our species. His story is one of layered improbabilities: That his skeleton was preserved by favorable burial conditions, discovered and donated to a curatorial institution, dated and studied by archaeologists, and chosen for ancient DNA analysis. Based on genomic estimates of large population numbers, his life was one of many thousands that have gone unobserved, yet here we have a small window into the humanity of our ancestors.

Funding

This research was funded in part by the Social Sciences and Humanities Research Council of Canada. The research of ML is supported by an African Origins Platform Grant (98815) awarded by the National Research Foundation of South Africa.

Acknowledgments

We thank curators Gavin Whitelaw and Alan Morris, who gave permission to study the curated materials. An earlier version of this research was presented at the Biennial Meetings of the Society of Africanist Archaeologists, Toronto, Canada, June 18–21, 2018.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ijpp.2018.10.008>.

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