

5 Aquatic Features in Fossil Hominids?

Marc Verhaegen

SUMMARY

The hominid fossil record is examined in this chapter in the light of comparative anatomy and molecular biology. Four hypotheses are proposed:

- (1) Nothing in the palaeontological data invalidates the idea of semi-aquatic adaptations in hominid evolution from more than 4 million years ago until less than 1 million years ago.
- (2) African hominoids – humans, chimpanzees and gorillas – are descended from australopithecine ancestors.
- (3) Early australopithecine locomotion resembled that of the modern proboscis monkey, with potential for hanging from branches with the arms, swimming and diving, and wading bipedally.
- (4) *Homo erectus* and *H. neanderthalensis* possessed adaptations for littoral diving, and lost the arboreal adaptations of their australopithecine ancestors.

PALAEO-ENVIRONMENTAL EVIDENCE

Hominid fossils have been found in places that either are or were the sites of rivers or lakes. Pre-, gracile and robust Australopithecines, as well as early *Homo* (Tables 5.1, 5.2; Figure 5.1), stem from very wet palaeoenvironments with algae, sponges or reeds, and bivalves, swamp-snails, crabs, fish, frogs, aquatic turtles, crocodiles, water-fowl and hippos, often in the shallow water of a lake margin, lagoon or river delta (for example, Pickford, 1975; Ward and Hill, 1987; Martyn and Tobias, 1967; Radosevich and Retallack, 1988; Johanson, Taieb and Coppens, 1982; Bonnefille, 1976; Brain, 1981, p. 189; Carney *et al.*, 1971; Leakey, Clarke and Leakey, 1971; Ninkovich and Burckle, 1978; Potts, 1988). Lucy, the most complete skeleton of an *Australopithecus afarensis*, from Hadar, was discovered amid crocodile and turtle eggs and crab claws in near-shore deposits, and Johanson and Taieb (1976) preclude the possibility that Lucy's remains had been moved over any great distance. Also, the *Homo erectus* boy WT-15000,* an even more complete skeleton, was found amid typical lacustrine forms: 'the only other fauna found so far in the fossiliferous bed are many opercula of the swamp snail *Pila*, a few bones of the catfish *Synodontis* and two fragments of indeterminate large mammal bone' (Brown, *et al.*, 1985). Some fragmentary fossils – often skull bones or mandibles, the skeletal parts that

* See Table 5.2 for abbreviations used to denote East African fossil sites.

Table 5.1 Survey of fossil hominids

<i>Australopithecus afarensis</i> , c.4–3mya, *	E. Africa: e.g., Lucy from Hadar
<i>A. africanus</i> , c.3–2.5 mya,	S. Africa
<i>A. robustus</i> , c.2–1.5 mya,	S. Africa
<i>A. boisei</i> , c.2.5–1 mya,	E. Africa
) the robust Australopithecines
<i>Homo (Australopithecus?) habilis</i> , c.2 mya,	E. Africa
<i>H. erectus</i> , less than 2 mya,	Africa, Java, China
<i>H. neanderthalensis</i> or <i>H. sapiens neanderthalensis</i> ,	prior to 35,000 years ago,
	Europe and Middle East

Not all species are well defined, nor do all hominid fossil remains fit well into one of these 'species'. E.g., *A. afarensis*, *H. habilis* and *H. erectus* are not very homogeneous (Ferguson, 1987a, 1987b). The large intraspecific variation could be due to being composed of different taxa (*afarensis* or *habilis*), to a wide geographical (*erectus*), or temporal (*boisei* or *erectus*) distribution or to large sexual dimorphism. The Australopithecines prior to 4 mya are often referred to as *A. cf. afarensis* or pre-Australopithecines.

Table 5.2 Some East African fossil sites: abbreviations used

AL	Afar locality, Hadar in Ethiopia	
ER	East Rudolf, e.g., Koobi Fora)
WT	West Turkana or West Lake Rudolf)
CH	Chesowanja (late <i>A. boisei</i>))
KP	Kanapoi)
TH	Tugen Hills)
) pre-)
) Australopithecines)
) (Figure 5.1 (b)))
LT	Lothagam)
OH	Olduvai hominid)
LH	Laetoli hominid)
) Tanzania	

* Million years ago.

Fig. 5.1 (b)

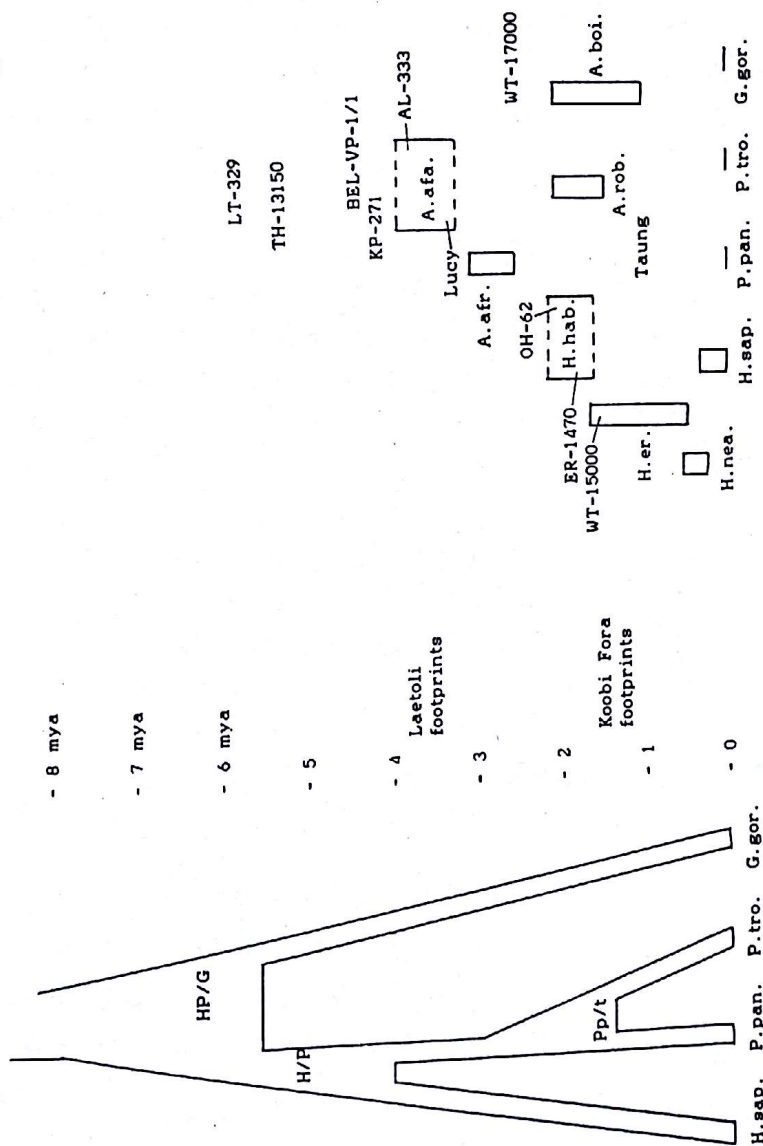


Fig. 5.1 (a)

Figure 5.1 Evolutionary tree of African hominids.

(a) Molecular tree (after Hasegawa, Kishino and Yano, 1985; 1987)
 HP/G = split between *Homo-Pan* and *Gorilla*; H/P = split between *Homo* and *Pan*; Pp/t = split between pygmy chimp (*bonobo*) and common chimpanzee.

mya = million years ago

(b) Fossil tree (after Delson, 1987)

BEL-VP-1/1 = pre-australopithecine frontal bone from Ethiopia (Clarke *et al.*, 1984); LT-329 and TH-13150 = *A. cf. afarensis* mandibles (Ward and Hill, 1987); KP-271 = Kanapoi distal humerus.

are left until last in the consumption process of large cats (Morden, 1988) – of *A. afarensis* from Laetoli come from wind-worked tuffs, but even these were found not far from ancient rivers (Leakey *et al.*, 1976). Also, the australopithecine remains found in South African cave deposits were probably the left-overs of sabre-tooths or leopards that were eating their prey in a riverside tree (Brain, 1981).

The findings do not constitute proof that the early hominids lived exclusively in or near the water. Watery sites provide silt in which bones are more likely to be preserved, and in river-valley locations there may be later water erosion to expose the layers which contain the fossils. It is possible to argue that while some of these hominids lived and died by the lake, others may have been living out on the open savannah, and that the prevalence of watery locations is indicative of the preconditions for fossilisation rather than of the hominid's habitat.

One palaeo-anthropological objection advanced against the Aquatic Ape Theory is the negative one that 'long-term adaptation along African coastlines should have left some traces, particularly if early hominids were exploiting shellfish (whose remains preserve remarkably well)' (Jurmain *et al.*, 1981, p. 326; see also Washburn and Moore, 1980, p. 132). But 'aquatic' does not necessarily mean 'marine'. Our ancestors could have been semi-aquatic in tropical lagoons, or in gallery or mangrove forests. They could have eaten vegetables instead of animal food. Besides, primates are not in the habit of collecting food and taking it back to a base. If they ate shellfish they would have originally eaten them only a few at a time *in situ*, as sea-otters do. Dating from at least about 0.3 million years ago, when *Homo* had acquired the practice of communal eating, traces of shellfish exploitation are found, for example, at Terra Amata in southern France.

COMPARATIVE ANATOMY OF FOSSIL HOMINIDS

Body size

Body enlargement, when comparison is made with Old World monkeys, is obvious in fossil and living hominoids (see Tables 5.3, 5.4). A body weight of more than 30 kg is rare in arboreal animals, whereas increased body mass is a striking feature of all aquatic mammals as compared with their closest terrestrial relatives.

However, increased body weight cannot in itself be regarded as evidence of aquatic influence, since it can also be seen – though usually on a less spectacular scale – in other circumstances (Simpson, 1959; Clutton-Brock and Harvey, 1977). For example, animals tend to be larger when they live in colder environments (Bergmann's Rule), when they live in open grasslands as opposed to forests, or in seas as opposed to rivers. A shift from insectivorousness to frugivorousness, or from

frugivorousness to folivorousness, could also favour a larger body size. Ground-dwellers tend to be larger than climbers, so that ceasing to be arboreal may in itself have been a major factor leading to increased body size.

Brain volume

The cranial capacity of the Australopithecines ranged from 375 to 525 ml, which is about as large as that of apes (Tobias, 1983; Falk, 1985, 1987). There has been a marked increase since early *Homo* ER-1470, who had a cranial capacity of probably more than 750 ml (Falk, 1980). Neanderthal man had a brain 15 per cent larger than modern man. Various theories have been advanced to account for the brain enlargement in *Homo* (Table 5.5). One is the evolution of speech (Verhaegen, 1988); songbirds also have large relative brain size (as measured by encephalisation quotient) compared with other birds (Wyles, Kunkel and Wilson, 1983). Other suggested explanations are the danger of over-heating the brain (Fialkowski, 1986), the need for throwing accuracy (Calvin, 1983), and the possible intellectual demands imposed by tool use, hunting or warfare (McHenry, 1982).

Most of these explanations are related to behaviour rather than to habitat, but one environment which appears to increase brain size is *water*. Brain enlargement is very common in aquatic mammals, notably pinnipeds (seals, walruses and sea-lions) and toothed whales (sperm and killer whales, dolphins and porpoises). A few years ago it was thought that a higher basal metabolism in marine mammals accounted for this (Armstrong, 1983), but recently more accurate measurements have failed to discern a difference in metabolic rate between terrestrial and aquatic mammals (e.g., Folkow and Blix, 1987). Another suggestion is made by Michael Crawford: since omega-3 fatty acids result from a marine or a mixed land/water diet, the very high content of these marine-based fatty acids in the human nervous system could have permitted – as in dolphins – the evolution of very large brains (S.C. Cunnane, personal communication). On the other hand, brain enlargement may be due to the same reason as body enlargement: the need for miniaturisation of the body and especially of the brain is low in an aquatic milieu, because the surrounding water greatly reduces the energy costs of sustaining the extra weight (Verhaegen, 1988).

Explanations advanced for modern man having a somewhat smaller brain than his ancestors and than Neanderthal man are summarised in Table 5.6.

Brain endocasts

Fossil brain endocasts make it possible to attempt to date the emergence of typically human brain centres. Two of these are closely connected

Table 5.3 Classification of living primates

I	Strepsirhini (e.g., lemurs, indris, loris, galagos)
II	Tarsiers
III	Anthropoids (monkeys, apes and man):
A	Platyrrhini or New World monkeys (e.g., spider-monkeys, marmosets)
B	Catarrhini or Old World monkeys (Africa and Asia)
1	Cercopithecoidea or Old World monkeys:
(a)	Colobinae (e.g., langurs, proboscis monkey (<i>Nasalis larvatus</i>))
(b)	Cercopithecinae (e.g., macaques, baboons)
2	Hominoidea (apes and man):
(a)	Hylobatidae or lesser apes (gibbons and siamang, S. E. Asia)
(b)	Large hominoids (great apes and man):
–	orang-utan
–	African hominoids: man, chimp and bonobo, gorilla

Table 5.4 Living hominid and pongid species

<i>Pongo pygmaeus</i> or orang-utan, the great ape from S.E. Asia	
<i>Gorilla gorilla</i>)
<i>Pan troglodytes</i> or common chimpanzee)
<i>Pan paniscus</i> or bonobo or pygmy chimp) the great apes from Africa
)
<i>Homo sapiens sapiens</i> or anatomically modern man)

Table 5.5 Brain weights of various mammals, adult and premature, weighing 50–70 kg (Smith, 1984)

Man	c.1300 g
Porpoise	537 g
Great apes	c.400–450 g
Zebra	410 g
Ruminants	140–334 g
Suids	125–178 g
Carnivores	154–175 g

Table 5.6 Explanations for neolithic reduction of cranial capacity in man (partly after Henneberg, 1988)

-
- auto-domestication (domestic animals have 20–30% less brain tissue than their wild relatives)
 - 'stasis' between two punctationalistic leaps
 - selection for smaller body size (e.g., after leaving the aquatic habitat, or as a result of population growth and subsequent food shortages)
 - relaxation of selection for intelligence, with the development of more complex societies (cf. auto-domestication)
 - internal reorganisation of the brain superseding further increases in size (cf. computer miniaturisation)
 - decreased protein consumption in the Holocene
 - reduced muscle robustness or muscle control
 - by-product of generalised structural reduction (gracilisation of the skeleton)
 - selection for smaller brain weight (e.g., after leaving the aquatic habitat)
-

with speech. *Broca's area* in the left frontal lobe coordinates the primary motor cortex that commands the muscles of mouth and larynx, for instance, for speaking. *Wernicke's area* in the left parieto-temporal lobe is used in decoding spoken language.

Tobias (1983) was unable to detect Wernicke's area in fossil endocasts earlier than *H. habilis*, around 2 million years ago. Both Tobias and Falk (1983) believe that the Australopithecines, lacking this structure, could not have been capable of verbal communication. Tobias detected signs of a Broca-like expansion in *A. africanus* fossils of about 2.5 million years ago, but this is questioned by Falk, who believes that only early *Homo* ER-1470 of about 2 million years ago had an obvious Broca's area, and that the Australopithecines still had an ape-like frontal lobe. Morgan and Verhaegen (1986) speculated that the earliest Broca-like structures were an adaptation for improved control of mouth and breathing muscles as required in a diving mammal, an essential precondition for the evolution of speech.

Falk (1986) also studied the cranial venous sinus system in fossil hominid endocasts, and found that the occipital/marginal venous sinus was enlarged in *A. afarensis* and the robust Australopithecines, but seldom in other hominoids (except human foetuses and neonates). She believed that the enlarged occipital/marginal sinus was a haemodynamic adaptation to incipient bipedalism. Extensive, valveless, anastomotic vertebral venous networks are found in man (Falk and Conroy, 1983) and also in a variety of other mammals subjected to frequent and sudden changes in head and trunk position, possibly because they operate in a

medium where movement is three-dimensional – that is, water or air. Examples include climbing or flying mammals such as sloths, cats and bats, and especially diving mammals such as seals, sea-cows and whales. Slijper (1979) suggests that aquatic mammals use these venous networks to buffer the sudden pressure changes they encounter when diving.

Still another suggestion is made by Cabanac (1986). He believes that our extensive venous networks at the skull base are part of a cooling system of the brain (see also Wheeler, 1985; but cf. Verhaegen, this volume, chapter 11).

Table 5.7 Explanations for skull vault thickening in fossil *Homo* (partly after Foster, 1987)

-
- the insertion of very powerful masticatory and/or nuchal muscles on the skull vault
 - mechanical protection of the brain
 - a negative correlation with brain capacity
 - a positive correlation with cranial capacity
 - with certain hunting habits
 - with inter-group aggression
 - with sexual dimorphism
-

Cranial vault

H. erectus, even more than *H. neanderthalensis*, had very thick cranial vaults, thicker than those of monkeys and apes, or of modern man; and thicker also than those of *H. habilis* and the Australopithecines (Kennedy, 1985). Several explanations have been proposed for this feature (Table 5.7). Most of them are variations on the theme of mechanical protection for the growing brain: they relate this to behavioural factors such as hunting, inter-group aggression and sexual dimorphism.

The heavy cranial vault of *H. erectus* was accompanied by very dense bones in the rest of the skeleton (humerus, ulna, pelvis, femur, tibia). These cannot have been directly related to protection of the brain, and would be less obviously advantageous in a hunting hominid for whom speed was at a premium. Really heavy skeletons are only seen in slow littoral bottom-feeders like sea-cows, probably compensating for their abundant subcutaneous fat (density 0.9) in a milieu with a density of 1.026 instead of the 1.000 of pure water (Hildebrand, 1974, pp. 586–7; Wilson, 1979, pp. 793–4). The fast-swimming seals have thinner skulls than dogs (van Nie, personal communication), but the slow walruses have extremely thick cranial vaults, presumably for keeping the head down easily while seeking shellfish. If *H. erectus* had thick skull bones for the same reason, he too must have sought food at the lake or sea bottom.

We can deduce that at least some of the Neanderthals were habitual divers. Skulls of middle-aged Shanidar I and Chapelle-aux-Saints males had extensive and bilateral ear exostoses, while the *H. erectus* skull-X from Zhoukoudian demonstrated a discrete lesion in one ear (Kennedy, 1986). In modern man, these anomalies are only seen in populations who exploit marine or freshwater resources through diving in water of 18°C or less; they are almost invariably 'associated with a history of cold water exposure over long periods of time'; 'a long and impressive history of aquatic habits, usually beginning before their teenage years, was described by all patients' (quoted in Kennedy). There is no reason to believe that this was different in *H. neanderthalensis*. It strongly suggests that the male Neanderthals – at least in some seasons – dived regularly, probably every day, in the cold rivers along which they lived.

Another feature of the cranial vault in *H. erectus* and *H. neanderthalensis*, especially the males, is the pronounced supra-orbital torus (bony eyebrow ridge), found also in robust Australopithecines, African apes and baboons. It is weakly or variably developed in modern humans, orang-utans, gibbons and some Old World monkeys, and is absent in all smaller primates and most other mammals. Masticatory and eye-protective explanations are usually advanced (Table 5.8).

Table 5.8 Explanations for supra-orbital torus development in *H. erectus* and *H. neanderthalensis* (after Russell and replies, 1985)

-
- a differential growth process among various regions of the skull due to non-mechanical factors
 - an allometric correlation with large body size
 - a defence against possible blows, especially in primates with their frontally placed eyes
 - an adaptation that resists the stress over the eyes during anterior biting, e.g., before the use of fire (cooking)
 - a consequence of powerful masticatory muscle insertions just dorsal to the torus (cf. Table 5.9)
-

Compatible with these explanations is that the presence of a well-developed torus in fossil man in contrast with modern man is a result of the more dorsally placed brain. In *H. erectus* and *H. neanderthalensis* the brain case is placed behind the face rather than above it, and it is also flattened (platycephalic), with its widest point behind the ears, at the base of the skull and not well up in the vault as in *H. sapiens* (Stringer, 1978). Both the flattening and the dorsal shift of the brain case seem to indicate a streamlining of the skull, such as would be required by the diving

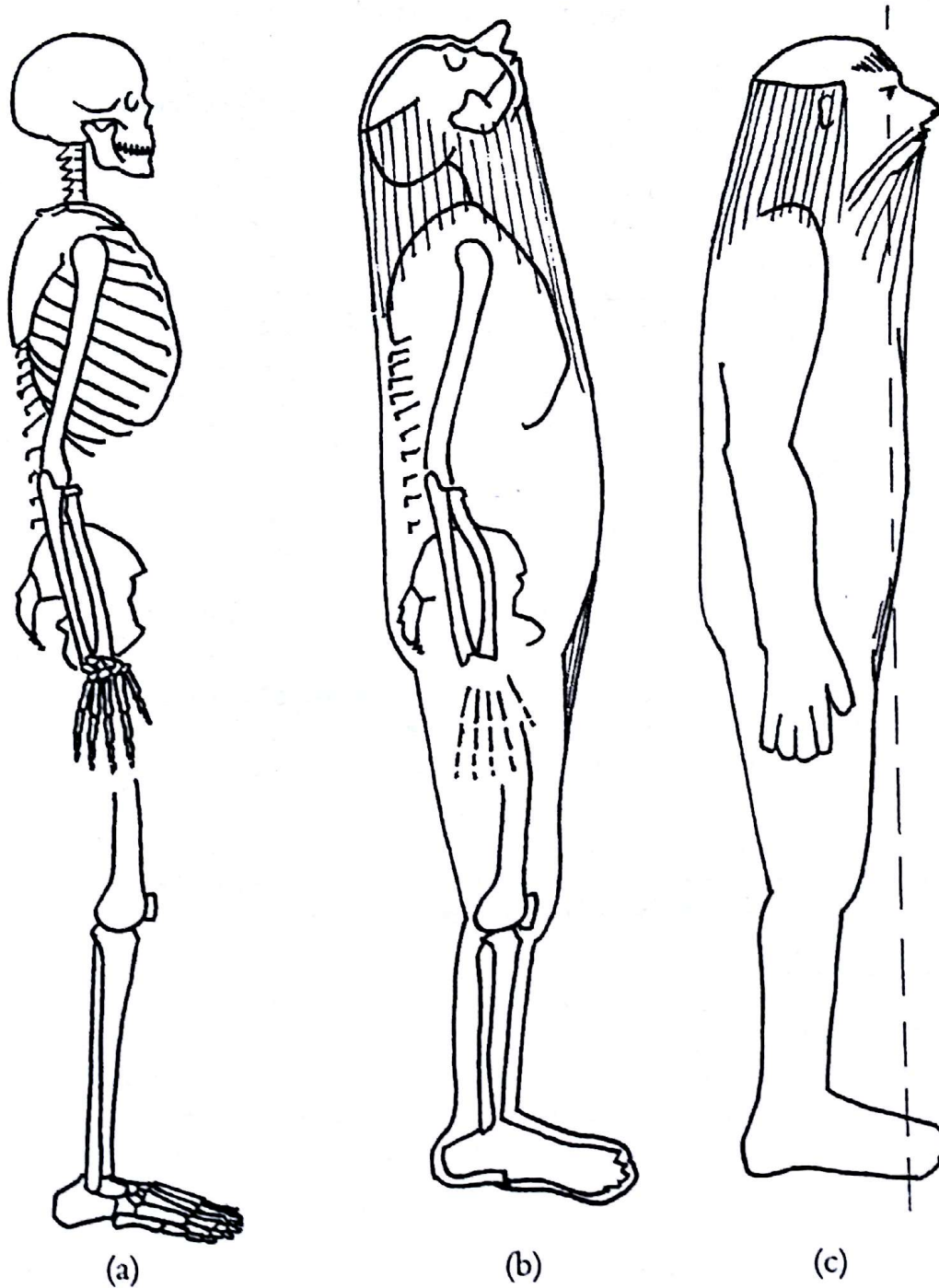


Figure 5.2 Side view of a male Neanderthal compared with modern man.

(a) modern skeleton; (b) diving Neanderthal (note streamlining of head and body); (c) floating Neanderthal (note projection of nose above water surface).

A reconstruction is necessarily speculative in respect of the soft tissues. The assumptions made in (b) and (c) are that the nostrils were anterior, the hair long, the belly thick and the head bald on top (Verhaegen, 1985, 1987a, 1987b). (b) and (c) are based on comparisons of Neanderthal fossils with modern man: skull lower and longer; mid-face projects anteriorly, jaws more robust; spinous processes of vertebrae longer and more horizontal; superior pubic rami reach more anteriorly; hand slightly broader, little finger longer; radius and femur bowed more strongly; patella larger; tibia somewhat shorter.

Table 5.10 Pneumatisation in fossil hominids

-
- *A. afarensis* AL-199 and AL-200-1 had large maxillary sinuses (Johanson and Taieb, 1976)
 - Temporal squama pneumatisation in *A. afarensis* AL-333-45, early *A. boisei* WT-17000, and some gorillas and male chimps, was more pronounced than in later *A. boisei*, S. African Australopithecines and *H. habilis* (Kimbel, White and Johanson, 1984; Johanson, 1985; McHenry, 1986; Walker *et al.*, 1986)
 - Robust Australopithecines generally show more extensive paranasal pneumatisation and inflated mastoids, but less inflated temporal squamae (Leakey and Walker, 1988; Wood, 1978; Kimbel, White and Johanson, 1984)
 - The S. African Australopithecine from Taung shows a much larger maxillary sinus than comparable chimp or human juveniles; pneumatisation has also extended into the hard palate (as in *A. robustus* and *P. troglodytes*) and zygoma (Conroy and Vannier, 1987)
 - Early *Homo* ER-1470 had extensive mastoid, maxillary and especially frontal pneumatisation (Day *et al.*, 1974)
 - The mid-Pleistocene *H. erectus* from Bodo had extensive maxillary sinuses (Conroy *et al.*, 1978)
 - The frontal sinuses in modern man (in blacks more than in Eskimos and Australian aborigines), and certainly in Neanderthal man, are much larger than in apes (Blaney, 1986)
-

External nose

The human projecting external nose became apparent in *H. erectus*, most markedly in the superior nasal region (Franciscus and Trinkaus, 1988b). In Neanderthals the whole mid-face region was very protruding, with the large, broad, highly placed nasal aperture projecting anteriorly (Figure 5.2 (c)). The Monte Circeo skull from the Tyrrhenian coast, which had the lowest skull vault of all Neanderthals, also had the most highly placed nasal aperture (Moerman, 1977, pp. 265, 144). When Otto Hauser discovered the Moustier Neanderthal in 1908, the external nose was still recognisable, and the nostrils were directed more anteriorly instead of inferiorly as in modern man (Moerman, p. 80).

Special adaptation of the nasal aperture is a feature of all aquatic mammals, and of mammals with an external nose: the proboscis monkey and some closely related colobine monkeys, saiga, elephant seal and bladder-nose seal, elephants, tapirs, swine and peccaries, coati and some other carnivores, and diverse sniffing insectivores. In *Homo*, the external nose has been viewed as a compensation for the reduction of the anterior dentition, or as an adaptation for moisture conservation in arid

environments (Table 5.13). The Neanderthal protruding mid-face has been explained as a masticatory adaptation for better opposing rotational forces on the anterior teeth (Rak, 1986), or as an adaptation to extreme cold (Coon, 1962; but see Rak). An aquatic explanation is the lengthening of the airways for better closure, the streamlining of the head when diving (Figure 5.2 (b)), and the projection of the nose above the water surface when swimming on the back (Figure 5.2 (c)), as sea-otters do when opening shellfish, or proboscis monkey babies clinging to their swimming mothers (Ellis, 1986).

In contrast with *Homo*, the Australopithecines still had the flat, non-protruding nose of their primate ancestors. Nevertheless, a few peculiarities may be noticed. As in all hominoid taxa, the nasal region is highly variable (Eckhardt, 1987, 1988). Guttered margins of the nasal aperture are especially prominent in robust Australopithecines (Walker *et al.*, 1986). Robust Australopithecines also display a unique inferior tapering of the nasal bones. The only living primate in which a similar condition exists is the snub-nosed langur, a close relative of the proboscis monkey (Corruccini and Ciochon, 1979). The function of these adaptations is not clear, but might be connected with incipient aquaticity.

Table 5.11 Pneumatisation in other animals

<i>Extensive pneumatisation</i>	<i>Small paranasal sinus</i>
Crocodiles (freshwater)	Most reptiles
Most fossil hominids	Monkeys, carnivores
Swine	Hippopotamuses
Elephants	Marine mammals

- Most mammals (e.g., monkeys, lions and cats) have small sinuses with broad ostia, unlike man (Blanton and Biggs, 1968; Harrison, 1958)
- Dogs have larger frontal sinuses, which are almost completely filled with ethmo-turbinates used in olfaction (V. E. Negus, in Blanton and Biggs, 1968)
- Most herbivores (e.g., koalas, horses, ruminants and especially swine) have well developed sinuses (Loeffler, 1981, pp. 111-31; Kratzing, 1984)
- Elephants have very large sinuses, hippos (which usually stand and walk on the river bottom) very small ones
- Marine mammals have reduced or absent sinuses other than those associated with the middle ear (Hempleman and Lockwood, 1978, p. 27)

Table 5.12 Possible explanations for skull pneumatisation

-
- 1 *As surveyed by Blanton and Biggs (1968):*
 - to impart resonance to the voice
 - to humidify and warm the inspired air
 - to increase the area of the olfactory membrane (dog frontal sinus, see Table 5.11)
 - to absorb shock applied to the head
 - to secrete mucus for keeping the nasal chambers moist
 - to thermally insulate the nervous centres
 - to aid facial growth and architecture
 - to exist as evolutionary remains and/or unwanted space
 - to lighten the bones of the skull for maintenance of proper balance of the head
 - 2 *Other or more detailed possibilities:*
 - to set wider apart eyes or ears (stereo), horns or antlers (herbivores), teeth or tusks (elephants); or to permit the insertion of masticatory (herbivores) or other cranial muscles
 - to make the head look bigger for intra- or inter-specific intimidation
 - to narrow the nasal passages, e.g., for better closure during diving
 - to keep more air – and oxygen – in the body during diving
 - to lower the specific gravity of (parts of) the head for floatability and/or for stabilising the position of the head in or outside the water
-

Table 5.13 Possible functions of an external nose

-
- preparation of inspired air: e.g., dust-filtering, wet cleaning, purification, humidification and temperature modification (Franciscus and Trinkaus, 1988b)
 - water and/or heat retention from expired air: e.g., moisture retention in dry climates in *H. erectus* and *H. neanderthalensis* (Franciscus and Trinkaus, 1988a,b)
 - water and/or heat dissipation: e.g., heat dissipation through broad nares of a possibly hyperactive Neanderthal man (Franciscus and Trinkaus, 1988a)
 - secondary response to the primary reduction of facial and dental dimensions
 - visual intra-specific intimidation (as in the bladder-nose seal, and possibly the proboscis monkey)
 - sound resonance (see also Ellis, 1986)
 - odour detection: e.g., when sniffing in wet ground (swine, coati, etc.)
 - manipulation of objects (elephant), or rooting in wet ground
 - snorkel or nose-closing device in the water, by lengthening and/or narrowing the airways (Morgan, 1982, pp. 80–2)
-

Spine

The Australopithecines had the foramen magnum located relatively farther back on the skull base than modern man, but less so than the gorilla or common chimp. Some of the males, especially, had a large and steeply rising nuchal plane, almost similar to that in apes (Kimbel, White and Johanson, 1984; Johanson, 1985). *H. erectus* also had a much larger nuchal plane than *H. sapiens*. These features could have been correlated with an often more dorsiflexed head, and perhaps with the smaller brain case.

A. afarensis, like *Homo*, exhibits a univertebral pattern for the first rib: the head of this rib articulates only with the body of the first thoracic vertebra, and there is no articular facet for the first rib on the seventh (the most inferior) cervical vertebra as in other mammals (Ohman, 1986). The only exceptions are some kangaroos which have a different sort of univertebral first-rib articulation, and some chimpanzees, which are intermediary in showing quasi-facets on the seventh vertebra. Ohman postulates four hypotheses: the univertebral pattern 'increases the volume of the neck, which would compensate for the loss of the laryngeal airsac system in hominid vocalisation; it is a consequence of the barrel-shaped thorax in hominids; of functional modifications in the hominid shoulder girdle; and/or modifications in the hominid first rib while breathing in an upright stance'.

A more barrel-shaped thorax (as in aquatic mammals), certain shoulder girdle modifications (for example, for swimming with arms above the head, or for streamlining), and a greater capacity for a deep intake of breath would also be needed in an aquatic milieu. The univertebral pattern may also have allowed a greater cervico-thoracic dorsiflexion of the head (Figure 5.2 (b)), and probably a greater flexibility of the first rib. More flexible ribs are a feature of aquatic mammals (Hildebrand, 1974, p. 591; Hempleman and Lockwood, 1978, p. 27).

The spinous processes of the vertebrae are longer and less inclined in *A. afarensis*, *H. erectus* and *H. neanderthalensis* than in modern humans (Johanson and White, 1979; Brown *et al.*, 1985; Trinkaus, 1987). Probably this was related to a thicker muscle layer, and perhaps a thicker fat layer, than in modern man, so that the dorsal mid-line reached farther backwards, which made the trunk rounder, less dorsoventrally flattened than in *H. sapiens*. In aquatic mammals a round trunk helps to withstand the water pressure on the lungs, especially in the deep-diving species (C.J. van Nie, personal communication).

Thorax

Quadrupedal terrestrial mammals have latero-laterally flattened thoraxes (Figure 5.3 (a)). So do most monkeys (Figure 5.3 (b)). The human thorax, however, is rather broad, and it is flattened in the opposite plain,

dorsoventrally. It is difficult to reconstruct the precise shape of the thorax in the different fossil hominids. P. Schmid believes that Lucy had an ape-like thorax (inverted funnel-shaped), while C.O. Lovejoy considers that it more nearly resembled our own barrel-shaped thorax (Ohman, 1986). The Neanderthals must have had a very wide thorax (Moerman, 1977, pp. 133, 235).

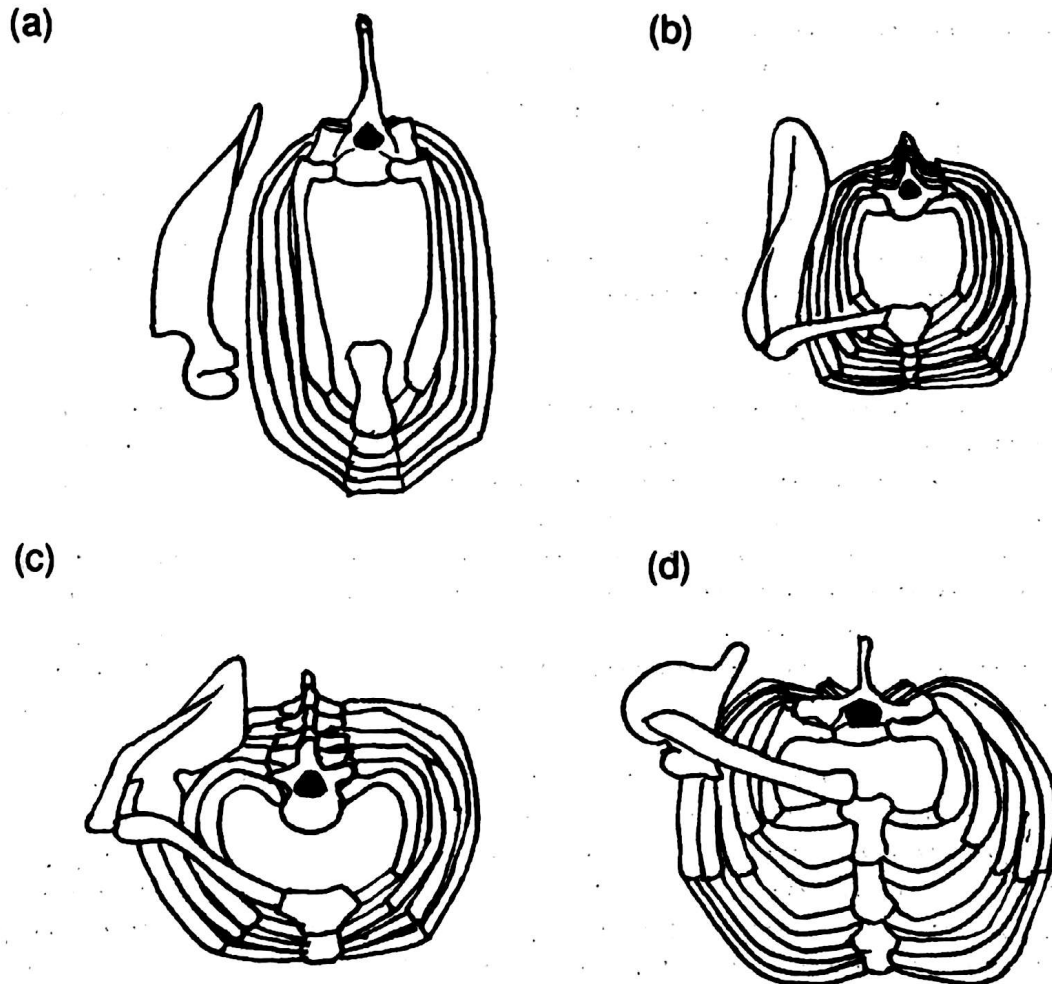


Figure 5.3 Comparison of thorax form, after Campbell (1974, figure 4.10) and Hildebrand (1974, figure 20.6).

Cranial view of thorax and shoulder girdle (scapula and clavicle, right half) of (a) a quadrupedal terrestrial mammal: deer (*Odocoileus*); (b) a quadrupedal arboreal mammal: monkey (*Macaca*); (c) a bipedal mammal: man (*Homo*); (d) a semi-aquatic mammal: beaver (*Castor*).

Bipedality or normally upright position is the classic explanation for having a round thorax. A barrel-shaped thorax was noted by E.J. Slijper in a goat born without forelimbs, which jumped forward on its hind limbs in a semi-upright position (Ohman). The narrow chest of quadrupeds can best be explained as an adaptation for reducing the

distance between the points of support of the forelimbs, and for allowing the scapula to rotate in the same plane in which the leg swings (see Figure 5.3 (a); and Hildebrand, 1974, p. 494). A broad thorax is seen in arm-hangers like the great apes (inverted funnel), gibbons (barrel-shaped) and spider-monkeys (Hildebrand, figure 22.9). Perhaps these brachiators do not need a latero-laterally flattened chest because they hang with their arms rather than lean upon them. Or the broad thorax could be an adaptation for maintaining an erect posture (as in Slijper's goat), or for being able to reach farther laterally with the arms with more dorsal scapulae (Figure 5.3 (c)).

Most marine mammals have round, barrel-shaped thoraxes (Slijper, 1979). Human fetuses, too, have round thoraxes, but adults have broader thoraxes, as do the common seals (van Nie, 1983) and freshwater mammals like the duck-billed platypus, hippopotamus and beaver (Figure 5.3 (d)).

Arms

The shoulder blades of the gracile Australopithecines resembled those of apes. Lucy had a smaller antero-posterior diameter of the humeral head (as in the wholly arboreal orang-utan), while *A. africanus* was more chimp-like in the larger height of the glenoid fossa (the humeral articulation surface of the scapula) (McHenry, 1986). In both fossils, the glenoid fossa was orientated 15° more upward than in man. The usual explanation for this ape-like orientation is that they were partly arboreal (brachiating), but Morgan (1984) remarked that swimmers and divers also spend part of the time with their arms extended above their heads. Very long arms are especially typical of tree-hangers such as sloths, spider-monkeys and apes, but could also have evolved for other purposes, such as knuckle-walking, collecting (whether fruits or, for example, mussels), swimming, or throwing.

Lucy had a relatively short humerus (Jungers, 1982), and a rather ape-like humerus and ulna (Stern and Susman, 1983). The Kanapoi distal humerus, of 4 million years ago, resembled that of man more closely than did some much later specimens of *A. boisei* (Oxnard, 1975, pp. 96, 121; Feldesman, 1982). The ulna of *boisei* was about 30 per cent longer than that of *H. sapiens*, and morphologically intermediate between man and apes (Feldesman). Also, OH-62, possibly a *H. habilis*, had relatively longer arms than modern man (Johanson *et al.*, 1987). While the Neanderthal humerus was no longer than ours, the forearm of the Kiik Koba child was about 10 per cent longer than in a comparable human baby (Moerman, 1977, p. 130). (This contradicts the hypothesis, quoted earlier, that the Neanderthals' extremities were reduced as an adaptation to withstand cold, according to Allen's rule.)

Several features of the Neanderthal skeleton suggest a hypertrophic upper limb, especially for ab- and adduction and for exo- and endo-rotation (Trinkaus, 1976; Trinkaus and Churchill, 1988; Churchill and Trinkaus, 1988; Ben-Itzhak and Smith, 1988). Swimming certainly is one of the activities in which strong arm muscles would be needed. One remarkable finding is that the right humerus in male Neanderthals was much broader and heavier than the left (Moerman, 1977, pp. 253–7; Ben-Itzhak and Smith; Ben-Itzhak, Smith and Bloom, 1988). This could be explained by arm specialisation in collecting (fruits, mussels), or in making or manipulating tools (pebbles, harpoons, spears), and by vascular anomalies such as patent ductus arteriosus with right-to-left shunt, or preductal coarctatio aortae (see also van Nie and Roede, this volume, p.292).

In OH-62, which is said to belong to *H. habilis*, the shaft of the radius exhibits mediolateral bowing (Johanson *et al.*, 1987). This is also seen in Neanderthal man. It has the effect of broadening the forearm, which may be a paddle-like adaptation, but is usually considered a result of stronger muscularity.

Hands

There is no evidence that any of the fossil hominids ever used their front limbs for walking on their knuckles, as the African apes do. In *A. afarensis* from AL-333, the wrist and hand were strikingly chimp-like, with strongly curved phalanges as in the pygmy chimp, which suggests climbing or arm-hanging, but it lacked the very short thumb and the knuckle-walking features of the African apes (Stern and Susman, 1983; Bush, 1980). The hands of *A. robustus* from Swartkrans showed features of both chimpanzees and humans; like *afarensis*, they lacked the knuckle-walking adaptations and probably also the diminished importance of the thumb, but the phalanges, as in man, were less curved than in apes or *afarensis* (Lewis, 1977; Susman, 1987). *H. habilis* OH-7 did show strongly curved phalanges, very broad at mid-shaft, suggesting powerful grasping potential like the chimpanzee (Napier, 1962; Susman and Stern, 1982). Most fossil hominids had phalanges with even broader shafts than man. Humans have relatively broader hands than other primates, but the Neanderthals had even broader hands with relatively longer little fingers and – in contrast with their long limb bones – even less curved hand bones than humans (Moerman, 1977, pp. 52, 256, 129).

The curved phalanges with broad mid-shafts of *A. afarensis* and *H. habilis* are usually seen as a hanging or climbing adaptation, and certainly this palmar concavity is different from the ulnar deviation of the phalanges seen in sea-turtles, penguins, sea-lions, or dolphins (Hildebrand, 1974, figure 23–14). The broad Neanderthal hands could

be explained by strong muscularity (grip); their cup form, for drinking or digging up tubers (van Nie, personal communication); or flipper-like adaptations: broad hands with broad phalanges are seen in all aquatic mammals.

Pelvic girdle

Abitbol (1987) found that the lumbo-sacral angle in Lucy (about 30°) was greater than in dogs (9°) and human new-born babies (20°), only slightly greater than in macaques and spider-monkeys (27°), but less than in chimps (44°), gibbons (60°) and man (77°). A wide lumbo-sacral angle was thought to have evolved to accommodate the large foetal head at the time of delivery, but it is more likely to correlate with habitually extended thighs (Abitbol, 1987), which are found in striding mammals (humans, and gibbons walking on branches), and in all swimming mammals. Morgan (1982, pp. 58–61) regarded aquaticness as a preadaptation for erect stance and locomotion.

The pelves of Lucy and *A. africanus* were very similar, and different from both apes and man (Stern and Susman, 1983). The bi-acetabular diameter was relatively much broader than in man and apes (Berge and Kazmierczak, 1986). The auricular articulation (with the sacrum) and the acetabular (with the femoral head), as in apes, were relatively much smaller than in humans (Oxnard, 1975). The lateral enlargement of the iliac blades was more ape-like, but the ilia, as in man, were much lower than in apes and monkeys. Both apes and monkeys have longer iliac blades than *Australopithecus* and *Homo*, but otherwise the apes' pelves are distinct from the monkeys' (Steudel, 1978).

Suggested explanations for these features of gracile Australopithecines' pelves have included: a bipedal gait different from and less efficient than our own, but with a better abductor mechanism for the thigh; semi-arboreality; obstetric factors; and the requirements of visceral accommodation and support during erect locomotion (Berge and Kazmierczak, 1986; Tague and Lovejoy, 1986). Some of the factors suggesting that bipedality was not well developed in the early Australopithecines are perhaps the small articulation surfaces and long and more horizontal femoral necks, which would make for less efficient weight-bearing, and the larger bi-acetabular diameter which would have made it more difficult to retain balance (Figure 5.4). In a semi-aquatic context, the broad pelvis could be compared with the broad trunk of aquatic mammals, especially freshwater species, and the small iliac height is comparable with the pelvic reduction characteristic of all aquatic mammals.

The pelvis of the adolescent *H. erectus* WT-15000, as well as his proximal femur, retained some Australopithecine-like aspects, but the bi-

acetabular diameter was much narrower (Johanson *et al.*, 1987; Brown *et al.*, 1985). The femoral neck was orientated much more horizontally (with a neck-shaft angle of only 110°) than in robust Australopithecines ($115\text{--}120^\circ$), Lucy (123°) or man ($121\text{--}133^\circ$), and was much longer – in accordance with the strong iliac flare and small bi-acetabular diameter – than in man and certainly apes, and relatively as long as in robust Australopithecines; the femoral head was as large as in man, and much larger than in Australopithecines and apes (Brown *et al.*; Stern and Susman, 1983).

The meaning of the long and horizontal femoral neck in fossil hominids is not clear (Tompkins, Heller and Franciscus, 1988), but it is difficult to explain in an arboreal or bipedal context, although the narrower bi-acetabular diameter and larger femoral head of *H. erectus* could suggest a more frequent bipedality than in gracile Australopithecines (see Figures 5.4 (a) and 5.4 (b)). More horizontal femoral necks and flared ilia are also seen in the Neanderthals. Their pelves had slender, elongated, and very ventrally reaching superior pubic rami, clearly different from modern man (Rak and Arensburg, 1987). The broad sacrum (Ivanhoe, 1985), iliac flaring and long and ventrally reaching superior pubic rami are evidence of a larger trunk diameter than in man. Obstetric adaptations to the larger head of the Neanderthal foetus are unlikely to have been the cause (Rak and Arensburg).

Legs

The early hominids up to and including OH-62 had much shorter legs than later *Homo* (Figure 5.4). The relative length of the australopithecine leg resembled that of the orang-utan, the most arboreal of the great apes. But, as opposed to the orang, their legs are more reduced at the knees and still more at the ankles, rather than at the hip end (Oxnard, 1975). This distal leg reduction could be compared with that of aquatic mammals. WT-15000, the sub-adult *H. erectus*, had a long femur, slightly longer than in a present-day twelve-year-old boy, but a relatively shorter tibia (Brown *et al.*, 1985). Neanderthals also had somewhat shorter tibiae (Moerman, 1977, pp. 53, 253). The shortening is sometimes said to be an adaptation to cold, but this does not fit with considerations of time and space (Rak, 1986).

In *H. erectus* and *H. neanderthalensis* not only was the femur long, but also its shaft showed an anterior convexity, and in *erectus* it was compressed dorso-ventrally as compared with these features in modern man (Geissmann, 1986; Moerman, pp. 34, 61). All this could be correlated, for example, with different muscular arrangements in the thighs, with a different pattern of weight transmission in the legs (Kennedy, 1985), or with the broader pelves. It would also be consonant

with paddle-like adaptations, since femoral broadening would improve the propulsive force of thigh-stretching in swimming. Dorso-ventrally flattened femora are characteristic of pinnipeds (Wyss, 1988).

The cortex of femora and tibiae of *neanderthalensis*, and certainly of *erectus*, is much thicker than in man, Australopithecines and apes. As Kennedy commented:

the presence of such thickened bone is extraordinary; very few animals show similar generalised thickened bone. Manatees and dugongs show not merely thickened bone and medullary stenosis, but complete loss of a medullary canal . . . The adaptive advantage of such heavy, dense bone to the sirenians is apparently to counterbalance the buoyancy of their large lung volume while submerged. Amedullary bones, presumably reflecting a similar selective pressure, are also found in certain Mesozoic marine reptiles and in living humpback whales.

Sea-cows 'graze' lying or 'walking' with the front limbs on the sea bottom. Tertiary freshwater sirenians had much less massive bones than marine ones (Sickenberg, 1934, pp. 173-4). Surface-feeding ducks have a density of only 0.6; most fish are about as dense as the water that surrounds them; but bottom-dwellers are much denser (Hildebrand, 1974, pp. 584-9; Wilson, 1979, pp. 793-5; McFarland *et al.*, 1979, pp. 167-8, 212-16, 613-17).

It is, of course, impossible to know the body density of the fossil hominids. Man has a density of 1.02-1.09, partly depending on whether the lungs are inflated (Patrick, and Ghesquiere and Bunkens, this volume, chapters 14 and 16, respectively). This is slightly lower than the 1.07 of sheep, dogs and cats (Wind, 1976). Aquatic mammals have very thick subcutaneous fat layers - up to half of the body weight in slow-diving species - and smaller lung volumes, especially in deep-diving species. Humans standing in water of 25°C have their lungs compressed by almost half a litre (Choukroun, Kays and Varène, 1989), and long-distance swimmers have much more subcutaneous fat than normal (Pugh and Edholm, 1955). So we may assume that our semi-aquatic ancestors - with much more fat than us, and somewhat smaller lungs - would have had less density than modern man, other things being equal. This would make diving more difficult:

Perhaps in *H. erectus* and *H. neanderthalensis* the dense bones were adaptations to the density of (salt) water to compensate for the thick fat layers. The high density could anchor the body against water currents; in diving mammals that do not go very deep, the time below is longer than that between successive dives. The heavy bones would also enhance the descent rate; human divers frequently use counterweights during descent,

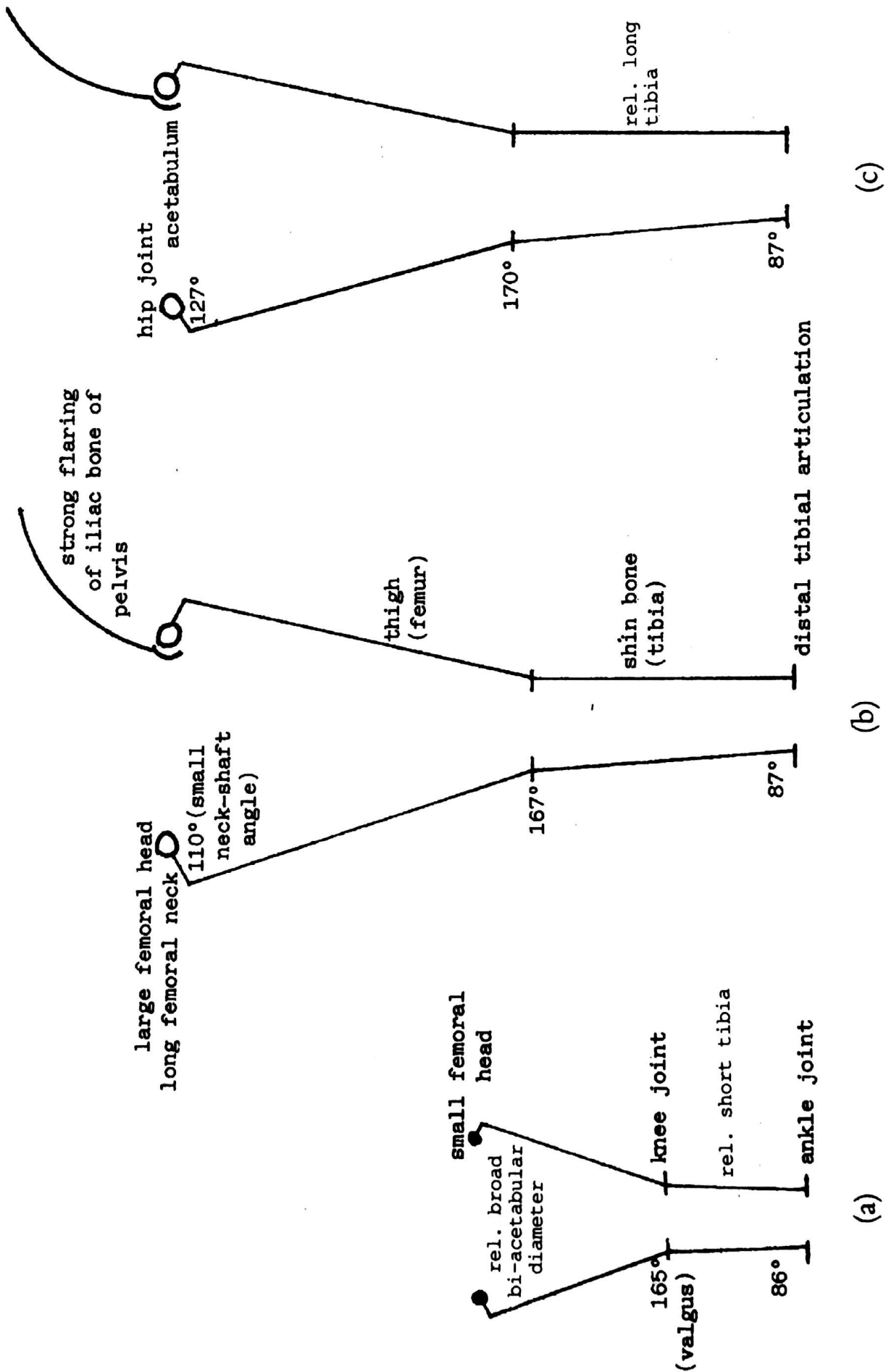


Figure 5.4 Schematic anterior view of hominid lower limbs (broadly to scale).

(a) 'Lucy', AL-288-1, a small *A. afarensis* c.3 mya; (b) WT-15000, a sub-adult *H. erectus*, c.1.6 mya; (c) modern *H. s. sapiens*.

whereas, during ascent, too rapid decompression can cause accidents (Hong, 1988). The massive skull, and more specifically the thick occipital part of it, could have stabilised the head while floating on the back (Figure 5.2 (c)). The heavy leg bones, and in particular the dense distal femora as in *H. erectus* from Trinil, suggest kneeling on the bottom while collecting food. The heavier right humerus of male Neanderthals could suggest collecting with the right arm.

Homo erectus fossils from inland sites (Zhoukoudian, located near a big river and possibly a lake) have denser femora than island specimens from Trinil. This could perhaps be explained by thicker fat layers (more weight on land and less density in water) in colder climates, by sexual dimorphism (Trinil-I was probably a woman), and by the immediately preceding evolution of these groups (phylogenetic inertia). For other – not necessarily conflicting – speculations for medullary stenosis, see Table 5.14.

Table 5.14 Possible explanations for medullary stenosis of femur and tibia in *Homo erectus* (after Kennedy, 1985, and references therein)

-
- a greater need for resisting torsional or bending stresses
 - fatigue stress
 - more weight, e.g., a broader trunk or more muscle or fat
 - certain growth disturbances
 - hypothyroidism (with lower basal metabolism and body temperature, which would allow longer dives)
 - vitamin A, vitamin D, parahormone and calcium anomalies, e.g., by cyclic consumption of fruits instead of meat
 - a reservoir for calcium, phosphorus or other minerals
-

The Neanderthals displayed very large patellae. This is in accordance with the robustness and the large epiphyses of most of their long bones (Moerman, 1977, pp. 52, 253). The human knee is unique among living primates in that only *H. sapiens* has a posterior insertion for the lateral meniscus on the tibial plateau. *A. afarensis* had no posterior insertion, but early *Homo* ER-1481 had two insertions like us (Tardieu, 1986). This means that the knee of *A. afarensis* was less stable than that of *Homo*.

Femur and tibia form an angle of about 165° in gracile Australopithecines and 3–4-year-old human children (valgus knee); 170° in the large Hadar specimens (AL-333) and in adult humans; 175° in orangutans and spider-monkeys; and 180° in other apes and monkeys (Stern and Susman, 1983; McHenry, 1986). J. Prost (in Stern and Susman) suggested that the hominid valgus knee could have evolved to meet the

demands of climbing, since among non-human primates the greatest degree of valgus is found in oranges and spider-monkeys. But more often it is believed to be a sign of bipedality, because it places the foot more directly under the centre of gravity of the body during the phase of single-limb support in walking (Stern and Susman, 1983). Yet a valgus knee is likely to be less stable than a straight one. In an aquatic milieu, centrally placed distal legs (Figure 5.4) would be even more indispensable, as we can see in the streamlined hind limbs of marine mammals.

The distal tibial articulation faces infero-laterally in apes, and makes an angle of about 75° with the tibial shaft in chimps. It faces more inferiorly in man and fossil hominids for which information is available ($85-90^\circ$). This suggests that *A. afarensis* had a more perpendicular tibia than apes, and it is thought to be an adaptation for bipedality (Latimer, Ohman and Lovejoy, 1987). Equally likely, it is simply correlated with the valgus knee (Figure 5.4).

Among living primates only man had a highly positive (that is, external) tibial torsion (toeing-off), but Lucy, like many human children still, had a pronounced negative tibial torsion (Sarmiento, 1987). Toeing-in could be an advantage for better grasping trees or branches. Toeing-out, in contrast, is typical of sea-lions (Morgan, 1982, figure 9). If the central position of the hominid shin bones was an adaptation for bipedality, it may be asked why we developed toeing-out instead of either toeing-in (which was probably the ancestral condition) or, alternatively, the absence of torsion (which would have been more effective for terrestrial locomotion).

Feet

The bipedal footprints discovered at two Laetoli sites, of about 3.5 million years ago, provide one landmark for dating the evolution of bipedalism. Of the two sets of prints, those at site A prove controversial. White and Suwa (1987) called them 'enigmatic', and Tuttle (1985) believed they could have been made by a bear. It is more probable, however, as affirmed by Leakey and Hay (1979), that they must be attributed to a hominid. The prints are relatively very broad and the stride is very short, suggesting that the gait could perhaps best be compared with that of a penguin on land (Morgan, 1982, p. 61). The footprints at site G bear a much clearer resemblance to human footprints: they are relatively broader than those of modern man, and the stride is shorter. These features, together with the long and adducted first metatarsals (mid-foot bones) but 'oblique alignment of the ray I phalangeal impressions' and 'anterior encroachment of the lateral toes' (White and Suwa) would be compatible with the hypothesis of flipper-like adaptations.

Fossilised foot bones of *A. afarensis* from the same period yielded other details about the anatomy. An examination of three heel bones from AL-333 established that they were nearer to apes in size and perhaps morphology (Stern and Susman, 1983; Deloison, 1985; but see Latimer and Lovejoy, 1989). The virtual absence of the human lateral process (which enlarges and stabilises the supporting surface of the heel) led Deloison to conclude that '*A. afarensis* could not rest its foot on the ground and walk as modern man does'. Aspects of heel and mid-foot are suggestive of a plantigrade foot with strong plantar ligaments (Stern and Susman); the phalanges were 'strikingly ape-like', slender but with mid-phalangeal thickening, highly curved and much longer than in man (Stern and Susman). As in the case of the curved hand bones, this is usually regarded as a climbing adaptation. Another view is that the curved toes served partly to keep a foothold on rough, stony or muddy ground (Latimer *et al.*, 1982). The foot of *afarensis*, plantigrade and with somewhat less developed heel and longer forefoot than in modern man, also bears remarkable resemblances to that of the sea-lion (Figure 5.5).

More recently, the OH-8 talus, possibly from a *H. habilis*, was much less human-like than that of *H. erectus* ER-813 of a similar period (Wood, 1974). The OH-8 foot bears several close resemblances to the chimpanzee, but with human-like exceptions such as a limited rotation of the calcaneo-cuboid joint, a less divergent first metatarsal, and a fifth metatarsal which was even more robust than in modern man (Lewis, 1980; Day and Napier, 1964, figure 2). The impression of a flat foot is reinforced by the OH-10 terminal first toe phalanx of about the same time, which was relatively much broader than that of man, and certainly than that of a chimpanzee (Oxnard, 1975, figure 62). Also, the Neanderthals had broader feet than most people have today (Moerman, 1977, pp. 257, 129, 64).

Long, flat, broad feet with robust first and last digital rays are typical of wading, swimming and diving birds and mammals (Figure 5.5), but terrestrial and arboreal animals have narrower feet with the central digits being those most emphasised (Wyss, 1988). Indeed, the rather human-like (though still shorter-strided) Koobi Fora footprints, possibly from a *H. erectus* of about 1.6 million years ago, appear to have been made in water less than ten centimetres deep (Behrensmeyer and Laporte, 1981). They confirm that, as in modern man, the common integumentary covering of the foot encloses a much higher percentage of the toe bones than in any extant primate. It extends in humans to approximately the mid-point of the basal phalanx, and F. Wood Jones once referred to it (albeit in quotation marks) as 'webbing' (Morgan, personal communication).

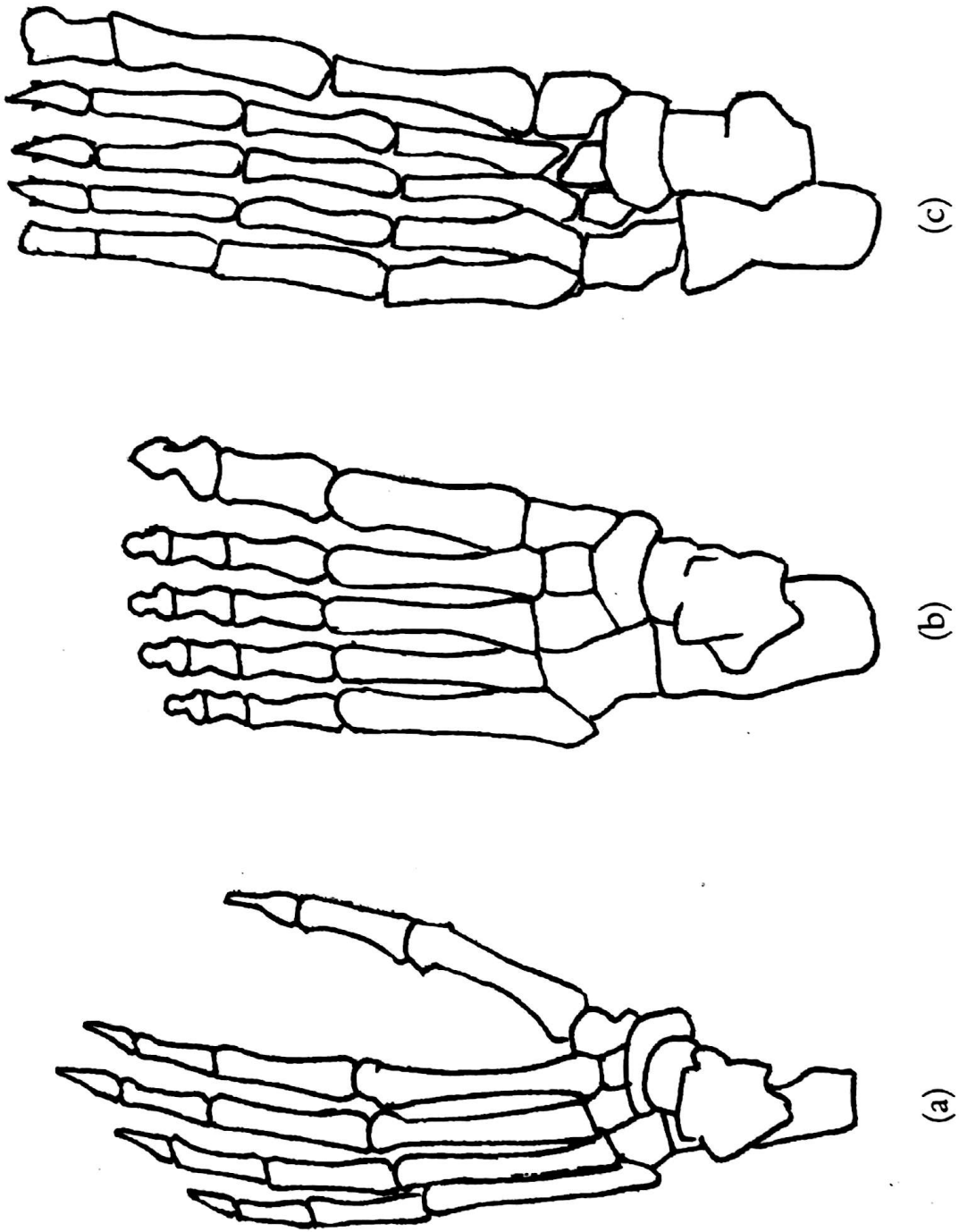


Figure 5.5 Comparison of foot skeletons (after Campbell, 1974; Wyss, 1988).
(a) chimpanzee (*Pan troglodytes*); (b) man (*Homo sapiens*); (c) Steller's sea-lion (*Eumetopias jubatus*).

DISCUSSION

The morphological, physiological and molecular study of *living* animals is the richest source of evidence about our evolutionary history. Hitherto, much of the discussion of the AAT has been based on morphological and physiological rather than palaeontological data. But the fossil hominid record, although its findings are meagre prior to 4 million years ago (Pickford, 1986, p. 125), is well documented compared with that of many other mammals. A fresh look at the evidence suggests some possible new interpretations.

Australopithecine ancestors for all African hominoids?

From the researches of molecular biologists a few conclusions may be drawn (see also Gribbin and Chérfas, 1983, pp. 180–5; Hasegawa, Kishino and Yano, 1985, 1987; Diamond, 1988):

- (1) Humans and chimpanzees are more closely related than either one of them is to the gorilla.
- (2) The splitting time between the lineage leading to the gorilla and that leading to man and chimpanzee may be situated between 10 to 6 million years ago.
- (3) That between man and chimpanzees may be situated between 8 and 4 million years ago (Figure 5.1 (a)).

Palaeontologists sometimes contest this chronology, and retain their conviction that the man/ape split occurred earlier. But when molecular and palaeontological data appear to be in conflict, the molecular evidence is the more reliable. Morphological characters (*a fortiori* of fragmentary fossil bones) are too much subject to the pitfalls of parallel and convergent evolution, as the *Ramapithecus* controversy of the 1970s illustrated.

One widespread assumption is that *Australopithecus* was closer to man than to the African apes because it has a smaller anterior dentition, thicker molar enamel and shorter iliac bones than chimps and gorillas, a more human orientation of the distal femoral and tibial articulations, and a univertebral articulation of the first rib. (The thicker molar enamel is no real argument, since the ancestors of the African apes are known to have had thick enamel (Martin, 1987).)

Other australopithecine features, however, more closely resemble *Pan* or *Gorilla*. For the cranial features, see Table 5.15. The human-like features of australopithecine limb bones also tend to have been exaggerated in the literature (Lewis, personal communication). Understandably, palaeontologists first notice resemblances with man, but more comprehensive comparisons afterwards also reveal the ape-like

features. Most Hadar postcranials are different from both man and apes, but scapula, humerus, ulna, knee, hand and foot bones are more ape-like (Stern and Susman, 1983). The shoulder blade of *A. africanus* is rather chimp-like (Vrba, 1979). Arm and foot bones of robust Australopithecines are intermediate morphologically, with *A. robustus* being closer to man than *A. boisei* in this respect (Lewis, 1977, 1980; Feldesman, 1982; Susman, 1987). In *A. afarensis*, the ilia were short as in man, which is the chief reason why Lucy is thought to have been bipedal. But though they were short, they were orientated like an ape's (Stern and Susman, figure 6).

Table 5.15 Some cranial resemblances between apes and Australopithecines

-
- Brain size and sulcal pattern of the australopithecine endocasts appear to be ape- rather than human-like (Falk, 1985)
 - The reconstructed skull from Hadar (mostly AL-333) is reminiscent of a female gorilla (Johanson and Edey, 1981, p. 351); that of *A. africanus*, of a female pygmy chimp (Zihlman *et al.*, 1978); already in 1925, A. Hrdlicka wrote that the Taung skull approached that of chimpanzees (Howells, 1985; see also Bromage, 1985)
 - *A. boisei* WT-17000 had extremely convex infero-lateral margins of the orbits, such as found in some gorillas (Walker *et al.*, 1986)
 - The nasal bone arrangement in some chimpanzees resembles that of robust Australopithecines (Eckhardt, 1987)
 - The incus (ear ossicle) of *A. robustus* resembles *Pan* and perhaps *Homo* more than *Gorilla* (Rak and Clarke, 1979)
 - Intra-palatal extension of the maxillary sinus has only been reported in Taung, robust Australopithecines and chimps (see Table 5.10)
 - The australopithecine dentition was closer to apes in morphology (*A. afarensis*, Johanson and White, 1979; Johanson and Edey, 1981), molar microwear (Poirier, 1987, pp. 126, 179), enamel growth rate (Beynon and Wood, 1987), and development pattern (Conroy and Vannier, 1987, 1988; Bromage and Dean, 1985; Smith, 1987)

In sum, the impression is that most E. African Australopithecines (the larger specimens of *A. afarensis* and all *A. boisei*) were closer to the *Gorilla* lineage, and the South African *A. africanus* and *A. robustus* to the *Homo* and/or *Pan* lineages. This impression is strengthened by the postcranial evidence.

The question at issue is whether Lucy – or whatever fossil hominid – was evolving away from or towards an ape-like condition (Verhaegen, 1990). In the palaeo-anthropological literature, 'primitive' is sometimes used instead of 'ape-like', 'chimp-like' or 'gorilla-like' and 'advanced' instead of 'human-like'. It is not impossible that the African apes'

ancestors were *more* bipedal than their descendants today (Gribbin and Cherfas, 1983, p. 125; Hasegawa, Kishino and Yano, 1985; Edelstein, 1987). Chimpanzees often walk bipedally on muddy ground (Nishida, 1980). The pygmy chimpanzee frequently practises ventro-ventral copulation, often believed to occur in *H. sapiens* as a consequence of bipedalism. If this concept is accurate, the African apes' pelvis could have evolved from a Lucy-like pelvis by re-elongation of the iliac blades. Two possibly relevant facts derive from foetal development in the apes. One is that chimpanzee embryos have very human-like feet, with very long and adducted first digital rays (Coon, 1954). The other was recorded by Huxley:

During most of the latter half of the prenatal life the human embryo, like the ape's, is covered all over with a coat of short, downy hair; so is an ape embryo of corresponding age. Before birth both ape and man shed this short hair and develop long hair on the head while remaining almost hairless on the body. Man retains this condition throughout life, while the newborn ape soon acquires its thick permanent garment. (Wells, Huxley and Wells, 1929.)

Taken in conjunction, these facts suggest a new scenario. It is possible that all African hominoids descended from an ancestor partly arboreal and partly aquatic, and bipedal in shallow water and on land. While the line leading to *Homo* became more aquatic (littoral), the *Pan* and the *Gorilla* lineages – probably independently – returned to a more arboreal existence and redeveloped some simian features suitable for that habitat, such as longer ilia, larger anterior teeth and thinner molar enamel, perhaps opposable big toes and even a slightly smaller brain.

African hominoids have limited hand and finger dorsiflexion, but increased supinatory motility of the forearm as compared with monkeys. These features are also found in seals and other marine mammals. If they were an inheritance of their semi-aquatic past, they could have hindered their becoming branch-runners again, like monkeys, and could have promoted their branch-hanging habits and very long arms. Indeed, it is only *after* birth – late in ontogeny – that an ape's arms become disproportionately long. Lucy did not show very long arms: its humerus was even shorter than in a female human pygmy, and much shorter than in a female pygmy chimpanzee. But one or two million years later, *A. boisei* displayed arms of gorilla length (Omo L-40-19 ulna). The branch-hanging adaptations – very long arms with limited hand dorsiflexion and hooked hands – could then become a preadaptation for terrestrial knuckle-walking in the African apes. (Also, some New World monkeys walk on the ground with 'tucked-under' phalanges (Zwell and Conroy,

1973).) To be sure, it is not suggested here that gorillas and common chimpanzees have descended from *robust* Australopithecines, although that possibility may not be fully excluded.

That molecular biology forces us to accept several parallel adaptations in the chimp and the gorilla lineages is only apparently a problem, since similar forms tend to develop similar adaptations in response to similar environmental or climatic changes; and parallel, convergent, reverse and even fluctuating evolution of morphological characters is extremely widespread, and often even more remarkable (Darwin, 1903, p. 171; White and Harris, 1977; Sheldon, 1988; Seger, 1987) than a parallel evolution of knuckle-walking in semi-erect, long-armed, hook-handed apes with limited hand dorsiflexion.

***A. afarensis*: some *Nasalis*-like locomotion features**

The clearest evidence for australopithecine bipedality is that afforded by the Laetoli site A and G footprints. It is not known whether one of these sets of prints – and if so, which one – was made by a hominid of the same species as Lucy. And although it is evident that some of the early hominids walked on two legs for at least part of the time (Latimer and Lovejoy, 1989), it is not clear from the fossilised bones how well they were adapted to this mode of locomotion. Resemblances with man in iliac reduction, valgus knee, perpendicular distal tibial articulation and adducted first metatarsal bone are thought to represent adaptations for a bipedal stance and gait; but other explanations are possible, and the resemblance between Lucy and ourselves in respect of pelvis, knee and foot is far from complete.

The most obvious differences are the ape-like orientation of Lucy's ilia, the small femoral head (but long neck), the absence of a posterior insertion for the lateral meniscus, the short legs, and the curved toes. If these hominids were bipedal on the ground, their bipedality was different from ours. Susman (1987) states: 'The conception of the earliest hominids as savannah-dwelling, terrestrial bipeds does not account for the small size, relatively short lower limb, mobile ankle, long forefoot, curved toes, and ape-like toe-joints of *A. afarensis*'. The inference is that the early Australopithecines did not spend all their time on the ground, but had a habitat only partly terrestrial. Susman maintains that the non-terrestrial aspect of Lucy's environment was arboreal, and the evidence for (semi-)arboreality in the Hadar hominids is strong: orang-like features of the shoulder blades, with upward orientation of the glenoid fossae, curved hand and foot bones, negative tibial torsion, mobile ankle and knee, relatively short legs, monkey-like lumbo-sacral angle.

Another possible combination is terrestrial/aquatic. There are several indications that at least the early Australopithecines were semi-aquatic: distally reduced legs, with centrally placed tibiae, long and adducted big

toes, short pelvis, broad trunk, loose rib articulation, and perhaps extensive skull pneumatization and guttered nasal aperture. The mobile knees and ankles would be compatible with either climbing or swimming. If the early hominids were semi-aquatic, there is insufficient evidence to establish whether they originally lived in fresh or salt water, and whether they dived or only swam on the surface. The strong pneumatization suggests frequent floating or swimming on the water surface, especially in fresh or weakly saline water habitats (Pickford, 1975; Bishop *et al.*, 1975; Bonnefille, 1976; Brain, 1981, p. 189).

It would be a mistake to assume that the arboreal and aquatic explanations are mutually exclusive. Perhaps the best available model for Lucy's modes of locomotion is to be found in the proboscis monkey, *Nasalis larvatus*. This monkey, which lives in the mangroves of Borneo, swims and dives very well, walks bipedally in shallow waters across the water courses of the estuary and on muddy ground, and climbs and even hangs from the branches with its arms (Ellis, 1986, 1991; Napier and Napier, 1967, p. 232). It has a protruding nose, a relative body enlargement and forelimb lengthening compared with other colobine monkeys. Detailed correlation is not to be expected, since taxonomically *Nasalis* belongs to the monkeys and Lucy to the hominoids; but the ways in which they diverge from their respective archetypes (see, e.g., figure 2 of Feldesman, 1982) show points of convergence which could well indicate comparable habitat and locomotor behaviour.

One million years later, the robust Australopithecines, like the giant panda, showed extremely broad and thick-enamelled cheek teeth. If they ate bamboo at the riverside, they often swam (but seldom dived) and waded, climbed and sat with erect trunks.

Fossil *Homo*: probably semi-aquatic

Fossil *Homo* shows much stronger signs of aquatic adaptation than *A. afarensis*. Evidence of this from the fossil record includes body and brain enlargement, Broca's area in the brain, ear exostoses, possible platycephaly, short iliac bone, flat femur, broad feet and hands with relatively long and robust first and fifth digital rays, and the use of pebble stone tools (like sea-otters). In the case of *H. erectus*, arguments for a salt-water habitat are the dense bones, and possibly his 'fast' dispersal to South East Asia and the East Indies (in an overland journey through the forests a terrestrial/arboreal primate would have encountered enough geographical obstacles to slow down or even stop this dispersal, as compared with a migration along the Indian Ocean). Presumably, different lineages from an ancestral coast-dwelling stock followed the rivers inland. *H. erectus* shows no clear adaptations for an arboreal habitat; although his tibiae were somewhat shorter than ours, his bipedal gait on the ground must have resembled our own.

Some Neanderthals are discovered near sea coasts, but most are found in river valleys. They share with *H. erectus* the large body and (even larger) brain, the platycephaly and the (slightly less) massive bones. They may have been descended from some *erectus* populations that moved up the rivers, since the less dense bones and the strongly enlarged frontal sinuses suggest a freshwater milieu. The Neanderthal broad arms and feet, and especially the ear exostoses, clearly indicate frequent diving (in cold water). The very protruding mid-face and nostrils and the large frontal sinuses suggest frequent floating on the back: the anterior air-filled sinuses and the posterior dense skull would have stabilised the head in the water with the nose upwards – the standard at-rest position adopted by the sea-otter.

The best available model for the kind of life led by *H. erectus* and *H. neanderthalensis* must be the still existing human communities where one or more sexes dive for seaweeds or shellfish (Hong, 1988; Kennedy, 1986; see also Verhaegen, 1991).

CONCLUSION

Palaeontological data do not rule out the possibility of semi-aquatic ancestors. There is some evidence for aquatic features in the Australopithecines, and they may not have been fully adapted for bipedality; there are indications that the gracile Australopithecines were at least partly arboreal.

There is a stronger case for assuming aquatic adaptations in fossil *Homo*. *H. erectus* had a very dense skeleton, which is found otherwise only in littoral bottom-feeders. The most unequivocal piece of evidence concerns Neanderthal man. Ear-canal exostoses are virtually pathognostic of frequent diving in colder water. Their abundance in the Neanderthals establishes beyond reasonable doubt the semi-aquatic nature of these people.

ACKNOWLEDGEMENTS

This survey has only been possible thanks to the numerous detailed anatomical descriptions and comparisons of fossil hominids by so many palaeontologists. I have to thank M. Pickford, J. de Vos, O.J. Lewis, S.J. Edelstein, S.C. Cunnane, M. Hasegawa, J. Wind, D. Ellis, W.M.A. De Smet, and especially C.J. van Nie, J.M. Patrick, D. Falk, Machteld Roede and Elaine Morgan for invaluable discussions, corrections and comments, and Morien Morgan for typing the manuscript.

REFERENCES

- Abitbol, M.M., 1987, Evolution of the lumbosacral angle. *American Journal of Physical Anthropology*, **72**, 361–72.
- Armstrong, E., 1983, Relative brain size and metabolism in mammals. *Science*, **220**, 1302–4.

- Behrensmeyer, A.K. and Laporte, L.F., 1981, Footprints of a Pleistocene hominid in Northern Kenya. *Nature*, **289**, 167-9.
- Ben-Itzhak, S. and Smith P., 1988, A radiographic study of fossil and recent humeri. *American Journal of Physical Anthropology*, **75**, 186-7.
- Ben-Itzhak, S., Smith, P. and Bloom, R.A., 1988, Radiographic study of the humerus in Neanderthals and *Homo sapiens sapiens*. *American Journal of Physical Anthropology*, **77**, 231-42.
- Berge, C. and Kazmierczak, J.B., 1986, Effects of size and locomotor adaptations to the hominid pelvis: evaluation of australopithecine bipedality with a new multivariate method. *Folia Primatologica*, **46**, 185-204.
- Beynon, A.D. and Wood, B.A., 1987, Patterns and rates of enamel growth in the molar teeth of early hominids. *Nature*, **326**, 493-6.
- Bishop, W. W., Pickford, M. and Hill, A., 1975, New evidence regarding the Quaternary geology, archaeology and hominids of Chesowanja, Kenya. *Nature*, **258**, 204-8.
- Blaney, S.P.A., 1986, An allometric study of the frontal sinus in *Gorilla*, *Pan* and *Pongo*. *Folia Primatologica*, **47**, 81-96.
- Blanton, P.L. and Biggs, N.L., 1968, Eighteen hundred years of controversy: the paranasal sinus. *American Journal of Anatomy*, **124**, 135-48.
- Bonnefille, R., 1976, Implications of pollen assemblage from the Koobi Fora Formation, East Rudolf, Kenya. *Nature*, **264**, 4030-7.
- Brain, C.K., 1981, *The Hunters or the Hunted?* (Chicago: University of Chicago Press).
- Bromage, T., 1985, Taung facial remodelling: a growth and development study. In *Hominid Evolution*, ed. P.V. Tobias (New York: Liss), 239-45.
- Bromage, T.G. and Dean, M.C., 1985, Re-evaluation of the age at death of immature fossil hominids. *Nature*, **317**, 525-7.
- Brown, F.H., Harris, J.M., Leakey, R.E. and Walker, A., 1985, Early *Homo erectus* skeleton from West Turkana, Kenya. *Nature*, **316**, 788-92.
- Bush, E., 1980, The thumb of *Australopithecus afarensis*. *American Journal of Physical Anthropology*, **52**, 210.
- Cabanac, M., 1986, Keeping a cool head. *News in Physiological Sciences*, **1**, 41-4.
- Calvin, W., 1983, A stone's throw and its launch window. *Journal of Theoretical Biology*, **104**, 121-35.
- Campbell, B.G., 1974, *Human Evolution* (Chicago: Aldine), 2nd ed.
- Carney, J., Hill, A., Miller, J.A. and Walker, A., 1971, Late Australopithecine from Baringo District, Kenya. *Nature*, **230**, 509-14.
- Choukroun, M. L., Kays, C. and Varène, P., 1989, Effects of temperature on pulmonary volumes in immersed human subjects. *Respiration Physiology*, **76**, 255-66.
- Churchill, S.E. and Trinkaus, E., 1988, Neanderthal scapular glenoid fossa morphology. *American Journal of Physical Anthropology*, **75**, 196.
- Clark, J.D., Asfaw, B., Assefa, G., Harris, J.W.K., Kurashina, H., Walter, R.C., White, T.D. and Williams, M.A.J., 1984, Palaeoanthropological discoveries in the Middle Awash Valley, Ethiopia. *Nature*, **307**, 423-8.
- Clutton-Brock, T.H. and Harvey, P.H., 1977, Primate ecology and social organization. *Journal of Zoology, London*, **183**, 1-39.
- Conroy, G.C., Jolly, C.J., Cramer, D. and Kalb, J.E., 1978, Newly discovered fossil hominid skull from the Afar depression, Ethiopia. *Nature*, **276**, 67-70.
- Conroy, G.C. and Vannier, M.W., 1987, Dental development of the Taung skull from computerized tomography. *Nature*, **392**, 625-7.
- Conroy, G.C. and Vannier, M.W., 1988, The nature of Taung dental maturation continued. *Nature*, **333**, 808.
- Coon, C.S., 1954, *The Story of Man* (New York: Knopf).
- Coon, C.S., 1962, *The Origin of Races* (New York: Knopf).

- Corruccini, R.S. and Ciochon, R.L., 1979, Primate facial allometry and interpretation of australopithecine variation. *Nature*, **281**, 62–4.
- Darwin, C., 1903, *On the Origin of Species by Means of Natural Selection* (London: Watts).
- Day, M.H., Leakey, R.E.F., Walker, A.C. and Wood, B.A., 1974, New hominids from East Rudolf, Kenya. *American Journal of Physical Anthropology*, **42**, 461–76.
- Day, M.H. and Napier, J.R., 1964, Fossil foot bones. *Nature*, **201**, 969–70.
- Deloison, Y., 1985, Comparative study of calcanei of primates and *Pan–Australopithecus–Homo* relationship. In *Hominid Evolution*, ed. P.V. Tobias (New York: Liss), 143–7.
- Delson, E., 1987, Evolution of palaeobiology of robust *Australopithecus*. *Nature*, **327**, 654–5.
- Diamond, J.M., 1988, Relationships of humans to chimps and gorillas. *Nature*, **334**, 656.
- Eckhardt, R.B., 1987, Hominid nasal region polymorphism and its phylogenetic significance. *Nature*, **328**, 333–5.
- Eckhardt, R.B., 1988, Primate phylogenetic patterns preserve persistent polymorphism. *American Journal of Physical Anthropology*, **75**, 207.
- Edelstein, S.J., 1987, An alternative paradigm for hominoid evolution. *Human Evolution*, **2**, 169–74.
- Ellis, D., 1986, Proboscis monkey and aquatic theory. *Sarawak Museum Journal*, **XXXVI** new series, **57**, 251–62.
- Ellis D., 1991, Is an aquatic ape viable in terms of marine ecology and primate behaviour? (This volume, chapter 4.)
- Falk, D., 1983, Cerebral cortices of East African early hominids. *Science*, **221**, 1072–5.
- Falk, D., 1985, Hadar AL 162–28 endocast as evidence that brain enlargement preceded cortical reorganization in hominid evolution. *Nature*, **313**, 45–7.
- Falk, D., 1986, Evolution of cranial blood drainage in hominids: enlarged occipital/marginal sinuses and emissary foramina. *American Journal of Physical Anthropology*, **70**, 311–24.
- Falk, D., 1987, Hominid paleoneurology. *Annual Review of Anthropology*, **16**, 13–30.
- Falk, D., and Conroy, G.C., 1983, The cranial venous system in *Australopithecus afarensis*. *Nature*, **306**, 779–81.
- Feldesman, M.B., 1982, Morphometric analysis of the distal humerus of some Cenozoic catarrhines: the late divergence hypothesis revisited. *American Journal of Physical Anthropology*, **59**, 73–95.
- Ferguson, W.W., 1987a, Revision of the subspecies of *Australopithecus africanus* (Primates: Hominidae), including a new subspecies from the late Pliocene of Ethiopia. *Primates*, **28**, 258–65.
- Ferguson, W.W., 1987b, Reconstruction and re-evaluation of the skull of *Homo antiquus* (Hominoidea: Homininae) from Hadar. *Primates*, **28**, 377–91.
- Fialkowski, K.R., 1986, A mechanism for the origin of the human brain: a hypothesis. *Current Anthropology*, **27**, 288–90.
- Folkow, L.P. and Blix, A.S., 1987, Nasal heat and water exchange in gray seals. *American Journal of Physiology*, **253**, R833–9.
- Foster, K., 1987, Evolution of cranial thickness: a consequence of cranial capacity? *American Journal of Physical Anthropology*, **72**, 198.
- Franciscus, R.G. and Trinkaus, E., 1988a, The Neanderthal nose. *American Journal of Physical Anthropology*, **75**, 209–10.
- Franciscus, R.G. and Trinkaus, E., 1988b, Nasal morphology and the emergence of *Homo erectus*. *American Journal of Physical Anthropology*, **75**, 517–27.
- Geissman, T., 1986, Length estimate for KNM–ER 736, a hominid femur from the Lower Pleistocene of East Africa. *Human Evolution*, **1**, 481–93.
- Gribbin, J. and Cherfas, J., 1983, *The Monkey Puzzle* (London: Triad, Paladin).
- Harrison, R.J., 1958, *Man the Peculiar Animal* (Harmondsworth: Penguin Books).
- Hasegawa, M., Kishino, H. and Yano, T., 1985, Dating of the human/ape splitting by a

- molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, **22**, 160-74.
- Hasegawa, M., Kishino, H. and Yano, T., 1987, Man's place in Hominoidea as inferred from molecular clocks of DNA. *Journal of Molecular Evolution*, **26**, 132-47.
- Hempleman, H.V. and Lockwood, A.P.M., 1978, *The Physiology of Diving in Man and other Animals* (London: Edward Arnold).
- Henneberg, M., 1988, Decrease of skull size in the Holocene. *Human Biology*, **60**, 395-405.
- Hildebrand, M., 1974, *Analysis of Vertebrate Structure* (New York: Wiley).
- Hong, S.K., 1988, Man as a breath-hold diver. *Canadian Journal of Zoology*, **66**, 70-4.
- Howells, W.W., 1985, Taung: a mirror for American anthropology. In *Hominid Evolution*, ed. P.V. Tobias (New York: Liss), 19-24.
- Ivanhoe, F., 1985, On the neanderthal pubis and acromegaly. *Current Anthropology*, **26**, 526-9.
- Johanson, D.C., 1985, The most primitive *Australopithecus*. In *Hominid Evolution*, ed. P.V. Tobias (New York: Liss), 203-12.
- Johanson, D.C. and Edey, M.A., 1981, *Lucy, the Beginnings of Mankind* (London: Granada).
- Johanson, D.C., Masao, F.T., Eck, G.G., White, T.D., Walter, R.C., Kimbel, W.H., Asfaw, B., Manega, P., Ndessokia, P. and Suwa, G., 1987, New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. *Nature*, **327**, 205-9.
- Johanson, D.C. and Taieb, M., 1976, Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. *Nature*, **260**, 293-7.
- Johanson, D.C., Taieb, M. and Coppens, Y., 1982, Pliocene hominids from the Hadar formation, Ethiopia (1973-1977). *American Journal of Physical Anthropology*, **57**, 373-402.
- Johanson, D.C. and White, T.D., 1979, A systematic assessment of early African hominids. *Science*, **203**, 321-30.
- Jungers, W.L., 1982, Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature*, **297**, 676-8.
- Jurmain, R., Nelson, H., Kurashina, H. and Turnbaugh, W.A., 1981, *Understanding Physical Anthropology and Archeology* (St Paul: West Publishing Co.).
- Kennedy, G.E., 1985, Bone thickness in *Homo erectus*. *Journal of Human Evolution*, **14**, 699-708.
- Kennedy, G.E., 1986, The relationship between auditory exostoses and cold water: a latitudinal analysis. *American Journal of Physical Anthropology*, **71**, 401-15.
- Kimbel, W.H., White, T.D. and Johanson, D.C., 1984, Cranial morphology of *Australopithecus afarensis*, a comparison study based on a composite reconstruction of the adult skull. *American Journal of Physical Anthropology*, **64**, 337-88.
- Kratzing, J.E., 1984, Anatomy and histology of the nasal cavity of the koala (*Phascolarctus cinereus*). *Journal of Anatomy*, **138**, 55-65.
- Latimer, B.M., Lovejoy, C.O., Johanson, D.C. and Coppens, Y., 1982, Hominid tarsal, metatarsal and phalangeal bones recovered from the Hadar Formation: 1974-1977 collections. *American Journal of Physical Anthropology*, **57**, 701-19.
- Latimer, B.M. and Lovejoy, C.O., 1989, The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. *American Journal of Physical Anthropology*, **78**, 369-86.
- Latimer, B., Ohman, J.C. and Lovejoy, C.O., 1987, Talocrural joint in African hominoids: implications for *Australopithecus afarensis*. *American Journal of Physical Anthropology*, **74**, 155-75.
- Leakey, M.D., Clarke, R.J. and Leakey, L.S.B., 1971, New hominid skull from Bed I, Olduvai Gorge, Tanzania. *Nature*, **232**, 308-9.
- Leakey, M.D. and Hay, R.L., 1979, Pliocene footprints in the Laetolil beds at Laetoli, Northern Kenya. *Nature*, **278**, 317-23.

- Leakey, M.D., Hay, R.L., Curtis, G.H., Drake, R.E., Jackes, M.K. and White, T.D., 1976, Fossil hominids from the Laetolil Beds. *Nature*, **262**, 460–6.
- Leakey, R.E.F. and Walker, A., 1988, New *Australopithecus boisei* specimens from East and West Turkana, Kenya. *American Journal of Physical Anthropology*, **76**, 1–24.
- Lewis, O.J., 1977, Joint remodelling and the evolution of the human hand. *Journal of Anatomy*, **123**, 157–201.
- Lewis O.J., 1980, The joints of the evolving foot, Part III. The fossil evidence. *Journal of Anatomy*, **131**, 275–98.
- Loeffler, K., 1981, *Anatomie und Physiologie der Haustiere* (Stuttgart: Eugen Ulmer).
- Martin, L., 1987, Significance of enamel thickness in hominoid evolution. *Nature*, **314**, 260–3.
- Martyn, J. and Tobias, P.V., 1967, Pleistocene deposits and new fossil localities in Kenya. *Nature*, **215**, 476–80.
- McFarland, W.M., Pough, F.H., Cade, T.J. and Heiser, J.B., 1979, *Vertebrate Life* (London: Collier Macmillan).
- McHenry, H.M., 1982, The pattern of human evolution: studies on bipedalism, mastication and encephalization. *Annual Review of Anthropology*, **11**, 151–73.
- McHenry H.M., 1986, The first bipeds: a comparison of the *A. afarensis* and *A. africanus* postcranium and implications for the evolution of bipedalism. *Journal of Human Evolution* **15**, 177–91.
- McHenry, H.M. and Skelton, R.R., 1985, Is *Australopithecus africanus* ancestral to *Homo*? In *Hominid Evolution*, ed. P.V. Tobias (New York: Liss) 221–6.
- Moerman, P., 1977, *In het spoor van de Neanderthal-mens* (Baarn: Boekerij).
- Morden, J., 1988, Towards a hominid taphonomy: carnivore consumption of human carcasses. *American Journal of Physical Anthropology*, **75**, 251.
- Morgan, E., 1982, *The Aquatic Ape* (London: Souvenir Press).
- Morgan, E., 1984, The aquatic hypothesis. *New Scientist*, **1405**, 17–19.
- Morgan, E. and Verhaegen, M., 1986, In the beginning was the water. *New Scientist*, **1498**, 62–3.
- Napier, J.R., 1962, Fossil hand bones from Olduvai Gorge. *Nature*, **196**, 409–11.
- Napier, J.R. and Napier, P.H., 1967, *A Handbook of Living Primates* (New York: Academic Press).
- Nie, C.J. van, 1983, A comparative study of the morphology and the topography of the heart of the *Arctocephalus australis* (fur or ursine seal) and the heart of the *Phoca vitulina vitulina* (common or harbour seal) in their relation to the type of locomotion. *Aquatic Mammals*, **10**, 79–82.
- Nie, C.J. van and Roede, M.J., 1991, Some cardiac topographic and morpho-physiological observations of the common seal and of man. (This volume, pages 290–3).
- Ninkovich, D. and Burckle, L.H., 1978, Absolute age of the base of the hominid-bearing bed in Eastern Java. *Nature*, **275**, 306–8.
- Nishida, T., 1980, Local differences in reactions to water among wild chimpanzees. *Folia Primatologica*, **33**, 189–209.
- Ohman, J.C., 1986, The first rib of hominoids. *American Journal of Physical Anthropology*, **70**, 209–29.
- Olson, T.R., 1985, Taxonomic affinities of the immature crania from Hadar and Taung. *Nature*, **316**, 539–40.
- Oxnard, C.F., 1975, *Uniqueness and Diversity in Human Evolution* (Chicago: University of Chicago Press).
- Pickford, M., 1975, Late Miocene sediments and fossils from the Northern Kenya Rift Valley. *Nature*, **256**, 279–84.
- Pickford, M., 1986, Geochronology of the Hominoidea: a summary. In *Primate Evolution*, ed. J.G. Else and P.C. Lee (Cambridge: Cambridge University Press), 123–8.
- Poirier, F.E., 1987, *Understanding Human Evolution* (Englewood Cliffs: Prentice-Hall).

- Potts, R., 1988, Contexts of *Homo erectus/Homo sapiens* at Kanjera and Olorgesailie, Kenya. *American Journal of Physical Anthropology*, **75**, 258.
- Pugh, L.G.C. and Edholm, O.G., 1955, The physiology of Channel swimmers. *Lancet*, **6893**, 761-8.
- Radosevich, S.C. and Retallack, G.J., 1988, Paleoecology of hominids from the site AL-333, Hadar, Ethiopia. *American Journal of Physical Anthropology*, **75**, 258.
- Rak, Y., 1986, The Neanderthal face: a new look to an old face. *Journal of Human Evolution*, **15**, 151-64.
- Rak, Y. and Arensburg, B., 1987, Kabara 2 Neanderthal pelvis: first look at a complete inlet. *American Journal of Physical Anthropology*, **73**, 227-31.
- Rak, Y. and Clarke, R.J., 1979, Ear ossicle of *Australopithecus robustus*. *Nature*, **279**, 62-3.
- Romer, A.S. and Parsons, T.S., 1977, *The Vertebrate Body* (Philadelphia: Saunders).
- Russell, M.D., 1985, The supraorbital torus: 'a most remarkable peculiarity'. Replies of Garn, S.M., Shea, B.T., Girgis, F., Turkel, S. and Zivanović, S. *Current Anthropology*, **26**, 337-60.
- Sarmiento, E.E., 1987, Long bone torsions of the lower limb and its bearing upon the locomotor behavior of australopithecines. *American Journal of Physical Anthropology*, **72**, 250-1.
- Seger, J., 1987, El Niño and Darwin's finches. *Nature*, **327**, 461.
- Sheldon, P., 1988, Making the most of the evolution diaries. *New Scientist*, **1596**, 52-4.
- Sickenberg, O., 1934, *Beiträge zur Kenntnis Tertiärer Sirenen* (Brussels: Koninklijk Natuurhistorisch Museum van België).
- Simpson, G.G., 1959, *The Meaning of Evolution* (New Haven: Yale University Press).
- Slijper, E.J., 1979, *Whales* (London: Hutchinson).
- Smith, B.H., 1987, Maturational patterns in early hominids. *Nature*, **328**, 674-5.
- Smith, R.J., 1984, Allometric scaling in comparative biology: problems of concept and method. *American Journal of Physiology*, **246**, R152-R160.
- Stern, J.T. and Susman, R.L., 1983, The locomotor anatomy of *Australopithecus afarensis*. *American Journal of Physical Anthropology*, **60**, 279-317.
- Studel, K., 1978, A multivariate analysis of the pelvis of early hominids. *Journal of Human Evolution*, **7**, 583-95.
- Stringer, C.B., 1978, Some problems in Middle and Upper Pleistocene hominid relationships. In *Recent Advances in Primatology*, ed. D.J. Chivers and K.A. Joysey (London: Academic Press).
- Susman, R.L., 1987, Pygmy chimpanzees and common chimpanzees; models for the behavioral ecology of the earliest hominids. In *The Evolution of Human Behavior, Primate Models* (Albany: State University New York Press), 72-86.
- Susman, R.L. and Stern, J.T., 1982, Functional morphology of *Homo habilis*, *Science*, **217**, 931-4.
- Tague, R.G. and Lovejoy, C.O., 1986, The obstetric pelvis of AL 288-1 (Lucy). *Journal of Human Evolution*, **15**, 237-55.
- Tardieu, C., 1986, The knee joint in three hominid primates: application to Plio-Pleistocene hominids and evolutionary implications. In *Current Perspectives in Primate Biology*, ed. D.M. Taub and F.A. King (New York: Van Nostrand Reinhold), 182-92.
- Tobias, P.V., 1983, Recent advances in the evolution of the hominids with especial reference to brain and speech. In *Pontifical Academy of Sciences, Scripta Varia* **50**, 87-140.
- Tompkins, R.L., Heller, J.A., Franciscus, R.G., 1988, Hominid femoral neck angle and biomechanical neck length. *American Journal of Physical Anthropology*, **75**, 279.
- Trinkaus, E., 1976, A functional interpretation of the axillary border of the Neanderthal scapula. *Journal of Human Evolution*, **6**, 231-4.
- Trinkaus, E., 1987, The Krapina hominid postcrania. *American Journal of Physical Anthropology*, **72**, 264.
- Trinkaus, E. and Churchill, S.E., 1988, Neanderthal radial tuberosity orientation.

- American Journal of Physical Anthropology*, **75**, 15–21.
- Tuttle, R.H., 1985, Ape footprints and Laetoli impressions: a response to the SUNY claims. In *Hominid Evolution*, ed. P.V. Tobias (New York: Liss), 129–33.
- Verhaegen, M., 1985, The aquatic ape theory: evidence and a possible scenario. *Medical Hypotheses*, **16**, 17–32.
- Verhaegen, M., 1987a, The aquatic ape theory and some common diseases. *Medical Hypotheses*, **24**, 293–300.
- Verhaegen, M., 1987b, Vertonen de fossiele hominiden tekens van wateraanpassing? *Marswin*, **8**, 142–51.
- Verhaegen, M., 1988, Aquatic ape theory and speech origins: a hypothesis. *Speculations in Science and Technology*, **11**, 165–71.
- Verhaegen, M., 1990, African ape ancestry. *Human Evolution*, **5**, 295–7.
- Verhaegen, M., 1991, Aquatic Ape Theory and fossil hominids. *Medical Hypotheses* (in press).
- Vrba, E., 1979, A new study of the scapula of *Australopithecus africanus* from Sterkfontein. *American Journal of Physical Anthropology*, **51**, 117–30.
- Walker, A., Leakey, R.E., Harris, J.M. and Brown, F.H., 1986, 2.5–myr *Australopithecus boisei* from west of Lake Turkana. *Nature*, **322**, 517–22.
- Ward, S. and Hill, A., 1987, Pliocene hominid partial mandible from Tabarin, Baringo, Kenya. *American Journal of Physical Anthropology*, **72**, 21–37.
- Washburn, S.L. and Moore, R., 1980, *Ape into Human* (Boston: Little, Brown).
- Wells, H.G., Huxley, J. and Wells, G.P., 1929, *The Science of Life* (London: Amalgamated Press), vol. 1: 264.
- Wheeler, P., 1985, The loss of functional body hair in man, *Journal of Human Evolution*, **42**, 12–27.
- White, T.D. and Harris, J.M., 1977, Suid evolution and correlation of African hominid localities. *Science*, **198**, 13–21.
- White, T.D. and Suwa, G., 1987, Hominid footprints at Laetoli: facts and interpretations. *American Journal of Physical Anthropology*, **72**, 485–514.
- Wilson, J.A., 1979, *Principles of Animal Physiology* (New York: Macmillan).
- Wind, J., 1976, Human drowning: phylogenetic origin. *Journal of Human Evolution*, **5**, 349–63.
- Wood, B.A., 1974, Evidence on the locomotor pattern of *Homo* from early Pleistocene of Kenya. *Nature*, **251**, 135–6.
- Wood, B.A., 1978, Classification and phylogeny of East African hominids. In *Recent Advances in Primatology*, ed. D.J. Chivers and K.A. Joysey (London: Academic Press), vol. 3: 350–72.
- Wyles, J.S., Kunkel, J.G. and Wilson, A.C., 1983, Birds, behavior, and anatomical evolution. *Proceedings of the National Academy of Science, USA*, **80**, 4394–7.
- Wyss, A.R., 1988, Evidence from flipper structure for a single origin of pinnipeds. *Nature*, **334**, 427–8.
- Zihlman, A.L., Cronin, J.E., Cramer, D.L. and Sarich, V.M., 1978, Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees and gorillas. *Nature*, **275**, 744–6.
- Zwell, M. and Conroy, G.C., 1973, Multivariate analysis of the *Dryopithecus africanus* forelimb. *Nature*, **244**, 373–5.