

Aquarboreal ancestors?

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According to biomolecular data, the great apes split into Asian pongids (orang-utan) and African hominids (gorillas, chimpanzees and humans) 18–12 million years ago (Mya) and hominids split into gorillas and humans–chimpanzees 10–6 Mya. Fossils with pongid features appear in Eurasia after c. 15 Mya, and fossils with hominid fossils appear in Africa after c. 10 Mya. Instead of the traditional savannah-dwelling hypothesis, we argue that a combination of fossil (including the newly discovered *Orrorin*, *Ardipithecus* and *Kenyanthropus* hominids) and comparative data now provides evidence showing that: (1) the earliest hominids waded and climbed in swampy or coastal forests in Africa–Arabia and fed partly on hard-shelled fruits and molluscs; (2) their australopith descendants in Africa had a comparable locomotion but generally preferred a diet including wetland plants; and (3) the *Homo* descendants migrated to or remained near the Indian Ocean coasts, lost most climbing abilities, and exploited waterside resources.

Human evolution is usually discussed within an environmental framework that includes forests and savannahs [1–3]. Unique human features, such as bipedalism and furlessness, are therefore often argued to have evolved in forests, on the savannah, or within a transitional zone [1–3]. We argue that a third environmental factor, namely water, also played an important role in the evolution of the great apes and humans. Our 'comparative approach', a method pioneered by Hardy [4] and Morgan [5], combines comparative data with fossil, geographical and biomolecular evidence. We argue that the ancestors of gorillas, chimpanzees and humans had an 'aquarboreal' lifestyle in which they climbed and waded in swampy or coastal forests. Gorilla and chimpanzee ancestors adapted to drier forests where they knuckle-walked and continued to climb and wade where necessary. Human ancestors, however, evolved fully upright and linear bipedalism, furlessness, a larger brain and voluntary breath control as adaptations for wading and diving in a coastal environment. Climbing abilities became less important as coastal forests dwindled and seafood became a more important dietary source.

Here, hominid refers to gorillas *Gorilla* spp., chimpanzees *Pan* spp., humans *Homo sapiens* and their AUSTRALOPITH-like (see Glossary) fossil relatives. Pongid refers to the orang-utan *Pongo* spp. and their fossil relatives. Biomolecular evidence (DNA) suggests PONGIDS and HOMINIDS separated 18–12 million years ago (Mya),

gorillas and humans–chimpanzees separated 10–6 Mya, and chimpanzees and humans 8–4 Mya [6,7].

It is generally assumed that gorilla and chimpanzee ancestors are poorly represented in the fossil record and that australopiths were ancestral only to humans. Evidence for australopiths being bipedal (fossilized footprints and skeletal remains) is used to support this hypothesis because it is widely believed that bipedalism emerged only after the chimpanzee and human lineages had separated. Several authors [8–12], however, have argued independently that the African apes might have had australopith-like ancestors and that the common ancestors of humans, chimpanzees and gorillas might have been already partly bipedal. This has recently been supported by discoveries of early hominids that are argued to have had both bipedal and climbing adaptations (*Orrorin tugenensis* [13] Kenya c. 6 Mya and *Ardipithecus ramidus* [14] Ethiopia c. 5 Mya).

Were early hominids–pongids aquarboreal?

Most primates are quadrupedal tree-dwellers with very flexible spines and limbs, which enable them to reach, climb or leap through trees and to stand or walk bipedally when necessary. Human-like 'erect bipedalism', although less common than 'HOPPING BIPEDALISM', is seen regularly in lowland gorillas that seek sedges in forest swamps [15], in proboscis monkeys that wade between mangrove trees [5], and possibly in *Oreopithecus bambolii* (Table 1), whose diet might have included wetland plants and whose anatomy 'provides evidence that bipedal activities made up a significant part of the positional behavior' [16]. We find nonwading explanations for human bipedalism [1–3] (e.g. standing up to reach fruit in trees, aggressive posturing, looking over savannah grass and carrying tools, food or babies) unconvincing, because the advantages appear to be only of a temporary nature, and because no other primates or savannah mammals have developed bipedalism for similar reasons.

The features that typically distinguish apes from monkeys (i.e. large size, tail loss and arm hanging) could have been adaptations for what we call an 'aquarboreal' locomotion in an environment that included both trees and water. A vertical posture and an ability to climb with the arms raised above the head could have helped a wading primate to enter or leave the water by grasping overhanging branches or waterside vegetation, and to grasp fruits above the water. Body enlargement and tail reduction would hinder agile arborealism, whereas a larger body is more easily supported in water and helps reduce heat loss (explaining why aquatic mammals are larger than related terrestrial forms). Tails would be of little use for a wading and/or swimming primate and would cause both drag and heat loss.

Early hominids could have waded bipedally in swamp forests using the trees for refuge, sleep, and fruit gathering, whilst also finding part of their food in shallow

water. Although most Miocene hominid–pongid (Box 1) and Plio–Pleistocene hominid fossils (Table 2) have been discovered in areas that were then forested and close to water, this in itself is not a strong argument for a wading lifestyle because most fossilization occurs in water-deposited sediments.

The geographical distribution of extinct and extant hominids–pongids, combined with the comparative evidence outlined here, suggests a basic middle Miocene hominid–pongid population that was clustered in coastal or swamp forests somewhere between what are now the Mediterranean and Arabian Seas. This cluster could have given rise to the DRYOPITH-like apes that have been discovered in southern Eurasia, and to the Mio–Pliocene australopith-like hominids found in Africa (Box 1).

Were australopiths wetland waders?

Our extensive survey of the literature [17] suggests that most hominids might have dwelt in ‘wet’ rather than ‘dry’ habitats, and this has been confirmed by recent discoveries [14,18,19]. Palaeo-ecological reconstructions are notoriously difficult and our view has been contested by supporters of traditional savannah interpretations [1–3,17,19], yet it appears clear that all australopiths lived near trees, with early species generally living in wet and well-wooded environments, and later species living more often in more open wetlands (Table 2). Our interpretation is corroborated by: (1) comparisons of POSTCRANIAL skeleton; (2) tooth enamel microwear; (3) strontium:calcium ratios; and (4) isotopic evidence.

Postcranial skeletal comparisons

Fossilized footprints and skeletal remains suggest that australopiths had a mix of bipedal, tree-climbing and probably [20] KNUCKLE-WALKING features. These would have been ideal for wetlands: bipedalism in waist-deep water, knuckle-walking in knee-deep water, and well-developed overhead arm mobility for grasping fruits and climbing in the waterside vegetation, as seen to varying degrees in modern pygmy chimpanzees and lowland gorillas in flooded rainforests or forest swamps [15]. Australopith short-legged bipedalism was different from human bipedalism [21], probably including a somewhat forward-leaning trunk posture [22], and would have been suitable for aquarboralism. The *Australopithecus africanus* StW-573 foot from Sterkfontein, South Africa, for instance, ‘had both bipedal and climbing adaptations. This skeleton’s foot morphology is consistent with the bipedal Laetoli footprints, which are not those of fully human feet, but which have very clear ape-like morphology’ [23]. Tree-climbing features (which are less obvious in the robust australopiths) include apelike upward-directed shoulder joints and curved finger and toe phalanges.

Tooth microwear

Tooth microwear studies indicate that *Australopithecus afarensis* molar enamel had a glossy polished surface that is typical of the molars of capybaras *Hydrochoerus hydrochaeris* and mountain-beavers *Aplodontia rufa* [24]. Both these semi-aquatic rodents feed mainly on riverside herbs, grasses and the bark of young trees. The

microwear of *Australopithecus boisei* displays more pits, wide parallel striations and deep-recessed occlusal dentine features than that of *A. afarensis* [25,26], resembling the microwear of beavers *Castor fiber*, which feed on riverine herbs, roots of water-lilies, bark and woody plants. Apparently, an early australopith diet of fruits (larger front teeth) and swamp herbs (polishing) was supplemented with woody plants in the robust australopiths (more wear). Walker’s suggestion that *A. boisei* were bulk-eaters of ‘small, hard fruits with casings, pulp, seeds and all’ [27] could explain the deep-recessed dentine, but not the heavily polished enamel that is typical of marsh-plant feeders [24,25].

Strontium:calcium ratios and isotopic evidence

The microwear data are consistent with those from two studies on South African australopiths [28,29]. Sillen provides three possibilities for low strontium:calcium ratios in *Australopithecus robustus*: partial carnivory; eating leaves and shoots of forbs and woody plants; and eating food derived from well-drained streamside soils [28]. Sponheimer and Lee-Thorp state 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’ [29]. However, regular consumption of savannah grasses is incompatible with the polished, rounded microwear [24,29] and predominant meat eating is unlikely in view of the blunt molars [27]. More probable is a diet of sedges and other marshland plants supplemented with fruits and animals (e.g. tools attributed to *A. robustus* now suggest termite-eating [30]).

Independent lines of evidence thus suggest that different australopith species regularly waded for shallow-water plants, possibly like lowland gorillas do today [15], only much more frequently. Papyrus or reed sedges were abundant in australopith environments (Table 2) and are part of the diet of extant hominids. Gorillas eat bamboo shoots and stalks, as well as swamp herbs and sedges (Table 1); all hominids eat cane; bipedally wading chimpanzees and humans collect water lilies; and rice growing in shallow water, and other cereals are staple foods for humans.

Were *Homo* ancestors waterside omnivores?

Late Plio- or early Pleistocene human ancestors could have migrated to or remained near the coast and exploited marine resources. Dolphins and seals have larger brains than do their terrestrial relatives of equal size [31] and human brains are three times those of chimpanzees. The long-chain, polyunsaturated lipid ratios of shellfish and fish are more similar to the ratios in the human brain than are any other known food source [32]. This highly nutritious diet is argued to have been important for building and fuelling large brains [32].

Eating hard-shelled foods, such as shellfish and nuts, generally requires thick enamel, which is typically seen in sea otters [27], capuchin monkeys [33] and most living and fossil hominids–pongids (Box 1, Table 2). Walker wrote that if ‘a mammalogist who knows nothing about hominids were asked which mammalian molars most

resembled those of *Australopithecus*, the answer would probably be orang-utan molars. If asked to look outside the order Primates, the answer would probably be the molars of the sea otter (*Enhydra lutra*). This species possesses small anterior teeth, and large, flat molars with thick enamel [27]. A recent study [34] indicated that *Australopithecus* or *Homo habilis* microwear resembled that of chimpanzees (and orang-utan [35]), *Homo ergaster* resembled that of capuchin (more hard or brittle foods), and neither taxon specialized on raw meat [34,35]. Sea otters, capuchin and chimpanzees all open shells by hammering them with hard objects. The most dextrous mammals, besides humans, are raccoons, otters, capuchin and chimpanzees. Conceivably, human–chimpanzee ancestors used stones to remove and open coconuts growing on palm-trees, and oysters on mangrove roots (Fig. 1) in the same way that mangrove capuchin do [33]. If chimpanzee ancestors moved inland, stone use might have become confined to nut cracking, but, for coastal human ancestors, stone use would have become more important, and the long association with coconuts and shellfish might explain the use of stone tools during the Stone-Age.

Today, breath-hold diving is practised by human subsistence cultures that gather shellfish or seaweed. Diving mammals, such as cetaceans and pinnipeds, are able to take a deep breath whenever they intend to dive, and comparative data suggest that voluntary breath control in humans is much better developed than in monkeys, apes, dogs and pigs [5,36,37]. Many tree- (e.g. gibbons) and water-dwellers (e.g. otters, dolphins and humpback whales) have well-developed sound-producing capabilities [36]. Vocal communication might have been important during wading activities, when smell and body language would have been less effective [5]. Along with voluntary breath control and a large brain, this could have contributed to the evolution of human speech [5].

Anatomically (*Homo rudolfensis*) and archaeologically (OLDOWAN tools), the genus *Homo* appears in East Africa c. 2.5 Mya, at about the beginning of the Pleistocene, when increased glaciation was locking large amounts of water in ice-caps and causing sea levels to drop. If the coastal lagoons produced more food for a tool-using omnivore than did the decreasing forests, it could explain why *Homo* reduced its climbing abilities, evolved diving abilities and dispersed along the Indian Ocean. If *Homo* lived in such environments during glaciations, their remains would have been deposited at Pleistocene beaches, which, in most cases, are now some hundred metres below sea level.

Archaic *Homo* fossils, footprints and tools have been discovered near coasts all over the Old World [17], from Boxgrove (UK) and Hopefield (South Africa), to Mojokerto (Indonesia). The Mojokerto fossil, found amid barnacles, corals and molluscs [38] in a river delta probably c. 1.8 Mya, might be among the oldest *H. erectus* fossils ever discovered. Archaeological evidence suggests that *Homo erectus* crossed a 19-km-wide strait to reach the Indonesian island of Flores more than 0.8 Mya, well before any evidence of boat-building [3]. Stone tools found

in 0.12 My-old Eritrean reefs [39] support the idea that *Homo* spp. have a long history of coastal resource exploitation.

Arguably, modern humans evolved from beachcombers who gradually became more suited to wading and diving (Fig. 1), developing more linear bodies, longer legs, larger brains and tool-using skills. This coastal phase could help explain furlessness, subcutaneous fat and voluntary breath-control – features that are unique among primates but common to walruses, seacows, babirusas, hippos, whales and dolphins [4,5]. It could also help explain why humans are more efficient swimmers and divers than other primates [4,5,37,40].

We propose that several *Homo* populations, including *Homo sapiens*, returned to a more terrestrial existence, colonized coastal areas and river valleys in Africa and Eurasia, exploited waterside plants and animals, including waterfowl, turtles, stranded whales, antelope and hippo, but were unable to adopt a more chimpanzee-like form of quadrupedalism because, whereas knuckle-walking gorillas and chimpanzees evolved directly from short-legged wader–climbers, *Homo* already had long legs and a more linear build. Terrestrial bipedalism is slower than quadrupedalism and leads to backaches, hip and knee problems but also ‘frees’ the hands for communication and the manipulation and transport of food, water, weapons, tools and babies.

Hypothesis and further research

The combination of comparative, dental, skeletal, fossil, biomolecular and geographical evidence suggests that hominid ancestors climbed and waded bipedally in swampy or mangrove forests and supplemented their mainly herbi–frugivorous diet with shellfish. The australopiths and ancestors of gorillas and chimpanzees might have lived near swampy forests and preserved their climbing abilities, whereas hominid populations that remained near or returned to the coast could have given rise to the various *Homo* spp.: big-brained, long-legged waders and divers who were able to take full advantage of the resources associated with coastal environments. They dispersed along the Indian Ocean and followed rivers inland. This scenario helps to explain the long legs of humans, as well as furlessness, subcutaneous fat, infant tolerance to immersion, voluntary breath control, big brains and the development of language and technology.

Traditional palaeo–anthropology relies to a large extent on savannah-based interpretations of the hominid fossil record [1–3]; nonsavannah-based explanations are rarely considered and the fragmented nature of the fossil record means that much conjecture is needed in trying to build coherent models. A more realistic approach is to incorporate comparative data and accept the possible role of nonsavannah environments in the evolution of hominids. We expect that extensive, detailed and consistent comparisons with other mammals will provide unexpected insights into hominid evolution.

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Glossary

Australopith: Plio–Pleistocene hominid fossils from Africa, such as *Australopithecus* and *Ardipithecus*.

Dryopith: Miocene hominid–pongid fossils from Eurasia.

Hominids: African apes (common chimpanzees, pygmy chimpanzees and gorillas) and humans and their fossil relatives (as opposed to pongids).

Hopping bipedalism: with hips and knees flexed when at rest, e.g. tarsiers, indris, jerboas and kangaroos.

Knuckle-walking: walking on the dorsal side of the middle phalanges of the fingers (gorillas and chimpanzees).

Oldowan: earliest stone tool industries, usually attributed to early *Homo*.

Pongids: orang-utan and their fossil relatives (as opposed to hominids).

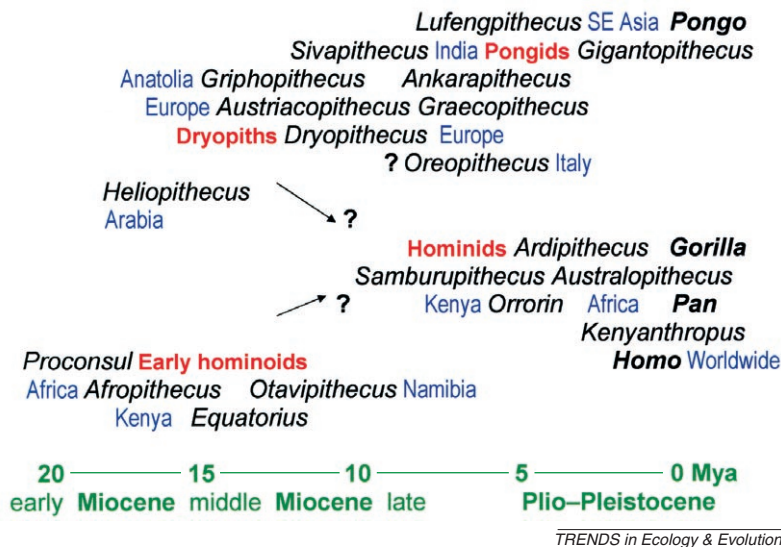
Postcrania: body parts, e.g. fossil bones, which do not belong to the skull or dentition

Box 1. Fossil hominids–pongids

Extant hominoids comprise HYLOBATIDS (see Glossary) and hominids–pongids. Hylobatids and pongids live in Asia, whereas hominids probably stem from Africa. Between 13 and 7 million years ago (Mya), most hominid–pongid fossils (except, e.g. *Samburupithecus*) came from Europe, Anatolia and India. Although the common hominid–pongid ancestors might have lived near the Middle East [a], the

possibility remains that the ancestral line leading to the hominids was always present on the Afro–Arabian continent [b] (the Arabian peninsula was then part of Africa).

The taxonomy of the fossil great apes remains very contentious and researchers often have conflicting opinions. Figure 1 illustrates the temporal and geographical diversity of the Miocene great apes and provides a rough temporal and geographical framework for the reader. We have tried to group the fossils according to geographical location and morphological similarities but want to stress that the exact relationships remain uncertain. Schematically, we discern three groups (Fig. 1).



Early and Middle Miocene great apes in Africa–Arabia

Proconsul, *Afropithecus* (*Morotopithecus*), *Equatorius* (*Kenyapithecus*) and *Otavipithecus* might have been stem hominoids, rather than hominid–pongids. The 17-Mya-old ‘Saudi ape’ *Heliopithecus leakeyi*, discovered near ‘the tropical shores of the Tethys epi-continental sea’ [c], is possibly the earliest known dryopith and hominid–pongid [c,d] (although a newly discovered thick-enameled hominoid from southern Germany is said to be older [e]).

Middle and Late Miocene hominids–pongids in Eurasia

The thick-enameled dryopith *Austriacopithecus weinfurteri* (Slovakia–Austria, c. 14 Mya, possibly belonging to *Griphopithecus* [c,f]) was also found in marine nearshore sands [f,g]. *Dryopithecus* spp. [f,g] (Europe, 13–9 Mya) and *Oreopithecus* (possibly not a hominid–pongid, see Table 1), both with thinner molar enamel and arm-hanging adaptations, dwelt in swampy forests. *Graecopithecus* (*Ouranopithecus*) and *Ankarapithecus* are superthick-enameled late dryopiths from more open environments. *Sivapithecus* (*Ramapithecus*), *Lufengpithecus* and *Gigantopithecus* are thick-enameled Asian pongids. If all Eurasian hominid–pongid fossils are pongid, as argued by Pickford [b], the last marine transgression that isolated Eurasia from Africa c. 16 Mya [e,f] could have separated pongids (north of Tethys) and hominids (south of Tethys).

Late Miocene and Plio–Pleistocene hominids in Africa

Samburupithecus, of gorilla size and outlook, but with thicker molar enamel, might be the earliest known hominid [b]. *Orrorin* is believed to have had both bipedal and climbing features and might have belonged to the *Homo–Pan* branch of hominids [h]. *Ardipithecus* is a thinner-enameled forest-dwelling early hominid with bipedal as well as climbing features [i]. In our opinion, *Australopithecus* is a paraphyletic taxon that possibly comprises members of the *Gorilla*, *Pan* and/or *Homo* branches of hominids [j]. *Kenyanthropus* might belong to the *Homo* branch of hominids [k].

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Box Glossary

Hylobatids: the lesser apes gibbons and siamangs (as opposed to the extant great hominoids: hominids and pongids).

Fig. 1. Great ape and human evolution. Hypothetical reconstruction of the ancestral diet and locomotion based on comparative anatomy, DNA and geographical distribution of living hominid-pongoid species. Fossil hominids (*Samburupithecus*, *Orrorin*, *Ardipithecus*, *Australopithecus* and *Kenyanthropus*) are not included here because their exact place is uncertain.

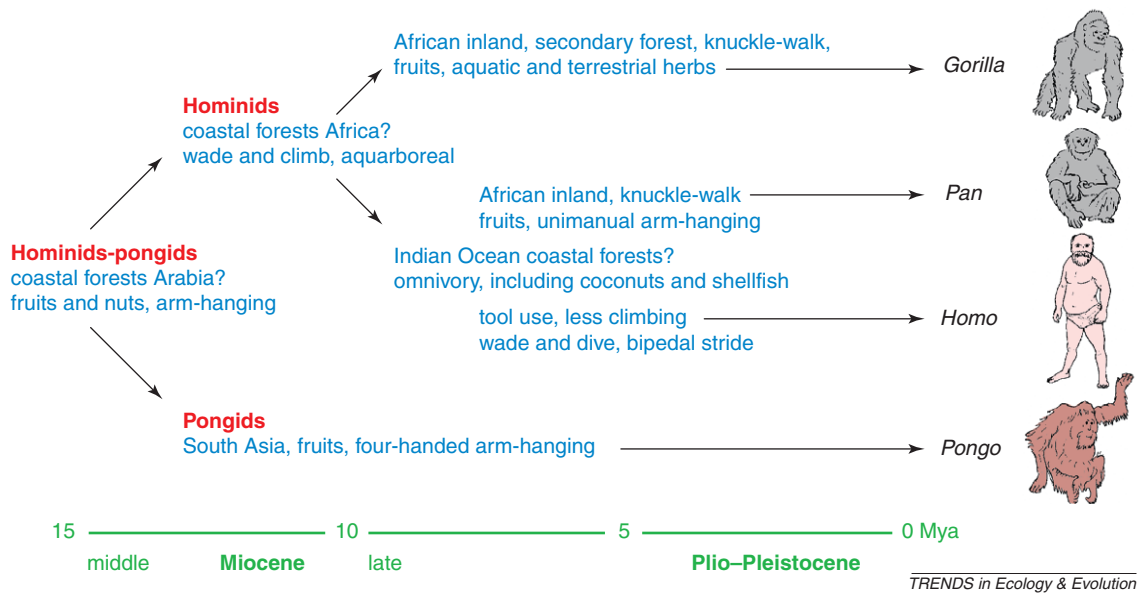


Table 1. Examples of possible arboreal-to-aquarboreal transitions in mammals

Species	Diet and habitat	Locomotion and body build	Aquatic foods	Aquatic locomotion	Refs
Two- and three-toed sloths <i>Choelopus</i> and <i>Bradypus</i> spp. (edentates)	Folivores in tropical forest in the Amazon basin	Slow arm-hanging arboreals (suspensory). Broad thorax, very short tail	No aquatic food	Swimming (kind of breast-stroke) between trees (flooded season)	41
Mangrove capuchin <i>Cebus a. apella</i> (New World monkey)	Frugi-omnivore. Thick enamel and tools used to open nuts, oyster shells, etc.	Generalized arboreal quadruped. Typical monkey: long tail, no broad thorax	No aquatic food, except mangrove oysters	Occasional swimming (dog paddle) or wading	33
The 'swamp ape' <i>Oreopithecus bambolii</i> c. 9–7 Ma (probably hominoid)	Thin enamel. Folivore? Coal-swamp deposits on island of Tuscany-Sardinia	Arm-hanging. Aquarboreal? Medium-sized, broad build, no tail	Aquatic plants, such as water lilies, reed, sedges, cattail, pondweed, horsetails and stoneworts?	Frequent bipedal wading presumed. Swimming unknown (fossil)	16
Lowland gorilla <i>Gorilla g. gorilla</i> (hominid)	Herbi-frugivore on forest floor and in lower canopy (secondary forest)	Knuckle-walking and arm hanging. Largest primate, broad thorax and no tail (as all hominoids)	Aquatic herbaceous vegetation (e.g. Cyperacea and Hydrocharitaceae, makes up c. 2 % of diet)	Knuckle-walking and bipedal wading in forest swamps. Occasional swimming (breast-stroke)	15
Proboscis monkey <i>Nasalis larvatus</i> (Old World monkey)	Folivore, mostly in mangrove trees	Leaping arboreal quadruped, some arm-hanging. Large monkey (short tail in <i>N. concolor</i>)	No aquatic food	Bipedal wading between mangroves and occasionally on dry ground, occasional swimming (usually dog-paddle but breast-stroke and overarm also observed)	5

Table 2. Overview of hominid fossils in Africa

Fossil species	Age^a	Tooth enamel^b	Body build^c	Example of site (description)^d	Refs
<i>Samburupithecus kiptalami</i>	c. 9.5 Mya	Probably thick	Very large	Samburu Hills: lacustrine, open woodlands	42
<i>Orrorin tugenensis</i>	c. 6 Mya	Thick	Rather large	Tugen Hills: shallow lake fringed by trees	18
<i>Ardipithecus ramidus</i>	5.6–4.4 Mya	Rather thin	Rather large	Middle Awash: wet and wooded	14
<i>Australopithecus anamensis</i>	c. 4 Mya	Thick	Rather large	Kanapoi: wide gallery forest	17
<i>A. afarensis</i>	c. 4–3 Mya	Thick	Gracile–large	Hadar: swale-like, streamside gallery woodland	17
<i>Kenyanthropus platyops</i>	c. 3.5 Mya	Thick	Gracile	Turkana: shallow lake and forest edge	19
<i>A. africanus</i>	c. 3 Mya	Thick	Gracile	Sterkfontein: sub-tropical forest, thick bush	3,17
<i>A. aethiopicus</i>	c. 2.5 Mya	Very thick	Very large and robust	Turkana: overbank deposits, amid reedbucks	17
<i>A. robustus</i>	c. 2 Mya	Very thick	Robust	Kromdraai: streamside reedbeds, amid parrots	17
<i>Homo rudolfensis</i>	2.4–1.8 Mya	Thick	Rather large	Chemeron: lacustrine, shelly limestones	17
<i>A. or H. habilis</i>	c. 2–1.6 Mya	Thick	Small, gracile	Olduvai: swamp vegetation and papyrus reeds	17,35
<i>A. boisei</i>	2.1–1.2 Mya	Very thick	Very large and robust	Chesowanja: warm, shallow lagoon, amid reeds	17
<i>H. ergaster</i>	c. 1.6 Mya	Thick	Large	Turkana: amid molluscs, swamp-snail and catfish	17

^aAbbreviation: Mya, million years ago.

^bThick, as in humans and orangutans. Thin, as in gorillas. (Depends on body size. Chimpanzees have intermediary enamel thickness.)

^cLarge, similar to humans or chimpanzees; small, c. 30 kg; robust, with heavily and broadly built bodies and cheek teeth; Gracile, with more slender body. (Exact body sizes of fossils are unknown and difficult to estimate, e.g. using human measurements as a guide for lower limbs might underestimate australopith weights, whereas using dental formulas gives much higher body sizes.)

^dDescriptions to illustrate possible aquariboreal lifestyle. Note that 'drier' interpretations, more savannah-oriented, are often possible.