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Mollusk and tortoise size as proxies for stone age population density in South Africa: Implications for the evolution of human cultural capacity

Tamaño de los moluscos y tortugas como representantes para la densidad de población de la edad de piedra en Sudáfrica: implicaciones para la evolución de la capacidad cultural humana

KEY WORDS: Middle Stone Age, Later Stone Age, South Africa, population density, modern human origins.
PALABRAS CLAVE: Paleolítico Medio, Paleolítico Tardío, Sudáfrica, densidad de población, orígenes de los humanos modernos.

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ABSTRACT

Research on the evolution of fully modern human cognitive capacities and cultural behaviors has flourished in recent years. Here, we focus on distinguishing between the two best-described models. The first hypothesizes a rapid, abrupt development of fully modern human behavior about 50,000 years ago (50 kya), at the transition from the Middle Stone Age (MSA) to the Later Stone Age (LSA) of Africa. The second proposes a gradual accumulation of advanced behavioral traits within the MSA (250-50 kya), ultimately coalescing in the LSA. The alternatives differ in the proposed relationship between population density and cultural change within the MSA, and this allows a test with the archaeological record of South Africa. In the Abrupt and Late Model, human population density in the MSA should be generally lower than in the LSA and there should be no trend towards higher population densities during the most recent MSA. In the Gradual Accumulation Model, human population densities should increase during the MSA, in keeping with the gradual or piecemeal development of advanced behaviors that presumably enhanced reproduction and survival. Past human population densities are impossible to calculate, but size changes in marine mollusks and tortoises can be used to track changes in density through time. This is because mollusks and tortoises grow continuously; they can be collected without special technology or risk; and human collectors tend to take the largest ones first, for reasons of visibility and food value. More intensive collection will thus reduce average mollusk or tortoise size, and during the stone age, the intensity of collection probably depended mainly on the number of collectors. A shift toward significantly smaller mollusks or tortoises thus implies larger, or at least denser, human populations. Mollusk and tortoise size observations summarized here suggest that MSA populations tended to be less dense than LSA populations on the south and west coasts of South Africa, and the difference appears to owe more to culture than to environment, because the MSA and LSA localities represent a range of environments, scattered widely in time and space. The difference tentatively supports the Abrupt and Late Model. More conclusive support will require additional observations, particularly from early LSA sites, antedating 13 kya.

RESUMEN

La investigación sobre las capacidades cognitivas y los comportamientos culturales totalmente humanos ha florecido en los últimos años. En el presente documento nos centraremos en distinguir los dos modelos mejor descritos. El primero establece la hipótesis de que se produjo un abrupto desarrollo del comportamiento del humano totalmente moderno hace aproximadamente 50.000 años, en la transición entre el Paleolítico Medio (PM) al Paleolítico Tardío (PT) en África. El segundo propone una acumulación gradual de rasgos conductuales avanzados dentro de la PM (250.000-50.000 años) que acaban fusionándose en la PT. Las alternativas varían en la relación propuesta entre la densidad de población y el cambio cultural dentro de la PM, lo que permite realizar una prueba con el registro arqueológico de Sudáfrica. En el Modelo Abrupto y Tardío, la densidad de población de la PM debería ser por lo general inferior a la de la PT y no debería existir ninguna tendencia hacia mayores densidades de población durante la PM. En el Modelo de Acumulación Gradual, la densidad de población humana debería crecer durante la PM al ritmo del desarrollo gradual o poco sistemático de los comportamientos avanzados que se supone que mejoraron la reproducción y la supervivencia. Las densidades de las poblaciones humanas del pasado resultan imposibles de calcular, aunque los cambios en

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los tamaños de los moluscos marinos y de las tortugas nos sirven para hacer un seguimiento de los cambios de densidad a lo largo del tiempo. Eso se debe a que los moluscos y las tortugas crecen de manera continua; pueden recogerse sin ninguna tecnología ni riesgo especiales; y los recolectores humanos tienden a coger primero los de mayor tamaño por motivos de visibilidad y de valor alimenticio. Una recolección más intensiva reducirá así el tamaño medio de los moluscos y de las tortugas y, durante la edad de piedra, la intensidad de la recolección probablemente dependió sobre todo del número de recolectores. Un cambio hacia moluscos o tortugas más pequeños significa así una población humana mayor o por lo menos más densa. Las observaciones sobre el tamaño de los moluscos y de las tortugas que se resumen aquí sugieren que las poblaciones de la PM tendían a ser menos densas que las de la PT en las costas del sur y del oeste de Sudáfrica y que la diferencia parece deberse más a motivos culturales que al entorno porque las ubicaciones de la PM y de la PT representan una gama de entornos diseminados ampliamente en el tiempo y en el espacio. La diferencia parece apoyar de forma tentativa al Modelo Abrupto y Tardío. Contar con apoyos más concluyentes requerirá más observaciones, en particular en los yacimientos de las primeras épocas de la PT anteriores al 13.000.

LABURPENA

Azken urteotan gorakada izugarria izan dute berriaz gizakiari dagozkion gaitasun kognitibo eta jokabide kulturalen gaineko ikerketek. Lan honetan, orain arte modurik zehatzenean deskribatu diren bi ereduak aztertuko ditugu. Lehenengo ereduak ezarritako hipotesiaren arabera, duela 50.000 urte inguru, Erdiko Harri Arotik (EHA) Harri Aro Berantiarreko (HAB) igarobidean, Afrikan bat-bateko jautzia eman zuen gizakiaren bilakaerak jokabide guztiz modernorantz. Bigarren hipotesiak ezartzen duenaren arabera, ordea, Erdiko Harri Aroaren barruan (250.000tik 50.000 urtera bitartean) mailaz maila metatuz joan ziren jokabide-ezaugarri aurreratuak, eta horiek guztiak bat egin zuten Harri Aro Berantiarrean. Proposatzen diren bi aukeren arteko aldea EHAn barruko biztanleriaren dentsitatean eta kultur aldaketan oinarritzen da, eta horrek aldi berean aukera ematen du Hego Afrikako erregistro arkeologikoan proba bat egiteko. Lehenengo hipotesiko ereduari, Erdiko Harri Aroan bat-bateko jautzia eman zela adierazten duenean, alegia, biztanleriaren dentsitatea, oro har, Harri Aro Berantiarrean baino txikiago behar zukeen izan, eta EHAn zehar ez zegokeen dentsitate handiagorako inolako joerarik. Bigarren hipotesiaren arabera, hau da, mailaz mailako metaketaren ereduari proposatzen duenaren arabera, ugalketa eta biziraupena ustez hobetu zuten jokabide aurreratuak garatu ziren heinean areagotu zen giza biztanleriaren dentsitatea. Iragan urruneko giza populazioen dentsitateak kalkulatzeko ezinezkoa da. Hala ere, denboran zehar dentsitate horiek egindako bilakaeraz ohartzeko modua badago itsas moluskuen eta dortoken tamainak aztertuz. Horretarako, kontuan hartuko da moluskuak eta dortokak etengabe handitzen direla neurritz; eta horiek biltzek ez duela eskatzen inolako teknologia berezirik eta ez duela inolako arriskurik. Bestalde, biltzaileek tamaina handienekoak biltzeko joera dute, bai errazago ikusten direlako bai elikagai gehiago dutelako. Bilketa intentsiboaren ondorioz, harrapatutako moluskuen eta dortoken batz besteko tamaina murriztu egingo litzateke. Eta Harri Aroaz ari garelarik, bilketaren intentsitate-neurria biltzaile kopuruaren arabera ezarri ahal izango litzateke. Moluskuen eta dortoken tamaina txikiarantz aldatzeko giza populazio altua edo biztanleriaren dentsitate handiagoa adieraziko luke. Honako lan honetan bildu diren molusku eta dortoken tamainuari buruzko azterketaren argitan ondorioztatzen denez, Hego Afrikako hegoalde eta mendebaldeko itsasertzean kokatutako biztanleriari dagokionez, HABn baino dentsitate txikiagoa zegoen EHAn. Horrenbestez, badirudi bi aroen arteko aldea arrazoi kulturaletan oinarritzen dela gehiago inguruari dagozkionetan baino, Erdiko Harri Aro eta Harri Aro Berantiarreko kokalekuak denbora eta espazioan ondo barreiatuta daudelako eta gainera era askotako inguruetan. Badirudi, dentsitatearen desberdintasun horrek bat-bateko aldaketa berantiarreko ereduaren alde egiten duela, baina arrazoi erabakigarriak lortzeko, beharrezkoa da gaia ikertzen jarraitzea, batez ere 13.000 urtetik goragoko antzinatasuna duten Harri Aro Berantiarreko aztarnategietan.

THE ORIGIN OF MODERN HUMAN BEHAVIOR

Research on the evolution of fully modern human cognitive capacities and cultural behaviors has flourished in recent years. HENSHILWOOD & MAREAN (2003) summarize current alternative models, all of which assume that fully modern behavior evolved sometime during the Middle or Late Pleistocene in Africa. The models differ mainly on the timing of this evolution. Here we focus on testing the two best-described models. The first, or Abrupt and Late Model, posits a rapid or abrupt evolution of human cultural behavior about 50,000 years ago (50 kya), during the transition from the Middle Stone Age (MSA) to the Later Stone Age (LSA) of Africa. The second, or Gradual Accumulation Model, proposes a gradual accumulation of advanced behavioral traits throughout the MSA, culminating in the LSA.

Proponents of the Abrupt and Late Model argue that MSA Africans and Middle Paleolithic Europeans were behaviorally similar and that they shared derived behaviors such as sophisticated stone flaking, active hunting, pigment collection, and the control of fire. However, neither the Africans nor the Europeans routinely produced art

objects or ornaments, buried their dead with grave goods, commonly worked antler, bone, or ivory, or often transported raw materials over long distances. In these respects and others, they differed from many human populations after 50-40 kya, including most historic hunter-gatherers, whose material culture commonly reflected such behaviors. According to the Abrupt and Late model, the MSA ended abruptly when a small group of people came to resemble historic hunter-gatherers in their behavioral capabilities and then spread to replace or swamp non-modern people elsewhere, first in Africa and then in Eurasia. Klein has suggested that the development of fully modern (LSA and later) behavior followed on a genetic mutation that fostered the fully modern brain (KLEIN, 2000; KLEIN & EDGAR, 2002). In his view, it was the modern brain, with its seemingly infinite capacity for innovation, which promoted the modern diaspora, first through Africa and then beyond. Others who accept the Abrupt and Late Model believe that the biological (neural) capacity for modern human behavior existed long before 50 kya, but that rapid technological, sociocultural, and/or demographic change were the factors that made it manifest (BAR-YOSEF, 1998, 2000; WHITE,

1992). All proponents of the Abrupt and Late Model believe that the advanced behaviors associated with the LSA conferred fitness advantages that promoted larger LSA population sizes and their eventual dispersal from Africa.

The Gradual Accumulation Model postulates that anatomical and cognitive modernity emerged together at least 100 kya in Africa and perhaps at the time when the MSA first emerged, 250-200 kya. Archaeological markers of modern cognition and behavior then evolved in a gradual and piecemeal way during the MSA, culminating in the LSA about 50 kya. Armed with the full-blown LSA, fully modern humans then expanded to other regions of the world (DEACON & DEACON, 1999; HENSHILWOOD *et al.*, 2002; McBREARTY & BROOKS, 2000). McBREARTY & BROOKS (2000:532) suggest that new technologies and risk-management strategies linked to modern cognition and behavior increased infant survivorship and decreased overall mortality beginning at least 100 kya, promoting population growth and geographic expansion. Alternatively, environmental deterioration could have concentrated populations in some regions, increasing their density and leading to the invention of new technologies and survival strategies. McBREARTY & BROOKS (2000) did not specify whether population increase occurred only in certain parts of Africa or more or less everywhere the MSA existed. However, much of the archaeological evidence they cite for advanced MSA behavior comes from South Africa, which must then mean that MSA population density increased in southern Africa, at least sporadically. The Gradual Accumulation Model has gained support recently from the discovery of advanced artifacts in the MSA levels of Blombos Cave on the south coast of South Africa (D'ERRICO *et al.*, 2005; HENSHILWOOD *et al.*, 2001a; HENSHILWOOD *et al.*, 2004; HENSHILWOOD *et al.*, 2002). The artifacts include bone points, engraved ochre fragments, and purported shell beads, all of which are taken to indicate a level of behavior of the kind that becomes commonplace only after 50 kya with the LSA.

One way to determine which model is more likely to be correct is to develop predictions that can be tested in the archaeological record. The models differ conspicuously in their predictions for changes in population density and its effect on behavior. The Abrupt and Late Model predicts that human population density should be relatively low throughout the MSA and there should be no trend toward higher density through MSA time. The Gradual Accumulation Model predicts that

populations should increase during the MSA, particularly associated with the appearance of occasional bone artifacts, beads, and other markers of advanced behavior. The Gradual Accumulation model does not specify whether higher human population densities should precede advanced behaviors or vice versa, but archaeological indicators of human population density could help to decide this issue. The main obstacle to this may be sufficient temporal resolution to determine whether population density or behavior changed first.

A larger problem is that a postulated difference in population density between the MSA and the LSA could never be absolute, because density depends not just on technology but also on environment. Thus, LSA populations in relatively impoverished environments would be expected to have low, MSA-like population densities regardless of their advanced technology. One way to confront this confounding effect of environment is to compare MSA and LSA populations over a wide range of ancient environments, to determine if a general MSA/LSA contrast in population density still emerges. This is the approach we have chosen here. Ultimately, as more data accumulates, we plan to use sediments, mammalian fauna, and other paleoenvironmental indicators to control for environmental effects more directly.

At the present time, only South Africa presents an archaeological record that can be used to test the population predictions of the alternative models, and assemblages from the south (Indian Ocean) and west (Atlantic Ocean) coasts are particularly pertinent for their number and rich faunal associations (Figure 1 and Table 1). The two coasts have long differed environmentally, which means that comparisons between them can be used to determine the extent to which apparent chronological variation in MSA behavior and population density reflects a general trend or only local idiosyncrasy. For this reason, it is important to examine both coasts simultaneously.

MOLLUSKS AND TORTOISES AS PROXIES FOR HUMAN POPULATION DENSITY

Estimating human population densities and sizes from archaeological site densities is notoriously difficult, because different settlement patterns may generate different numbers of sites and younger sites tend to be more numerous than older ones for reasons of preservation alone. However, it may still be meaningful that LSA sites significantly outnumber MSA sites even though

the MSA spanned a much longer time. This is true even when temporally equivalent MSA and LSA segments are considered, leaving the impression that MSA people were generally less numerous.

Size changes in marine mollusks and tortoises offer another way to track human population density (BUCHANAN *et al.*, 1978; DE BOER *et al.*, 2000; KLEIN *et al.*, 2004; KLEIN & CRUZ-URIBE, 1983, 1987, 2000; MANNINO & THOMAS, 2002; PARKINGTON, 2003; SPETH & TCHERNOV, 2002; STINER *et al.*, 2000; STINER *et al.*, 1999). Mollusks and tortoises can be captured without special technology or risk, and they grow continuously. People usually take the largest ones first, either because these provide the highest food return, because they are more visible, or sometimes because they taste better. It follows that more intensive collection will tend to reduce average individual tortoise or mollusk size.

Ethnographic and ecological research in the Transkei on the southeast coast of South Africa illustrates the potential of mollusk size to illuminate the intensity of collection. Not surprisingly, the research has shown that the number of human collectors determined the annual number of mollusks removed per kilometer of rocky shore (HOCKEY *et al.*, 1988). It has further shown that the collectors preferred large mollusks, in part because they believed that larger mollusks tasted better (BIGALKE, 1973; LASIAK, 1991, 1992). In some species of limpets, larger individuals occur higher on the rocky shore, making them more visible, available longer, and therefore easier to collect (BRANCH, 1975; HOCKEY & BOSMAN, 1986). The research supports a hypothesized link between increased human exploitation and reduced mollusk size, because when collectors were given access to previously protected coastal areas, various mollusks they collected, including brown mussels (*Perna perna*) and goat's eye [*Patella (Cymbula) oculus*] and granular [*Patella (Scutellastra) granularis*] limpets, were larger than those from sites that had been long exploited; brown mussel size even decreased during a single study period (HOCKEY & BOSMAN, 1986; LASIAK, 1991, 1992). The role of human predation in reducing granular limpet size became especially clear when protected and exploited areas were paired for similar geomorphology, topography, and exposure to wave action, and exploited areas produced much smaller limpets (HOCKEY & BOSMAN, 1986). However, some taxa, including turban shells (*Turbo sarmaticus*), did not differ in average size between the protected and unprotected areas, suggesting that susceptibility

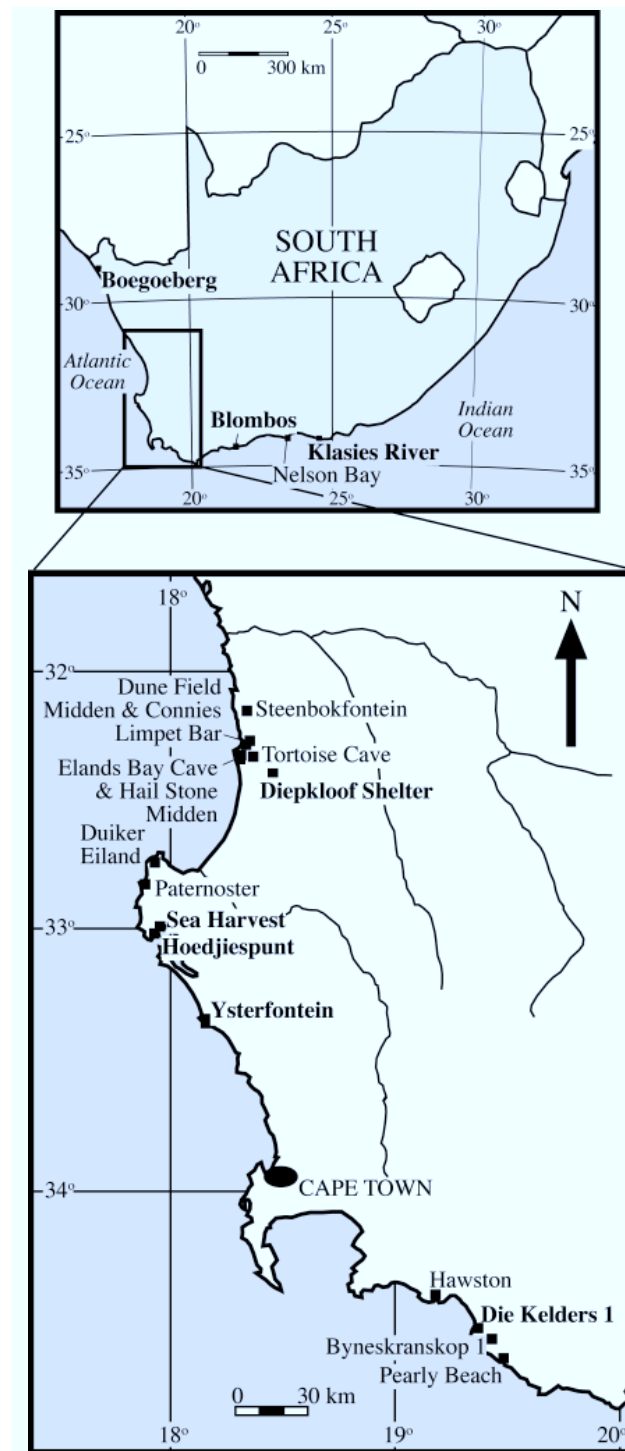


Figure 1. Map showing the approximate locations of the MSA and LSA sites cited in the text and Figures 2-4. Sites with MSA occupations are shown in boldface.

Blombos Cave	BBC	D'ERRICO <i>et al.</i> (2005); HENSHILWOOD <i>et al.</i> (2002); HENSHILWOOD <i>et al.</i> (2001b)
Boegoeberg 2		KLEIN <i>et al.</i> (1999)
Byneskranskop 1	BNK1	KLEIN & CRUZ-URIBE (1983); SCHWEITZER & WILSON (1982)
Connies Limpet Bar		BUCHANAN (1988)
Die Kelders 1	DK1	GRINE <i>et al.</i> (1991); KLEIN & CRUZ-URIBE (2000); MAREAN <i>et al.</i> (2000); TANKARD & SCHWEITZER (1976)
Diepkloof Rock Shelter	DRS	PARKINGTON (1987)
Duiker Eiland		ROBERSHAW (1979)
Dune Field Midden		ORTON (2002); PARKINGTON <i>et al.</i> (1992)
Elands Bay Cave	EBC	KLEIN & CRUZ-URIBE (1987); PARKINGTON (1988)
Hail Stone Midden		BUCHANAN (1988)
Hawston		AVERY (1976)
Hoedjiespunt 1 & 3	HDP	BERGER & PARKINGTON (1995); STYNDER <i>et al.</i> (2001)
Klasies River Main	KRM	DEACON (1995); SINGER & WYMER (1982)
Nelson Bay Cave	NBC	DEACON (1984); INSKEEP (1987); KLEIN (1972)
Paternoster 1062		YATES (1998)
Pearly Beach		AVERY (1976)
Sea Harvest		VOLMAN (1978)
Steenbokfontein	SBF	JERARDINO & SWANEPOEL (1999); JERARDINO & YATES (1996)
Tortoise Cave	TC	JERARDINO (1993; 1995); ROBAY (1987)
Ysterfontein 1	YFT1	HALKETT <i>et al.</i> (2003); KLEIN <i>et al.</i> (2004)

Table 1. List of MSA and LSA sites discussed in the text, the site abbreviations used in the figures, and some key references.

of mollusks to heavier exploitation is related to the life history characteristics and habitat preferences of each taxon (LASIAK, 1991, 1992). Limpet size is particularly likely to reflect the intensity of human collection, because unlike many other species, especially mussels, limpets lack subtidal stocks from which intertidal populations can be quickly replenished. This special vulnerability makes limpets especially useful as a proxy for human collector intensity.

Tortoises resemble limpets in many respects, including relatively long life spans, continuous growth, late reproductive maturation and high hatchling mortality, which means that they also broadly resemble limpets in their age structure and size distribution. STINER *et al.* (2000) note that intense tortoise collection for the illegal pet trade has diminished mean individual size in North Africa and Spain. Collection for pets is especially biased towards larger individuals, because they are more visible and have greater market value. STINER *et al.* (2000) add that in some tortoise species adult females are larger than males of the same age, so that removing the largest individuals from a population tends to reduce the reproductive output of the population and its ability to recover from exploitation. With this in mind, STINER *et al.* (2000) simulated the effects of varying levels of predation on tortoises using a range of fertility and mortality parameters and concluded that tortoises are highly sensitive to predation and can easily be driven to local extinction.

MOLLUSK SIZE DURING THE MSA AND LSA OF SOUTH AFRICA

A wide variety of mollusks inhabit the intertidal zones on the south and west coasts of South Africa, but limpets and mussels dominate archaeological shell deposits. The mix of species on each coast is different, largely reflecting differences in the offshore waters and in the dominant current systems. The warm, tropical Agulhas current flows from east to west along the south coast, favoring intertidal species that prefer or can tolerate warm water. On the far west of the south coast, periodic upwelling produces cooler temperatures, allowing warm and cold water marine communities to co-exist (BRANCH *et al.*, 1981; BRANCH *et al.*, 1994). Besides endemic limpets and mussels mentioned above, the south coast houses abalone or perlemoen (*Haliotis midae*), turban shells (*Turbo* spp.), and other edible mollusks. For reasons of preservation (durability), the opercula of turban shells are particularly conspicuous in archaeological sites.

The cold Benguela current flows from south to north along the west coast, and prevailing westerly winds promote upwellings of cold, nutrient rich waters (BRANCH *et al.*, 1981; BRANCH *et al.*, 1994). The west coast intertidal fauna thus tends to be comprised of species like black mussels (*Choromytilus meridionalis*) and granite limpets [*Patella (Cymbula) granatina*] that prefer relatively cool temperatures. Other common

species include Argenville's limpet [*Patella (Scutellastra) argenvillei*] and the granular limpet, which also occur sporadically on the south coast.

Limpet size is commonly documented from maximum shell length, while turban shell size is estimated from the maximum diameter of the operculum. Figures 2-5 use box plots to document archaeological size variation for five species – Cape turban shells, granite limpets, granular limpets, and Argenville's limpets – that are commonly represented by easily measured specimens in south or west coast sites. In each figure, the vertical line near the center of each boxplot marks the median for a sample; the shaded rectangles designate the 95% confidence limits around the median; the open rectangle encloses the middle half of the data (between the 25th and 75th percentiles); the horizontal line bisecting the plot marks the range of continuous measurements; and open circles and starbursts mark outliers. When the 95% confidence limits for two sample medians do not overlap, their medians differ at or below the 0.05 significance level.

The figures show that MSA turban shells, granite limpets, granular limpets, and Argenville's limpets all tend to be significantly larger than their LSA counterparts. The pattern is particularly clear for the Cape turban shell and for the granite limpet, which is the species for which we have the greatest number of observations. Median sizes of MSA black mussels tend to vary within the range of LSA mussels (Figure not shown. See HALKETT *et al.*, 2003; PARKINGTON, 2003). This was probably expectable, since unlike the turban shells and especially the limpets, black mussels thrive in both the intertidal and subtidal zones. Mollusks that occur only in the subtidal zone are rare or absent in stone age sites, suggesting that the people did not collect below low tide, probably because of treacherous currents that could wash them out to sea. The undisturbed black mussels that live subtidally would thus have provided an unexploited reservoir for rapid replenishment of even heavily exploited intertidal populations. Relative to limpets, black mussels could also recolonize an area more quickly because they mature more rapidly. The bottom line is that only short-term collection events, which are not visible in most of our samples, might reveal a difference between MSA and LSA impact on black mussels.

TORTOISE SIZE DURING THE MSA AND LSA OF SOUTH AFRICA

By far the most common tortoise species on the west and south coasts of South Africa is the angulate (or bowsprit) tortoise (*Chersina angulata*). Males grow larger, with a maximum recorded body weight of about 2.3 kg, maximum shell length of about 280 mm, and maximum shell breadth of about 160 mm (Rose 1962 as cited in KLEIN & CRUZ-URIBE, 1983; VAN HEEZIK *et al.*, 1994). Densities range from 6-15 to 31-34 individuals per hectare (AVERY *et al.*, 2004; VAN HEEZIK *et al.*, 1994). Their activity pattern varies with temperature and humidity, but they are generally available throughout the year (RAMSAY *et al.*, 2002), and they are a reliable, gatherable resource.

In archaeological sites, the most abundant part for estimating tortoise body size is the distal humerus. Figures 6 and 7 use the same boxplot format as Figures 2-5 to summarize the mediolateral diameter ("breadth") of distal humeri in south and west coast MSA and LSA tortoise samples, respectively. LSA specimens sometimes approach or equal MSA specimens in median size, but in general MSA tortoises are larger.

DISCUSSION

The figures show that in general, MSA Cape turban shells, granite limpets, granular limpets, Argenville's limpets, and angulate tortoises all tend to be larger than their LSA counterparts. Among the species for which we have measurements, only black mussels fail to show a similar difference, and this was probably expectable, for reasons we explained above. We suggest that generally larger MSA mollusk and tortoise size reflects more limited MSA predation pressure due to smaller MSA populations, but we must also consider the possibility that environmental difference was the controlling factor (CABRAL & DA SILVA, 2003; JERARDINO, 1997; MANNINO & THOMAS, 2002; SPETH & TCHERNOV, 2002). Mollusk growth rates, for example, are affected by temperature, population density, water turbidity, geomorphology, topography, and exposure to wave action (BRANCH & ODENDAAL, 2003; JERARDINO, 1997; MANNINO & THOMAS, 2002). MANNINO & THOMAS (2001) studied samples of the topshell (*Monodonta lineata*) from Mesolithic sites in southern England, and sought to control for environmental effects by combining extensive modern ecological surveys with counts of shell growth increments. The increments provide a

direct indication of the age distribution within each topshell sample, and the increment analysis showed that a progressive reduction in mean shell size was associated with a reduction in mean age. The accompanying ecological studies suggested that probable past environmental change should have increased not decreased mean shell size and age, and humans predation was thus the most plausible explanation for a reduction in topshell size through time. JERARDINO (1997) estimated sea-surface temperatures from oxygen-isotope ratios in black mussel shells and then compared estimated temperatures to black mussel size in late Holocene deposits on the west coast of South Africa. She found no correlation between temperature and size. She did, however, find a tendency for large mussels to occur in horizons that showed little evidence of water turbidity. The explanation may be that mussels in relatively calm waters can devote more energy to growth and less to finding food. However, not all the samples in her stratigraphic sequence fit the pattern, and the period of most rapid shell accumulation coincided with the smallest mussel sizes and low water turbidity. JERARDINO related the decrease in mussel size to intensive collection by humans during this period. Finally, DE BOER *et al.* (2000) compared modern middens to ones that were less than 200 years old to reduce the likelihood that climate change and sea level fluctuations seriously affected mollusk exploitation on Inhaca Island, Mozambique. They found significant reductions in mollusk size and species diversity in the modern middens, and they attributed this to increasing human exploitation resulting from increasing human population size on the island.

SPETH & TCHERNOV (2002) investigated the relationship between a decrease in size of spur-thighed tortoises (*Testudo graeca*) near the end of the Middle Paleolithic sequence at Kebara Cave, Israel, and changes in paleoclimate, site function, seasonality of site use, and the ranges of species or sub-species. They argued that the tortoises tended to be larger during warmer, moister intervals, when Kebara was used ephemerally, and during warm-season occupations. They accepted that human predation probably played a role in causing the decline in tortoise size, but they concluded that ambient temperature or other environmental factors had to be considered before reaching a definitive conclusion.

The current study does not address environmental controls on size directly, but the samples were drawn from a range of geographic settings and time periods that represent different

temperature regimes, precipitation levels, sea levels, floral and faunal communities, and coastal configurations, as well as different seasons of mollusk and tortoise collection and different probable site functions. This makes it likely that the tendency for both mollusks and tortoises to be larger in the MSA reflects human predation pressure more than climate or other environmental variables. In support of this conclusion, Figures 3 and 4 contain data from modern samples ("10-minute samples") of limpets that were collected from normally unexploited intertidal rocks near some of the key west coast LSA and MSA sites. Some of the LSA sites are subhistoric (less than 2000 years old), and they almost certainly formed under environmental conditions that closely resemble modern ones. In each case, however, the LSA limpets tend to be significantly smaller than those in the "10-minute samples", implying that it was LSA exploitation – not environment—that produced the relatively small archaeological limpets (BUCHANAN *et al.*, 1978; HALKETT *et al.*, 2003; LASIAK, 1992). In our on-going research, we hope to employ oxygen-isotope analysis and other methods that will provide more direct control over key environmental factors.

This work builds on previous comparisons between MSA and LSA mollusk and tortoise size in South Africa (HENSHILWOOD *et al.*, 2001b; KLEIN *et al.*, 2004; KLEIN & CRUZ-URIBE, 1983, 2000; PARKINGTON, 2003; PARKINGTON *et al.*, 2004). KLEIN *et al.* (2004) and PARKINGTON (2003) both analyzed mollusk size on the west coast, and we use many of the same samples here. They found that MSA samples not only tend to contain larger limpets, but they differ from LSA assemblages in other conspicuous respects, including a more limited range of mollusk species and a significantly smaller number of granular limpets relative to granite and Argenville's limpets. Granular limpets tend to occur higher on the shore, but they are smaller than the other two species, and they would probably be more commonly overlooked if limpet collection were less intensive. Combined with other observations, such as the rarity or lack of fish bones in MSA sites and the absence of rock lobster (*Jasus lalandii*) chelipeds, the limpet observations clearly suggest that MSA people exploited coastal resources more selectively or less intensively than their LSA successors.

The research we discuss was designed to generate archaeological observations that can be used to test alternative models for modern human behavioral evolution. The models differ not only in how they interpret occasional modern archaeological

markers in the MSA, but also in what they imply about the relationship between behavioral change and changes in population size or density. We know that population size increased significantly by the end of the MSA 50 kya, if only because fully modern Africans then expanded to Eurasia. Most researchers agree that the behavioral changes indicated by advanced archaeological markers would have enhanced human reproduction and survival, which means that they should have promoted larger human populations. Our mollusk and tortoise data so far fail to reveal population increase that might be predicted from the appearance of modern behavioral markers within the MSA. A possible explanation is that the markers occur only sporadically, and it was only when they became commonplace, in the LSA, that populations grew significantly. This explanation,

however, begs the question of why the earliest (MSA) manifestations of advanced behavior failed to become more common more quickly, assuming as we do that they conferred greater fitness.

We recognize that much more research is necessary to clarify the relationship between mollusk and tortoise size on the one hand and MSA and LSA human population size on the other, and in particular to control for the effects of environment. We note also that our LSA observations come entirely from sites younger than 13 kya, and a full test of the any hypothesis about the relationship between technological change and population size will require data from much earlier LSA sites, nearer to 50-40 kya in age, and also from regions other than the south and west coasts of South Africa.

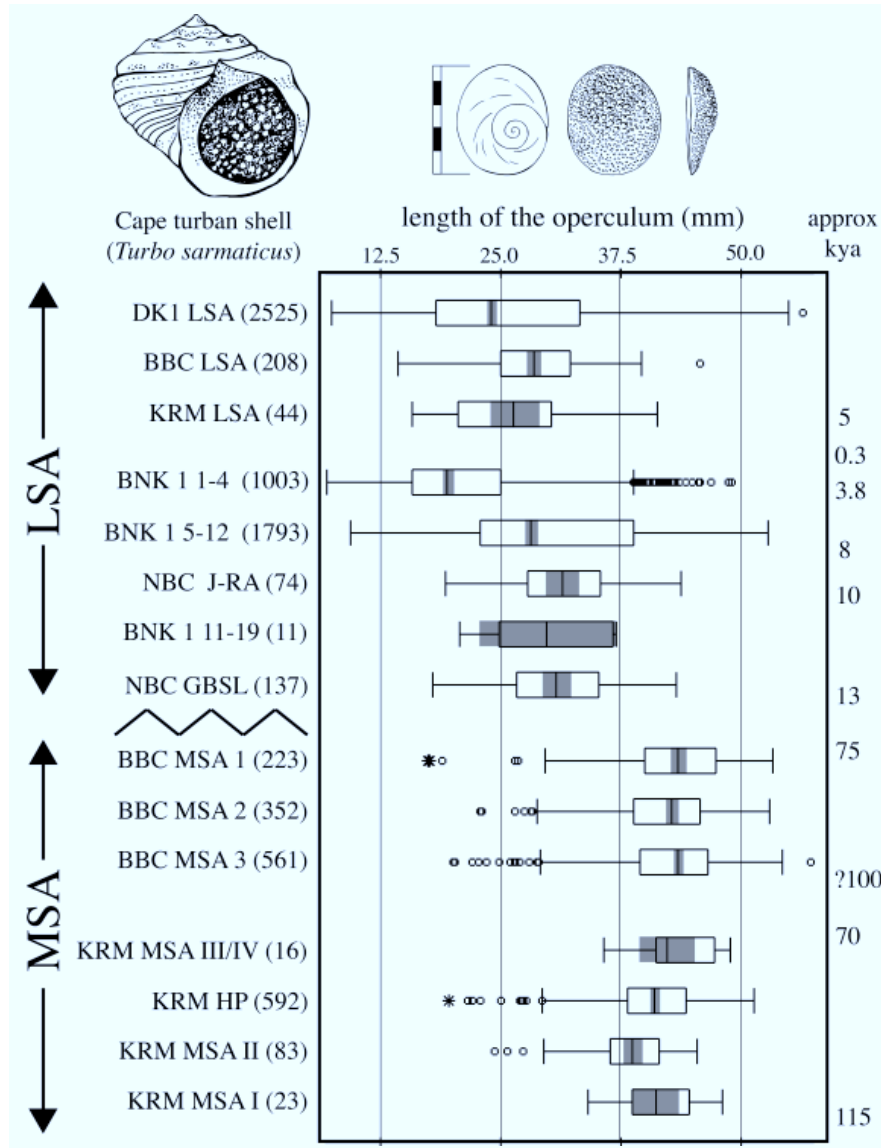


Figure 2. Box plots summarizing the maximum length of Cape turban shell opercula from MSA and LSA sites on the south coast of South Africa.

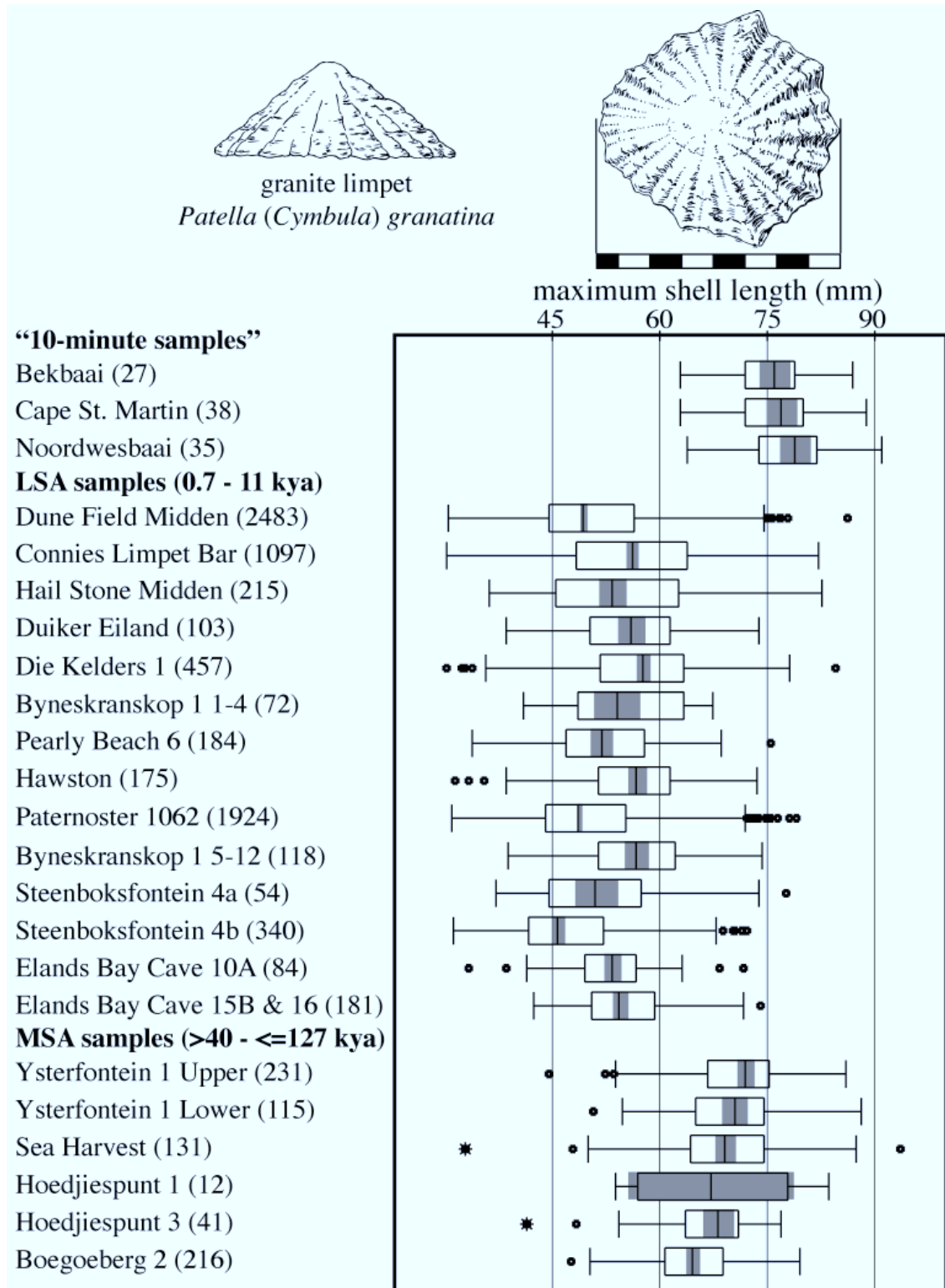


Figure 3. Box plots summarizing the maximum length of granite limpets from MSA and LSA sites on the west coast of South Africa.

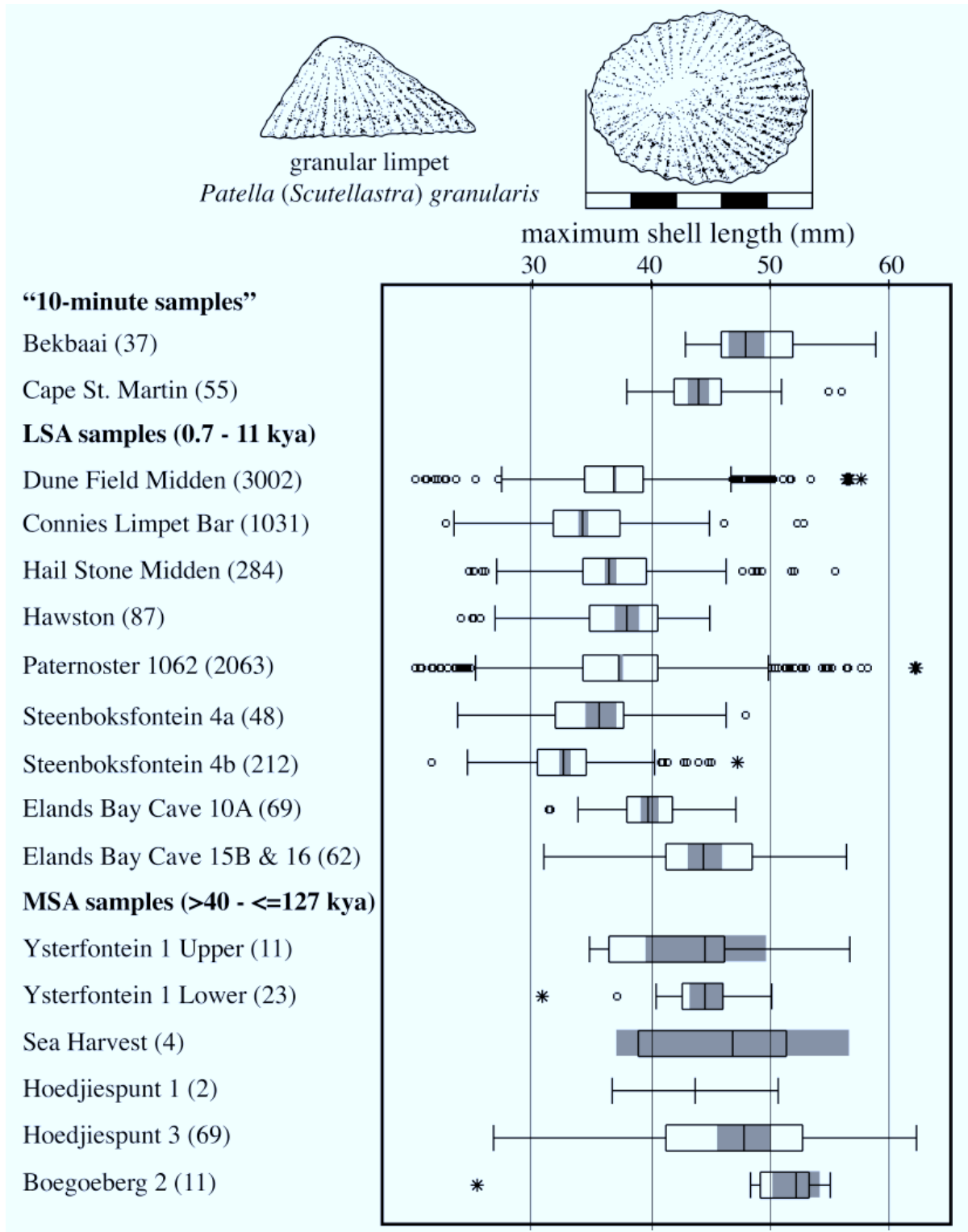


Figure 4. Box plots summarizing the maximum length of granular limpets from MSA and LSA sites on the west coast of South Africa.

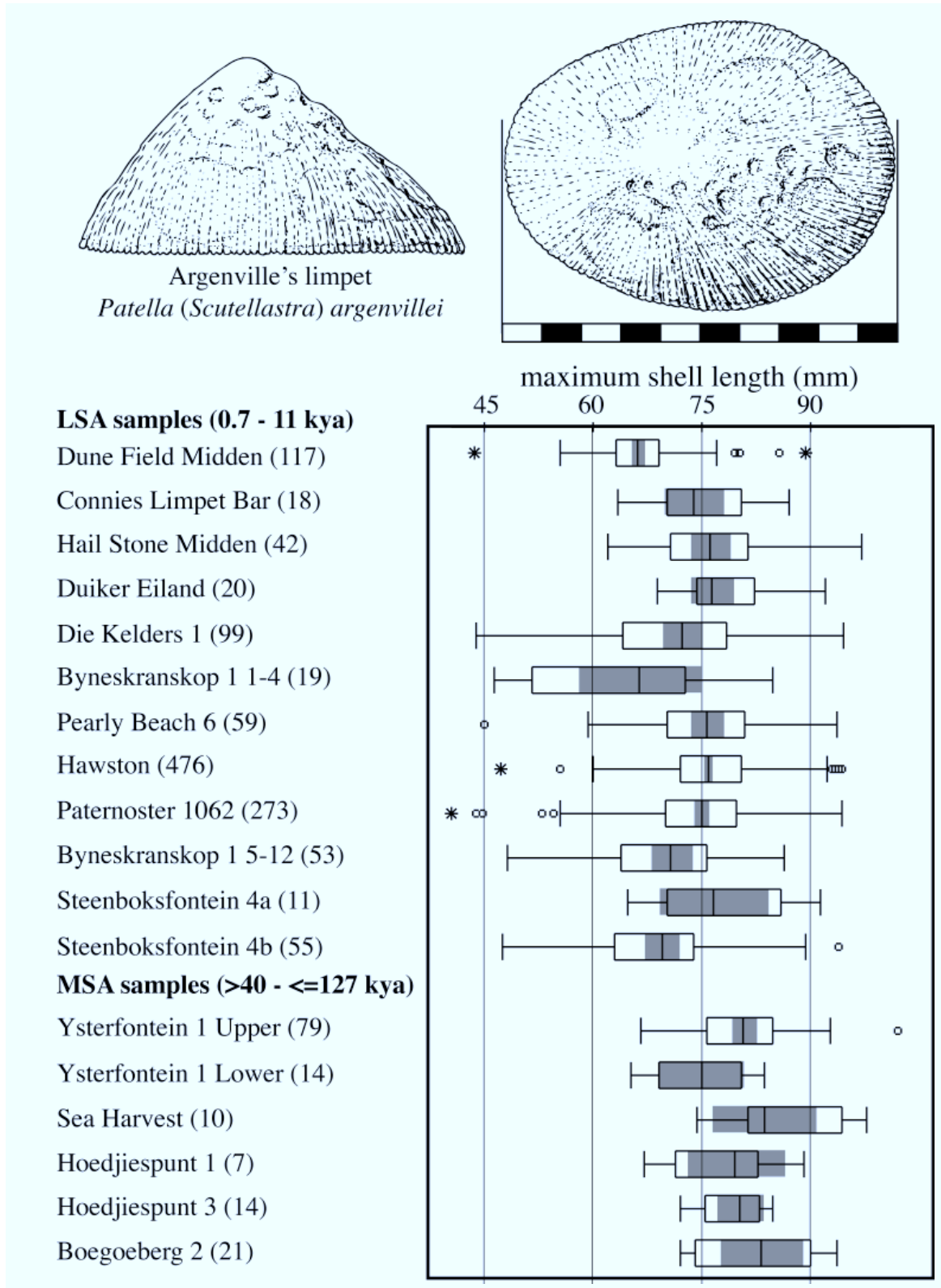


Figure 5. Box plots summarizing the maximum length of Argenville's limpets from MSA and LSA sites on the west coast of South Africa.

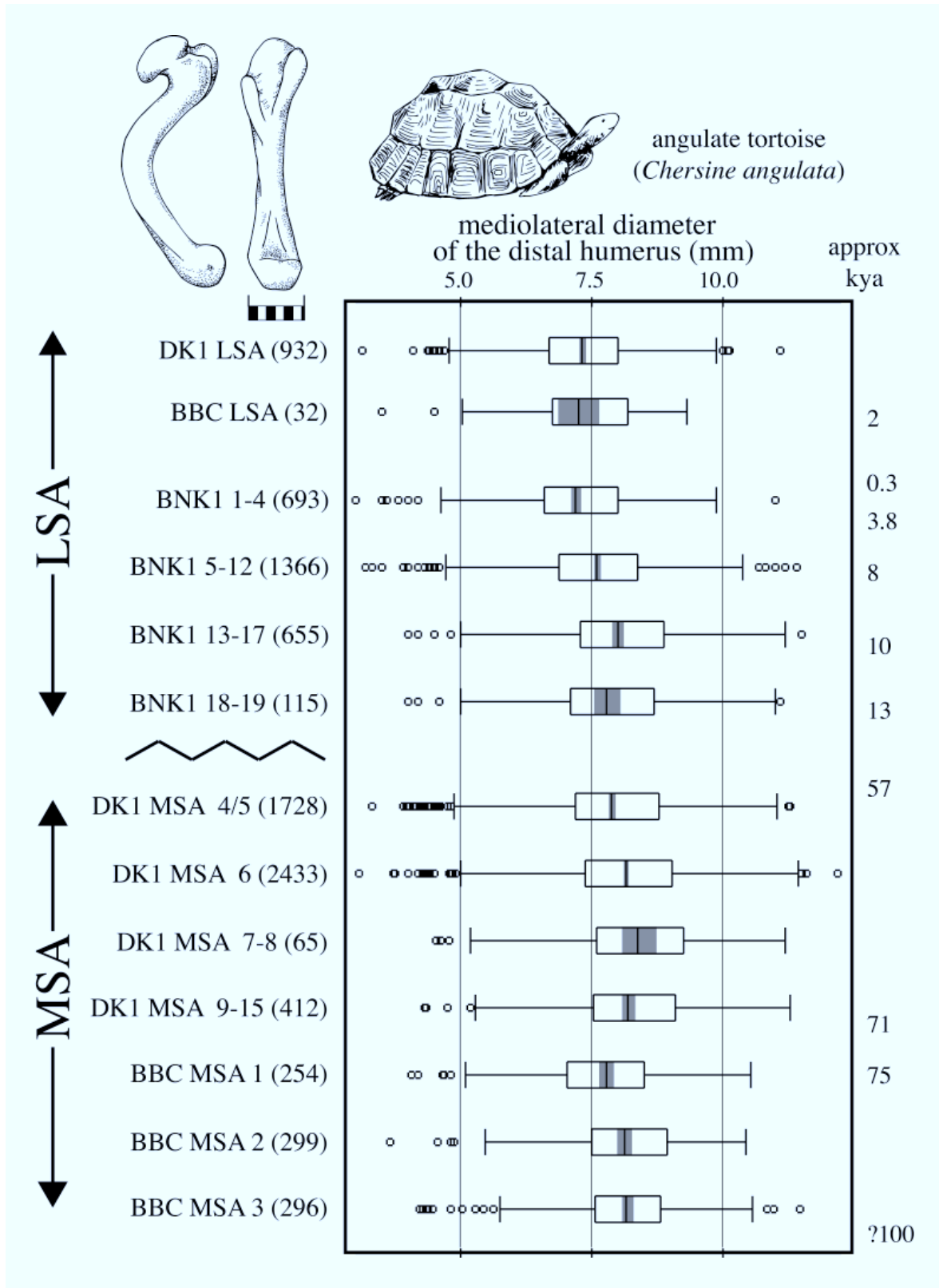


Figure 6. Box plots summarizing the mediolateral diameter ("breadth") of angulate tortoise distal humeri from MSA and LSA sites on the south coast of South Africa. The site list is different from the one for south coast turban shells in Figure 2, because not all sites with turban shells have provided abundant tortoises and vice versa.

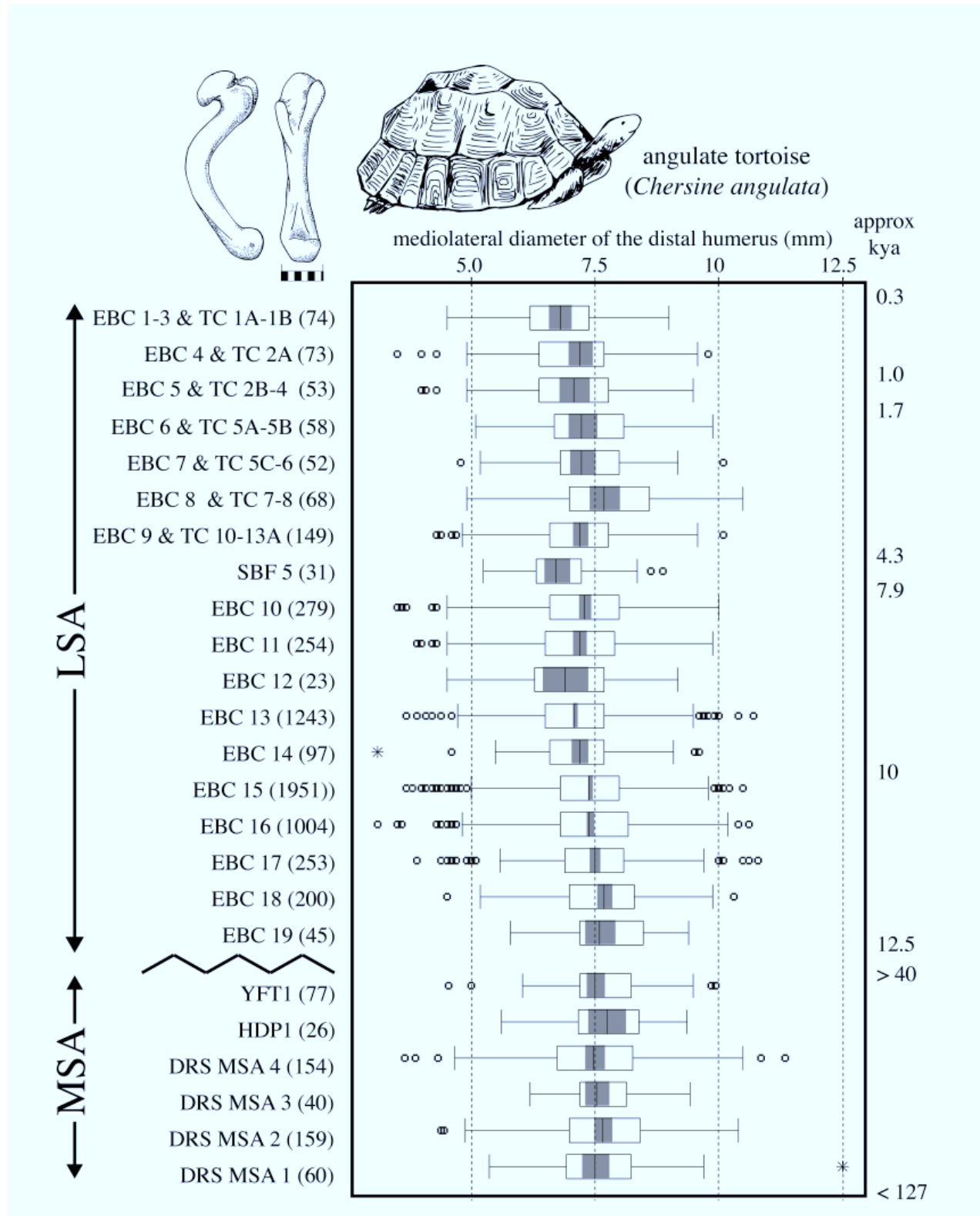


Figure 7. Box plots summarizing the mediolateral diameter ("breadth") of angulate tortoise distal humeri from MSA and LSA sites on the west coast of South Africa. The site list is different from the ones for limpets in Figures 3-5, because not all sites with limpets have provided abundant tortoises and vice versa.

CONCLUSIONS

Specialists agree that humans became fully modern in their behavior during the transition from the MSA to the LSA about 50 kya, but they disagree on whether the behavioral shift occurred gradually within the MSA or abruptly at its end. The contrasting perspectives, which we refer to as the Gradual Accumulation Model and the Abrupt and Late Model, differ in their expectations for human population size change within the MSA. The Gradual Accumulation model suggests that populations should have been growing, at least in the later part of the MSA after 100 kya, and the Abrupt and Late Model suggests they would have fluctuated around a relatively low average, with a sharp increase at the MSA -to-LSA transition. Mollusks and tortoises in MSA sites offer a means to test the alternatives, because average mollusk and tortoise size is a function of the intensity of human collection, which generally reflects the number of human collectors. Our data show that in general, MSA mollusks and tortoises are larger than their LSA counterparts, which suggests that MSA people lived at lower population densities.

There is the complication that the number of human collectors reflects both culture (mainly foraging technology) and environment, and we have not fully controlled for environmental change. However, our MSA sites sample a wide range of times and places, and this makes it unlikely that the environment is a primary factor in explaining the tendency for MSA mollusks and limpets to be so large. Thus, our data suggest that MSA populations were generally smaller than LSA populations, and to the extent that the data were drawn from a long interval during the later MSA (after 100 kya), they support the Abrupt and Late model more strongly than its Gradual Accumulation alternative. Additional samples and more thorough environmental controls will one day allow a firmer conclusion.

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