

Australopiths wading? *Homo* diving?

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Abstract

Asian pongids (orangutans) and African hominids (gorillas, chimpanzees and humans) split 14-10 million years ago, possibly in the Middle East, or elsewhere in Eurasia, where the great ape fossils of 12-8 million years ago display pongid and/or hominid features. In any case, it is likely that the ancestors of the African apes, australopithecines and humans, lived on the Arabian-African continent 8-6 million years ago, when they split into gorillas and humans-chimpanzees. They could have frequently waded bipedally, like mangrove proboscis monkeys, in the mangrove forests between Eurasia and Africa, and partly fed on hard-shelled fruits and oysters like mangrove capuchin monkeys: thick enamel plus stone tool use is typically seen in capuchins, hominids and sea otters.

The australopithecines might have entered the African inland along rivers and lakes. Their dentition suggests they ate mostly fruits, hard grass-like plants, and aquatic herbaceous vegetation (AHV). The fossil data indicates that the early australopithecines of 4-3 million years ago lived in waterside forests or woodlands; and their larger, robust relatives of 2-1 million years ago in generally more open milieus near marshes and reedbeds, where they could have waded bipedally. Some anthropologists believe the present-day African apes evolved from australopithecine-like ancestors, which would imply that knuckle-walking gorillas and chimpanzees evolved in parallel from wading-climbing 'aquarborealists'.

After the human-chimp split some 6-4 million years ago, our ancestors could have stayed at, or returned to the Indian Ocean shores, where they elaborated their shellfish-eating, tool-using, beach-combing and wading-diving skills. From here the different *Homo* species could have colonized Africa and Eurasia by following the rivers as bipedal omnivores. *Homo erectus* crossed Wallace's Line and reached Flores before 0.8 million years ago, and the earliest *erectus* fossils are found in beaches and swamps from Java to Georgia and Kenya 1.8-1.6 million years ago. Voluntary breath-holding, an essential requirement for diving, probably facilitated the evolution of human speech.

Key words

Hominid evolution, bipedalism, speech origins, dryopithecines, *Australopithecus*, *Homo erectus*, aquatic herbaceous vegetation, enamel microwear, stone tools.

Introduction

There is a strong belief within certain sections of the anthropological community that australopithecines were ancestral to humans, and that the ancestors of chimpanzees and gorillas are not represented in the African fossil record. Evidence suggesting that australopithecines were bipedal, such as fossilized footprints and skeletal remains, is often used to support this hypothesis.

Of course, this hypothesis is based partly on the assumption that chimpanzees and humans descended from ancestors that were not yet bipedal, and that bipedalism only emerged after the ancestral lines leading to chimpanzees and humans had separated. A popular theory once held that bipedalism emerged when human ancestors moved out of the forests into a more open and arid environment.

We believe, however, that an alternative hypothesis may be more accurate, namely that the australopithecines were no closer to the ancestral line leading to humans than they were to the ancestral lines leading to the African apes. Further, we believe the common ancestor of humans, chimpanzees and gorillas was already at least partly bipedal, regularly wading in flooded forests such as coastal mangrove forests. Gorillas and chimpanzees, according to this hypothesis, evolved knuckle-walking features independently, in parallel, after moving from the coast to the African interior via rivers and gallery forests.

Humans, on the other hand, descended from a hominid population that remained nearer the coast and which gave rise to efficient waders and divers, and eventually to the various species of the *Homo* genus, some of which later returned to a more terrestrial lifestyle. This hypothesis, in our opinion, helps explain many unique human adaptations including the development of human tool manufacturing skills and the origins of speech.

Hominid fossils and scenarios

The evolutionary history of all animals, including our ancestors, has been influenced by a number of environmental factors. Thus, we believe many evolutionary insights can be gained by comparing the parallel and convergent adaptations of different animals in similar environments. In fact, we believe evidence gained from comparative anatomy and physiology of living species is as important to evolutionary studies as fossil evidence.

The fossil record displays well-known shortcomings. It is biased and incomplete. For instance, it could be possible that hominids living in certain environments were less likely to leave fossilized remains than hominids living in other milieus. More specifically, geologists note that fossilization is extremely difficult in mangrove areas because tidal water movements spread the bones over a vast area, and the high acidity of the water dissolves the bony remains. Moreover, in mangrove areas the sea floor is flat, so there is almost no chance that a landslide would ever cover remains.

Because of the scantiness of the fossil record, paleontologists now generally accept the late Colin Patterson's view that the direct ancestors of living species are unlikely to be found within it (Nelson 1998). As a result, it is probable that most, if not all, fossil hominid species found to date are simply extinct side-branches of the lines leading to the present living hominids. In part, it was this likelihood that led us to be extremely cautious about using the fossil record as the sole basis for attempting to develop a viable hominid 'family tree'. Instead, we adopted the practice of assembling and considering all the credible available evidence in a comparative and systematic methodology. While the totality of the evidence remains incomplete, the multiple cross-checking process does produce a cautious confidence in the tentative scenarios it suggests.

Primate locomotion

Most primates are four-legged tree-dwellers with very mobile spine and limb joints, enabling them to reach, climb and leap through trees. Thanks to this locomotor flexibility they can easily adopt a bipedal stance and gait when necessary.

Many primates adopt this bipedal gait when they wade through water. For example, the western lowland gorilla has been observed wading on its hind limbs through forest swamps in search of edible sedges and aquatic herbs (Chadwick 1995, Doran & McNeillage 1997). The mangrove-dwelling proboscis monkeys also cross stretches of water to move from one mangrove tree to another, and they always walk on two legs when making these treks; in

fact, they are even sometimes seen using bipedal locomotion on dry ground (Morgan 1997).

This erect bipedal wading gait is very different to the more common hopping bipedalism that other primates and mammals such as indris, tarsiers, jerboas and kangaroos use when moving on the ground. This latter gait incorporates bent knees and hips rather than the more linear stature preferred for wading. The advantage of the erect wading posture is that it allows primates to hold their body and head as far as possible above the water surface, allowing them to cross deeper stretches of water.

Most anthropologists still base their estimates of when human bipedalism emerged on the available fossil evidence. Up until a few years ago many were convinced that bipedalism arose some four million years ago in a savanna environment. Recent studies, however, as well as fossil finds such as *Ardipithecus ramidus* and *Australopithecus anamensis*, have forced a reconsideration of this traditional view. Today, most anthropologists accept that bipedalism probably emerged earlier, in a wooded or forested habitat (Tobias 1998).

We believe the common ancestors of chimpanzees, gorillas and humans formed a population which waded and climbed in mangrove forests somewhere between what is now the Mediterranean and the Arabian Sea. There is presently no evidence to discount the idea that hominid bipedalism evolved in a milieu where both trees and water were present. Most, if not all, early hominid fossils have been discovered in what were then forested areas close to water (*e.g.* see below, the quotations from Radosevich *et al.* 1992, Rayner 1993, and Tobias 1998), and much the same can be said of the great apes at the time of the pongid-hominid split (see below, Steininger 1986, Mein 1986). However, it is important to note that although in our opinion the last common hominid ancestor was a regular wader, it almost certainly continued to use the trees for refuge, sleep and food gathering.

African ape evolution

Humans belong to the hominoid biological group, which consists of the lesser apes (hylobatids) and the great apes (pongids and hominids). Today, hylobatids (gibbons and siamangs) and pongids (orangutans) live in Asia, whereas hominids (humans, chimpanzees and gorillas) live in Africa. Between 13 and 9 million years ago, however, nearly all great apes, such as *Dryopithecus*, *Graecopithecus*, *Ankarapithecus* and *Sivapithecus*, lived in

Europe, Anatolia and India (*e.g.* Andrews 1995, Algaput *et al.* 1996, Cameron 1997). This suggests Asian pongids and African hominids may have split somewhere near the Middle East (Stewart & Disotell 1998).

In 1974, a partial maxilla and teeth of *Heliopithecus*, 'a primitive branch of the Dryopithecinae', some 17 million years old, were collected at Ad-Dabtiyah, eastern Saudi Arabia, between continental sandstones-clays and marine limestones-marls (Whybrow & Bassiouni 1986). According to the authors, 'their habitat seems to have been near to the tropical shore of the Tethys epi-continental sea'. Andrews *et al.* (1987) believe this Saudi ape may have been the first recognizable member of the great-ape branch. The oldest European dryopithecine-like fossils, *Austriacopithecus* from Dêvinská Nová Ves and Kleinhadersdorf near the Slovakian-Austrian border, about 14 million years old, also lay in marine nearshore sands, and *Dryopithecus* fossils 13-10 million years ago derive from swampy forests (Steininger 1986, Mein 1986).

We believe a basic great-ape population may have clustered somewhere around what is now the Arabian peninsula, which once formed part of the African continent. This cluster may have given rise to different offshoots, such as the dryopithecine-like apes that moved into Europe, Anatolia and India, and later to the hominids that entered the African inland by following the rivers upstream. These African migrations, in our opinion, led to the australopithecines and to the chimpanzees and gorillas. Meanwhile, part of the population may have remained at, or returned to, the coast, where they became efficient waders and divers, and this population could have given rise to species which eventually returned to the land, becoming predominantly terrestrial bipeds.

According to molecular evidence, the great apes split into pongids and hominids some 14 to 10 million years ago. The ancestral line leading to the gorillas separated from the line leading to humans and chimpanzees about 8 to 6 million years ago, and the ancestors of chimpanzees and humans separated between about 6 and 4 million years ago (*e.g.* Takahata & Satta 1997, Caccone & Powell 1989).

We propose that the ancestral line leading to the gorilla branched off from the stem hominid group when it moved from the coastal mangrove forests into the African interior, perhaps by following the rivers and gallery forests of the African Rift Valley. It is not impossible that this ancestral line might have given rise to the very large australopithecine species such as *Australopithecus boisei* (Kleindienst 1975).

The ancestral chimpanzee population probably moved from the coast to the African interior a few million years after the gorilla, also by following rivers and gallery forests. By the time the chimpanzee and human ancestral lines had separated, hominid populations may have inhabited coastal forests on different parts of the Indian Ocean coast, including the east African coast.

It seems probable that different hominid branches would have evolved in parallel as they moved inland. Shellfish and other marine resources would have become rarer as they followed the rivers upstream, so other plant and animal food would have been needed to replace these foods in the diet. The inland populations would have re-adapted to a more traditional primate diet, become more herbivorous, and spent less and less time in the water. The ancestors of chimpanzees, according to this hypothesis, stayed longer at the coast than the ancestors of gorillas, and we would therefore expect them to have remained more omnivorous than gorillas, because the opportunity for harvesting shellfish, for example, would have been greater on the coast than in more inland milieus, and their ancestors would have had less opportunity to re-adapt to a more traditional primate lifestyle.

Australopithecine lifestyle

It has become increasingly clear that most, if not all, hominids dwelt in 'wet' rather than 'dry' habitats, and there is little doubt that the early australopithecines of between four and three million years ago dwelt in well-wooded and even forested milieus such as swampy woodlands or streamside forests. For example, Radosevich *et al.* (1992), in a paper on *Australopithecus afarensis* from Hadar, East Africa, said: 'The bones were found in swale-like features ... it is very likely that they died and partially rotted at or very near this site ... this group of hominids was buried in streamside gallery woodland'. In addition, Rayner *et al.* (1993) wrote that the *A. africanus* fossils of Makapansgat, South Africa, were found in 'very different conditions from those prevailing today. Higher rainfall, fertile, alkaline soils and moderate relief supported significant patches of sub-tropical forest and thick bush, rather than savannah ... sub-tropical forest was the hominins' preferred habitat rather than grassland or bushveld, and the adaptation of these animals was therefore fitted to a forest habitat'. Moreover, last year, Tobias (1998), on the same species, wrote:

'From Sterkfontein, suggestions of greater woodland cover at the time when *Australopithecus* was deposited in Member 4, had emerged from studies on fossil pollen, but these were not compelling. Then Wits team member Marian

Bamford identified fossil vines or lianas of *Dichapetalum* in the same Member 4: such vines hang from forest trees and would not be expected in open savannah. The team at Makapansgat found floral and faunal evidence that the layers containing *Australopithecus* reflected forest or forest margin conditions. From Hadar, in Ethiopia, where 'Lucy' was found, and from Aramis in Ethiopia, where Tim White's team found *Ardipithecus ramidus*, possibly the oldest hominid ever discovered, well-wooded and even forested conditions were inferred from the fauna accompanying the hominid fossils. All the fossil evidence adds up to the small-brained, bipedal hominids of four to 2.5 million years ago having lived in a woodland or forest niche, not savannah.'

The later robust australopithecines, of two to one million years ago, clearly lived in more open environments, apparently near riverbanks, lake margins and reedbeds. For example, Kromdraai *A. robustus* was found near grassveld and streamside or marsh vegetation, in the vicinity of quail, pipits, starlings and swallows, as well as parrots, lovebirds and similar psittacine birds (Brain 1981). Turkana *A. aethiopicus* was discovered in 'overbank deposits of a large perennial river', amid water- and reedbeds (Walker *et al.* 1986). Chesowanja *A. boisei* lay in a lagoon amid exclusively aquatic species: 'Abundant root casts ... suggest that the embayment was flanked by reeds and the presence of calcareous algae indicates that the lagoon was warm and shallow. *Bellamyia* and catfish are animals tolerant of relatively stagnant water ...' (Carney *et al.* 1971).

This impression of marsh vegetation – the early australopithecines in more wooded and the robusts in more open milieus – is compatible with all other information we have on australopithecines: postcranial skeleton, masticatory and dentitional data, enamel microwear, strontium/calcium ratios, and isotopic evidence.

Fossilized footprints and skeletal remains suggest that australopithecines were bipedal. Early australopithecines also show clear indications of tree climbing features such as upward directed shoulder joints (glenoid fossae) and curved finger and toe phalanges, whereas such features are less obvious in the later robusts.

Dental studies suggest that whereas gracile australopithecines preferred softer fruits and vegetables, the robusts' diet included harder food items (*e.g.* Robinson 1954, DuBrul 1977, Walker 1981, Puech 1992, Lee-Thorp *et al.* 1994). Estimates of robust australopithecine bite force suggest 'low-energy food that had to be processed in great quantities' and food objects that were 'hard and round in shape' (Demes & Creel 1988). DuBrul (1977) noticed

striking dental parallelisms between the robust australopithecines and the bamboo-eating giant panda (broad, high and heavy cheekbones, reduced prognathism and front teeth, very broad molar teeth, premolar molarization), when compared to gracile australopithecines and non-panda bears respectively.

Students of fossil hominid teeth agree that such broad molars with thick enamel and rounded cusps, while unsuitable for the regular processing of tough foods like leaves or meat, are suitable for the processing of hard food items. Papyrus and reed were abundant in the paleo-environment of the later australopithecines (*e.g.* Olduvai, Chesowanja, Kromdraai), and Cyperaceae and Gramineae are part of the diet of living African hominoids. Gorillas eat sedges and bamboo shoots and stalks, all African hominids eat cane, chimpanzees and humans eat water lilies, and rice and other cereals are staple food for humans. Supplementing their diet with hard parts of grass-like plants might have enabled the robusts to bridge the dry season, when fruits and soft vegetables may have been less available.

Studies of dental enamel microwear provide further details. In the early *A. afarensis* (Garusi-Laetoli and Hadar), the cheekteeth enamel has a typical glossy polished surface and the microwear has resemblances to that of capybaras and mountain beavers (Puech *et al.* 1986). These animals are semi-aquatic rodents that feed mainly on succulent marsh and riverside herbs, grasses and bark of young trees. It has recently become clear that Western lowland gorillas spend some time eating what the researchers call AHV (aquatic herbaceous vegetation) such as Hydrocharitaceae herbs and Cyperaceae sedges (Doran & McNeilage 1997).

Comparisons of molar enamel in South African fossils show that *A. robustus* ate substantially more hard food items than the earlier *A. africanus* (Grine & Kay 1988). Incisal microwear suggest that *A. robustus* may have ingested foods that required less extensive incisal preparation than the foods consumed by *A. africanus* (Ungar & Grine 1991), and incisal reduction in *A. robustus* also suggests a less frugivorous diet, since 'incisors need not be employed in the manipulation of hard objects' (Ungar & Grine 1989).

The enamel of the East African robusts (*A. boisei* of Olduvai and Peninj) displays more pits, wide parallel striations and deep recessed dentine. This microwear pattern has some resemblances with that of beavers, which feed on riverine and riverside herbs, roots of water lilies, bark and woody plants (Pierre-François Puech, personal communication). It thus seems probable that an early australopithecine diet of fruits (larger front teeth) and aquatic herbs (polishing) was supplemented with woody plants in the robusts (more wear).

The suggestion of Walker (1981) that *A. boisei* KNM-ER 406 and 729 were bulk-eaters of whole fruits, 'small, hard fruits with casings, pulp, seeds and all', could explain the deep recessed occlusal dentine, but not the glossy appearance of the heavily polished enamel, which is more typical of marsh plant feeders. In terrestrial grazers, tooth wear is very different (Sponheimer & Lee-Thorp 1999). In sheep, for instance, it is faster, has a different gradient and produces fabric-like grooves (Pierre-François Puech, personal communication).

These microwear data are consistent with the strontium/calcium ratios (Sillen 1992), as well as with the isotopic data of South African australopithecines (Sponheimer & Lee-Thorp 1999). Apart from partial carnivory, Sillen provides two possible explanations for the low Sr/Ca ratios of *A. robustus*: eating leaves and shoots of forbs and woody plants, and eating food derived from a wet microhabitat, for instance, from well-drained streamside soils. Sillen (1992) as well as Sponheimer & Lee-Thorp (1999), perhaps influenced by earlier 'hunting hypotheses', prefer the regular consumption of animal food as an explanation for the Sr/Ca ratios and the isotopic data in *A. robustus*, rather than considering the altogether more logical explanation that they might have eaten cyperaceous sedges and other marshland plants. Sponheimer & Lee-Thorp (1999) say that *A. africanus* 'ate not only fruits and leaves but also large quantities of carbon-13-enriched foods such as grasses and sedges or animals that ate these plants, or both'. Since terrestrial grasses are incompatible with the polished microwear (*e.g.* Sponheimer & Lee-Thorp 1999, Puech *et al.* 1986), and regular meat-eating is incompatible with the small front teeth and the huge and broad cheekteeth (*e.g.* Wood & Aiello 1998, DuBrul 1977, Walker 1981), their diet more probably included marshland plants such as Cyperaceae, as is shown by the very different studies by Puech (1992), Sillen (1992) and Sponheimer & Lee-Thorp (1999).

In conclusion, the coincidence of several *independent* lines of evidence – paleo-milieu, postcranial skeleton, dental morphology, enamel microwear, Sr/Ca ratios, isotopic data – suggests that some or all australopithecines regularly waded bipedally in search of plants growing in and near shallow waters. They might have waded in much the same way as living hominid species such as bonobos and Western gorillas do today, only much more frequently (Chadwick 1995, Doran & McNeilage 1997). This does not exclude the possibility, however, that early hominids, including some australopithecine species, might have processed and consumed animal food when available (Roche *et al.* 1999, de Heinzelin *et al.* 1999), particularly considering they may have evolved from mangrove-dwelling, tool-using omnivores.

The Emergence of Homo

In our view, a population of hominids remained in, or returned to, forests near the coast, where they became more and more adept at exploiting the available aquatic resources. We believe this population gave rise to the various *Homo* species. Initially, they might have fed partly on foods such as the oysters fixed to mangrove trunks exposed at low tide. This high-caloric and highly nutritious diet could have been important for building and fuelling a large brain. Note that the long-chain polyunsaturated lipid ratios of tropical fish and shellfish are more similar to the ratios in the human brain than any other food source known (Broadhurst *et al.* 1998).

Presumably these hominids had thick tooth enamel (Martin 1985), like earlier hominoids such as *Graeco-*, *Ankara-* and *Sivapithecus*, and later *Australopithecus* and *Homo* (some hominoids, however, like the Miocene *Dryopithecus* and the Pliocene *Ardipithecus*, had relatively thin enamel). Enamel is extremely hard, and thick enamel is typical of species like orangutans, capuchin monkeys and sea otters that consume hard foods such as hard-shelled fruits, nuts and molluscs. Walker (1981) even wrote: 'If, for example, a mammalogist who knows nothing about hominids were asked which mammalian molar most resembled those of *Australopithecus*, the answer would probably be the molars of the sea otter (*Enhydra lutris*). This species possesses small anterior teeth, and large, flat molars with thick enamel.'

(Walker believes the thick enamel in sea otters may not be for cracking shells, but for the occasional hard inclusions inside the shells which would otherwise damage the dentition. It should be noted that seaweed consumers might also need thick enamel because seaweed often houses small molluscs. Some seaweeds contain high levels of vitamin C, a necessary element in the diet of hominoids, who mostly find this vitamin in fruits. Seaweeds, like other seafoods, also contain a high content of iodine, which absence causes endemic goiter, cretinism and myxedema in areas away from the seacoast. But seaweeds are often difficult to digest.)

Tool use is seen in many animals, but perhaps the most obvious mammalian examples, excluding humans, are capuchin monkeys, chimpanzees and sea otters. They all try to open hard-shelled foods by hammering them with hard objects. Sea otters, for instance, crack open shellfish with stones while floating on their backs. Capuchins crack open nuts and shellfish with stones, and Fernandes (1991) reports that mangrove capuchins even use oyster shells

where stones are not available. Chimpanzees also crack open nuts with stones. It seems likely, therefore, that tool use in hominids may have begun with shellfish or nut eating.

We propose that our ancestors began using hard objects as tools to remove or crack open the shellfish that grew on the trunks of the mangrove trees in the forests in which they lived. For the hominids that moved inland to areas where molluscs were less common, tool use may have become confined to nut-cracking and other activities seen in chimpanzee populations today. For the hominids that stayed near the coast, tool use would have remained an essential behavioral adaptation, and perhaps the extraordinary stone tool industries we associate with the various *Homo* species is a reflection of their long association with shellfish.

All diving mammals have the ability to take a deep breath at will whenever they intend to dive. Many of them, like dolphins and seals, also have larger brains than land mammals of equal size (Armstrong 1983). Today, breath-hold diving is practiced by some subsistence human cultures that gather shellfish or seaweed. Voluntary breath control in humans is most probably an adaptation for diving, and this is clearly illustrated when one compares the human respiratory system with that of non-human primates and freshwater or marine mammals (Schagatay 1996).

Many primates, like gibbons, and other arboreal animals have an aptitude for vocal and musical expression. They share this capacity for making and interpreting a wide range of sounds with many marine mammals. Vocalization was probably a very important communicative device in an aquatic environment, where more traditional devices such as smell and body language would have been less effective. This, combined with an inherent talent for complex vocal exchange, as well as voluntary breath control and a large brain, may have been the prerequisites for human language.

The totality of the available evidence leads us to propose that the *Homo* genus evolved from part-time bipedal waders and beach-combers who evolved longer legs, and who gradually became also more suited to swimming and diving, and who, as a result, developed a more streamlined and linear body with a larger brain. Eventually, these long-legged *Homo* species colonized coastal areas and river valleys in Asia, Africa and Europe, where they probably used their tool-using skills to exploit other available resources such as scavenged carcasses of hippos and other mammals. The Javanese Mojokerto fossil, discovered in a river delta amid marine and freshwater molluscs (Ninkovich & Burckle 1978), which is probably 1.8 million years old, might well be the oldest *Homo erectus* fossil ever discovered. There is

even archeological evidence that *Homo erectus* reached the island of Flores, also in Southeast Asia, some 800,000 years ago, well before any evidence of boat building appears in the archeological record (Morwood *et al.* 1998, Tobias 1998). We propose that *Homo erectus*'s superior swimming skills enabled them to cross the great natural water barrier known as Wallace's Line.

Eventually, at least some of these long-legged hominid species returned to a more terrestrial existence. But just as no *Homo* species may ever have ceased being at least partly terrestrial, it is possible that no *Homo* species ever ceased being at least partly aquatic either. When members of the *Homo* genus did become more terrestrial, they were unable to revert to knuckle-walking quadrupedalism, like gorillas and chimpanzees, because, whereas gorillas and chimpanzees evolved directly from short-legged climbing-wading 'aquarboresalists', *Homo* was already a part-time wader and diver with long legs and a more linear build.

Terrestrial bipedalism is a slower form of locomotion than quadrupedalism, is more conspicuous, less energy efficient and leads to many ailments such as backaches, hip and knee problems. However, it also has many advantages, mainly associated with the freeing up of the hands so that they can be used more effectively for communication, and to carry food, water, babies and tools.

We believe the semi-aquatic phase helps explain human features such as furlessness, subcutaneous fat and voluntary breath control, features unique among primates, but common within various water mammals such as seacows, hippopotamuses, walruses, dolphins and whales (Morgan, 1997). It may also help explain why we are much more efficient swimmers and divers than other primates (Bender 1999, Bender *et al.* 1997, Schagatay 1996).

In our opinion, it should not be a question of whether members of the *Homo* genus were ever aquatic, but rather *how* aquatic were they. For example, the fossilized remains of Neandertals, traditionally viewed as fully terrestrial, have been discovered exclusively next to coastlines and rivers. Moreover, the presence of ear exostoses (bony outgrowths of the ear canal, a condition only seen after life-long diving in modern humans) is evidence that at least some Neandertal individuals practiced frequent diving, and traces of cattails on some stone tools suggest wading activities (Shreeve 1995). We believe Neandertals evolved from even more water-based *Homo erectus* populations that moved up the rivers from the coasts into the Eurasian interior. Like some modern human populations, such as the Korean Ama, they probably maintained elements of a wading or diving lifestyle.

Conclusion

Our hypothesis proposes that the last common ancestors of the African hominids lived in coastal mangrove forests, where they waded bipedally and were omnivorous, supplementing their mainly herbi-frugivorous diet with shellfish and perhaps seaweed. The ancestors of the gorillas and chimpanzees, as well as the australopithecines, in our opinion, migrated inland along rivers and gallery forests.

The population that remained near the coast, due to geological factors, left fewer fossilized remains. This coastal population gave rise to the various species of the *Homo* genus: big-brained, long-legged waders and breath-hold divers, able to take full advantage of the available resources naturally associated with a coastal milieu. These hominids populated the coastal regions of the Indian Ocean and they moved up rivers into the interiors of Asia, Africa and Europe. Many unique human features including long legs, big brains, voluntary breath control, fur loss, the adoption of subcutaneous fat and infant tolerance to immersion can be explained by this evolutionary scenario. In addition, this wading-and-diving phase may help explain the development of our unique tool manufacturing skills and language use.

This hypothesis, in our opinion, is detailed enough that it can be tested against new evidence as it becomes available, and can also be used as a predictive tool. As such, its success or failure will either confirm or negate its value as the basis for a potentially definitive theory of human evolution.

Possible figures

Figure 1 – Map of Miocene hominoid fossils:

- Africa-Arabia ca.20-14 mya: *Proconsul*, *Moroto-*, *Helio-*, *Kenyapithecus* ...
- Europe-Anatolia ca.14-8 mya: *Austriaco-*, *Dryo-*, *Graeco-*, *Ankarapithecus*...
- India ca.12-8 mya: *Sivapithecus*

Figure 2 – Lowland gorilla wading bipedally in search for sedges. Illustration of possible lifestyle of robust australopithecines (photo by Michael Nichols, in Chadwick 1995).

Figure 3 – Evolutionary tree of hominids: hypothetical and schematic reconstruction of African ape and human evolution, based on comparative anatomy and behavior, geographical distribution and biomolecular data of living hominids. Fossil species *Ardipithecus*, *Australopithecus* and *Homo* are sidebranches of the lines leading to the living hominids.

References

- Algaput B., Andrews P., Fortelius M., Kappelman J., Temizsoy I., Celebi H. & Lindsay W. 1996. A new specimen of *Ankarapithecus meteai* from the Sinap Formation of central Anatolia. *Nature* **382**, 349-351.
- Andrews P. 1995. Ecological apes and ancestors. *Nature* **376**, 555-556.
- Andrews P., Martin L. & Whybrow P. 1987. Earliest known member of the great ape and human clade. *American Journal of Physical Anthropology* **72**, 174-175.
- Armstrong E. 1983. Relative brain size and metabolism in mammals. *Science* **220**, 1302-1304.
- Bender R. 1999. *Die evolutionsbiologische Grundlage des menschlichen Schwimmens, Tauchens und Watens*. Bern, Switzerland: University of Bern.
- Bender R., Verhaegen M. & Oser N. 1997. Der Erwerb menschlicher Bipedie aus der Sicht der Aquatic Ape Theory. *Anthropologischer Anzeiger* **55**, 1-14.
- Brain C. K. 1981. *The Hunters or the Hunted?* Chicago: University of Chicago Press.

Broadhurst C. L., Cunnane S. C. & Crawford M. A. 1998. Rift Valley fish and shellfish provided brain-specific nutrition for early Homo. *British Journal of Nutrition* **79**: 3-21.

Caccone A. & Powell J. R. 1989. DNA divergence among hominoids. *Evolution* **43**, 925-942.

Cameron D. W. 1997. A revised systematic scheme for the Eurasian Miocene fossil Hominidae. *Journal of Human Evolution* **33**, 449-477.

Carney J., Hill A., Miller J. A. & Walker A. 1971. Late australopithecine from Baringo District, Kenya. *Nature* **230**, 509-514.

Chadwick, D. 1995. Ndoki – last place on earth. *National Geographic* **188**, 2-43.

Demes B. & Creel N. 1988. Bite force, diet, and cranial morphology of fossil hominids. *Journal of Human Evolution* **17**, 657-670.

Doran D. M. & McNeilage A. 1997. Gorilla ecology and behavior. *Evolutionary Anthropology* **6**, 120-130.

de Heinzelin J., Clark J. D., White T., Hart W., Renne P. WoldeGabriel G., Beyenne Y. & Vrba E. 1999. Environment and behavior of 2.5 million-year-old Bouri hominids. *Science* **284**, 625-629.

DuBrul E. L. 1977. Early hominid feeding mechanisms. *American Journal of Physical Anthropology* **47**, 305-320.

Fernandes M. E. B. 1991. Tool use and predation of oysters by the tufted capuchin in brackish water mangrove swamp. *Primates* **32**, 529-531.

Grine, F. E. & Kay, R. F. 1988. Early hominid diets from quantitative image analysis of dental microwear. *Nature* **333**, 765-768.

Kleindienst M. R. 1975. On new perspectives on ape and human evolution. *Current Anthropology* **16**, 644-646.

Lee-Thorp J. A., van der Merwe N. J. & Brain C. K. 1994. Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. *Journal of Human Evolution* **27**, 361-372.

- Martin L. B. 1985. Significance of enamel thickness in hominoid evolution. *Nature* **314**, 260-263.
- Mein P. 1986. Chronological succession of hominoids in the European Neogene. In Else J. G. & Lee P. C. *Primate Evolution*. Cambridge University Press, Cambridge, pp. 59-70.
- Morgan E. 1997. *The aquatic ape hypothesis – the most credible theory of human evolution*. London: Souvenir.
- Morwood M. J., O’Sullivan P. B., Aziz F. & Raza A. 1998. Fission-track ages of stone tools and fossils on the east Indonesian island of Flores. *Nature* **392**, 173-6.
- Nelson G. 1998. Colin Paterson 1933-1998. *Nature* **394**, 626.
- Ninkovich D. & Burckle L. H. 1978. Absolute age of the base of the hominid-bearing bed in Eastern Java. *Nature* **275**: 306-308.
- Puech P.-F. 1992. Microwear studies of early African hominid teeth. *Scanning Microscopy* **6**, 1083-1088.
- Puech P.-F., Cianfarani F. & Albertini H. 1986. Dental microwear features as an indicator for plant food in early hominids: a preliminary study of enamel. *Human Evolution* **1**, 507-515.
- Radosevich S. C., Retallack G. J. & Taieb M. 1992. Reassessment of the paleoenvironment and preservation of hominid fossils from Hadar, Ethiopia. *American Journal of Physical Anthropology* **87**, 15-27.
- Rayner R. J., Moon B. P. & Master, J. C. 1993. The Makapansgat australopithecine environment. *Journal of Human Evolution* **24**, 219-231.
- Robinson J. T. 1954. Prehominid dentition and hominid evolution. *Evolution* **8**: 324-334.
- Roche H., Delagnes A., Brugal J.-P., Feibel C., Kibunjia M., Mourre V. & Texier P.-J. 1999. Early hominid stone tool production and technical skill 2.34 Myr ago in West Turkana, Kenya. *Nature* **399**, 57-60.
- Schagatay, E. 1996. *The human diving response – effects of temperature and training*. Lund, Sweden: University of Lund.

- Shreeve J. 1995. *The Neandertal Enigma: solving the mystery of modern human origins*. New York: Morrow.
- Sillen A. 1992. Strontium-calcium ratios (Sr/Ca) of *Australopithecus robustus* and associated fauna from Swartkrans. *Journal of Human Evolution* **23**, 495-516.
- Sponheimer M. & Lee-Thorp J. A. 1999. Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Science* **283**, 368-370.
- Steininger F. F. 1986. Dating the Paratethys Miocene hominoid record. In Else J. G. & Lee P. C. *Primate Evolution*. Cambridge University Press, Cambridge, pp. 71-84.
- Stewart C.-B. & Disotell T. R. 1998. Primate evolution: in and out of Africa. *Current Biology* **8**, R582-588.
- Takahata N & Satta Y. 1997. Evolution of the primate lineage leading to modern humans: phylogenetic and demographic inferences from DNA sequences. *Proceedings of the National Academy of Sciences USA* **94**, 4811-4815.
- Tobias P. V. 1998. Water and Human Evolution. *Out There* 35: 38-44.
- Ungar P. S. & Grine F. E. 1989. Maxillary central incisor wear in *Australopithecus* and *Paranthropus*. *American Journal of Physical Anthropology* **78**, 317.
- Ungar P. S. & Grine F. E. 1991. Incisor size and wear in *Australopithecus africanus* and *Paranthropus robustus*. *Journal of Human Evolution* **20**, 313-340.
- Walker A. 1981. Diet and teeth – dietary hypotheses and human evolution. *Philosophical Transactions of the Royal Society of London B* **292**, 57-64.
- Walker A., Leakey R., Harris J. M. & Brown F. 1986. 2.5 Myr *Australopithecus boisei* from west of Lake Turkana. *Nature* **322**, 517-522.
- Wood B. & Aiello L. C. 1998. Taxonomic and functional implications of mandibular scaling in early hominids. *American Journal of Physical Anthropology* **105**, 523-538.

Whybrow P. J. & Bassiouni M. A. 1986. The Arabian Miocene: rocks, fossils, primates and problems. In Else J. G. & Lee P. C. *Primate Evolution*. Cambridge University Press, Cambridge, pp. 85-91.