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THE AQUATIC APE THEORY*

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THE AQUATIC APE: Fact or Fiction? • Roede e

# THE AQUATIC APE: Fact or Fiction?

*The first scientific  
evaluation of a controversial  
theory of human evolution*

*Edited by:  
MACHTELD ROEDE  
JAN WIND*

# THE AQUATIC APE: FACT OR FICTION?

*The First Scientific Evaluation  
of a Controversial Theory of Human Evolution*

*Edited by*

Machteld Roede, Jan Wind,  
John M. Patrick and Vernon Reynolds

SOUVENIR PRESS (E&A) LTD

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First published 1991 by Souvenir Press (Educational & Academic) Ltd,  
43 Great Russell Street, London WC1B 3PA  
and simultaneously in Canada

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ISBN 0 285 63033 4

Printed in Great Britain by  
WBC Print Ltd, Bridgend, Mid Glamorgan

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## Preface

In Valkenburg, in the hilly southern part of the Netherlands, above limestone caves in which fossils like the *Mosasaurus* bear witness to a former marine environment, a conference, organised by the European Sociobiological Society and the Dutch Association of Physical Anthropology, was held in August 1987. Its aim was to evaluate the pros and cons of Sir Alister Hardy's daring idea about the Aquatic Ape, a presumed early ancestor of humans.

The number of fossil data relating to our evolutionary origins is increasing all the time; molecular studies further extend our understanding of hominid phylogeny. Hence the uncertainties and controversies surrounding reconstructed pictures of our early progenitors are decreasing. Though various interpretations of the fossil data exist, there is a growing consensus that about 5 million years ago there was a split of the lineages that finally led, on the one hand, to man, and on the other, to the chimpanzee. Humans are in various aspects so different from other mammals – including other primates – that, according to Darwinian theory, we could only have evolved when our earliest hominid ancestors occupied a specific niche, quite different from that of the other contemporary primates. Accordingly, there has been much discussion about our Miocene ancestors. Unfortunately, very few fossil data are available for that period, and so the dawn of mankind remains wrapped in mist.

Yet it is generally accepted that during that period the proto-hominids abandoned living in the trees and started to move, with the first steps of a primitive bipedalism, into a new environment. At the Valkenburg meeting the question of whether this was the savannah or, rather, an aquatic environment was raised.

Raymond Dart was among the first to suggest a transition from an arboreal into a savannah niche. The latter was the environment where later, about 3.5 million years ago, 'Lucy' (*Australopithecus afarensis*) and her australopithecine mates kindly left sufficient fossilised traces to enable us today to make statements about their morphological and physiological features, as well as about their behaviour. Dart's idea has been taken for granted ever since, and its acceptability has hardly ever been tested in the light of our knowledge of our physiological and motor development capabilities. Hitherto, possible scenarios for evolutionary paths have been

proposed almost exclusively by experts on bones, few of whom are acquainted, for instance, with the specific demands on the bone-muscle apparatus involved in the specific skills and behaviours of a decreasingly quadrupedal creature, or with the special physiological demands posed by living in hot, open plains.

In accordance with the rule that the human mind is inclined to select from among new facts only those which fit into the pattern of concepts already shaped, and with our resistance to new, strongly deviating facts, the idea that hominid speciation was initiated during a (semi-)aquatic period has been ignored or played down. This occurred despite the fact that this new idea gave rise to various quite reasonable explanations, some more acceptable than those that have arisen from the Savannah Theory.

The aim of the present volume is to compare the traditional savannah scenario with the alternative aquatic one, and by so doing to attempt to reconstruct our very first hominid ancestors. Arguments both in favour of and against the savannah and the aquatic theories will be presented. One of the values of the present approach lies in the fact that in comparing the pros and cons, soft tissue such as fat and hair, and also tears, as well as skeletal structure, have been taken into account. Moreover, hypotheses have been tested in the light of current understanding of respiratory and other physiological processes, and particularly of behaviour. There is also a chapter on the underlying mechanism whereby an alternative idea such as the Aquatic Ape Theory tends to be rebuffed and rebuked.

This volume mainly offers the contributions presented at the Valkenburg meeting; but it is more than simply a collection of proceedings. The speakers were asked to write out their contributions, incorporating the discussions held during the conference. Other scientists were also asked to contribute, and it was decided to include presentations by young scientists as well as some by more senior scholars, all of quite diverse backgrounds.

The contents of the book are organised into three main parts. Part I starts with a survey of the history of Sir Alister Hardy's idea and an elaboration of the concept by Elaine Morgan. This is followed by a suggestion for the most likely place of origin of our presumed aquatic progenitors – the Danakil Alps – by Leon P. LaLumiere, an evaluation of the ecological wetlands conditions by Derek Ellis, and a survey of fossil material by Marc Verhaegen. Part II starts with a discussion by Graham Richards of why the Aquatic Ape Theory has encountered so much resistance. Then follow essays written from different angles, both protagonist and antagonist. Martin Pickford comments on the lack of geological and palaeontological evidence, and Alan Turner refers to the current debate in evolutionary biology about the significance of apparent

adaptations. At particular points the debate concentrates on physiological characteristics such as thermoregulation in relation to water balance (Verhaegen), fat distribution (Caroline Pond), and hair pattern and hairlessness (Peter Wheeler, Paul Leyhausen). John Patrick and Erika Schagatay discuss respiratory adaptations for swimming and diving; Holger and Signe Preuschoft, and Joseph Ghesquiere and Helene Bunkens concentrate on buoyancy and locomotion. Jan Wind also discusses swimming, and provides evolutionary explanations of the human proneness to drowning. Shorter contributions cover comparisons of humans and apes (Karl-Erich Fichtelius) and of humans and sea mammals (Cornelis van Nie and Roede), and a proposal by Sarah B. M. Kraak that the Aquatic and Savannah Theories should be combined, while Schagatay offers some original speculations on breastfeeding, and suggests why the presumed aquatic niche was abandoned. Machteld Roede surveys the relations between man and the sea today. Part III comprises a concluding essay by Vernon Reynolds and an epilogue by the editors.

We wish our readers as much enjoyment and interest as we ourselves felt during the very stimulating meeting at Valkenburg, and while preparing this book.

October 1990  
Machteld Roede, Jan Wind,  
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## Part I

### THE AQUATIC APE THEORY



# 1 The Origins of a Theory

Elaine Morgan

## SUMMARY

The theory of a possible aquatic phase in human evolution was first presented in 1942 by Max Westenhöfer in Germany; it was also independently conceived by Alister Hardy in 1929 and published by him in 1960. This chapter quotes Hardy's reasons for delaying the publication, describes the reception accorded to his ideas, and outlines some subsequent developments.

## THE BEGINNINGS

Alister Hardy first conceived the idea of a possible aquatic phase in human evolution in 1929 on reading the following passage from Wood Jones's *Man's Place Among the Mammals*:

The peculiar relation of the skin to the underlying superficial fascia is a very real distinction, familiar enough to anyone who has repeatedly skinned both human subjects and any other members of the primates. The bed of subcutaneous fat adherent to the skin so conspicuous in man, is possibly related to his apparent hair reduction, though it is difficult to see why, if no other factor is invoked, there should be such a basal difference between man and the Chimpanzee.

Hardy's response was immediate. As a marine biologist, he was more familiar with the skinning of sea mammals than of either human or non-human primates. The phenomenon described by Wood Jones in connection with human bodies reminded him irresistibly of his own first-hand experience of the skin of various species of aquatic mammals in which a layer of subcutaneous fat is the norm. He wondered whether in man also it might initially have been an adaptation to a more aquatic way of life.

Other parallels between man and aquatic mammals soon sprang to his mind, such as the naked skin, the relatively streamlined silhouette of human beings compared with that of other primates, and the occasional incidence of interdigital webbing. He reasoned that for a primate which spent much of its time wading in water, an erect posture would become obligatory and, at the same time, easier to sustain without overbalancing. The precision hand-grip and the unusual arrangement of hair tracts on the human body (much debated at the time) could have been acquired in the same way.

He did not publish his ideas for over thirty years. His friends warned him that if he publicly advocated such a bizarre theory it would blight his career. They were probably right. At the end of his life he was refreshingly candid about his reasons for keeping silent: 'I wanted to get a good professorship; I wanted to be a Fellow of the Royal Society'. As it turned out, long before he was ready to publish, a version of the hypothesis appeared in print in Germany, as one passage in a book entitled *The Unique Road to Man* (*Der Eigenweg des Menschen*), written in 1942 by Max Westenhöfer, a professor at the University of Berlin.

Westenhöfer's account of the aquatic theory was that of a man who had not made up his mind about it. He made no claim to be the originator; neither did he credit anyone else with originating it. He seemed, rather, to assume that it had been around for some time and that his readers were likely to be familiar with it in general terms. It is quite conceivable, since Hardy spoke of his ideas to some of his friends and pupils in the interwar years, that speculation about it had already spread farther afield than Oxford, and had crossed to the Continent without being traceable to any particular source.

Westenhöfer searched the literature of primate anatomy for any reference to aquatic influence, and for species-specific features of human anatomy which remained unaccounted for. He made no attempt to identify the aquatic phase with any specific date, place or causative event. One of the papers, written by G. L. Sera in 1924, hypothesises a very early aquatic phase. Sera sought to account for some differences between Old World and New World primates by suggesting that the ancestors of the platyrrhines had undergone a period of aquatic development not shared by the catarrhines. Westenhöfer's general conclusion was that an aquatic experience at some time or other was a promising hypothesis worthy of further consideration.

Unfortunately, Westenhöfer's book was published in the middle of the Second World War. Europe had other things on its mind, and the usual channels for the exchange of scientific ideas were silted up. By the time they ran clear again, the heretical hypothesis had apparently been forgotten. Certainly Hardy knew nothing of Westenhöfer; he died in 1985 at the age of eighty-nine without ever learning that he had been forestalled. By 1960 he had achieved the aims he had set his sights on: the Oxford professorship and the FRS, and a high reputation as the author of authoritative works in his own field. He now felt able to lower his guard sufficiently to outline his theory to a local sub-aqua club that he had been invited to address. A version of his speech was communicated to the local press, and it appeared in garbled form under sensational headlines in the Sunday newspapers. Hardy published one article and one

Since he was a man who inspired affection as well as respect, academic scholars adopted what they saw as the kindest and most British way of dealing with an embarrassing situation: they behaved as if he had not spoken or, at least, as if no one had happened to be listening at the time. Among many who were in all other respects his staunchest admirers this attitude never wavered, so that when he died his obituaries praised him for many things but conspired to ignore his aquatic 'indiscretion'. This has promulgated the myth in some quarters that Hardy had propounded the whole thing as an impish practical joke which some misguided people were naïve enough to take seriously. However, in the last year of his life he was interviewed about the subject on film\* and he made it absolutely clear that he regarded his hypothesis as revolutionary, and significant, and entirely valid.

I first came across Hardy's theory on reading a brief reference to it in 1970 in Desmond Morris's book *The Naked Ape*, and vainly searched through books and journals on evolution for further information or commentary about it. Apparently for ten years it had been silently sinking into oblivion. I therefore wrote to Hardy saying that I intended to write a book about it. He knew nothing about me, and I did not conceal that I had no qualifications for entering the arena other than my conviction that he was right. So my letter came to him as, in his own words, 'a bit of a shock', since he had never relinquished the idea of one day writing at greater length on the subject himself.

However, he responded with characteristic generosity. On 26 October 1970, he wrote:

Yes, of course you must go ahead and do so with my enthusiastic blessing. I hope it will be a great success. As it is turning out, it may well be the best arrangement from my point of view. You will be interesting – I hope and think exciting – the general public in the idea, and . . . preparing a wider public for my more zoological and anatomical treatment of the subject than I might otherwise expect. Press on with it as hard as you can, although I am in no hurry to publish quickly and my chapters are not written – just lots of notes.

I did not meet Hardy or discuss the contents of my book with him – or with any other scientist – until after it was published in 1972 under the title of *The Descent of Woman*. It featured some additional arguments which Hardy had not considered. Some of them – for example, the regression of the olfactory lobe and ventro-ventral copulation – had already occurred to Westenhöfer and were mentioned in his book (of which I knew nothing until Jürgen Hinrichs-Röhrig drew my attention

\* *Water Babies*. Golden Dolphin Productions, 21–3 McLaren Street, New Sydney 2060, Australia.



to it in 1986). Other arguments, based on weeping and voluntary breath control, were new.

Whatever the book's merits or demerits, it performed one vital service: it attracted enough attention to ensure that the aquatic theory would this time have a greater chance of remaining on the agenda of evolutionary theorists. It was translated into ten languages and blew the spores of the idea all round the world; they germinated in the minds of the young and receptive and of many who were already convinced that there was something missing in the conventional scenario of the emergence of man.

### THE HYPOTHETICAL AQUATIC MODE OF LIFE

For those interested in the history of this idea, the original documents are not always easy to retrieve. I therefore reprinted Hardy's papers on the subject in full in *The Aquatic Ape* (Morgan, 1982), and I append herewith a translation of the relevant passage from Westenhöfer's book.

The postulation of an aquatic mode of life during an early stage of human evolution is a tenable hypothesis, for which further inquiry may produce additional supporting evidence.

The shape of the human foot, broadening towards the front, could indicate a paludine habitat, especially when we note the observations of Mr O. Abel in his *Palaeobiology* (Stuttgart, 1912, pp. 229–30) where he discusses the secondary plantigradism of certain fossilised bog animals, for instance, *Mesodon* and *Coryphodon*, whose footprint shows a remarkable similarity to that of humans. For such a mammal, moreover, a move to an aquatic environment would mean that powerful teeth would become unnecessary due to the relative softness of the available food resources.

The fact that man lacks hair – but probably was hairy at some earlier stage – suggests an analogy with the relative absence of hair in water mammals (whale, sea-cow, hippopotamus), especially since so far there is no other plausible explanation. Another indication is the subcutaneous layer of fat in humans; its capacity for expansion appears to predate human civilisation. The so-called Venus statuettes, dating back to the Stone Age, support this assumption. The hitherto unsolved problem concerning pigmentation in humans may be related to this problem; rather than loss of pigment in the white races, there may have been increased pigmentation in coloured ones, corresponding to the post-natal increase in pigmentation in children of all races.

In his latest book *On the Significance of the Ear Muscle*, Mr B. Henneberg also proposes an aquatic mode of life in the prehuman primate. He assumes that this ancestral hominid featured a contractile

form of the ear muscle, with the anthelix (tragus and antitragus) differing in shape from that of *Homo*, and that this original form was subsequently lost during the transition to life on land. It is still easily possible to reproduce the original form in children by artificial means, and the original feature has in fact been observed in one living newborn baby. In his famous work *Physiology of Movement* [Philadelphia, 1949], Duchenne shows that electrical stimulation of the tragus and antitragus muscles in human beings is capable of closing the entrance of the ear, which is why he calls the two muscles 'constrictor conchae sup. and inf.'

Man shares with the water mammals the regression of the olfactory organ, the bulbus and lobus olfactorius which, according to A. Kappera and Count Haller, is connected with a certain development in the conformation of the brain, not found in the macrosomatic animals.

As further evidence of an earlier aquatic way of living for man, one could also point to the existence of mucous glands in small benign tumours in the skin of man's back which the Prague pathologist Schickel has investigated and which, in the absence of any other possible explanation, with reference to fish and frogs, he has called atavistic. Such mucous glands have survived as the normal condition in the hippopotamus as a physiological adaptation to its aquatic environment, while in humans they appear under pathological conditions about which little is understood.

To this can be added the not particularly rare web-like skin formation on the hand and toes (seen also in *Potamogale*, the otter shrew), and the direction of the body hair towards the elbow on the lower arm in human beings and anthropoids, as well as in other apes and quadrupeds. The usual explanation, that the direction of the hairs functions as protection against rain when the arms are placed over the head, is too naïve to be correct. Apart from the fact that the head does not even get covered, the water then would be conducted forward from the elbow between the hairs of the upper arm and thereby directly to the skin of the armpit and chest, which would hardly be advantageous. Even if this direction of the hairs were peculiar to man, I would see it as not insignificant support for my aquatic hypothesis, since such a direction of the hairs on the lower arm during swimming (stretching the arms forward) would have been useful.

This summary should not be concluded without some reference to the ideas of the anthropologist, G. L. Sera, in Naples. He takes the view that the form and development of the Adam's apple, the shortness of the outer auditory passage, the form of the musculus glutaeocruralis (m. tenuisimus), some characteristics of the female genitals, the formation of the kidneys, the form and development of the nasal cartilage, and the form of the ear muscle may constitute evidence of a



possible aquatic phase in the evolution of the platyrrhine New World primates. And finally, I would point out that man's way of mating is also the standard method among water mammals such as beavers, cetaceans and sirenians.

The aquatic theory remains an open question. But such hypotheses, which at first sound so improbable, should at least serve as a stimulus to further research, on the principle that a good detective follows up the least promising clues as well as those which seem to point to a simple solution.

## REFERENCES

- Hardy, A., 1960, Was man more aquatic in the past? *New Scientist*, 7, 642-5.  
 Morgan, E., 1972, *The Descent of Woman* (London: Souvenir Press).  
 Morgan, E., 1982, *The Aquatic Ape* (London: Souvenir Press).  
 Morris, D., 1967, *The Naked Ape* (London: Jonathan Cape).  
 Sera, G. L., 1938 *Archivio Zoologico Italiano*, Vol. 25.  
 Westenhöfer, M., 1942, *Der Eigenweg des Menschen* (Berlin: W. Mannstaede & Co.).  
 Wood Jones, F., 1929, *Man's Place Among the Mammals* (London: Edward Arnold).

## 2 Why a New Theory is Needed

Elaine Morgan

## SUMMARY

*Homo sapiens* is the anomalous member of the primate order. The orthodox version of our evolutionary emergence on the savannah leaves too many unique features unaccounted for. The Aquatic Ape Theory (AAT) offers a unitary solution to a higher proportion of these anomalies than does any other hypothesis.

### A SAVANNAH HABITAT?

Over a hundred years have passed since Darwin wrote *The Descent of Man*. During that time, despite intense research and speculation, the major questions – why man became bipedal, lost his body hair, learned to speak, developed a big brain – have come no nearer to solution. New hypotheses are regularly propounded, but none has yet commanded professional consensus or prompted the feeling that the search is now over. This record of failure has done little to weaken faith in the orthodox scenario – that is, that a move from the trees into a more open habitat was the ultimate and sufficient reason why hominids began to differ so radically from apes. A critique of this proposition is therefore an indispensable preliminary to advocacy of the Aquatic Ape Theory (AAT).

Other primates (baboons, patas monkeys, for instance) have made the transition to the savannah with minimal phenotypic or behavioural modification, and have flourished. There seems to be no inherent reason why the progenitors of hominids, faced by the same fairly simple problems of adaptation, could not have solved them just as economically. Instead, they resorted to a gradual but revolutionary restructuring of their methods of walking and running, breathing, regulating their temperature, and communicating with their fellows. The features distinguishing them from the apes are normally represented as adaptations making them fitter to survive on the savannah. But most of these adaptations, in the initial stages, must have been positively maladaptive in that environment. A few examples will serve to illustrate the point.

### LOCOMOTION

Quadrupedalism characterises the overwhelming majority of ground-dwelling mammalian species. It affords stable equilibrium, is efficient in



energy terms, lends itself readily to speed, and is easily learned by the young, often within hours of birth. It allows for emergencies: a quadruped with one injured leg walks on the other three while it heals. The gently arched and cantilevered spinal column has been perfected over millions of years to combine maximum strength with flexibility.

No animal could afford to sacrifice all these assets without an overwhelmingly powerful selective pressure. The cost of habitual plantigrade bipedalism is high. It is the most unstable method of mammalian progress known to zoology. Growing bipeds only perfect the art after years of practice and innumerable tumbles. Even in their prime, damage to one leg can cripple them; once past it, equilibrium again becomes a problem. The bipedal posture, with viscera and male sex organs exposed to attack, is ill designed for confronting an enemy or predator.

In a biped the vertebrae and intervertebral discs are subjected to weights and stresses which the spines of quadrupeds do not have to sustain. The S-shaped curve of the human spine minimises direct downward pressure but creates an area of instability in the lumbar region. The modified angle of the pelvis means that in childbirth the foetus has a more tortuous exit path to negotiate than is the case in quadrupeds. In man, the change from a quadrupedal to a bipedal stance raises the heart roughly twice as high above the ground, and the resultant pooling of the blood in the lower limbs puts additional strain on the vascular system. After millions of years of adaptation to bipedalism we are still plagued by pains and malfunctions such as chronic lower-back pain, inguinal hernia, and varicose veins.

The claim is often made that bipedalism was adaptive because it 'freed the hands'. But an ape's or monkey's hands are perfectly free except when it is moving from one place to another; human beings, likewise, normally engage in skilled manual operations only while sitting or standing, and very rarely while actually walking or running. It could as well be argued that bipedalism reduced our potential for dexterity, since the so-called freeing of the hands was accompanied *pro rata* by the 'enslavement of the feet' (Richards, 1986). This, in the long run, has halved our allowance of serviceable manipulative digits.

It was long argued that the hominid first evolved a big brain and the ability to fashion tools and weapons, and that bipedalism became necessary to enable him to carry a weapon to hurl at his quarry. All theories along these lines had to be abandoned after the discovery of the Afar hominids such as Lucy—small-brained creatures, clearly bipedal, with no evidence of tools or weapons. Three separate lines of argument have emerged in an attempt to replace the weapon-carrying hypothesis.

Carrier (1984) has argued that man's physiology may be evidence of strong selective pressure in favour of endurance running. He has published that over long distances bipedal running is an advantage to a

human hunter because his four-footed quarry becomes exhausted sooner than he does. This may well have been a fortunate consequence of bipedalism, but it is very unlikely to have been the cause, firstly because the fossil discoveries suggest that bipedal walking was well established before there was any evidence of hunting, and secondly because animals capable of covering short distances bipedally (for example, apes, bears, vervets, beavers) invariably revert to quadrupedalism when speed is required. To justify the contention that game-hunting led to bipedalism, it is not enough to demonstrate that modern *Homo sapiens* runs more effectively on two legs: it is necessary to demonstrate that an unadapted pre-Australopithecine anthropoid could have run more effectively on two legs than on four. Experiments with primates (Taylor and Rowntree, 1973) suggest that bipedalism is slower and consumes more energy.

Lovejoy (1981) envisages a pair-bonded male hominid foraging much farther afield than his mate and walking upright in order to carry food back to her. The concept of a hominid nuclear family is a persistent one, but improbable. Monogamous mammals display minimal sexual dimorphism, whereas *Homo* is unrivalled in the number and variety of epigamic markers. Lovejoy does not specify the type of food being carried. Any ape wishing to transport all or part of a dead animal would carry or drag it with one hand and run on three. Long treks with handfuls of seeds or berries would not repay energy output. The only kind of food conducive to primate bipedalism consists of armfuls of rather bulky items such as large tubers, bananas or coconuts. We need evidence that the savannah yielded such products.

Wheeler (1985) suggests that man descended from a meridional ape, which gained an edge over competitors by reducing the time needed to rest in the shade, and was thus able to devote more time to foraging. For this purpose, it is argued, the ancestral hominid adapted to withstand the sun's noonday heat by minimising the percentage of body surface presented to its perpendicular rays — that is, by standing erect. Some support for this thesis is provided by Newman (1970) and Sakura (1983). The assertion that bipedalism bestowed a competitive edge can only be assessed by considering what other species were competing for the same scant resources. The likeliest candidates would be savannah baboons such as the hamadryads. This successful species shows no signs of being disadvantaged by the habit (common in many primate species) of resting at midday: its siesta is combined with the visit to the water hole, which is obligatory for most savannah species at some time during the day. The marginal putative advantage conferred by day-long non-stop foraging would be unlikely to outweigh the considerable incidental costs of bipedalism and hair loss.

None of these theories offers an entirely satisfactory explanation of habitual bipedalism, a behaviour pattern so specialised that it only



emerged in one mammal, and so fraught with drawbacks that it would seem to have been adopted only under some kind of duress.

## FUR

Fur is another classic mammalian feature which *Homo* alone is supposed to have found incompatible with life on the plains. It is a prime asset which no land mammal could lightly afford to dispense with: a first line of physical defence against heat and cold and ultraviolet rays. It may also fulfil additional functions such as colour camouflage and threat signalling by pilo-erection.

Primates, particularly, would find it indispensable. Primate mothers are free to swing, leap, clamber, brachiate and run on all fours *only* because the young can hold on to their fur. The hominids were the only primate infants whose hands encountered smooth skin to which they could not cling. No other primate mothers are hampered, except for a brief neonatal period, by having to support their growing offspring in their arms. In the case of the hominid females the hands – even if they had been in any real sense freed by bipedalism – were promptly enslaved again (by the requirement to support offspring because of the loss of body hair) for the greater part of their lifespan.

Theories about hair loss normally refer to the problem of keeping cool during the hot tropical day. (The problem of keeping warm during the cold tropical night has received little attention.) It is not clear why the hominids' need in this respect is thought to have been unique. Reference has been made (Wheeler, 1985) to the lack of a carotid rete, yet the lack of it has not obliged other savannah primate species to shed their fur. The further suggestion that hominids needed new cooling strategies because of their reduced nasal chambers and turbinates is a circular one: if these organs had been important to the animal's well-being, they would not have been reduced.

Experiments with depilation have shown that fur (for example, in the camel) is an efficient barrier *against* heat gain from the environment (Schmidt-Nielsen, Schmidt-Nielsen, Jarnum and Houpt, 1957). The argument therefore hinges on hair loss as an important facilitator of sweat-cooling. But sheep, camels and the desert-dwelling wild ass effectively utilise sweat-cooling without having naked skin. At least one primate (the patas monkey) has, without denuding itself, evolved a highly efficient system of sweat-cooling, adequate to its needs even though it is reputedly the fastest running of all primates and is active all day long in its hot and often arid savannah habitat (Mahoney, 1980). The hominid could presumably have done the same. Newman (1970), exploring the relationship between bipedalism, nakedness and sweat, concluded that

nakedness was unlikely to have evolved in order to facilitate sweat-cooling in the heat of the savannah. He believed that nakedness predated sweat-cooling and that 'loss of hair must have stemmed from other causes, or predated the occupation of the habitat in question'.

On the question of hair tracts on the human body, it is doubtful whether their arrangement affords reliable evidence of evolutionary origin. There are some unique features, which Hardy (1960) cited because in his youth it was a subject much researched and debated. Two points should be noted in connection with the new 'aerodynamic' model offered by Wheeler (this volume, chapter 13) to explain the anomalies. Firstly, air currents produced by natural convection would only rise straight up around the body as long as the hominid was not only perpendicular but also stationary, and this would seldom be the case while he was foraging for scattered food sources. Secondly, the convection model does not purport to explain the anomalies in hair tracts on the upper part of the body, yet that is where some of the more striking examples are found (Kidd, 1903).

## SWEAT

Sweat-cooling is achieved by the evaporation of a film of liquid from the surface of the skin. In most land mammals which resort to sweat-cooling – other than man – the liquid is a suitable dilute secretion of the apocrine glands, which are found all over the body in association with hair follicles. In humans these apocrine glands are present prenatally but vanish before birth, except for specialised groups in axillary and pubic areas. They are replaced by millions of eccrine glands such as those commonly found in other species on palms, soles, paws and the underside of prehensile tails (volar eccrines). Some higher primates have non-volar eccrines over the body surface, but they are much fewer in number than in man, and in terms of thermoregulation they appear to be non-functional (Montagna, 1972).

A study of thermogenic sweating in three baboons (Hiley, 1976) established that sweating in the area of the chest was the product of epitrichial (that is, apocrine) glands. Another study (Elizondo, 1988) describes thermogenic sweat from the lateral calf of a patas monkey as eccrine; but the methodology fails to establish whether the sweat was exuded by the eccrine glands or by the apocrine glands with which they are interspersed.

In humans the rate of sweat secretion is higher than that of any other known mammal. However, in sweat-cooling, profusion as such is not necessarily an advantage. Sweat exuded more rapidly than it can evaporate is wasted: the excess liquid does nothing to reduce body



temperature. That is why in humid conditions sweating affords little or no relief.

Eccrine sweating has two disadvantages. Its onset is delayed (Newman, 1970); it is in the interval between a sudden temperature rise and the beginning of the sweat flow – which can be anything between five and thirty minutes – that human beings may succumb to heat stroke. The second disadvantage is that eccrine sweating continues to flow profusely even when dehydration and/or salt depletion are reaching dangerous levels. Water and salt are both scarce on the savannah, and increased water dependence would limit the range available for foraging. Such an environment would be unlikely to foster the emergence in the hominids of a cooling system so profligate of both these vital resources (Denton, 1982).

### THE LARYNX

In all land mammals, with the exception of man, the trachea extends from the lungs via the larynx into the back of the nasal passages; they are known as obligatory nose breathers. The obligation is not absolute: the epiglottis in many animals can, at need, be detached from the palate to afford temporary mouth breathing for purposes of vocalisation or thermoregulatory panting. But as soon as these efforts are relaxed, nose breathing resumes.

This near-universal system is highly efficient. It facilitates olfaction; it ensures that all air reaching the lungs has been filtered, warmed or cooled to near body temperature, and moistened by passing over the mildly bactericidal mucous linings of the nasal passages. It enables an animal to drink and breathe at the same time. It entirely rules out any possibility of an animal being inconvenienced by food and drink entering the airways.

In an adult human being these advantages and safeguards have been lost. The larynx has lost contact with the palate and descended to a point well below the back of the tongue, adjacent to the opening of the gullet. It is a development which mystified Darwin and Negus, among others. No one has been able to suggest any advantage which this change would bestow on a terrestrial mammal. The effects seem uniformly deleterious. The lungs are rendered more vulnerable. During sleep in a supine position the tongue may relapse into the back of the throat, blocking the airway entirely for a short period, and during deeper unconsciousness – for example, from concussion or anaesthetics – the blockage can be fatal. The respiratory tract of young babies initially resembles that of the rest of the animal kingdom. The gradual descent of the larynx at about four to six months coincides with the peak incidence of 'sudden infant death syndrome' and it has been argued that there may well be a causal link (Calkins, 1978). For example, if a throat infection caused a

partial obstruction of the airway, the infant's earliest reflexes would prompt a raising of the larynx to within the nasal passages; but if the larynx had partially descended, this could no longer be achieved and the attempt might cause the airway to be blocked by the uvula.

Current thinking about laryngeal descent envisages it as a fortuitous effect of the change in the angle of the human skull which followed adoption of the erect posture (Laitman, 1983; Lieberman, 1983). But this argument is weakened by the fact that in other animals where the larynx has descended (sea-lion, dugong) the basicranial angle has not changed.

### FAT

Man is unique among primates and among most land mammals in his propensity to accumulate comparatively large amounts of adipose tissue, especially in subcutaneous sites. This would seem an unlikely adaptation to a savannah environment, whether the hominids are envisaged as hunters or only as potential prey, since the extra weight would slow them down. The land mammals which regularly accumulate considerable fat stores are the hibernators and estivators, but in them the fat is seasonal, and in man it is not. In a comparison of 23 mammal species ranging from bats to whales, it was found that humans have at least ten times as many adipocytes as would be expected in proportion to their body weight (Pond, 1987; chapter 12).

It used to be argued that loss of body hair to keep cool was followed or accompanied by the acquisition of a fat layer in order to keep warm. But it has been demonstrated (Scholander, Walters, Hook and Irving, 1950) that in the air medium a layer of subcutaneous fat is an inefficient insulator, while in water – for example, in the seal – the fatty layer provides a better insulator against cold than the air layer in its fur.

Fossil evidence cannot establish whether the Australopithecines had already acquired a greatly increased supply of adipocytes, or whether this feature should be attributed to a later date, with the advent of agriculture and a more settled existence. Two considerations militate against the second possibility. One is the human baby. Maternal investment in the fatness of babies is considerable, both before and after birth. In a human neonate, fat constitutes 16 per cent of body weight as compared with 3 per cent in the baboon. For this feature to have become so firmly established in human ontogeny needs a much longer evolutionary history than the period since agriculture. The second consideration is that there are extant human populations practising a non-agricultural economy, but their babies have plump cheeks and their young women have rounded breasts and buttocks. It is reasonable to suppose that this development had its beginning early in hominid history.



## THE 'BABOON MARKER'

Even at the level of his DNA, *Homo* emerges as a bafflingly anomalous member of the community of African primates. In the 1970s a team of American cytologists revealed the presence in baboons of a non-defective endogenous type C retrovirus, harmless to the baboons but capable of being released and causing reactions in other primate species (Benveniste and Todaro, 1976). All surviving African primate species contain viral gene sequences closely related to the RNA genomes of the baboon virus and providing protection against it, suggesting that at one time the virus (although subsequently losing its virulence) was both pervasive and life-threatening.

The presence of the 'baboon marker' is thus indicative of ancestral contact with the baboon virus, just as sickle cells in the blood indicate ancestral contact with malaria. Forty different primate species were examined by the American team. Of these it was found that all the 23 African species, including the gorilla and the chimpanzee, carry the marker. None of the 17 Asian species carries it. The surprise discovery was that in *Homo sapiens* – of whatever race – there was no sign of the 'baboon marker'. This strongly suggests that at some time during the onset of their evolutionary separation from the apes, man's ancestors must have been isolated from the baboons and from the other African primates by some geographical barrier which entirely precluded contact. A stretch of ocean would be a classic example of such a barrier.

During this period of separation, the baboon retrovirus raged over continental Africa. Its advent could have been as sudden and threatening as that of the AIDS retrovirus. But it must have differed from AIDS in one respect. Since it affected all non-human primates of African origin, including the small nocturnal prosimians in the forest canopy, the virus was probably airborne. No mainland African primate species failing to develop the protective 'baboon marker' gene sequence has survived. To explain why humans are the only primates native to Africa not bearing the 'baboon marker', Todaro and Benveniste suggested that they descended from a *Homo erectus* strain which first emerged in Asia, and later migrated to Africa at a time when the baboon virus was no longer life-threatening.

The AAT offers an alternative and more parsimonious way of interpreting the facts. One scenario which appears totally untenable is that man's evolution continued unbroken on the baboon-haunted African savannah.

## AN ALTERNATIVE HYPOTHESIS

The preceding selection of unsolved questions about human evolution is far from exhaustive, but it supports the contention that the standard

scenario of human evolution on the savannah is inadequate. It leaves too many human features unaccounted for.

The Aquatic Ape Theory postulates that hominid speciation was initiated, and its nature determined, by a period of semi-aquatic or aquatic lifestyle. The sea-flooding of north-east Africa (LaLumiere, 1981) could have placed a hominid ape population under duress by marooning it on island habitats, necessitating the exploitation of rich marine food sources as sea levels continued to rise. The bipedal Afar hominids could have descended from survivors of that episode who found themselves once more on mainland Africa as the sea-flooded area first became land-locked and the water finally evaporated.

The split between apes and man is characterised by a genetic divergence of only 1 per cent, but this is accompanied by wide phenotypic and behavioural differences. This combination strongly suggests not only allopatric speciation but also adaptation to widely differing habitats. Coexistence with early ancestors of chimpanzees in forest-edge or savannah habitats would have led to chance encounters and interbreeding, which would have retarded the emergence of strongly divergent phenotypes.

An island would have provided both geographic isolation and a different ecological environment. On the basis of the AAT, many human features which are unique among primates can be explained in terms of convergent evolution, since parallels can be found in semi-aquatic and aquatic animals. Relatively large deposits of subcutaneous fat are found in the majority of aquatic species: it provides buoyancy, streamlining and insulation – and in water the added weight is no disadvantage. Hairlessness is common among aquatic mammals. It is true that small aquatic mammals (such as water-rats) are not hairless, but the hairless species include some, like the river-dolphin and the babirusa, which are as small as, or smaller than, *Australopithecus*. One reason for the descended larynx may have been the need, before a dive, to inhale large quantities of air more quickly than could be achieved through the narrower nasal passages. Wind (1976) reasons that laryngeal descent is unlikely to have been the definitive factor in the emergence of speech. He points to cerebral reorganisation as the decisive element facilitating vocal communication.

There is, however, one other vital prerequisite. When the reorganised brain forms the intention to initiate vocal communication, the message must first be sent not to the vocal tract but to the lungs. Conscious and finely tuned control of respiration (most highly developed in diving animals and man) is indispensable for the emergence of speech. The descended larynx (found nowhere except in some diving animals and man), while perhaps not indispensable, facilitates and enhances the flexibility of the vocal repertoire.



When a species departs from its previous behaviour pattern, firstly the change is normally gradual, and secondly some immediate advantage must accrue from the outset to reinforce the behaviour. In the case of bipedalism these conditions were not fulfilled. Step-by-step change from horizontal to vertical would not be viable; there is no practical halfway house between walking on four legs and walking on two. The disadvantages (instability, prolonged infant dependence, skeletal and vascular malfunctions) would be incurred immediately, would weigh most heavily at the outset, and only gradually decrease through evolutionary modification. Most of the disadvantages relate to the destabilising effect of gravitational forces on the newly orientated bones, blood and other organs. For example, the weight of our own viscera is sustained by a dish-shaped pelvis; the intestines of a savannah ape could not have rested comfortably on the vertical blades of its pongid ilia, as a bipedal gait would have required.

By contrast, the hypothetical advantages accruing to pre-*afarensis* bipedalism on the savannah would be minimal at the outset and only slowly increase. It has been suggested that the descendants of the foraging male might ultimately get into their stride and be able to carry back enough food to cement the pair bond; or that the descendants of the noonday apes might ultimately achieve coolness as their vertical stance was perfected and their body hair diminished. But no immediate benefits would have rewarded the initial clumsy steps in either scenario.

It is tempting to imagine that a time would have come when the graph of decreasing disadvantage intersected with the graph of increasing advantage, but that is a teleological concept. Bipedalism on land would never have begun to become more efficient unless it was already being regularly practised while it was inefficient – a fact which goes far to explain why no other animal ever resorted to it.

If we assume that the initial stage did not take place on land, none of these problems arises. For a wading ape the incentive to bipedalism and the accruing reward would be instantaneous: by standing on two legs it could keep its head above water. The disadvantages would be minimal at the outset because in water gravitational force is counteracted. Equilibrium would be less endangered, the bones would not be compressed, the blood would not pool, the viscera would not sag. Locomotion in water – whether wading or swimming – tends to force the adoption of a 180° angle between spine and hind limbs. Long adaptation to this posture would gradually but inevitably affect skeletal structure – especially in the pelvic region – to a point where the aquatic ape was imperfectly adapted for locomotion on land, whether on four legs or on two. On their return to the mainland, the virtual impossibility, for the female, of carrying a plump, hairless baby while proceeding on all fours would have favoured bipedalism.

Habitual bipedalism is found in no other extant species. However, it may have been characteristic of the fossil 'marsh ape', *Oreopithecus*. Remains of this primate are found in lignite layers, which also contain fossils of crocodiles and turtles, and palaeobotanical remains of reeds, fern spores and swamp algae (Azzaroli, Boccaletti, Delson, Moratti and Torre, 1986). The list of eighteen similarities between *Oreopithecus* and *Homo* drawn up by Hürzeler (1960) has been challenged and whittled down, but the well developed anterior superior and anterior inferior spines of the pelvis, found in *Oreopithecus*, are shared with no other primate but *Homo* (Harrison, 1986). Since the theory that *Oreopithecus* was ancestral to man has been abandoned, convergent evolution is the likeliest explanation of the resemblances.

The hotter and more dangerous environment on the open plains made some form of sweat-cooling desirable. But this does not explain why the hominid once again departed from the mammalian norm by resorting to eccrine glands for thermoregulation. Physiologists have speculated that these glands initially evolved for some other purpose. Montagna (1982) observed: 'The several million glands on the human body act principally as heat regulators, but this function is perhaps too recent to be totally effective'. The previous function may have been excretory. Eccrine glands (as the name implies) do not appear to be secreting anything; the sweat is generally described as being merely diffused or eliminated via the gland. And although non-volar sweat is normally hypotonic (less saline than blood), prolonged sweating causes the glands to become fatigued and to lose their power to keep the saline solution hypotonic (Weiner and Hellman, 1959).

It may be helpful to compare this with another anomalous feature involving a saline solution, namely weeping, or more specifically what Darwin described as 'psychic' as opposed to 'reflex' tears. Psychic weeping is activated by motor pathways in the nervous system different from those which control reflex lacrimation (Ashley Montagu, 1960). Similarly, our non-volar eccrines react to different stimuli from those activating volar eccrines (Weiner and Hellman, 1959). Both eccrine sweat-cooling and human weeping emerged after the ape/hominid split; neither represents the simple quantitative expansion of an existing system. In some pathological conditions such as cystic fibrosis both sweat and tears become very salty.

These facts are consistent with the supposition that human sweat and tears may at an earlier evolutionary stage have been hypertonic, and may have evolved simultaneously and for the same purpose – to perform a function complementary with that of the kidneys in controlling salt equilibrium. Some such auxiliary mechanism has evolved in many marine species to facilitate the excretion of salt from ingested sea water.



(Schmidt-Nielsen and Yangè, 1958). In the case of tears, the excretion may have been originally accompanied by an involuntary contraction of the gullet to prevent any more sea water being swallowed; no other explanation has ever been advanced for the cricopharyngeal spasm in the oesophagus ('lump in the throat') which often precedes or accompanies weeping.

Later, in an arid territorial environment, the hominid's now active and abundant eccrine glands would have been pressed into service as thermoregulatory sweat glands, because over most of the human body the apocrine glands are non-existent. An aquatic phase might account for their disappearance. A reduction in apocrine glands and a proliferation of sebaceous glands – also typical of *Homo* – is not uncommon among aquatic mammals (Ling, 1965).

For the period between the initial ape/man split and the appearance of *A. afarensis* no fossil evidence is available. The question confronting evolutionists is where and how the hominids lived during the fossil gap. One way of seeking an answer is to consider what kind of habitat is most likely to have been conducive to the development of the anomalous features in human physiology. Table 2.1 lists some of these features and the environment in which they are found in non-human species. (The 'Yes' in column 2 represents the pachyderms which are found on the savannah, but may have acquired their hairlessness in a different environment.)

Table 2.1 Human features shared with (a) savannah  
(b) aquatic mammals

Features	1 In man	2 In savannah mammals	3 In aquatic mammals
Loss of body hair	Yes	Yes	Yes
Habitual bipedalism	Yes	No	No
Descended larynx	Yes	No	Yes
Volitional breath control	Yes	No	Yes
180° spine/hind limbs angle	Yes	No	Yes
Increased non-seasonal fat deposits	Yes	No	Yes
Ventro-ventral copulation	Yes	No	Yes
Dorsal hair sparser than ventral	Yes	No	Yes
Proliferation of sebaceous glands	Yes	No	Yes

## CONCLUSION

Palaeontology offers no direct evidence about the conditions which triggered the change to bipedalism, because it occurred during the gap in the hominid fossil record. The Savannah Theory as an explanation of the

emergence of man, is therefore based on no hard evidence. It is widely accepted only because it is regarded as the simplest scenario. But man is not a simple animal, and the circumstances combining to produce such a remarkable species are unlikely to have been so commonplace. Many primate species have moved from the trees to the grasslands, but evidence of parallel or convergent evolution between any of these and *Homo* is virtually nil.

As a source of evidence about origins, comparative anatomy is at least as important and reliable as palaeontology. Its findings are often overlooked, or relegated to separate specialist pigeon-holes and forgotten, but once assembled they constitute a catalogue of physical anomalies impossible to reconcile with the orthodox scenario. The AAT claims to represent the 'best-fit' hypothesis of human emergence because it accommodates more of the anatomical data than does any other, and is not ruled out by any of the fossil discoveries to date.

## REFERENCES

- Ashley Montagu, A., 1960, Natural selection and the origin and evaluation of weeping in man. *Journal of the American Medical Association*, 174 (4), 392–7.
- Azzaroli, A., Boccaletti, M., Delson, M., Moratti, G. and Torre, D., 1986, Chronological and paleogeographical background to the study of *Oreopithecus bamboli*. *Journal of Human Evolution*, 15, 533–40.
- Benveniste, R. E. and Todaro, G. J., 1976, Evolution of type C viral genes: evidence for an Asian origin of man? *Nature*, 261, 101–8.
- Carrier, D. R., 1984, The energetic paradox of human running and hominid evolution. *Current Anthropology*, 25, 483–9.
- Crelin, E., 1978, Can the cause of AIDS be this simple? *Patient Care*, 12, 5.
- Denton, D., 1982, *The Hunger for Salt* (Berlin: Springer-Verlag).
- Elizondo, R. S., 1988, Primate models to study eccrine sweating. *American Journal of Human Primatology*, 14, 265–76.
- Hardy, A., 1960, Was man more aquatic in the past? *New Scientist*, 7, 642–5.
- Harrison, T., 1986, The phylogenetic relationship of *Oreopithecus*. *Journal of Human Evolution*, 15, 541–83.
- Hiley, P. G., 1976, The thermoregulatory responses of the galago (*Galago crassicaudatus*), and the baboon (*Papio cynocephalus*), and the chimpanzee (*Pan satyrus*) to heat stress. *Journal of Physiology*, 254, 657–71.
- Hürzeler, J., 1960, The significance of *Oreopithecus* in the genealogy of man. *Triangle*, 4, 164–74.
- Kidd, W., 1903, *The Direction of Hair in Animals and Man* (London: A. & C. Black), 89–92.
- Laitman, J. T., 1983, The evolution of the hominid upper respiratory system and implications for the origins of speech. In *Glossogenetics*, ed. E. de Grolier, (Amsterdam: Harwood Academic Publishers), 63–90.
- LaLumiere, L. P., 1981, The evolution of human bipedalism. *Philosophical Transactions of the Royal Society, London*, B292, 103–7.
- Lieberman, P., 1983, On the nature and evolution of the biological bases of language. In *Glossogenetics*, ed. E. de Grolier, (Amsterdam: Harwood Academic Publishers), 91–114.
- Ling, J. K., 1965, Functional significance of sweat glands and sebaceous glands in seals.

- Nature*, 208, 560-2.
- Lovejoy, C. O., 1981, The origin of man. *Science*, 211, 341-50.
- Mahoney, S. A., 1980, Cost of locomotion and heat balance during rest and running from 0°C to 55°C in a patas monkey. *Journal of Applied Physiology*, 49, 789-99.
- Montagna, W., 1972, Skin of non-human primates. *American Zoologist*, 12, 109-24.
- Montagna, W., 1982, The evolution of human skin. In *Advanced Views on Primate Biology* (Berlin: Springer-Verlag), 35-41.
- Negus, V. E., 1949, *The Comparative Anatomy and Physiology of the Larynx* (London: William Heinemann).
- Newman, R. W., 1970, Why man is such a sweaty and thirsty naked animal. *Human Biology*, 42, 12-27.
- Pond, C. M., 1987, Fat and figures. *New Scientist*, 114, 62-8.
- Pond, C. M., 1991, Adipose tissue in human evolution. (This volume, chapter 12.)
- Richards, G., 1986, Freed hands or enslaved feet? *Journal of Human Evolution*, 15, 143.
- Sakura, H., 1983, Characteristics of man. In *Evolution*, ed. S. Kondo (Tokyo: Yuzankaku), 211-66.
- Schmidt-Nielsen, K., Schmidt-Nielsen, B., Jarnum, S. A. and Houpt, T. R., 1957, Body temperature of the camel and its relation to water economy. *American Journal of Physiology*, 188-9, 103-12.
- Schmidt-Nielsen, K. and Yangé, R., 1958, Salt glands in marine reptiles. *Nature*, 182, 783.
- Scholander, P. F., Walters, V., Hock R. and Irving, L. 1950, *Biological Bulletin*, 99, no. 2.
- Taylor, C. R. and Rowntree, V. J., 1973, Running on two or four legs: which consumes more energy? *Science*, 179, 186-7.
- Weiner, J. S. and Hellman, K., 1959, The sweat glands. *Biological Review*, 35, 141-86.
- Wheeler, P. E., 1985, The loss of functional body hair in man: the influence of thermal environment, body form and bipedality. *Journal of Human Evolution*, 42, 12-27.
- Wheeler, P. E., 1991, Body hair reduction and tract orientation in man: hydrodynamics or thermoregulatory aerodynamics? (This volume, chapter 13.)
- Wind, J., 1976, Phylogeny of the human vocal tract, *Annals of the New York Academy of Sciences*, 280, 612-30.

### 3 The Evolution of Genus *Homo*: Where It Happened

Leon P. LaLumiere

#### SUMMARY

This chapter seeks to establish a possible location for an aquatic phase in hominid evolution. It lists the necessary conditions which such a location would have to fulfil and establishes that the highland area known as the Danakil Alps conforms to all of these. Geological evidence for the former isolation of the site by sea-flooding, combined with data from the fossil record, points to a possible scenario for the early stages of hominoid speciation and a suggested locality for further exploration.\*

A major obstacle to acceptance of the hypothesis of an aquatic phase in human evolution is the difficulty of envisaging precisely where and when this episode may have occurred, in what type of habitat, what first motivated the change to an aquatic way of life, and what brought it to an end. This chapter discusses some possible answers.

#### THE NECESSARY CONDITIONS

Reflection upon the Hardy (1960) hypothesis leads to the following conclusions concerning a possible location:

- (1) It must have been a forested area inhabited by apes.
- (2) It must have been isolated from the rest of Africa during the period in which the evolution of ape-like to man-like creatures occurred. This suggests an island.
- (3) The region must have later become reconnected to Africa, enabling the hominids to migrate to other parts of the continent. In combination, (2) and (3) suggest an area of continuing tectonic disturbance.

The first condition – a forested area inhabited by apes – does very little to narrow the field. The Hominoidea originated in Africa, and prior to about 16 million years before present flourished exclusively on that continent (Campbell and Bernor, 1976). But following the establishment of the Africa-Asia-Europe land bridge, they began to expand throughout the Old World evergreen woodland biome, which at its climax, between 12 and 8 million years ago, extended from the Atlantic to the Pacific and southward into subequatorial Africa on the eastern side (Bernor, 1983).

\* Some of this material has previously been published in *Philosophical Transactions of the Royal Society of London*, B292 (1981), and as 'Danakil Island, the evolution of human bipedalism' in Elaine Morgan's *The Aquatic Ape* (1982).