

# 9 The Aquatic Ape Theory, Seen from Epistemological and Palaeoanthropological Viewpoints

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## SUMMARY

In this chapter the Aquatic Ape Theory is evaluated according to epistemological criteria and its explanative value is compared with that of what AAT proponents call the Savannah Theory. To that purpose, the fossil record is reviewed, while employing the strictest 'functional' explanations for the morphological characters of the fossils. The known stages of human evolution are found to form an uninterrupted sequence of functional adaptations to arboreal, semi-arboreal/terrestrial and cursorial modes of locomotion. In many cases the adaptive value can be defined semi-quantitatively as mechanical advantages for a given type of locomotion. Our comparison made it necessary to develop some testable hypotheses about the locomotor behaviour of presumed aquatic ancestors, something that so far has not been proposed by AAT advocates. The morphological adaptations advantageous for some possible aquatic forms of locomotion do not exist.

We find that the Aquatic Ape Theory:

- does not explain more findings than do the more traditional ideas;
  - does not allow a more complete integration of accepted but unassociated facts;
  - does not contain fewer contradictions, nor leave fewer gaps;
  - does not allow more parsimonious explanations;
  - does not allow for more precise or more correct predictions of new findings;
  - does not yield hypotheses that can be tested in a more reliable, simpler or more convincing way than those deduced within the framework of the Savannah Theory.
- In fact, the weakest point of the new theory seems to be that its proponents do not develop hypothetical explanations that can be tested on the basis of known natural laws, or even on the basis of empirically well established rules.

It has to be admitted, though, that the promotion of the new AAT has stimulated a thorough reconsideration of what we believe to know, to investigate new facts, and to acquire new knowledge.

## INTRODUCTION

The Aquatic Ape Theory was designed to explain morphological and physiological characteristics of man, and to contrast with what AAT proponents call the Savannah Theory. By emphasising the latter term, they refer to the widespread belief that the evolutionary steps which led to the present human body shape took place in woodland or gallery forests in savannah-like landscapes, and later in grasslands scattered with

trees. In fact, the proponents of the Aquatic Ape Theory ascribe more uniformity and homogeneity to other current ideas on hominid evolution than we – and others – had attributed to them before. The traditional savannah scenario fits in fairly well with a large number of assumptions about the origins of important human traits (see p. 161), though admittedly it does not yield plausible explanations for all the features of our species.

The AAT postulates that human evolution has taken place in a completely different ecological scenario: namely, in or close to water. Consequently, the selective pressures assumed to have been responsible for the development of traits that distinguish human from non-human primates are different from those proposed by the majority of previous researchers. Therefore, we are confronted with two theories competing to offer better explanations of the same, uniquely human, features. Scientific seriousness demands an impartial judgement on the value of both theories. This is what is attempted in this chapter. Instead of trying to reach a decision on which theory is 'true' or 'false', we prefer to evaluate them on the basis of the following criteria:

- *explanative value*: the better theory is able to explain more findings than the other one;
- *integrative value*: the better theory allows for a more complete integration of commonly accepted but formerly unassociated facts;
- *extension and absence of contradictions*: a good theory does not imply contradictions and leaves few or no gaps between the partial explanations provided by it;
- *parsimony*: those explanations are to be preferred which are less complicated with respect to the causal mechanisms implied and the theoretical concepts referred to. A theory that embodies such explanations is more 'beautiful', or more 'elegant';
- *prognostic value*: the theory to be preferred is superior in its ability to make correct predictions of new findings;
- *testability*: to judge the prognostic value of a theory it must be possible to deduce testable hypotheses from that theoretical framework;
- *stimulus value*: a good theory should stimulate new approaches and research projects.

## SURVEY OF THE FOSSIL RECORD

Although the possibility cannot be ruled out that important stages of hominid evolution remain to be discovered, we should work within the

framework offered by the fossils available today when we attempt to reconstruct our ancestry, at least as long as we commit ourselves to the essentially empirical methods of natural science.

The evolution of man is now thoroughly documented (Vogel, 1974; Pilbeam, 1972; *National Geographic*, 1985; Johanson and Edey, 1982). We can trace back our ancestry through the stages of anatomically modern man of the Upper Palaeolithic (going back at least 40,000 years, perhaps even 80,000) and Neanderthal man of the middle Palaeolithic (about 150,000 years ago), to *Homo erectus* of the Early Palaeolithic (from 260,000 or 300,000 back to 1.6 million years ago; see Figure 9.1). The evolution of almost the entire skeleton is known, and there are few obvious differences that distinguish the body shape of Neanderthal man or *H. erectus* from that of modern man. Fossils of these forms have been found in Europe, Asia and Africa.

The probable ancestors of *H. erectus* were hominids called Australopithecines. In this context, it is not relevant to discuss the possible existence of a separate taxon, *H. habilis*. That discussion boils down to the question of whether there is a distinct evolutionary stage between *H. erectus* and *Australopithecus*. Certainly, the genus *Australopithecus* is split into robust and gracile forms and perhaps even into more than two species. Most parts of their skeletons are known, though unfortunately not all from the same sites. A conclusive analysis of australopithecine morphology is further hampered by the fact that essential skeletal parts are missing. At many sites remains of both forms, robusts and graciles, occur side by side. Australopithecine fossils date back to 3.5 million years ago and seem to be confined to East and South Africa. Some hominid-like fossils of greater age are known, but their taxonomical positions are not certain.

Those ancestors of the Australopithecines that we know are hominoids from the Miocene (more than 5.5 million years ago). They show dentitions and skull shapes very similar to those of modern apes. They have been found in several sites in Europe and Asia, in particular in the Siwalik foothills south of the Himalayas, and in Africa, east of the Rift Valley. The overall body shape and nearly all parts of the skeleton are known from a very complete find on Rusinga Island in Lake Victoria of a small species named *Proconsul africanus*. Nobody knows for sure whether it is representative of the entire group, because from other sites only fragments of the skeleton are known. Nevertheless, these fragments show no obvious differences from *P. africanus*. Surprisingly, the overall body shape of *Proconsul* resembles modern tree-living monkeys much more than modern apes. It is uncertain, however, whether the Miocene apes also possessed long tails. They are distinguished from modern apes by lacking their bulky trunk, short hind limbs and elongated forelimbs. Nor do they possess the typical features of modern gibbons (the 'lesser apes')



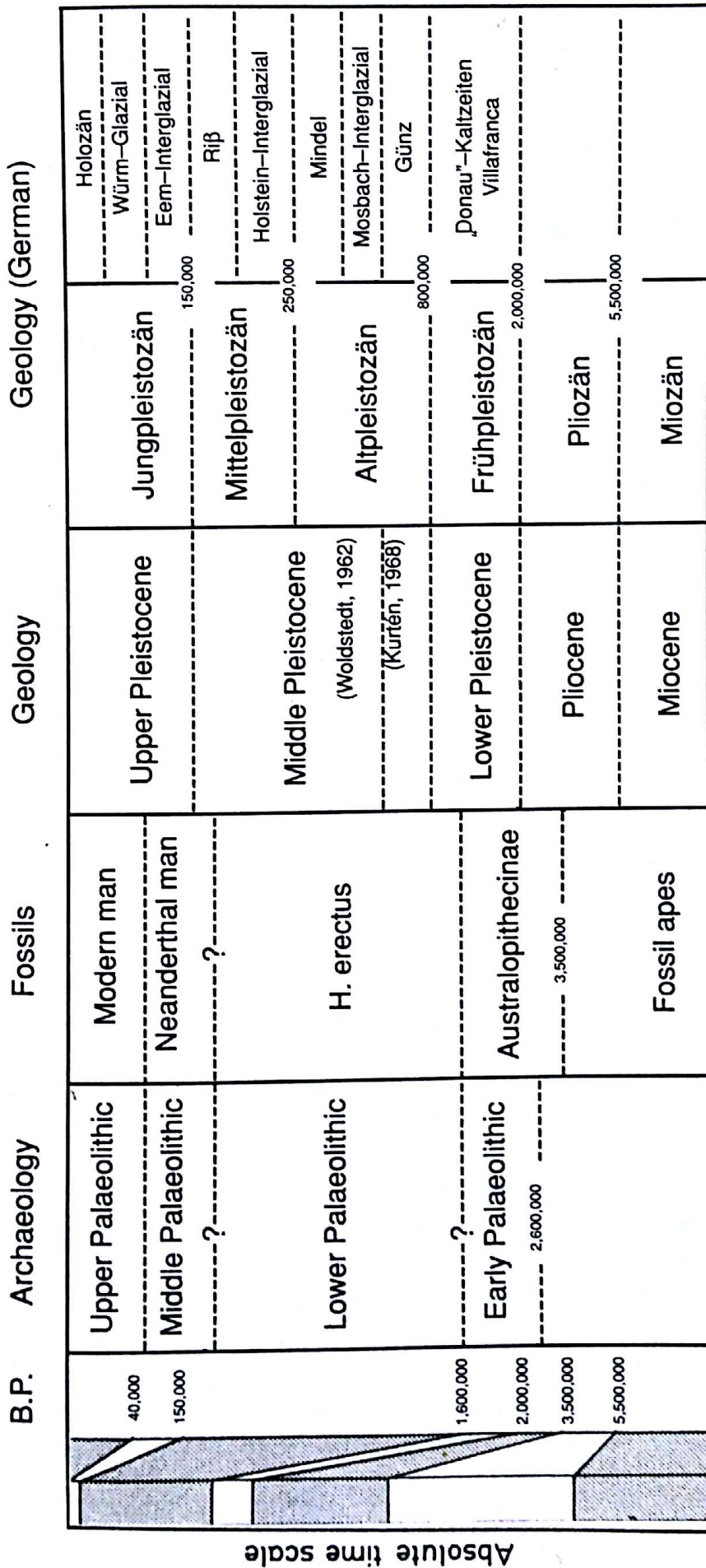


Figure 9.1 Chronology of hominid evolution.



no gap, contra Hardy/Magnus J  
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## The Aquatic Ape: Fact or Fiction?

such as the relatively slender trunk, the long hindlimbs and the extremely long forelimbs. Because of the similarity in their dentitions, but not in their body shapes, to those of modern pongids, the Miocene forms have been called 'dental apes'. We conclude that the bodily characteristics of both, lesser and great apes, are the result of more recent adaptations which have taken place roughly within the last 6 million years.

According to recent chronologies, the Miocene ended about 5.5 million years ago. That means that there is no longer a large gap in the known evolutionary history of hominids, as assumed until recently by palaeoanthropologists, who believed that the Miocene ended 10 million years ago. In fact, there are only some 2.5 or 3.5 million years that are without fossil records of our ancestry (see Figure 9.1). Hence, the starting-point for further considerations should be the known hominoids of the middle Miocene.

The environment in which the earliest of these evolutionary processes took place was, according to palaeo-ecological research (Pickford, 1986; Retallak, Dugas and Bestland, 1990), something between woodland and savannah, with gallery forests along rivers and freshwater lakes. The commonly used hypotheses imply a shift to bipedal locomotion and to a new diet because of the progressively dry, open grasslands which expanded during the late Miocene and early Pliocene. There are no known fossil documents to support the assumption that seashores were the habitats of these forms.

### A SELECTION OF HOMINOID CHARACTERS THAT CAN BE EXPLAINED FUNCTIONALLY

#### General remarks on functional explanations of morphological characters

It is purely speculative to create, as do the AAT proponents, a system of presumed functional needs believed to be advantageous under hypothetical ecological conditions which have perhaps never existed among our ancestors. In order not to unduly restrict the chances of finding positive answers, one should avoid focusing exclusively on human traits which seem to be enigmatic. Instead, features should be considered which can be readily understood according to current ideas, or which can be traced through our known ancestry. Bearing this in mind, it is reasonable to concentrate on dentition, skull shape, trunk shape, pelvis, hindlimbs, feet, fingers and toes.

In the present era of neo-Darwinian thinking, it has become customary to refer by the term 'adaptation' to both the character and the use made of it - that is, its 'function'. If we use the term 'adaptation' we have to indicate precisely what a given trait is 'good for', or which traits are advantageous for fulfilling a given 'function'. Explanations for the



acquisition or the loss of morphological traits can be given, according to Bock and von Wahlert (1965), on one of two levels: (a) that of biological role; (b) that of (mechanical) function. In this chapter, we restrict the use of the term 'function' to statements about how a feature works mechanically, depending on its physical properties. The use made of form characteristics during an animal's life history should be termed 'biological role'; in contrast to function, this can be ascertained only by observing animals in their natural environment.

The mechanical function must be fulfilled under all 'normally' occurring circumstances, enabling the structure not to fail in critical situations. The principle is now widely accepted that the body's shape must be such that its parts are suited to sustain the highest forces that can act on it under 'normal' conditions, while requiring a minimum of force or energy. The validity of that principle is underlined by the existence of a morphogenetic mechanism which causes an *intra vitam* remodelling of existing bones, tendons and ligaments. This leads to shape characteristics that fit optimally with the mechanical stresses induced by 'normal' locomotion or posture. Conversely, this means that the mechanical function can often be derived accurately from the shape of a fossil bone. It is this close connection between shape and function which leads us to put so much emphasis on the biomechanical approach to 'functions'.

'Biological roles' in the sense of Bock and von Wahlert (1965) are not tied so closely to morphology. In spite of this, most attempts to understand morphology are undertaken on the level of biological roles – as in the AAT debate. We prefer a strictly mechanical approach to function, because mechanical functions are more readily identifiable than biological roles (for further discussion, see Chivers *et al.*, 1984). In a terrestrial animal, the 'external' forces that can act on the body are limited by body weight (Preuschoft, 1985). These forces are usually concentrated on the hands or feet, or (while sitting) on the ischial callosities or equivalent structures.

### Miocene Apes

The remains of *Proconsul africanus* from Rusinga Island probably belong to one individual (Figure 9.2). Forelimbs and hindlimbs are of equal length, which indicates quadrupedal locomotion. The limbs are long and rather strong relative to the slender trunk. Both traits are typical of modern monkeys as well, and relate to the great step lengths that characterise monkey locomotion (Vilensky, 1983; Reynolds, 1985a, 1985b) in contrast to other, more specialised, cursorial quadrupeds. The hands and feet are of an elongate and slender form. Their prehensile propensities are shown by the length of the metapodials and the length and curvature of the phalanges, as well as by the positions and the shapes of the joints. According to Preuschoft (1970, 1971a, 1971b, 1973a, 1973b), the

A limited approach - to fossil bone structures as largely neglected source of info is kind of



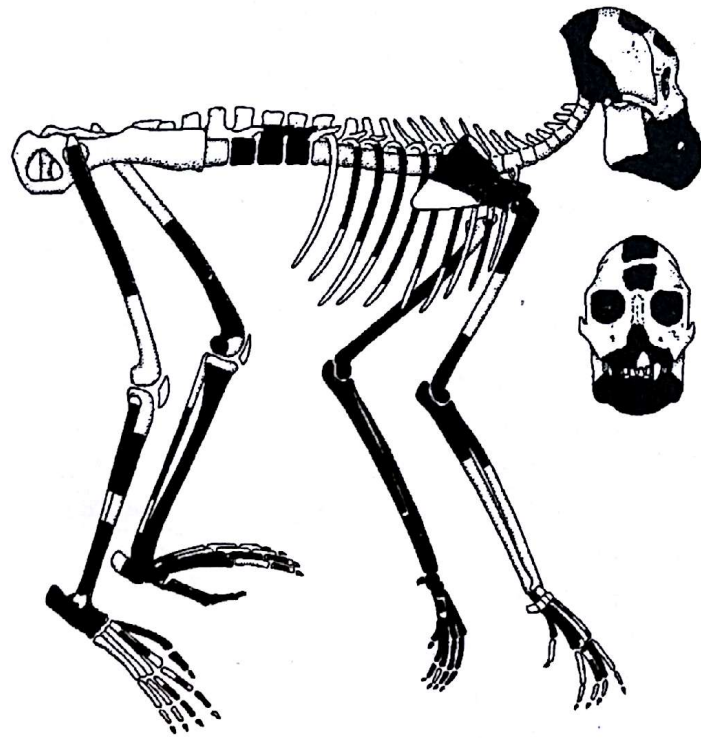


Figure 9.2 Reconstruction of *Proconsul africanus*, the best known among the potential forerunners of hominids (from Walker and Teaford, 1989).

curvature of the phalanges is an adaptation for grasping slim objects such as twigs. A phalanx (Figure 9.3) is exposed to bending moments caused by the action of the distal and proximal joint forces on one side, and to the pull of the flexor tendons and the force resulting from the redirection of the tendons running through the annular part of the tendon sheath. A curvature reduces bending moments by bringing the bone axis closer to the resultant force, which thus exerts more compression than bending. This alone gives strong evidence for an arboreal adaptation, as detailed by Preuschoft (1971b) for subfossil Madagascan lemuroids. The functional adaptation of other traits of *Proconsul* have been investigated by Preuschoft (1973b; see also Morbeck, 1972, for a different argument).

### **Australopithecines**

Most features which characterise Australopithecines as the earliest hominids and distinguish them from Miocene apes are intermediate between modern great apes and modern man.

The most intriguing trait, the relatively large brain, yields no direct evidence about the environment in which australopithecine evolution took place. In gracile Australopithecines, which were of approximately the same size as modern chimpanzees (30–40 kg: Jungers, 1982), the braincase volume is estimated to be 380–600 cm<sup>3</sup>, but for chimpanzees its volume is only 360–450 cm<sup>3</sup> (own data on *Pan troglodytes verus*, Frankfurt collection). In this context, it is important to recall that all primates, in



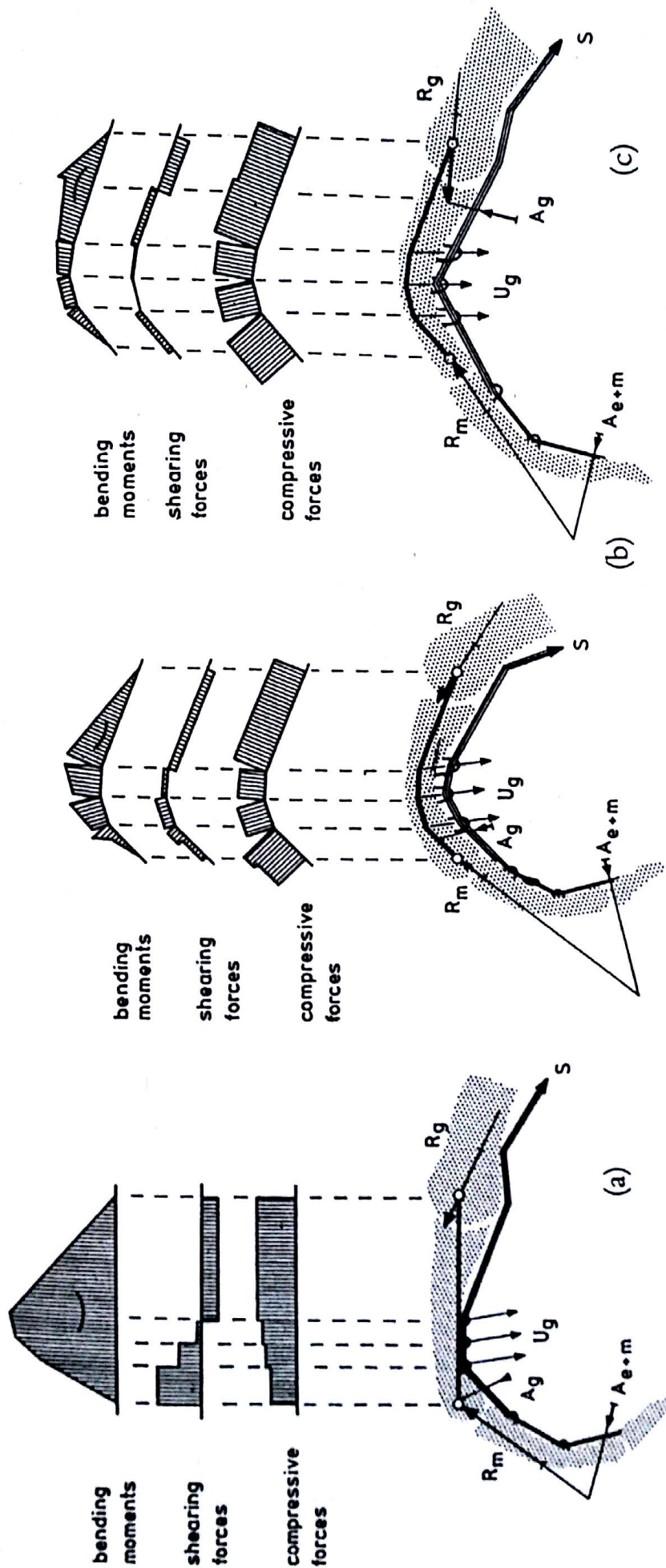


Figure 9.3 Stresses in finger bones of a primate present during a power grip, as used in climbing. The curvature of the phalanges reduces bending stresses, and thus can be considered an adaptation to climbing. (a) straight phalanx; (b) curved phalanx, flexed joints; (c) curved phalanx, more extended joints. The arrows indicate forces which act on the finger bones: A = reaction forces exerted by the substrate against the terminal plus middle phalanx ( $A_g$ ); S = muscle force on the flexor tendons. Both forces combine at the interphalangeal joint to form a resultant force  $R_m$  which pushes the middle phalanx against the proximal. The tendon force S is forced by the annular fibres of the tendon sheath to change its direction, and therefore exerts a force  $U_g$ , which is distributed over a part of the phalanx (illustrated as three partial forces at three points). All forces mentioned combine to a resultant  $R_g$ , which acts on the metacarpophalangeal joint.

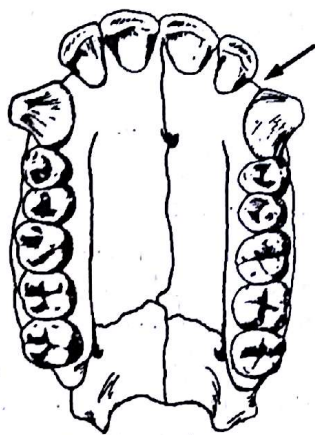
particular the monkeys and apes, possess large brains relative to their body size; and within these large brains, the neocortex is the most progressively developed part (Stephan, 1967; Starck, 1982). Recently, the assumption has gained ground that brain size as well as the elaborate cognitive abilities of monkeys and apes are related to the fact that all of them are group-living animals with very complicated social systems. Thus, a progressive coevolution of the brain and the cognitive abilities necessary for living in these social systems is assumed. The evolution of the cognitive capacities is very likely to be closely tied to the development of a sophisticated communication system.

The sensory capabilities of humans are very similar to those of other higher primates. All diurnal primates are characterised by elaborate visual capacities, and to a large extent their communication relies on visual signals of subtle gradation and short-lasting quality. This also holds true for modern humans. It would be a waste of energy and a source of error to develop visual communicative systems and sensory organs of this quality under the conditions of poor visibility typical of an aquatic environment. In addition, the vocal communication of modern man lacks the elements and features of vocalisation and sound reception typical of aquatic animals.

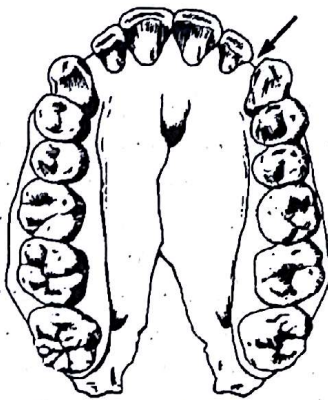
The entire configuration of the skull and dentition changed in the period between the pongid-like forms of the Miocene and the early hominids of the Pliocene. Whereas in the former the long, narrow, U-shaped dental arcade (Figure 9.4) was situated *in front of* a fairly small braincase, the latter had a shorter, rather parabolic dental arch *below* an enlarged braincase (Figure 9.5). Simultaneously, a reduction in the size of the canines as well as an enlargement of the molars occurred, plus a change in the cusp shape. Traditional considerations of biological roles converged on the idea that large canines became superfluous because hand-use replaced them as 'weapons', and hands replaced the mouth as tools for the intake of food (small-object-feeding, hunting). In a recent paper, Preuschoft (1989a) has traced a direct mechanical interdependence that must have existed between the evolution of these traits: the reduction in size of the front teeth indicates changes in diet, leading to 'small object feeding' (Jolly, 1970). The dome-shaped cusps are adapted to breaking down brittle and hard food items, like seeds and nuts – but also mollusc shells. According to Lucas, Corlett and Luke (1986a, 1986b), enlargement of the molar surfaces permits mastication of an equivalent amount of food if body size increases, but leads at the same time to a reduction in bite pressure. But the hardness of food items required an increase in bite pressure. Consequently, the muscles had to become enlarged and the load arms of the bite forces shortened. The latter was achieved by reducing snout length and increasing facial height. The characteristically flat or even concave face of robust Australopithecines (Robinson, 1972), or the pillar-like structures in



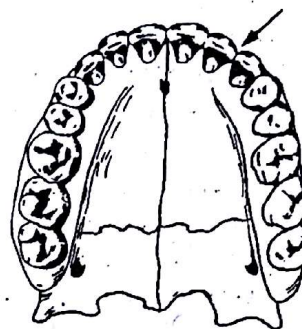
(a) Upper jaws



Chimpanzee

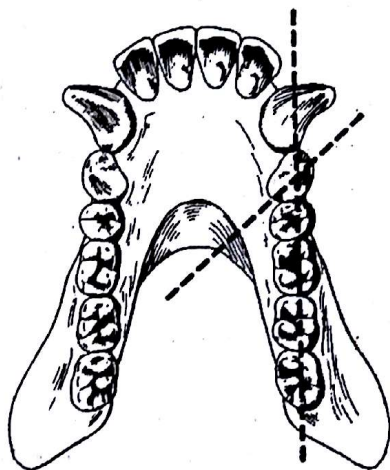


Australopithecus  
from Hadar

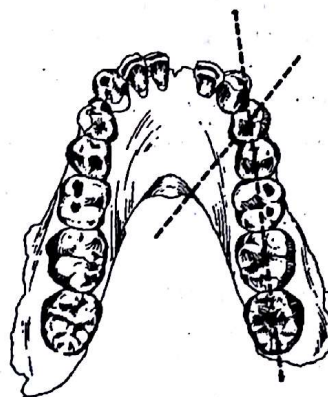


Man

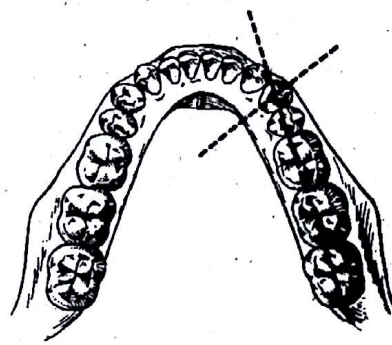
(b) Lower jaws



Chimpanzee



Australopithecus  
from Hadar



Man

Figure 9.4 The long narrow dental arcade of Miocene (and modern) apes has been transformed during hominid evolution into a short, parabolic dental arcade without large canines.

(a) Upper jaws: the arrows show the gap between the lateral incisor and the canine;  
 (b) Lower jaws: the broken lines indicate the angle of the tooth rows and the greatest diameter of the anterior premolar. (Not to the same scale; from Johanson and Edey, 1982.)



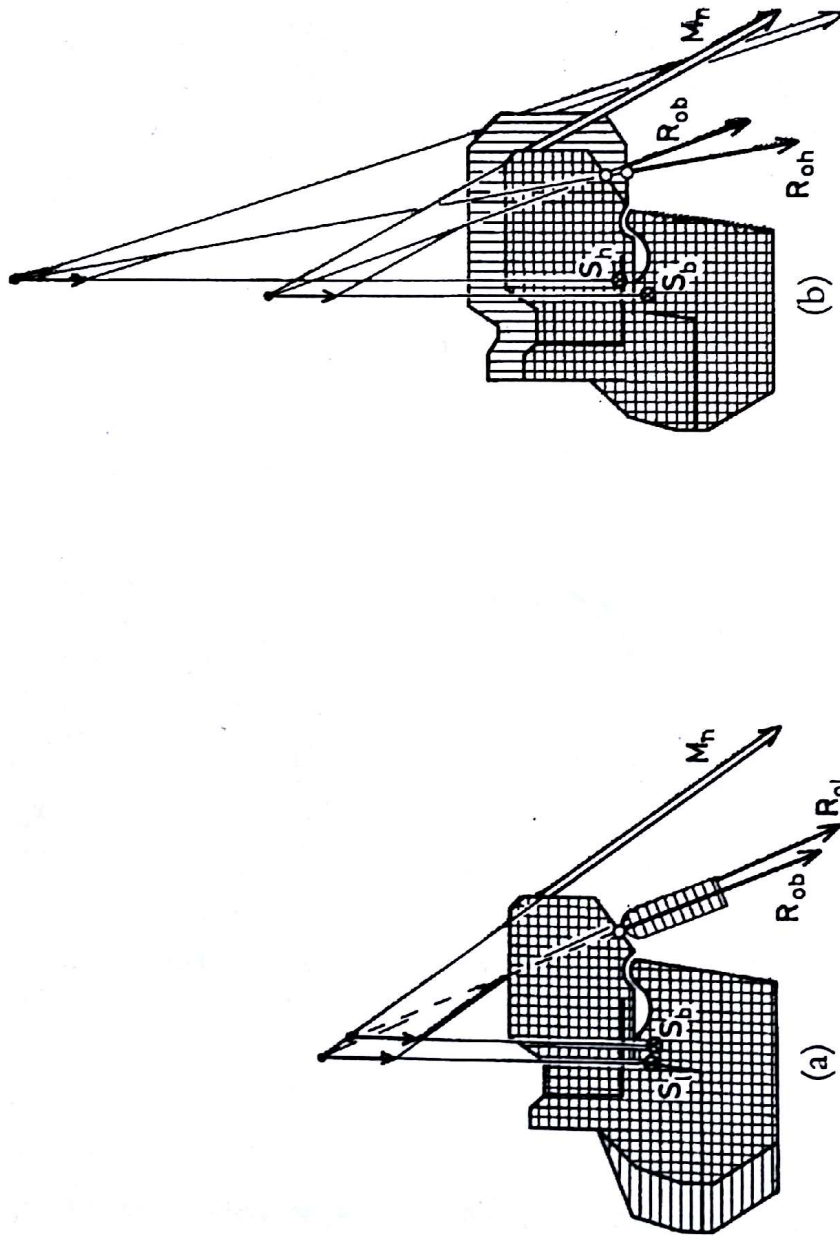


Figure 9.5 Schematic representation of the most marked changes of cranial shape during hominisation.  $S_l$  = centre of gravity, long snout;  $S_b$  = centre of gravity, short snout;  $S_h$  = centre of gravity, with increased vault height;  $M_n$  = nuchal musculature;  $R_o$  = resultant of muscle force and weight force, which passes through the occipital condyles, nearly perpendicular to the plane of the foramen magnum. The reduction of snout length as in (a), but not the enlargement of the braincase as in (b), shifts the centre of gravity dorsally. The resultant force which acts on occipital condyles and cervical vertebrae assumes a steeper direction in short-snouted skulls. Elevation of the vault (b) changes the direction of the nuchal muscles, so that the resultant  $R_o$  also assumes a steeper position. The higher face provides longer lever arms for the masticatory muscles.

graciles (Rak, 1983), served to give the upper jaw the strength necessary to sustain the increased bite forces (Preuschoft, 1989a).

This line of reasoning does not support the theory that Australopithecines were scavengers or hunters (as is assumed in other contributions to this volume), because the dentition of a meat-eater is exposed to different selective pressures. Rather, it favours the idea that early hominids tended towards open country and towards eating grass seeds or other hard objects. It would seem attractive (although it is not attempted here) to fit our argument into a scenario of hominids exploiting marine, coastal or benthic resources.

In non-human primates the head, which has its centre of gravity far in front of the condyles, must be balanced by considerable muscle force (Figure 9.5). The foramen magnum and the occipital condyles face backward in order to be perpendicular to the resulting force, as shown by Demes (1985). Given the short neck, so characteristic of primates, this seems to be inevitable for animals in the pronograde posture, because there is simply no possibility of moving the head above the level of the back. A major prerequisite for saving energy by balancing the head closer to its centre of gravity seems to be, in view of the short neck, upright posture of the trunk. Any enlargement of the brain, accompanied by increased vault height, moves the centre of gravity upward, in a cranial direction. This is not a disadvantage as long as the head is carried like humans carry it. The reduction of snout length contributes to shifting the centre of gravity of the head backward, in pronograde as well as orthograde posture. This reduces the load arm while increasing the power arms, thus reducing the muscular force necessary to keep the head balanced. The condyles, and with them the plane of the foramen magnum, tilt forward, following the swing of the resulting joint force.

Australopithecines apparently possessed a pronounced lordosis in a long lumbar spine of not less than six vertebrae (Robinson, 1972). This has been interpreted as evidence for upright body posture. Preuschoft, Hayama and Günther (1988) have investigated the mechanical conditions existing in long, slender-bodied Japanese macaques as a consequence of their acquisition of upright body posture (Figure 9.6). Under the influence of gravity (that is, without the help of buoyancy when submerged in water), a lordosis appears to offer an important advantage for an animal in an orthograde posture. It provides the erector spinae muscles with a longer lever arm, and moves the vertebral column towards the gravity vertical of the upper body. If a lordosis is present, shortening of the trunk is not necessary to keep the expenditure of muscle force low. Widening of the trunk in the frontal plane and a reduction of its dorso-ventral diameter are further traits which reduce the waste of energy connected with permanent, strong contraction of the erector spinae muscles. In fossils, the existence of these traits can be



deduced from the shape of the ribs (Schmid, 1983.) The shallow trunk of modern man implies a dorsal position of the centre of gravity: that is, it is closer to the vertebral column as the supporting structure. The same result is achieved by the shoulder blades having moved dorsally from their original position, which is lateral to the thorax in pronograde animals.

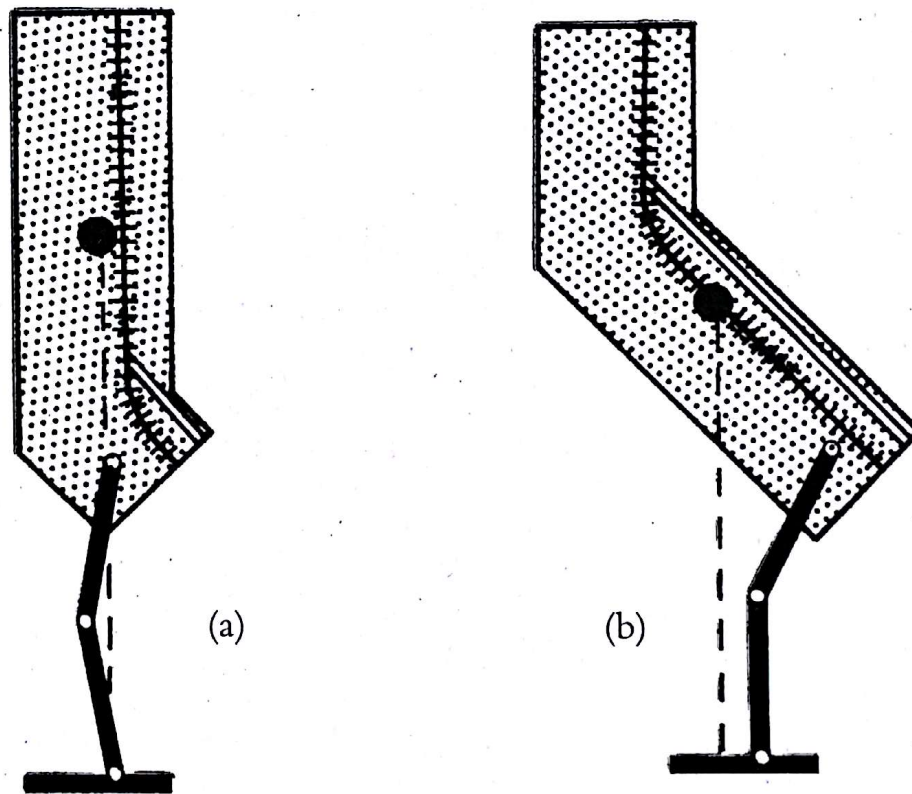
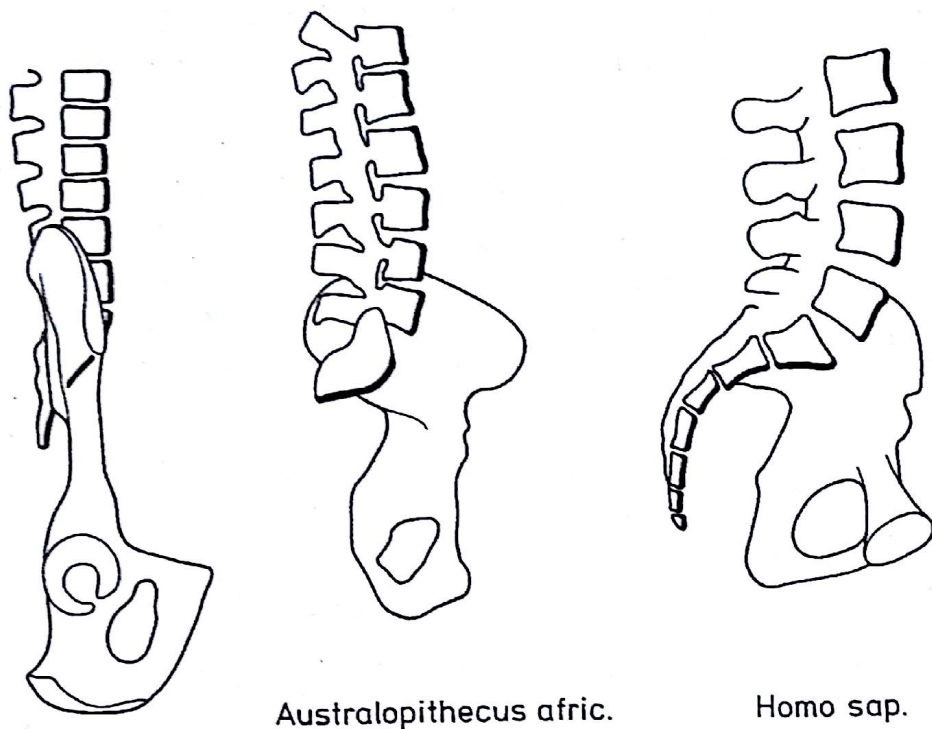


Figure 9.6 In upright trunk postures, a lordosis reduces the loadarm length of the more cranial sections of the body, while providing long power arms for the dorsal muscles.

In (a) the lordosis is shifted caudally into the pelvic region (i.e., to the iliac neck), so that the energy-saving effect is maximal (see also Preuschoft, Hayama and Günther, 1988).

The australopithecine pelvis (Figure 9.7) is commonly interpreted as being adapted 'to some degree' to an upright stance (Napier, 1967; Robinson, 1972; Preuschoft, 1971a; Lovejoy, 1973, 1975; Lovejoy, Heiple and Burstein, 1973). With regard to one detail, the length of the iliac neck, we can confirm this conclusion: the rearward shifting of the 'kink' in the trunk (shown in Figures 9.6 and 9.7) is limited by the length of the ilium. If its 'neck', the part between hip joint and ilio-sacral joint, is shortened, additional energy can be saved. This shortened iliac neck is one of the most characteristic features of the australopithecine pelvis as compared with the long ilium of modern pongids and the short one of

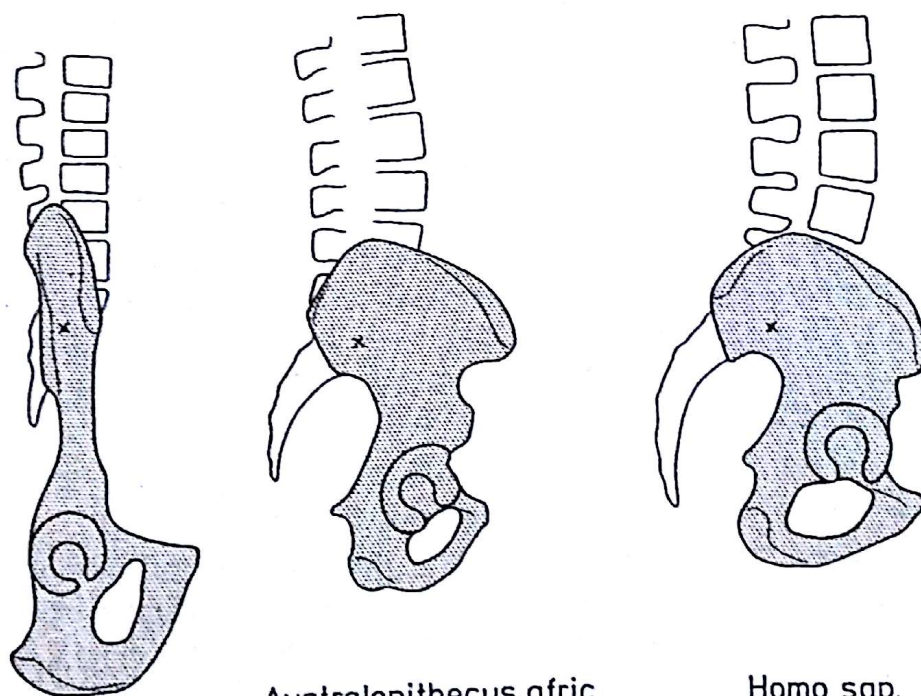




Pan trogl.

Australopithecus afric.

Homo sap.



Pan trogl.

Australopithecus afric.

Homo sap.

Figure 9.7 Side view of various primates' pelves to show the shortening and 'lordosising' of the iliac neck during hominid evolution.

modern humans. This will be worked out in detail by Preuschoft, Schmid and Berge in a forthcoming paper (in preparation).

In standing on one leg, or in the stance phase of walking, the human hindlimb is exposed to bending moments in the frontal plane (Figure 9.8 (a)). The well known valgus position of the knee joint causes a reduction of these bending moments at the knee joint and along the lower leg. This valgus position is apparent in the laterally open angle between the vertical and the femoral shaft, if placed upright on its condyles (Figure 9.9 (b)). The same trait already existed in Australopithecines (Preuschoft, 1971a), but is not present in modern pongids (Figure 9.8 (b)). As a consequence of this valgus position of the knee (Figure 9.9 (b)), the force produced by the quadriceps muscle and the force transmitted by the patellar ligament to the tibia also form a blunt, laterally open angle. This means that a laterally directed resultant acts on the patella. To prevent the patella from sliding, the lateral margin of the patellar facet (Figure 9.9(d)) is higher than the medial in *Australopithecus* and in later hominids (Lovejoy and Heiple, 1970; for additional details see Preuschoft, 1971a). In contrast, the knees of quadrupeds necessarily have a varus or neutral position, even in cases where an upright posture is assumed occasionally. Pongids (Figures 9.8 (b), 9.9 (a)) show the morphological characteristics favourable for climbing – namely, a marked varus position of the knee which allows strong abduction of the hip (see also Preuschoft, 1961, 1970) without placing the foot lateral to the gravity vertical.

Preuschoft (1971a) has shown that the metatarsals and the talus of the Australopithecine-like foot from Olduvai (OH-8) possess the shape characteristics of a rather rigidly built 'ground plate', well suited for walking on the ground (Figure 9.10). In this they resemble the respective elements in the human foot more closely than those in the foot of pongids (Figure 9.11). The anatomy of the australopithecine foot is known only incompletely (Davis, Day and Napier, 1964), but the toes are long and strong compared to those of modern man, and short compared to the toes of pongids. Stern and Susman (1983) have emphasised this in combination with other traits, and have argued that at least *A. afarensis* retained marked adaptations for climbing.

On the other hand, the conclusion that Australopithecines were bipedal is convincingly supported by the footprints and tracks found at Laetoli (Leakey, 1978, 1979; White, 1980). These documents of bipedal walking in a hominid are about 3.5 million years old and belong to the oldest known hominid fossils.

A lot of 'reasons' for the evolution of upright posture and locomotion in terms of biological role have been proposed: for instance, hunting, carrying of food or infants, use and transport of tools; better view over high grass, and higher speed (the latter seems doubtful). To these interpretations we can hardly contribute anything new. But all these traits

walking not even considered as apth...





make sense only if we imagine an animal which shifted from motor habitats similar to those of arboreal macaques or the versatile grey langurs (in forest areas) to bipedal travelling in more open landscapes. It may well be that the two-million-years' history of australopithecine bipedalism stretches from a still partly arboreal lifestyle to bipedal walking (Stern and Susman, 1983). The incompleteness of individual finds of early

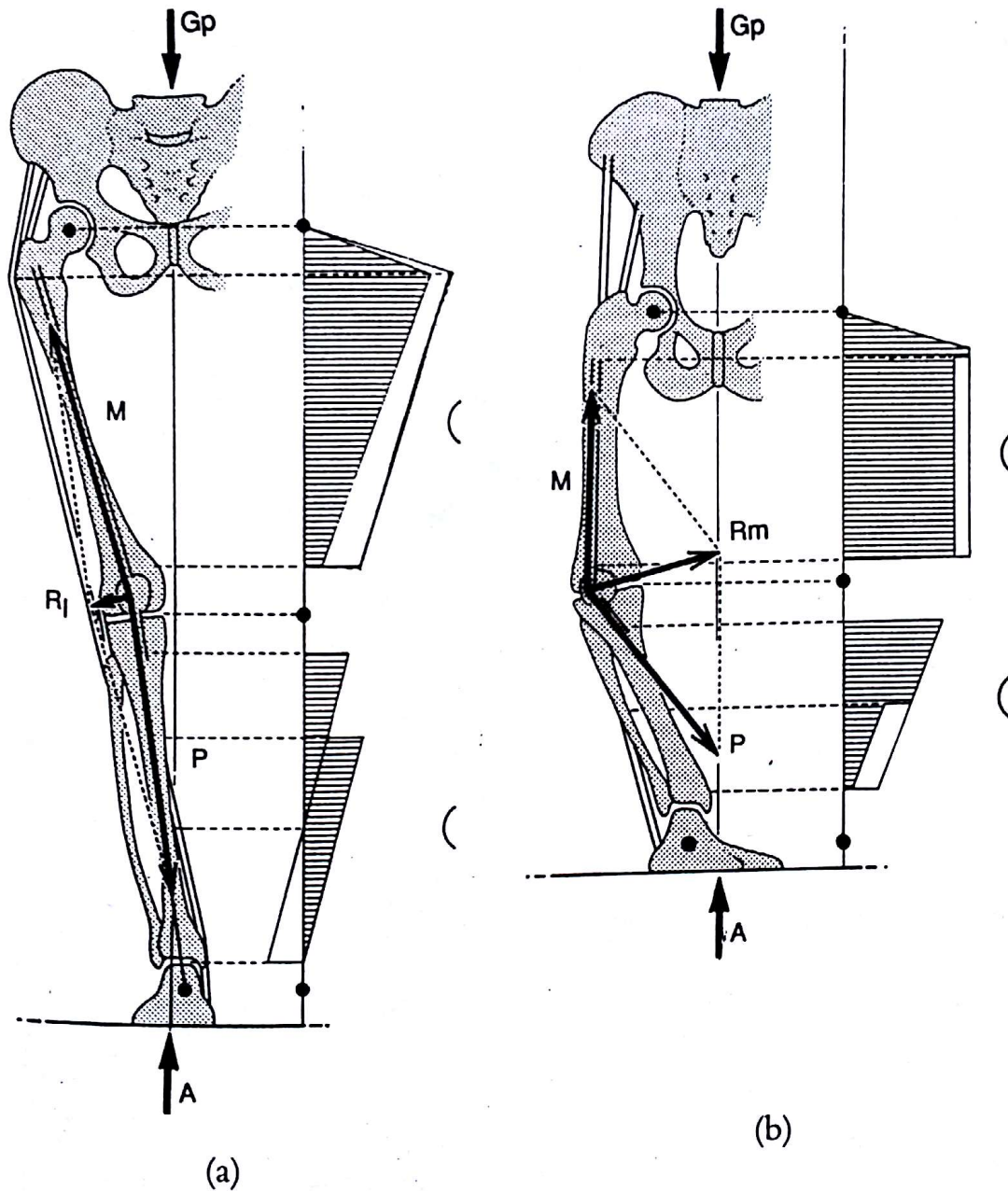


Figure 9.8 Right hindlimb under full body weight seen in frontal view.

(a) Human. The pulling forces of the quadriceps muscle (M) and of the patellar ligament (P) combine to form a laterally directed resultant (R<sub>1</sub>).  
 (b) Gorilla. The resultant R<sub>m</sub> applied to the patella is directed medially. Gp is the weight of the body above the pelvis; A is the ground reaction force. Note the difference of bending moments in both species.



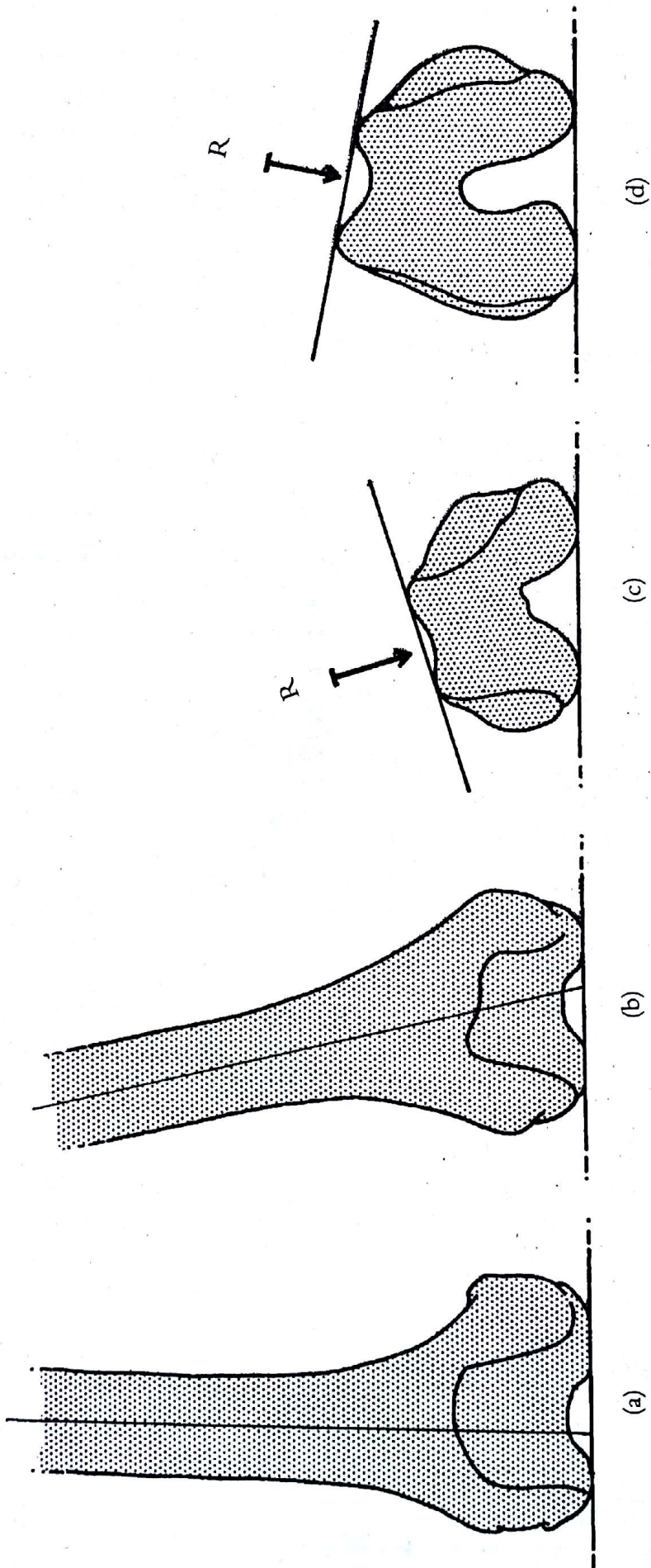


Figure 9.9 Valgus position of the right knee joint in *Homo sapiens* (b) compared to the varus position of the knee in *Gorilla* (a); and elevation of the medial margin in a pongid (*Gorilla*) (c) compared to the elevated lateral margin of the patellar facet, typical of *Homo* (and Australopithecines) (d). The patellar facets in both species are orientated almost perpendicularly to the resultant forces (R) acting on the patella as shown in Figure 9.8.

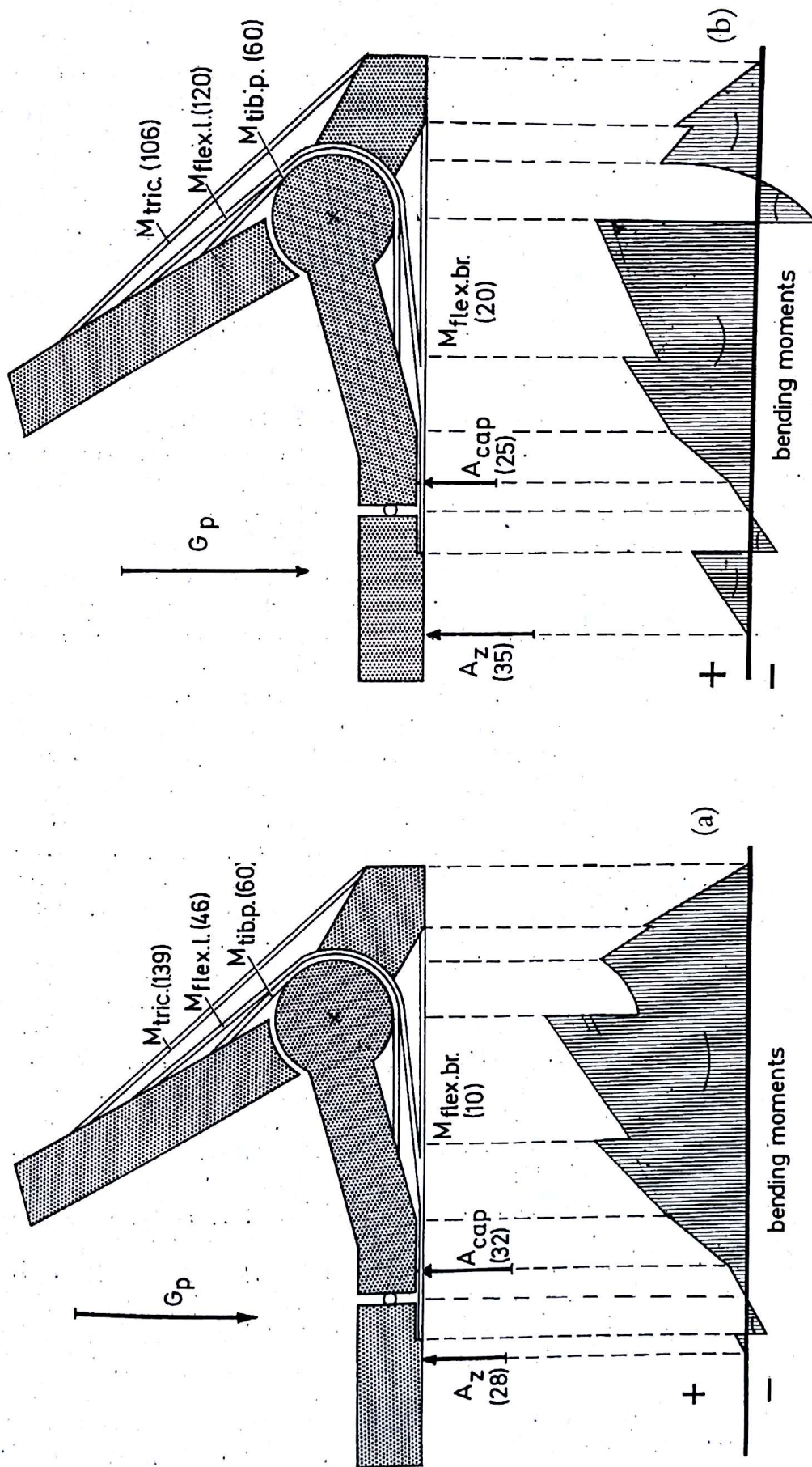


Figure 9.10 Stress patterns in the foot.

(a) A foot adapted to ground walking by having rather short toes (external force  $A_z$  close to metatarso-phalangeal joint), weak toe flexors, and a strong triceps muscle is under great bending stress. (b) A foot adapted to prehension by long toes ( $A_z$  far away from metatarso-phalangeal joint), necessarily strong toe flexors and consequently weak triceps, is exposed to smaller bending moments (from Preuschoff, 1970).



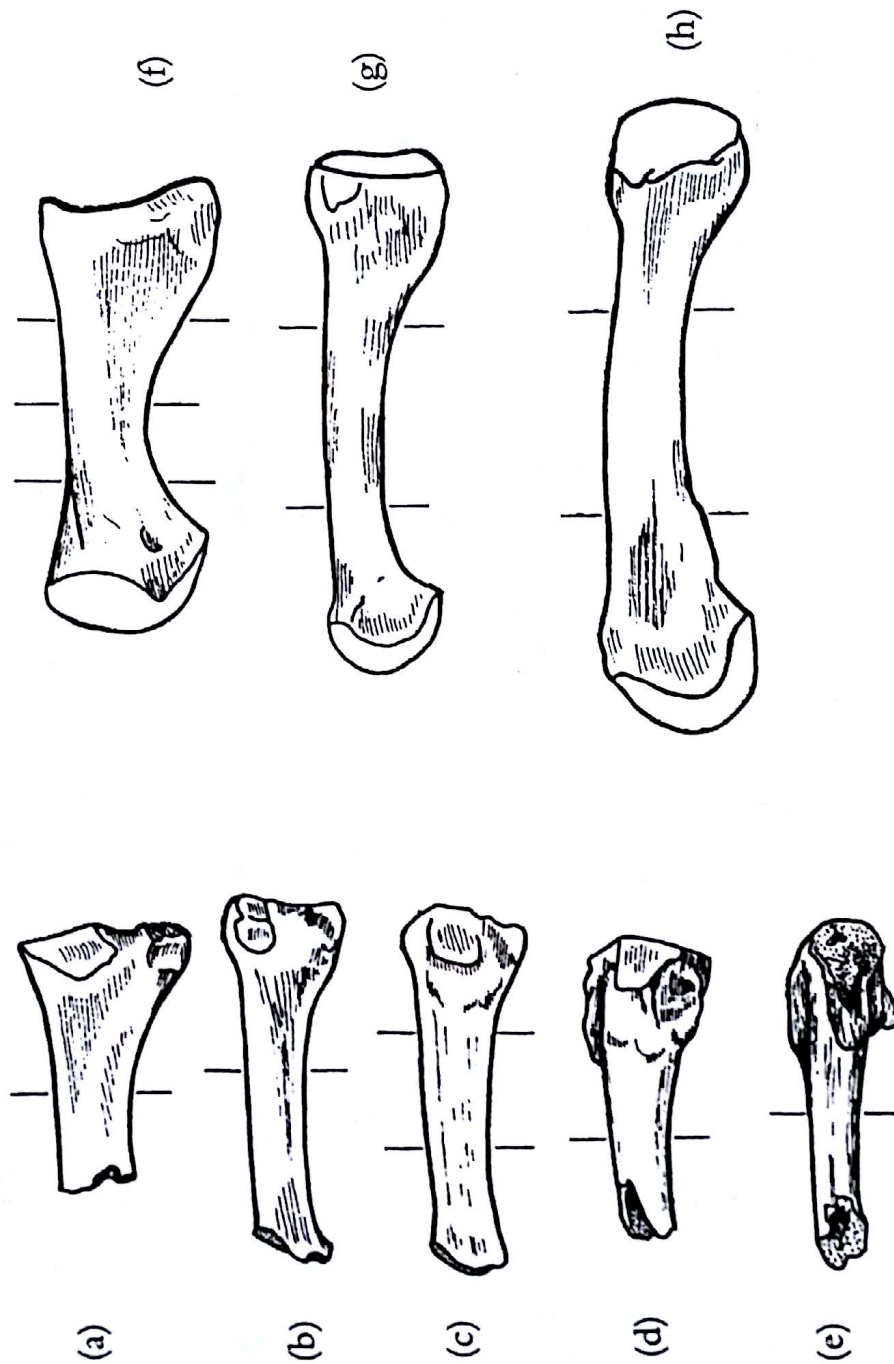


Figure 9.11 The metatarsals of the Olduvai foot OH-8 (a-e) possess relatively smaller diameters in their distal sections than a *Gorilla* (h), but are relatively 'high' in their proximal sections, thus resembling the shape typical of humans (f, g). Because bending resistance depends on the square of the diameters, a comparison with Figure 9.10 shows that the fossil metatarsals are less adapted to prehension than those of gorillas, but more so than those of humans. On the other hand, they are less adapted to serving as a ground plate than the feet of modern humans (from Preuschoft, 1971a).

Australopithecines (like Lucy), and of later stages of their evolution, does not yet allow us to spell out the development in detail.

### ***Homo erectus* and Neanderthal man**

Fossils of both forms are very similar to modern man with regard to body shape, proportions and size. Aside from inconspicuous and only metrically and statistically discernible details, *H. erectus* differs only in skull shape from present-day humans. This holds true for Neanderthal man as well. A recent study by Demes (1987) has demonstrated that the absence of the canine fossa and the associated width of the maxillary cavity in Neanderthal man's skull were a consequence of biting forces acting on the canines and anterior premolars. Therefore, these characteristics are identified as adaptive and functional, which indicates a behaviour peculiar to this form.

Between *Australopithecus* and *H. erectus* important evolutionary changes took place. The brain enlarged from less than 600 cm<sup>3</sup> to at least 800 and up to 1200 cm<sup>3</sup>. Bodily changes – that is, the elongation of the hindlimbs, the reshaping of the pelvis and the shortening of the vertebral column – conform to the acquisition of rather fast and enduring bipedal walking as the predominant mode of locomotion. Walking became faster and less energy-consuming in *H. erectus*, by comparison with former evolutionary stages. Seen from a biomechanical viewpoint, walking is a rhythmical exchange between potential and kinetic energy, as in a pendulum (Cavagna, Heglund and Taylor, 1977; Mochon and McMahon, 1980, 1981; Witte, 1991). The elongation of the hindlimbs as well as increased absolute body size offer means of increasing walking speed without additional input of energy. This has been evaluated for fossil hominids by Preuschoft and Witte (1991; Witte *et al.*, 1991). The same authors have shown that the proportions of arms and trunk must correlate to hindlimb length in order to compensate for undue rotational movements of the body caused by the forward and backward swinging of the long, heavy hindlimbs.

There is strong evidence that *H. erectus* knew how to use fire, and it is certain that he was able to produce a variety of tools. The 'cognitive' abilities of *H. erectus*, and even more those of later hominids, relaxed the selective pressure on what are normally called biological 'adaptations' by compensating for maladaptations which otherwise would have been subject to negative selection. Coevolution of cultural and biological traits seems to have started at this stage.

### **WHAT NEW INSIGHTS DOES THE AQUATIC APE THEORY OFFER?**

In contrast to most palaeoanthropologists, the proponents of the Aquatic Ape Theory have neither attempted to clarify the chronology of the



Comparative biology to be  
 based upon - but of course they  
 are placed in a context of  
 what is known to be possible

...: Fact or Fiction?

known fossil documents nor to interpret them in terms of their differences and similarities. Instead, they focus on the explanation of modern man's peculiarities as compared to modern apes and other mammals.

Among the features emphasised by the AAT are (1) some which are not at all peculiar to man, and (2) others which can be explained more satisfactorily within the framework of conventional ideas, which by no means imply an aquatic stage. Here, we will briefly discuss some examples of both categories.

1 Low hair-density is also found among modern large apes. According to Schultz (1936), gorillas, chimpanzees and orang-utans have about 300–500 hairs per  $\text{cm}^2$  – in contrast to the lesser apes and some monkeys which possess 2000–3000. The arrangement of body hair, as well as the importance of sweat glands for a primate who exposes himself to full sunshine, is discussed by Wheeler (chapter 13, this volume). Also, it should be noted that all primates in tropical regions usually avoid direct sunshine. Subcutaneous fat is arranged in similar deposits in many mammals, including primates (Pond, this volume, chapter 12).

2 Bipedality should be considered in connection with the fact that most primates are 'hindlimb-dominated' and show a tendency to sit upright when resting or investigating things closely. While standing or walking, most primates carry a larger part of their body weight on the hindlimbs than on the forelimbs (Figure 9.12). This has been found experimentally by Kimura, Okada and Ishida (1979) in Japanese macaques, and was later confirmed in chimpanzees by Kimura (1985, 1987). The animals put their hindlimbs forward, close to their gravity vertical (see also Reynolds, 1985a, 1985b). In addition, primates possess short necks, so that their centre of gravity is shifted caudally in comparison with other, cursorial mammals like dogs and hooved animals. As a consequence, the amount of body weight resting on the hindlimbs is increased, and the forelimbs are relieved (Preuschoft, 1990; see also Figure 9.12). For leapers among the primates the same holds true (Peters and Preuschoft, 1984; see also Günther, 1989; Demes and Günther, 1989a, 1989b). If a primate puts its feet slightly forward – that is, exactly beneath its centre of gravity – it can lift its hands from the ground, because its full weight rests on the hindlimbs. In fact, a variety of bipedal postures is readily assumed by many non-human primates, often for extended periods. The mechanical requirements of *permanent* bipedality under terrestrial conditions, and the resulting selective pressures, have been discussed above.

The biological role of upright sitting and bipedal standing in non-human primates is not completely understood. So it is not surprising that the biological role of bipedality in early hominids is so much discussed. A

clutching at heels -  
 functionally we are different  
 has an toy along it?  
 SC cat - babies, femur

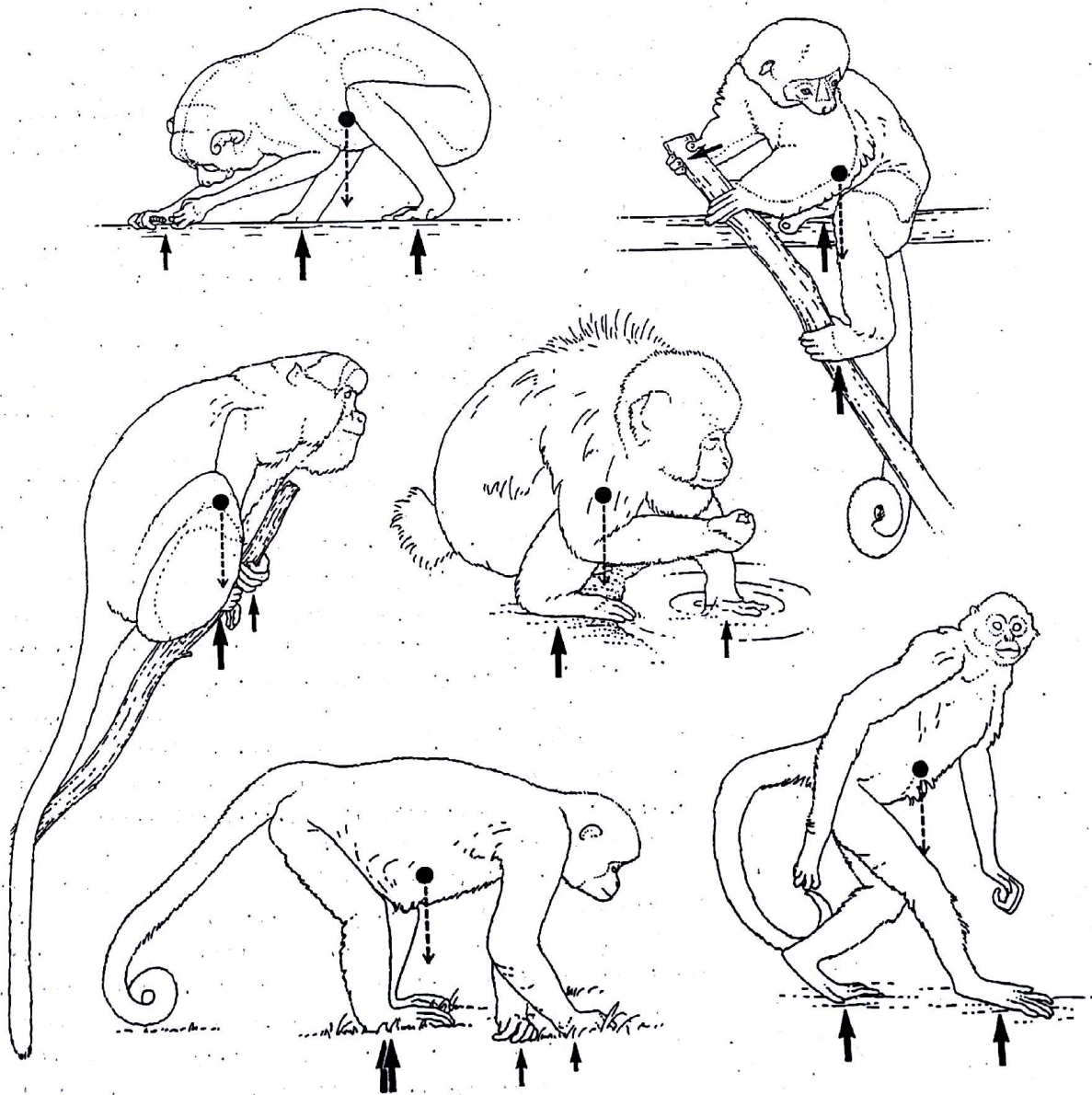


Figure 9.12 All primates carry a larger proportion of their body weight on the hindlimbs than other, cursorial, mammals do; primates are 'hindlimb-dominated', or 'preadapted' to bipedal posture and locomotion. The dots show the approximate positions of the centres of gravity, the broken arrows the direction of the weight force. The heavy arrows indicate the direction and sizes of the reaction forces to body weight.



of course hind limbs damaged  
is a pre-requisite but it  
is clearly insufficient as 'us  
own

promising new approach is contained in Wheeler's contribution to this volume (chapter 13). Undoubtedly, however, the tendency to carry much weight on the hindlimbs is related to the primates' characteristic mode of investigating and handling objects: they examine objects first by means of their hands, in contrast to most other mammals which use their lips, teeth, tongues and noses for exploration.

Interestingly, a mechanical investigation of bipedalism provides us with a hypothesis about the origin of another feature stressed by AAT adherents – namely, the 'diving reflex'. Experimental results (Nachemson, 1959, 1966; Nachemson and Elfström, 1970; Morris, Lucas and Bresler, 1961) indicate that the trunk is kept in equilibrium at the intervertebral discs not only by muscle contractions, but also by making use of the 'pneu' formed by the intestines in the abdomen and thorax, which are enclosed by the abdominal and thoracic wall muscles (see also Preuschoft, Fritz and Niemitz, 1979). Compression of the lungs requires the existence of a valve in the airways – that is, the larynx. Possibly this is the origin of the closing mechanism discussed by proponents of the AAT in the context of the 'diving reflex'.

Besides the features already emphasised, the AAT leaves open some important questions:

- When (in the chronological framework of Figure 9.1) would the pronounced aquatic phase of evolution have occurred?
- Which fossils in fact indicate an aquatic life?
- Which traits must be present in an aquatic primate to fulfil its immediate functional needs?

While the first and the second questions can be postponed until future finds provide us with the information that is lacking, the third requires the formulation of precise hypotheses that can be tested. The basis of any functional explanations of the morphological facts outlined above is empirical data, or at least precise hypotheses formulated in terms of biomechanics. Testable hypotheses of this kind, however, are usually missing in the AAT advocates' suggestions. Our attempts to obtain information from them about which of the evolutionary settings described below fits best with their theory, were unsuccessful. Apparently, they prefer raising questions to answering them. So, since testable hypotheses proposed by AAT defenders are lacking, we have ourselves tried to pin down the possibilities that exist for an 'aquatic' lifestyle. Concentrating on considerations discussed at the Valkenburg meeting, we can imagine only three variants that may serve as testable hypotheses:

- (1) The aquatic stage of hominid evolution took place along seashores. The ancestral hominids waded – searching for food, or avoiding predators – in shallow water (*marsh waders*).

aquatic phase, life raising  
they don't so 'we' don't  
testable...

compared to apes – they are  
better adapted as waders  
- and apes are  
better still



## Epistemological and Palaeoanthropological View

- (2) Our aquatic ancestors lived in somewhat deeper waters, either swimming close to the surface or diving (*shallow-water swimmers*).
- (3) Our ancestors were active, enduring swimmers, able to move rapidly in deep waters (*deep-water divers*).

Let us now try to investigate, for these three scenarios, the functional demands and their mechanical consequences.

If we assume variant (1), the *marsh wader* (Figure 9.13), we should expect the aquatic ape to have been equipped with long hindlimbs (which we indeed find in humans). Since water resistance will unduly slow down the forward swing of the limb, it is essential to raise the hindlimbs above the surface. This means that the wader has to avoid water more than knee-deep. Adaptation to wading will inevitably produce short femora and long tibiae. The locomotor mode shown in Figure 9.13 is admittedly expensive from an energetic point of view, but still more efficient than moving the swinging leg against water resistance. The proportions of femur to tibia as shown in Figure 9.13 are not present in the fossil record.

Regardless of the limb proportions, long extremities protect the trunk against becoming wet, which would lead to loss of body heat. The hindlimbs are immersed in water, which reduces their weight. Even partial immersion of the trunk, however, would greatly increase water resistance and make locomotion energetically very expensive and fleeing slow. In addition, the buoyancy of the trunk would relieve the vertical ground foot force to such an extent that wading became difficult because ground contact would be lost.

In humans and other primates the ratio of length of thigh to length of lower leg plus foot is commonly 1:1. This ratio leads to minimal angle displacement in walking movements, since the necessary lifting of the body's centre of gravity is combined with the smallest possible angle of excursion of the knee joint. Because mechanical work  $W$  is defined not only by

$$W = F \cdot s, \text{ but also by } W = M \cdot \phi$$

(where  $F$  is the force,  $s$  the distance covered,  $M$  the muscular force, and  $\phi$  the excursion of the knee joint in degrees), the 'work' required for these movements is also minimised. Therefore, the 1:1 length ratio minimises the energy required for terrestrial walking (Witte, 1991). In addition, soft substrates – as found frequently on the bottom of lakes or sea – favour a large area of support, which means long, wide feet. The 'rolling-off' of the human foot under these conditions implies a disadvantage, since it begins (heel strike) and ends (push-off by toes) with a load concentration on a reduced area of support. Everybody who has walked on soft ground knows its energy-consuming effect.

All good points if it were being proposed that humans were adapted to wading or like my recent ancestors... of course AHA isn't prehistoric - dismissed on the basis, not ability.

usually climbing usual gibbon a part of its repertoire  
✓ Deep water objectives

63  
3  
63  
74



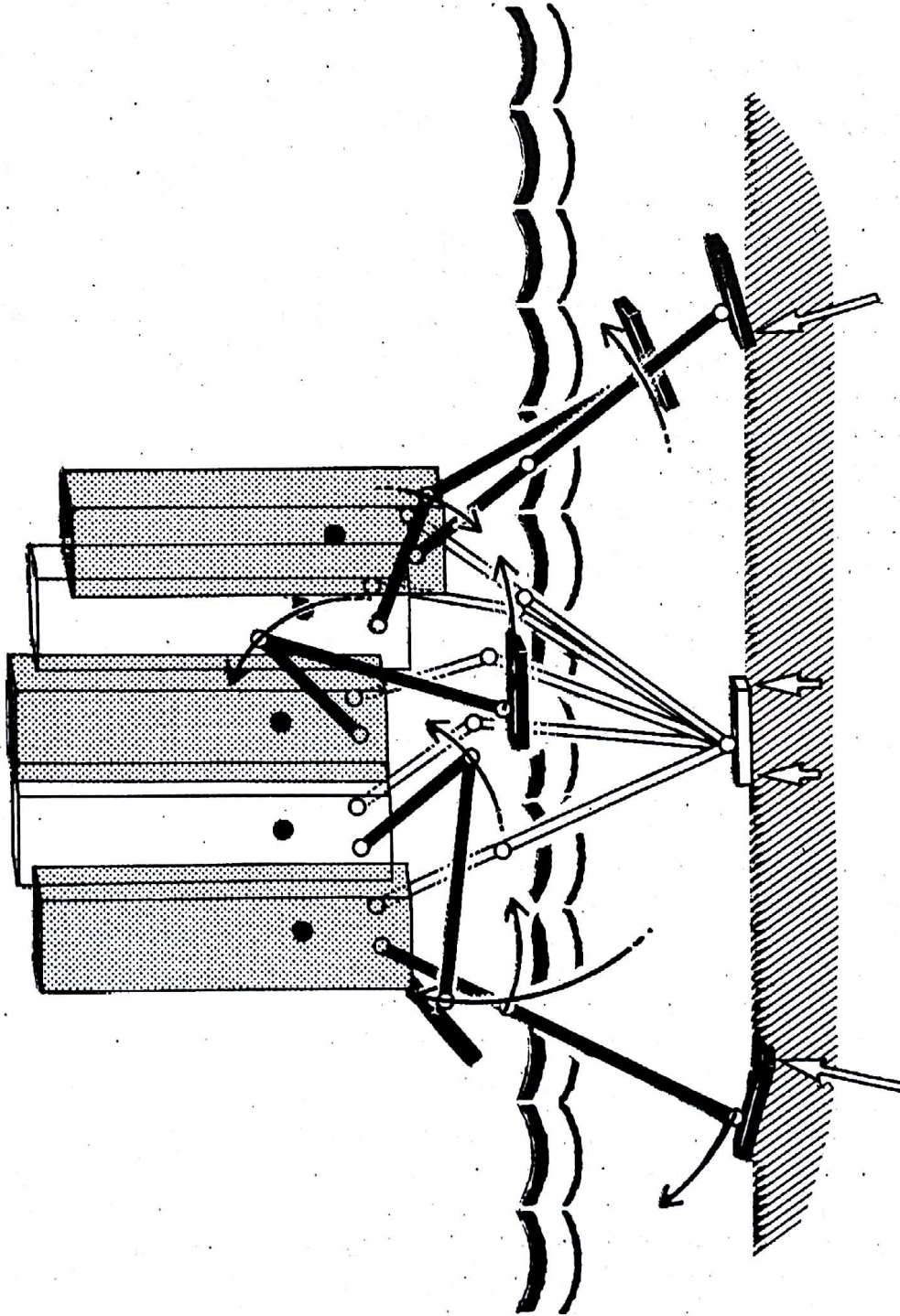


Figure 9.13 A 'marsh wader' has to keep its trunk, and swing its hindlimbs forward, above the water level. For the latter function, short thighs and long lower legs are advantageous. Note the reaction forces acting between ground and foot, varying with the shifting of the centre of gravity.

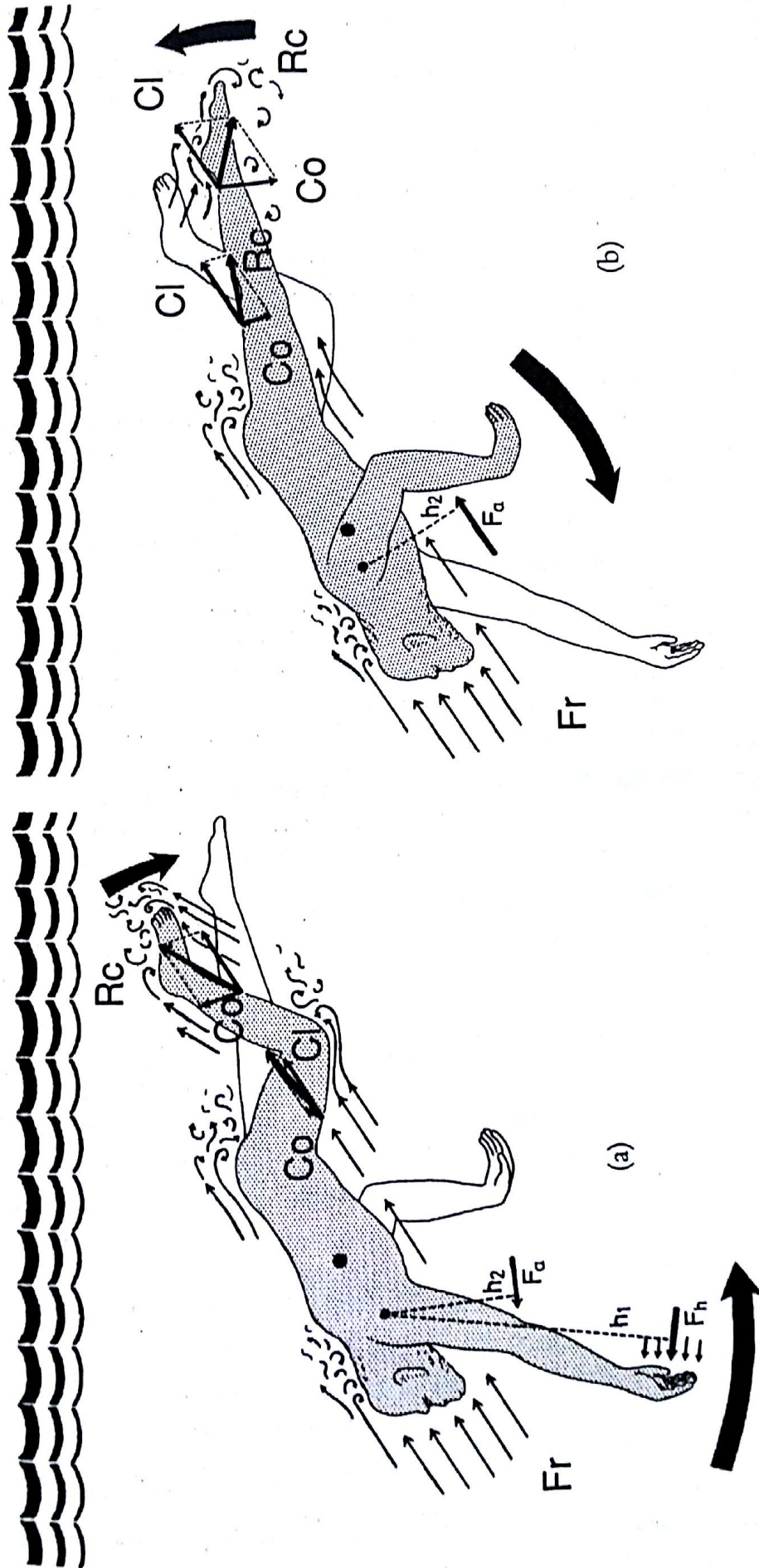


Figure 9.14 Forces (arrows) acting against the body of a swimming hominid.

(a) left arm moving backward during the propulsive stroke and left hindlimb moving ventrally; (b) left arm moving forward in the recovery stroke and left hindlimb moving dorsally. The propelling forelimb creates a moment (force  $F_a$  or  $F_h$ , multiplied by lever arm  $h_2$  or  $h_1$ , respectively) that rotates the head dorsally, towards the surface. At the moving hindlimbs, the water flow produced by locomotion (Cl) combines with the flow evoked by the up-and-down movement of the limbs (Co) to form a resultant water current (Rc). At the joints, as well as at the heels, turbulences are created that increase drag and make this animal's swimming slow and energetically expensive. To our knowledge, long scalp hair and a beard do not exclude water turbulence in the neck region.



Variant (2), the *shallow-water swimmer*, and (even more) variant (3), the *deep-water diver*, require the body density to be similar to that of water (Figure 9.14). This seems to hold true for most mammals, depending on the volume of air in their lungs and fur (Wind, 1976). One problem is the intake of air. The nostrils in all known primates are positioned frontally in the mid-face. So it is difficult for them to raise their nostrils above the water level, particularly since the neck is so short that head movements are limited.

The weight of a swimming body becomes negligible, and the forces that have to be exchanged between the body and its environment in order to cause propulsion are distributed over large areas of the body's surface. In animals not suspended in a dense, heavy fluid, body weight leads to a reaction force concentrated on the contact areas between body and ground. While swimming, all tetrapods maintain their usual pronograde orientation of the trunk axis, and their limbs move forwards and backwards as they do on the ground. The backward movements of the limbs serve to propulsion. In anteversion of the same limbs (recovery stroke), a smaller surface must be exposed to the resistance of the water to make the locomotion efficient (Wind, 1976). In the backward-directed power stroke, water resistance against the moving limb causes, as a side effect, a moment that rotates about the body's centre (Figure 9.14(a)). This increases with arm length. As long as the swimming animal remains at the surface, the backward rotation contributes to keeping the head above the water level. As soon as the animal starts diving, the ventral position of the limbs (the arms in Figure 9.14) below the trunk, which is inevitable for terrestrials, becomes a disadvantage. In fact, most tetrapods adapted to swimming have reduced limb length and the limbs are laterally placed or 'sprawled', so that (horizontal) rotation caused by one side is compensated for by the other. Enlargement of hands and feet provides them with larger paddles to make propulsion more efficient. These traits have never been found in fossil hominids. Neither in fossil nor in living primates do we find the shortened stylopodia or the broadened, elongated feet and hands which are the most obvious adaptations of habitually swimming tetrapods. Wide excursions, which include abduction to assume a 'sprawling' position, are admittedly possible in the shoulder and hip joints of many primates. But this is more probably connected with their climbing habits. Webs between the fingers and toes, which increase the surface in the power stroke while being folded in the recovery stroke, may have occurred in fossil forms – we just cannot recognise them on the skeleton. But they exist also in the indisputably non-aquatic modern apes, where they are even better developed than in humans.

Let us imagine that already orthograde hominoids took to a swimming mode of life – as shown in Figure 9.14. Because of the position of the

tetrapods swimming adaptation leads  
to limb reduction ✓  
Claws but apes have more webbing than  
humans.



## Epistemological and Palaeoanthropological View

Concedes that if upright posture  
can be late swimming hindlimbs would  
pose no problem  
- long limbs not suited for swimming  
- but they are for walking

lower limbs behind rather than ventral of the trunk, the balance of propulsive external forces would have posed no problem. But this presupposes what AAT proponents claim to explain: why these ancestors changed their body position from pronograde to orthograde on land before colonising the water.

Anyway, the body shape of modern humans is poorly adapted to swimming. The length of the hindlimbs as well as that of the forelimbs increases load-arm length without yielding more propulsion during swimming. This trait, therefore, clearly implies a waste of energy and hence a disadvantage. The existence of few joints between long segments leads to a disturbance of the water flow along the propulsive extremity, which results in a disadvantageous drag. This holds true not only for the thigh and the lower leg, but also for the metapodia and phalanges. A simple means often employed to increase the efficiency of a limb as a propulsive organ in water is to use it as a hydrofoil in both directions, up and down. This is only possible if joint excursions are possible in both directions, and if the segments are largely symmetrical. As emphasised by Wind (1976; this volume, chapter 17), in most or even all primates this holds true for the shoulder and carpal movements, but not at all for the elbow and finger joints, nor for the joints of the hindlimbs. In living as well as fossil primates, movements of the knee and ankle joints and finger and toe joints are limited at full extension, and at least the phalanges, and sometimes also the tibia, are curved, which makes them asymmetrical.

On the level of biological roles, we believe that the human affection for water depends on fashion. Today everybody seems fond of bathing, but a hundred years ago this was far less common. Another argument, just as attractive as the affectionate relationship of humans to water, should not be ignored: from the early stages of human history, on through all centuries, the wealthy classes have chosen to build their homes in places that exhibit a clear preference for open, diverse landscapes, with grassland interspersed with patches of woodland or individual trees, often embellished by flowing water or lakes: the parkland savannah. Man's evident dislike of dense forest may be illustrated by the extent of its intended total destruction.

## CONCLUSION

Current palaeoanthropological explanations do not satisfy AAT proponents. This is because current ideas do not (yet?) yield plausible reasons for *all* human characteristics, and AAT proponents insist that other questions about hominisation have to be raised. Therefore, the current ideas are rejected and new ones proposed.

A final evaluation of the AAT is impeded by the fact that it is vague in several respects. It leaves open the relative and absolute dating of the

who's being the hydro adapted and  
not? They want to have it  
both ways.

fashion? - there is a great deal of  
evidence that humans were  
very adept at diving -  
then diaspora likely to have  
been coastal



AAU - vague - dady of 'puzzle'  
 enigmatic features  
 biological roles not further (ch.)  
 - lack of testable hypotheses

presumed aquatic phase. It stresses some arbitrarily selected 'enigmatic' features of *Homo sapiens* and provides purely hypothetical explanations for them - without any attempt to give detailed, causal explanations for the origins of these traits. Because hitherto the AAT has been discussed only at the level of biological roles, not at the level of the mechanical functions fulfilled by the morphological structures that are found in fossils, the theory suffers from a lack of precision. The reason for, as well as the consequence of, this flaw is the absence of testable hypotheses and predictions deduced from them.

If not only the enigmatic characteristics, but others as well, are taken into account, it becomes evident that the AAT contains large *gaps*; its proposals are insufficiently *integrated* and by no means free from *contradictions*. Also, the *parsimony* of the AAT has to be questioned, because of the lack of explanations for less conspicuous traits. In its present form, the AAT is not able to produce satisfying *hypotheses that can be tested empirically*. One of its few *predictions* postulates the extension of the search for fossils into areas which have not yet yielded any finds. To be sure, by refusing to accept common opinions, the AAT has *stimulated* a reconsideration of ideas already available. Unfortunately, the AAT does not provide us with a more *complete understanding* of the facts about human evolution than we have got already.

On the other hand, detailed investigations of the mechanical function of several traits of modern humans, as well as of our fossil precursors, have been carried out. The results of these studies fit together, and are in accordance with, or even support, the traditional palaeoanthropological ideas which assume the evolution of hominids in a terrestrial, savannah-like habitat.

Although we feel attracted and, more so, challenged by some of the arguments derived from the Aquatic Ape Theory, we regret to conclude that we cannot offer any support to it. We do not agree that there is a need to postulate an aquatic phase in the evolution of man.

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AAT - has gaps  
 insufficiently integrated.  
 not free of contradictions  
 parsimony questioned  
 not testable

accords with  
 or support  
 ev. in  
 terrestrial  
 savannah-like



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