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Pachyosteosclerosis suggests archaic *Homo* frequently collected sessile littoral foods

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ABSTRACT

Fossil skeletons of *Homo erectus* and related specimens typically had heavy cranial and postcranial bones, and it has been hypothesised that these represent adaptations, or are responses, to various physical activities such as endurance running, heavy exertion, and/or aggressive behavior. According to the comparative biological data, however, skeletons that show a combination of disproportionately large diameters, extremely compact bone cortex, and very narrow medullary canals are associated with aquatic or semi-aquatic tetrapods that wade, and/or dive for sessile foods such as hard-shelled invertebrates in shallow waters. These so-called pachyosteosclerotic bones are less supple and more brittle than non-pachyosteosclerotic bones, and marine biologists agree that they function as hydrostatic ballast for buoyancy control. This paper discusses the possibility that heavy skeletons in archaic *Homo* might be associated with part-time collection of sessile foods in shallow waters.

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Introduction

The idea that littoral habitats may have played an important role in human evolution was first proposed more than half a century ago by Hardy (1960). Since then, littoral hypotheses have been supported on anatomical, physiological and nutritional grounds by a great number of authors (e.g. Sauer, 1962; Morgan, 1972; Cunnane, 1980; Verhaegen, 1985; Crawford and Marsh, 1989; Ellis, 1991;

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Niemitz, 2000). It is only recently, however, that more direct evidence of early Pleistocene consumption of aquatic foods has been advanced, e.g. *Homo erectus* from Trinil, Java, ~1.5 million years ago (Joordens et al., 2009), and hominins from East Turkana, Kenya, ~1.95 million years ago (Braun et al., 2010). In this paper, we argue that there is also comparative anatomical evidence that human forerunners during the Pleistocene might regularly have collected sessile, slow-moving or immobile littoral foods.

We present new data comparing bone thicknesses of fossil and extant hominoids to those of even-toed ungulates and Eocene cetaceans. We discuss whether archaic *Homo* fossils resemble slow, shallow-diving and wading species in having unusually heavy bones. We briefly review alternative hypotheses for pachyosteosclerosis, and address criticisms of this “littoral foraging hypothesis”.

Homo fossils are typically found in the presence of permanent bodies of water, including rivers, lakes and coastal deltas, and, at many of these sites, edible slow-moving or sessile foods including invertebrates were present. Our littoral hypothesis suggests that Pleistocene *Homo* populations may have dispersed by following permanent water bodies out of Africa along coasts – possibly during warmer periods, when the water temperature was suited to a tropical primate, or perhaps during glacial periods when increased water was locked in polar icecaps and glaciers, resulting in lower sea levels and the creation of new islands, reefs and beaches. Glacial periods in Africa were generally drier than interglacial periods (Hamilton and Taylor, 1991) and the replacement of forests with open landscapes is well documented for a number of late Pliocene and early Pleistocene east African sites (deMenocal, 1995; Reed, 1997; Vrba, 1985). These coastal populations may have beachcombed, waded and dived for littoral foods, from the high water mark to a few metres below sea level. From the coast, various *Homo* populations could have followed rivers inland to savannah wetlands including lakes and swamps.

Coastal populations could have originally inhabited forests that comprised mangrove elements, from which they may have plucked not only fruit from trees, as all apes do, but also oysters from the roots and trunks of mangrove trees. If human ancestors learned to exploit molluscs attached to trees, as capuchin monkeys (*Cebus apella apella*) do in mangrove forests using tools (Fernandes, 1991), it is only a small evolutionary shift to gathering molluscs also from under the water, though, to do this efficiently, significant changes in the anatomy would be expected.

Pachyosteosclerosis in tetrapods and hominids

The weight of a skeleton can be increased in different ways, including evolving denser bones, thicker bones, or narrower bone marrow cavities. Vertebrates with extraordinarily heavy skeletons are said to have generalised hyperostosis or pachyosteosclerosis, i.e. they display osteosclerosis (very dense bone histologically), pachyostosis (very thick bones compared to joint thickness) and medullary stenosis (narrow marrow canals). “Bone ballast in the form of osteosclerosis and hyperostosis is an unmistakable hallmark of an aquatic lifestyle” (Madar, 2007:198) and in tetrapods, “pachyostosis affects animals readapted to life in water” (Rage and Néraudeau, 2004). Whereas fast-swimming fish- and squid-eating aquatics have lightly built skeletons, heavy skeletons are typical of slow, shallow-water dwelling mammals such as seacows (especially the skull and ventral parts of ribs), walruses (especially the skull) and hippopotamuses (especially the limbs), and even of faster species such as sea otters (especially the limbs) that collect sessile foods at the sea bottom (Thewissen et al., 2007). Skeletal ballast is arguably most important in very warm and shallow waters, where evaporation causes saltier water, although during glacial periods, when rainfall decreases, there is less likelihood of freshwater runoff in some areas, which would also result in saltier water. No doubt, ballast is more important in the uppermost layers, where the lungs are still expanded, than at greater depths, where the lungs are compressed.

In order to descend (for food) and ascend (for oxygen) efficiently, diving tetrapods need to be about the same density as water, hence the overall density of marine tetrapods needs to be about 1.026 g/ml, and that of freshwater aquatics about 1.000 g/ml (e.g. Fish, 1990). This density tends to be distributed over the body, so as to stabilise the postures in the water. The pronograde seacows (Sirenia) have large dorsal lungs and very dense skulls and ventral rib parts (Gray et al., 2007; Nill et al., 1999). Incipient adaptations to wading often include heavy limb bones (pakicetids), and adaptations to slow bottom-diving typically include very heavy skulls (walruses, seacows, placodonts). Fast swimmers

Table 1

Cranial pachyostosis. Parietal thickness [mm] in fossil hominids and living primates.

Taxon	Approximate body weight [kg]	Parietal thickness [mm]
Homoidea		
<i>Gorilla</i>	120	3.6
<i>Pan</i>	41	5.3
<i>Australopithecus africanus</i>	?40	5.6
<i>Homo erectus</i>	?48	10.6
<i>Homo neanderthalensis</i>	?60	8.1
<i>Homo sapiens</i>	60	5.6
Primates		
Taxon	Approximate body weight [kg]	Parietal thickness [mm]
Primates		
Midparietal thickness (see Fig. 1), from Table 1 in Gauld (1996)		
<i>Cercopithecus</i>	4.8	1.2
<i>Colobus</i>	8.6	1.6
<i>Macaca</i>	9.5	1.7
<i>Papio</i>	18.9	2.9
<i>Hylobates</i>	5.9	1.3
<i>Symphalangus</i>	11.0	2.0
<i>Pongo</i>	60.3	4.9
<i>Gorilla</i>	123.5	5.2
<i>Pan</i>	41.0	4.2
<i>Australopithecus africanus</i>	?40.5	6.3
<i>Homo erectus</i>	?48.0	10.5
<i>Homo sapiens</i>	55.9	7.0

such as cetaceans and ichthyosaurs, on the other hand, secondarily evolve much less dense skeletons (e.g. Madar, 2007). Taylor (2000:15) writes: “. . . a new marine tetrapod clade will typically evolve bone ballast as part of its adaptation to life in water. Slow swimmers and grazers on sessile food, like sirenians and placodonts, develop it more strongly, but active predators like ichthyosaurs and cetaceans secondarily lose this character.”

‘Erectine grade’ populations are described as generally osteosclerotic, pachyostotic and having medullary stenosis, cranially and postcranially (Kennedy, 1985). Comparisons of different sources on parietal skull thickness in fossil and modern primates, including Old World monkeys, apes, australopithecines and *Homo*, show that skull vault thickness in *H. erectus* is more than twice that of equally large non-human primates (Table 1), that it is totally outside the normal range for primates (Fig. 1), that it is considerably more pronounced than in australopithecines and modern humans (Fig. 1), and that Neanderthal skulls are intermediate in this respect (Table 1). A comparison of relative cortex thickness of the femur at mid-shaft of fossil and modern hominoids, artiodactyls and fossil pakicetid (Eocene cetaceans) shows comparable results: some archaic *Homo* specimens had unusually heavy bones resembling amphibious species, and Neanderthals were intermediate in this respect (Table 2).

A number of alternative hypotheses have been put forward to explain the heavy bones of ‘erectine grade’ populations (Table 3), but these often fail to accommodate all available data. For instance, cursorials – whether fast (kangaroos, horses) or slow (human long-distance runners) – are typically slenderly built (Table 2) because “heavy skeletons are energetically expensive to move” (Madar, 2007:198). Also, it is not clear which activities in *H. erectus* could have led to thick as well as dense bones and medullary stenosis, not only in the arm and leg bones, but also in the skull.

The idea that high activity levels before puberty might have led to higher cortical robusticity throughout the skeleton later in life (Lieberman, 1996) leaves unanswered why most *H. erectus* were about twice as heavily built as chimpanzees, and even more heavily built than Neanderthals (Table 1), for instance, or why some archaic populations had large air sinuses in the frontal bones (especially Neanderthals), slender pubic bones (Trinkaus, 1976) or slender clavicles (Voisin, 2004).

Injuries to Neanderthal long bones have been described as resembling those of rodeo riders and attributed to extreme close quarter fighting with prey species (Berger and Trinkaus, 1995). This leaves

Table 2

Medullary stenosis. Comparisons of midshaft medullary/femur width [%] in fossil and extant cetartiodactyls and hominids.

Taxon Cetartiodactyla, extant and fossil	Description	Medulla [%] Mediolaterally, from Supplementary Table 3 in Thewissen et al. (2007)
<i>Tragulus</i>	~10 kg, mouse deer, tropical rain forest	63
<i>Saiga</i>	~30 kg, bovid, arid steppe	68
<i>Cainotherium</i> ?tylopod	Oligocene, ?rabbit-like herbivore, rabbit-sized	60
<i>Hippopotamus amphibius</i>	~2000 kg, amphibious, bottom-walking hippopotamus	55
<i>Sus barbatus</i>	~100 kg, bearded pig, tropical forest	70
<i>Indohyus</i>	Eocene raoellid, amphibious, racoon-sized, ?chevrotain-like, ?intermediate to Cetacea	42
<i>Poebrotherium</i>	Eo-Oligocene camelid, sheep-sized, hooves built for speed	75
<i>Merycoiodon</i>	Oligocene, short-limbed, large pig-sized, ?pig-like	68
<i>Leptomeryx</i>	Eo-Miocene tragulid relative, forested habitat, short forelimbs, small deer-like	64
<i>Ichthyolestes pinfoldi</i>	Eocene pakicetid, fox-sized, semiaquatic	25
<i>Nalacetus ratimitus</i>	Eocene pakicetid, wolf-sized, semiaquatic	54
<i>Ambulocetus natans</i>	Eocene ambulocetid, 3 metres long, crocodile-like	57
Taxon Hominoidea	Description	Medulla [%] Mediolaterally, from p. 480 in Aiello and Dean (1990)
<i>Homo sapiens</i>	Modern humans	42
<i>Homo</i> sp. 'rudolfensis'	Early Pleistocene, KNM-ER 1472 and 1481a	26
Non-human hominoids	~10–100 kg, apes, tropical rain forest	58
Taxon <i>Homo</i> species	Description	Medulla [%] Anteroposteriorly, from Table 1 in Kennedy (1985)
<i>Homo sapiens</i>	Male Romano-British ($n = 57$)	47
<i>Homo sapiens</i>	Female Romano-British ($n = 43$)	50
<i>Homo sapiens</i>	Males from Murray Valley, Australia ($n = 39$)	45
<i>Homo sapiens</i>	Females from Murray Valley, Australia ($n = 32$)	49
<i>Homo sapiens</i>	Khoisan, male and female ($n = 7$)	44
<i>Homo erectus</i> -like specimens	Zhoukoudian I and IV, KNM-ER 737 and 803, OH 28 ($n = 5$)	37
Taxon <i>Homo</i> species	Description	Medulla [%] Square root of medullary area, from Table 1 in Ruff et al. (1993)
<i>Homo sapiens</i>	Modern humans, Holocene ($n = 322$)	54
<i>Homo sapiens</i>	Early modern humans, late Pleistocene ($n = 6$)	47
<i>Homo neanderthalensis</i>	Neanderthals, late Pleistocene ($n = 10$)	44
<i>Homo erectus</i>	Archaic humans, middle Pleistocene ($n = 9$)	40
<i>Homo</i> sp. 'rudolfensis'	KNM-ER 1472 and 1481a, early Pleistocene ($n = 2$)	38

Table 2 (Continued)

Taxon	Description	Medulla [%] Anteroposteriorly and mediolaterally, from Table 1 in Croker et al. (2009)
Diverse mammals		
<i>Macropus</i> species	Kangaroo species ($n = 26$)	65
<i>Ovis aries</i>	Sheep, probably 12–19 months of age ($n = 24$)	75
<i>Homo sapiens</i>	Modern human females ($n = 46$) and males ($n = 43$), about fifty years old	48

unanswered, however, why *H. erectus* had even thicker bones than Neanderthals, or why chimpanzees are several times stronger and more muscular than modern humans (Vervaecke, 2002:141–142) and manipulate considerably heavier stone tools to crack open nuts (Mercader et al., 2007), yet have bone cortex densities and thicknesses in the range of non-human fossil and living primates, far below those of *H. erectus* and Neanderthals (Tables 1 and 2).

Another tentative explanation is that heavy cranial bones may have offered protection in conflicts with rivals, where some sort of banging with clubs was practiced (Knuckey, 1992; Boaz and Ciochon, 2004). There is, however, evidence that very dense bone tissue is less supple and more brittle than normal bone tissue (Madar, 2007). Moreover, head-banging does not explain why the postcranial bones are heavy, nor why the frontal skull, which contains paranasal air sinuses, has thinner walls than the occipital skull, which lacks air sinuses: if the skullcap had been for resisting blows, we would expect the densest bone to be at the front rather than the back, and we would expect the skullcap to be a round and vault-like ‘helmet’ as it is in modern humans, rather than the remarkably long and flat braincases of ‘erectine grade’ species. Moreover, ‘aggressive’ hypotheses of cranial vault thickness, such as fighting with rivals or with large prey, if they involve males, fail to explain why skullcaps in part of the *Homo sapiens* populations are thicker in women than in men (e.g. Ross et al., 1976; Li et al., 2007; see Table 4).

Special cases of hyperostotic bone such as the postcranial skeleton of *Homo ergaster* KNM-ER 1808, have been explained as resulting from pathological hypervitaminosis A, whether through high dietary intake of carnivore liver (Walker et al., 1982), or bee brood (Skinner, 1991). Generally we prefer non-pathological to ‘pathological’ explanations, but whether or not these hypotheses are correct, they fail to explain the shared heavy bones of ‘erectine grade’ populations at other places and times.

Discussion

‘Exertion’ explanations for the heavy bones of ‘erectine grade’ populations leave a number of critical questions unanswered. According to the comparative data, heavy-boned *Homo* populations resemble part-time, slow waders and divers in shallow waters. “Nasal sinuses and dense bones in *H. erectus* could certainly be interpreted as an adaptation to shallow diving, because of the sinuses tending to forbid deeper diving” (Michael Taylor, personal communication). Although we think it unlikely that human ancestors ever relied exclusively on seafood since this could have induced hypovitaminosis C, it is possible that human ancestors were once partly or strongly reliant on seafood, supplemented with terrestrial fruits, plants and animals. A number of palaeoanthropological papers have stressed the importance of aquatic resources such as molluscs, crabs, fish, marine mammals and shallow water plants in human evolution (e.g. Alperson-Afil et al., 2009; Erlandson, 2001; Erlandson and Moss, 2001; Gutierrez et al., 2001; Puech and Puech, 1993; Stewart, 1994; Stringer et al., 2008), and Joordens et al. (2009:656) conclude that “omnivorous hominins in coastal habitats with catchable aquatic fauna could have consumed aquatic resources.”

The littoral hypothesis appears to be supported by independent evidence:

- a) *Auditory exostoses*. The presence of auditory exostoses in several Neanderthal and some *H. erectus* skulls (Kennedy, 1986) suggests they engaged in some type of aquatic activity, since in *H. sapiens* these bony outgrowths of the ear canal are typically seen in people that dive for shellfish and aquatic

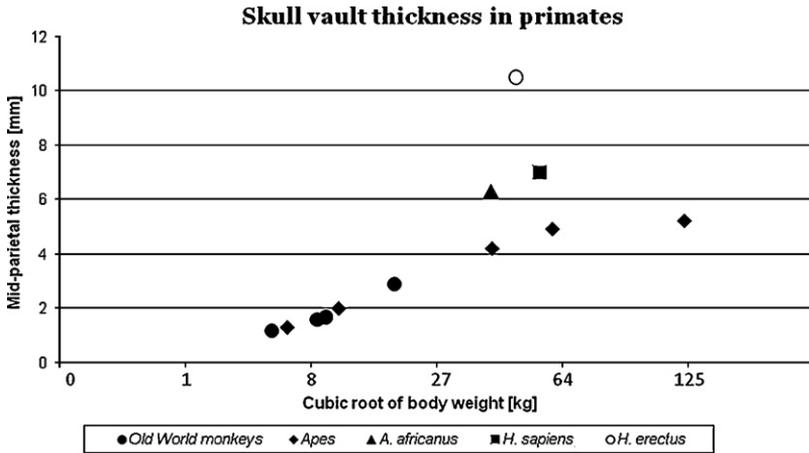


Fig. 1. Parietal skull vault thickness [mm] in primates, compared to body length (proxy: cubic root of body weight [kg]). Data from Gauld (1996), see Table 1.

resources in cold water (Frayer, 1988). Also, in a study by Ponzetta et al. (1997), auditory exostoses were found to occur more often in robust than in gracile individuals.

- b) *Heavier bones with marine diet.* Some modern human populations reliant on marine diets typically have thicker bone cortex than populations relying on land-based resources (Stock and Pfeiffer, 2001; Velasco-Vázquez et al., 1999). Whether this has to be explained by mechanical (e.g. the effect of wading or diving on bone formation) or dietary (e.g. the effect of minerals abundant in seafood) influences during lifetime, by natural selection (e.g. hydrostatic adaptations to diving or wading), or by combinations of these factors, is unknown to us.
- c) *DHA in aquatic foods.* Aquatic foods are many times richer in brain-specific long-chain polyunsaturated fatty acids such as docosahexaenoic acid (DHA) than terrestrial foods, and it is argued that the drastic expansions of the brain in the genus *Homo* may have coincided with consumption of aquatic, marine and other waterside foods (Broadhurst et al., 2011; Cunnane et al., 2007). The Neanderthal diet seems to have been very varied, including littoral (Stringer et al., 2008) as well as inland food resources (Richards et al., 2000); if they seasonally followed the rivers inland and ambushed herbivores in shallow water, this could explain their intermediate pachyosteosclerosis. It can also be argued that the later puberty in *H. sapiens* than in Neanderthals might be due to a diet poorer in DHA.

A number of hominid fossil or archaeological sites are found in association with open grassland habitats (e.g. Vrba, 1985). Human physiology (e.g. relatively low renal concentration power, high evaporative water losses, and high drinking needs), however, indicates that these open grassland habitats must have been close to permanent water bodies such as rivers, lakes and coasts. It is possible that the early diasporas of 'erectine grade' populations (the so-called Out of Africa 1) occurred not over semi-arid, open grasslands as has been hypothesised (e.g. Dennell and Roebroeks, 2005), but along open coasts and waterways, where human populations could have collected easy-to-catch littoral and waterside foods through walking and beachcombing as well as through wading and diving – activities all modern human populations are capable of, and many still practice (Bender et al., 1997). From these coasts, human populations could have moved to inland savannahs such as deltas, swamps, rivers and lakes.

The littoral foraging hypothesis would be severely weakened if fossils of heavy-boned *Homo* populations were found in habitats that lacked permanent water bodies containing edible aquatic foods. A number of palaeoecological data indicate that permanent water and edible littoral foods were a common feature of 'erectine grade' fossil sites (Broadhurst et al., 2011; Erlandson, 2001; Erlandson and

Table 3

Possible alternative hypotheses for pachyosteosclerotic features in 'erectine grade' and Neanderthal skeletons.

Anatomical region	Possible explanation	References
Lower extremities	Slow "endurance running" on open plains, e.g. savannahs	Dennell and Roebroeks (2005)
	"Dogged pursuit of prey"	Carrier (1984)
	Sprinting or fast running	Stewart and Hannan (2000)
	"Bouts of strenuous activity", especially on open terrain outside forests	Hanna and Brown (1983)
Upper extremities	"Higher load on the human femur, due to a larger body mass carried on two legs"	Crocker et al. (2009), see Table 2
	Tool manufacture and use, especially of stone tools	Abbott et al. (1998), Berger and Trinkaus (1995)
	Throwing or thrusting spears, especially for hunting and killing big game	Berger and Trinkaus (1995)
	Heavy struggles with animal prey, or with rivals	Berger and Trinkaus (1995)
Entire postcranial skeleton	Carrying heavy loads, e.g. stone tools, offspring, or prey	
Cheekbones and cranium	Harder biting (anterior dentition) and/or chewing (posterior dentition)	cf. Strait et al. (2007)
Cranial vault	Carrying loads on the head, especially in women (cf. Table 4)	
	Protection of larger brain in <i>Homo</i> , as opposed to non- <i>Homo</i> or non-hominin primates (cf. Fig. 1)	
	Inter- or intraspecific aggressive behavior, e.g. head-banging	Knuckey (1992), Boaz and Ciochon (2004)
Entire skeleton	Increased active exertion	Knüsel (1991), Ruff et al. (1993)
	Higher levels of sustained exercise prior to sexual maturity, inducing permanent systemic cortical robusticity, possibly through hormonal changes	Lieberman, 1996
	Combinations of the above (cranial plus postcranial explanations)	

Table 4Skull thickness in male and female *Homo sapiens*. The average thicknesses [mm] of 3000 living human skulls using CT scan images (from Li et al., 2007).

	Frontal bone	Parietal bone	Occipital bone
Men	6.58	5.37	7.56
Women	7.48	5.58	8.17

Moss, 2001; Marean et al., 2007; Munro, 2004; Verhaegen et al., 2007; Verhaegen and Puech, 2000), but more studies are needed to further test this hypothesis.

If the genus *Homo* dispersed along the coasts (e.g. Avery and Siegfried, 1980; Sauer, 1962) and even reached islands like Flores (Tobias, 1998), we expect they would have lived along saltwater during a considerable time span. The palaeolithic whale butchering at Dungo V, Baia Farta, Angola, occurred next to saltwater (Gutierrez et al., 2001), and Rift Valley sites such as Olduvai Gorge Bed II (from where OH 9 appears to have eroded) were sufficiently alkaline to contain the rotifers and other micro-organisms that flamingoes live on (Leakey and Hay, 1979). There is strong evidence that at Mojokerto *H. erectus* lived in a coastal delta (Huffman et al., 2006), that the earliest tools in northern Europe, at Pakefield, come from estuarine sediments (Parfitt et al., 2005), and that the type locality for *H. erectus*, Trinil, contains a number of marine faunal elements (Joordens et al., 2009).

On the other hand, the presence of unionoid mussels, which are generally intolerant of salt water, in Bed IV at Olduvai Gorge (OH 28), the KBS Member of Koobi Fora (KNM-ER 3883), the Chiwondo Beds of Lake Malawi (UR 501) and a number of other sites at which *Homo* remains have been found, including Pakefield, Trinil and Mojokerto, indicates that freshwater was also a common feature of many *Homo* palaeohabitats. This mix of fresh and salt water at various localities may account for some of the variation in bone thickness found in various *Homo* populations. Indeed, KNM-OL 45500, a thin-

boned *H. erectus* from Olorgesailie, Kenya, probably almost one million years old, had relatively thin cranial bones, which contradicts the exertion, rodeo, and head-clubbing ideas. Fossils found by sieving of the sandy silt adhering to the frontal bone include amphibian bones and a single tooth of the rodent *Otomys*, which inhabits thick grasses in and around modern East African swamps, lakes and rivers (Potts et al., 2004).

Some *H. sapiens* fossils, such as the Kow Swamp specimens (Kennedy, 1984), seem to have redeveloped archaic features and heavy skull bones. These Pleistocene populations consumed mussels and other aquatic foods. When the shellfish population at Kow Swamp became extinct about 19,000 years ago, the lake was abandoned soon after (Stone and Cupper, 2003).

Fig. 1 suggests that *H. sapiens* and *Australopithecus africanus* could have heavier bones than can be expected for their body size, although to a much lesser degree than Neanderthals and certainly *H. erectus*. The meaning of this is unclear to us: it may be due to the limited data, but in *H. sapiens* also due to phylogenetic inertia (e.g. a littoral past) or to aquatic food collection by many humans (e.g. Stock and Pfeiffer, 2001; Velasco-Vázquez et al., 1999), and in *A. africanus*, to uncertainties about their exact body weight, or to their possible dwelling in wetlands (Verhaegen and Puech, 2000; Wrangham, 2005).

Fossil, archaeological, isotopic (e.g. Richards et al., 2000) and even helminthic data (e.g. Zarlenga et al., 2006) suggest that several archaic populations butchered large herbivores. It has been hypothesised that a hunting lifestyle, possibly including fighting with large prey (Berger and Trinkaus, 1995), might explain the heavy bones of archaic people. However, the genus *Homo* is characterised by a remarkably poor olfactory sense, a small mouth and dentition, slow movements and weak muscularity, compared to chimpanzees and hunting mammals. Carnivorous animals typically have a keen sense of smell and a large and protruding muzzle with large front teeth, especially the canines. The quadrupedal chimpanzees chase, hunt and kill colobus monkeys without tools, and in the animal kingdom, stone tools are seen in durophagous animals such as sea otters, rather than in typical carnivores.

The archaeological, isotopic and helminthic evidence for large game consumption – combined with the fact that *Homo* species (weak postcranial muscularity and low speed, poor olfaction, small mouth opening, reduced dentition, MYH16 gene inactivation and weak masticatory muscles) seem uncharacteristic of most hunting animals – could be explained if the consumption of large game resulted from ambush hunting with weapons in swampy areas. Some *Homo* populations might have preyed upon animals hindered in their movements in muddy terrain or shallow water. Alternatively, they may have scavenged opportunistically, including on migrating herbivores drowned or trampled when crossing rivers, or beached whales (Gutierrez et al., 2001). Most, if not all, butchering sites in the archaeological record are in permanent waterside contexts, and they often involve waterside animals including whales, hippos, crocodiles and water-dependent bovids (Munro, 2004).

Conclusions

According to the comparative data presented here, the most parsimonious explanation for heavy skeletons in ‘erectine grade’ populations is that, as in other pachyosteosclerotic animals, their lifestyle included regular, possibly seasonal or tidal, collection of sessile foods in shallow waters – what we call the littoral foraging hypothesis. Neanderthals might have been intermediate in this respect between *H. erectus* and *H. sapiens*. Since *Homo* is typically durophagous (hard-object feeding with thick enamel and stone tools), pachyosteosclerotic populations could have gathered and consumed hard-shelled molluscs. This is supported by physiological data, and no fossil or archaeological data rule out this possibility. ‘Erectine grade’ sites virtually always contain aquatic molluscs suggestive of permanent water, even though “the inter-tidal environment tends to be badly preserved” (Michael Taylor, personal communication) and – even more importantly – during the Ice Ages, sea levels were up to 120 metres lower than today, so that remains of littoral lifestyles then are rarely visible in the fossil and archaeological record.

The ultimate test for the slow, shallow water foraging explanation for heavy bones in *H. erectus* would be to compare fossil *H. erectus* bones to those of other pachyosteosclerotic fossil and extant

animals, preferably by histological analysis, or, if that is impossible, by high resolution computer tomography.

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