



# Strontium isotope investigation of ungulate movement patterns on the Pleistocene Paleo-Agulhas Plain of the Greater Cape Floristic Region, South Africa

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## ABSTRACT

Middle Stone Age sites located within the Greater Cape Floristic Region on the South African southern coast have material culture with early evidence for key modern human behaviors such as projectile weaponry, large animal hunting, and symbolic behavior. In order to interpret how and why these changes evolved, it is necessary to understand their ecological context as it has direct relevance to foraging behavior. During periods of lowered sea level, a largely flat and vast expanse of land existed south of the modern coastline, but it is now submerged by higher sea levels. This exposed area, the Paleo-Agulhas Plain, likely created an ecological context unlike anything in the region today, as evidenced by fossil assemblages dominated by migratory ungulates. One hypothesis is that the Paleo-Agulhas Plain supported a migration ecosystem of large grazers driven by summer rainfall, producing palatable forage during summer in the east, and winter rainfall, producing palatable forage during winter in the west. Alternatively, ungulates may have been moving from the coastal plain in the south to the interior north of the Cape Fold Mountains, as observed for elephants in historic times.

In this study, we assess ungulate movement patterns with inter- and intra-tooth enamel samples for strontium isotopes in fossil fauna from Pinnacle Point sites PP13B and PP30. To accomplish our goals we created a bioavailable  $^{87}\text{Sr}/^{86}\text{Sr}$  isoscape for the region by collecting plants at 171 sampling sites and developing a geospatial model. The strontium isotope results indicate that ungulates spent most of their time on the Paleo-Agulhas Plain and avoided dissected plain, foothill, and mountain habitats located more than about 15 km north of the modern coastline. The results clearly exclude a north-south (coastal-interior) movement or migration pattern, and cannot falsify the east-west movements hypothesized in the south coast migration ecosystem hypothesis.

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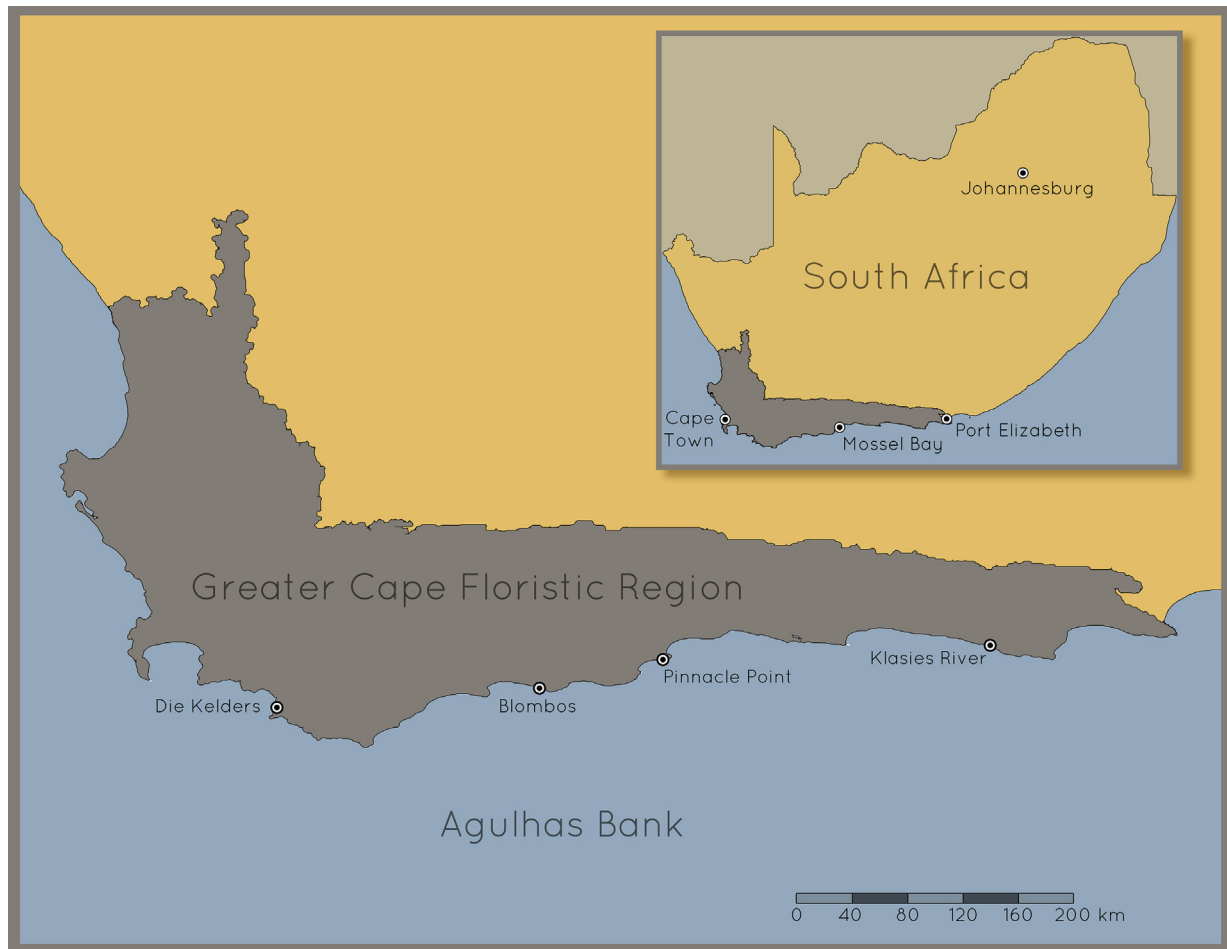
## 1. Introduction

A series of South African Middle Stone Age (MSA) sites dating

from ~160 to 50 ka provide evidence that has revised our understanding of the timing and pace of behaviors considered indicative of modern humans. Many of these sites are on the coast of the Greater Cape Floristic Region (GCFR) (Fig. 1), an area with Mediterranean climate and unique vegetation that is a plant biodiversity hotspot and center of endemism (Allsopp et al., 2014), but which is currently depauperate in large ungulates. The locality of our study

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**Fig. 1.** Map of southern Africa showing the extent of the Greater Cape Floristic Region with important cities (inset) and Middle Stone Age/Late Stone Age archaeological sites.

is Pinnacle Point, which is within the GCFR (Marean et al., 2014) and contains sites with the earliest evidence for stone tool microlithic technology ~71 ka (Brown et al., 2012), heat-treated stone tool production ~160 ka (Brown et al., 2009), and early evidence for humans using coastal resources ~160 ka (Marean, 2014; Marean et al., 2007). Genetic and fossil evidence suggest that the modern human lineage appears by at least ~200–160 ka (Clark et al., 2003; Gonder et al., 2007; McDougall et al., 2005), and of the handful of sites in Africa that are numerically dated to this time interval, only two are in South Africa (Border Cave and Pinnacle Point 13B) and one of these is in the GCFR (Pinnacle Point 13B) (Marean et al., 2007). It has been hypothesized (Marean, 2011, 2010) that the origin lineage of the indigenous inhabitants of the southern African sub-region, identified by genetic evidence (Henn et al., 2011; Pickrell et al., 2012; Schlebusch et al., 2012), found refuge along the southern shorelines during the long glacial cycle of Marine Isotope Stage (MIS) 6 (~195–125 ka) (Petit et al., 1999). For these reasons there is an ongoing multi-disciplinary effort to develop a detailed reconstruction of the paleoecological context of this region during the origins of modern humans (Franklin et al., 2015; Marean et al., 2014, 2015).

Klein (1983) noted that the faunal changes in the GCFR from the Pleistocene to the Holocene were greater than in any other African region with the possible exception of the Maghreb. Archaeological sequences dating to the Holocene –when the current sea levels and patterns of climate were rather stable and similar to modern – document a terrestrial fauna dominated by small-bodied

residential species such as grysbok, hyrax, dune mole rats, and tortoises (Marean et al., 2014). In contrast, the Pleistocene MSA and Later Stone Age (LSA) sequences found along the South African coast were dominated by large and medium-sized ungulates (both extinct and extant) that are typical of open-habitat migratory ecosystems (Klein, 1983). An early microlithic stone tool technology found at Pinnacle Point is further hypothesized to have been a component of projectile weapons designed to hunt large mammals safely and effectively (Brown et al., 2012). Open-habitat species that were present in the Pinnacle Point MSA levels (Rector and Reed, 2010) include black wildebeest (*Connochaetes gnou*), hartebeest (*Alcelaphus buselaphus*), springbok (*Antidorcas marsupialis*), zebra (*Equus cf. quagga*), and the extinct giant buffalo (*Syncerus antiquus*). Prior to fencing and habitat destruction, some of these species formed migratory associations of millions of animals in the interior well north of the south coast in the South African Highveld and Karoo that did not penetrate into the GCFR (Cronwright-Schreiner, 1925; Estes, 1991).

The dramatic faunal change between glacial and interglacial climates may seem surprising given that the GCFR was subject to rather muted climatic change through the Pleistocene (Chase and Meadows, 2007; Marean et al., 2014). Off the coast of the GCFR is the gradually descending and low-relief Agulhas bank, and during periods of lowered sea level varying portions of this landmass were exposed (Van Andel, 1989). A computer model of the changing character of this “Paleo-Agulhas Plain” shows that it was relatively flat, and during peak sea level regressions exposed about

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