

# 4 Is an Aquatic Ape Viable in Terms of Marine Ecology and Primate Behaviour?

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## SUMMARY

Tropical marine wetlands, often several types near each other, occur as mangrove salt-marshes, lagoons, and reef back-channels with islands. They are highly productive ecosystems with a diverse fauna and flora available as food for a dextrous, simple-tool-using, learning, wading ape, especially one capable of shallow dives. Three species of extant primates are known to use such habitats, and at least 15 primate species are able to swim and to perform some diving. In marine wetlands, a critical habitat requirement for safe nocturnal roosts is provided by cliffs and trees while, during daylight, home ranging is an expected primate behaviour.

The African Rift Valley, including the Red Sea, must have provided a suitable combination of sea level and habitat changes, about 5 million years ago, for an ape to become geographically isolated in marine wetlands, where aquatic selective pressures could have operated. Many modern humans' characters appear, in fact, to be adaptive to living in wetlands, and, once evolved, could have been functional in allowing the hominid stock to compete with baboons on inland riverine savannah. An aquatic ape is a likely ancestor of humans in terms of primate behaviour, marine ecosystems and geophysical timing.

## INTRODUCTION

This chapter brings together information about marine ecosystems, African rifting, the behaviour of primates, and some concepts of evolutionary theory, as a biologist's contribution to discussion of the Aquatic Ape Theory of human evolution. Marine ecosystems have not previously been considered in any great detail in this context, even when the theory was being expressed by marine biologist Hardy (1960). There is now an enormous literature on relevant habitats – for example, tropical marine wetlands. Primate behaviour is an overwhelmingly documented subject, too. But certain aspects which are relevant to the Aquatic Ape Theory are not well known, such as swimming and the behaviour of coastal populations. Or their relevance may not be immediately apparent: for instance, home ranging and circadian cycles. My point is that any postulated ancestor was a living, behaving animal with an integrated set of activities allowing it to survive and breed.

The third subject area, eco-ethological and evolutionary theory, is yet another that is enormous in scope, but nevertheless it must be taken into account by anyone hypothesising lines of descent. Several examples – the

concept of optimality theory, anagenesis–cladogenesis and allopatry–sympatry (two fundamental and simple pairs of evolutionary concepts), cline formation and subspeciation, punctuation and stasis – illustrate that relevant theory must be considered in developing a scenario for any postulated hominid clade.

My starting-point in getting involved in this topic was a very simple one, and based on several tenets of evolution theory. It was, in particular, the obviously over-simplified summary statement about the conventional (savannah) theory of human evolution: ‘Apes came down from the trees out on to the savannah’. Whether or not this arose under the selective pressure of reducing forests from Pliocene desertification does not matter. The ‘Direct Habitat Shift’ theory presents the difficulties listed in Table 4.1. How did apes survive on the savannah when there were fierce, fast predators there, day and night? How did they outcompete the several species of widely distributed baboons already there? And how were they isolated from the ape clade leading to chimpanzees and gorillas?

Table 4.1 Difficulties with the Savannah Theory of human evolution

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- 1 The variety of predators: e.g., lions, cheetahs, leopards, African hunting dogs
  - 2 Safety at night: e.g., from hyenas. Could it be secured by trees? Cliffs? Thorn barricades? Fire?
  - 3 Competitors: five or six species of baboons, widely distributed
  - 4 How was the prehuman stock isolated from the ape stock leading to chimpanzees and gorillas?
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The following information is set in the context of five general conclusions from the relevant literature.

### **The area of interest**

The geographical area of interest is in the eastern half of Africa, particularly the Rift Valley; but, also, it approaches the coastline at the Red Sea (the Danakil Depression) and the Zambezi River (Figure 4.1). That this area is the focus of attention is partly the consequence of the distribution of hominid fossiliferous beds from South Africa to Ethiopia (e.g., Lewin, 1984), and partly because the specific arguments of Kortlandt (e.g., 1972) are based on these fossils. And the area is also partly indicated by the implications of habitat diversity, clinal subspeciation and ecological catastrophe in a long (over 5000 km) rifting valley, continental and oceanic. Richards (1987) provides a comprehensive review of most aspects.

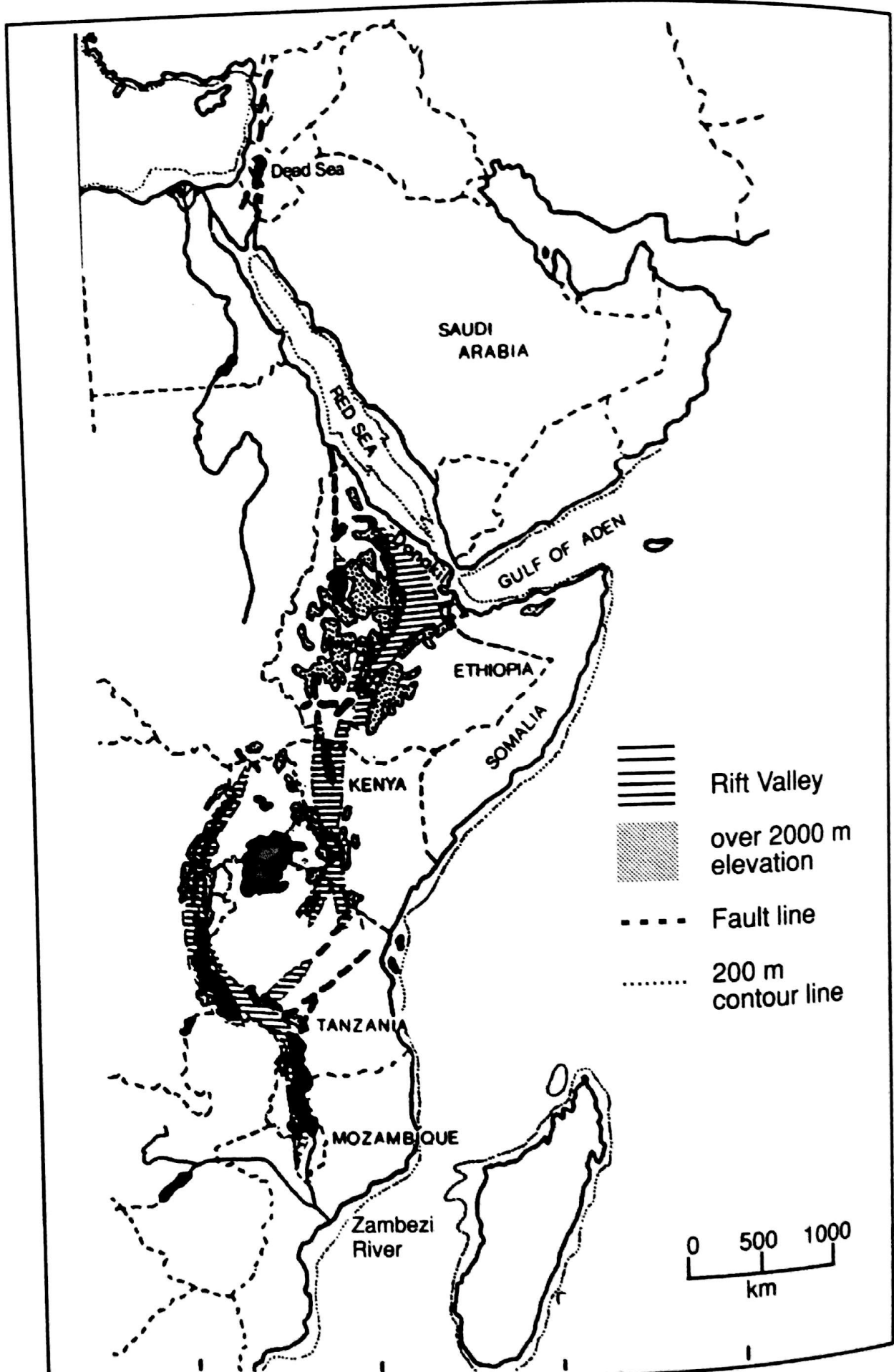


Figure 4.1 The African Rift Valley, including the Red Sea.

### **African wetlands and Red Sea rifting**

An aquatic ape would have been adapted to marine, rather than riverine-lake, wetlands. In principle, tropical marine ecosystems are richer in immobile and slow-moving food, and are less dangerous than freshwater wetlands. That the former offer a greater food supply is conventional wisdom among aquatic biologists, although I know of no one who has actually documented the relative diversity and abundance of edible aquatic plants, crustacea, bivalves, other invertebrates, fish, and so on. The relative danger is also difficult to document and I do not intend to do so, but it seems a reasonable conclusion to someone who has toured rivers infested with crocodiles and hippopotamuses as well as swum and scuba-dived in shark-inhabited lagoons. I do not swim in African rivers; I do swim, with care, in clear seawater there.

However, both arguments are subsidiary to an important African geomorphological event in the Pliocene. This is the oceanic Red Sea rifting, starting approximately 5 million years ago, which widened the previously formed sea-bearing extension of the African rift there (Cochran, 1983; Girdler, 1984; Girdler and Southren, 1987). This oceanic rifting will inevitably have created a geomorphologically active coastline with archipelagos, the result of fluctuating water levels arising partly from the rifting process and partly through climatic and sea-level changes. The Red Sea is a region with a geomorphologically dynamic aquatic (marine) regime appropriate to the Aquatic Ape Theory. Also, the continental Rift Valley will have been volcanically active and subject to catastrophic habitat destructiveness, lava flows and inferno at this time.

### **Forest and savannah habitat**

The forest habitat is a complex of sub-habitats (Richards, 1952), each occupiable by similar species with different adaptations. Thus there can be an upper canopy (with specialised primates such as the indri, howler monkey and gibbon), and several strata below down to the forest floor. These strata vary regionally depending on the amount and seasonality of rainfall, and the local topography creating standing or flowing water, such as swamps, rivers, lakes and estuaries. Thus there are rain-forests, and swamp, riverine and mangrove forests (Figure 4.2), as well as those on drier ground. Extensive stretches of these wet and dry forests in Africa, South-East Asia, Madagascar and South America support diverse species of primates, from upper canopy to ground.

The statement, 'Apes came down from the trees out on to the savannah', is misleading about forest and grassland ecology, as well as about primate biology. The common ancestors of catarrhine monkeys and hominoids, and of pongids and hominids, need not have been and probably were not upper-canopy species with their specialisations, even though both catarrhines and hominoids now have convergent species



Figure 4.2 Proboscis monkey on the ground in a mangrove swamp forest (G. Radcliffe, photo).

occupying that niche. The evolutionary problem is to transfer one or more stocks of apes from their niche as generalised lower-strata forest residents on to woodland savannah (tropical parkland) or riverine treed grassland, not the open savannah (tropical long-grass prairie).

Savannah is occupied by specialist long-ranging and fast cursorial herbivores and carnivores. Food would be hard to get there, hard to keep, and getting it would be dangerous enough for hunting parties, let alone camp-followers comprising elders, pregnant females and infants. In the process of adapting to parkland, not only the adult males, but also females and infants, would have to be viably adapted to the complexities of whatever ecosystem they were inhabiting at any one time (especially to predation) during the long series of anatomical, physiological and behavioural changes on the way to becoming human. And they would have to be able to push their way into the new ecological niche by adaptiveness superior to that of the baboons which had 'come down from the trees' before them.

### **Timing**

The period of interest must encompass not only the (roughly) 5 million-year separation of gorilla-chimpanzee-human stock (Lewin, 1984), but also the scale of Rift Valley formation (Bonatti, 1987) and the cladogenesis of apes from catarrhine monkeys. There are some intriguing anatomical differences between the two clades (Napier and Napier, 1985). For example, the survival value and behavioural implications of loss of the tail in apes needs considering, since apes and monkeys thereby had different anatomical starting-points when they produced their ground-living species. The time frame considered here thus extends back to the beginning of the Miocene epoch, some 25 million years ago. Note also that, if sexual maturity lay within the age range five to ten years, the number of generations for ape stocks would be 200,000–100,000 per million years.

### **Marine mammal adaptation**

The various clades of aquatic and semi-aquatic animals have different sets of adaptations. These match the Maynard-Smith (1975) concept of the equilibrium value of traits, the Evolutionarily Stable Strategies (ESSs). Thus the Cetacea are hairless, fully oceanic, with blubber, stern-oar tail-fluke and sonar. Soricidae and Mustelidae are amphibious with water-resistant hair, and land-usable legs functioning in water as paired side-oars or rear paddles. They are generally freshwater, but the coastal sea-otter *Enhydra lutris*, the rare sea-cat *Lutra felina*, and the Pacific coast so-called river-otter *Lutra canadensis* are notable exceptions. Another aquatic group is the pinnipeds and sirenids, with hair reduction and blubber. They are coastal, and the pinnipeds retain land birthing, and some, at least, much

infant hair. These families are all derived from quadrupedal forms, present members of which, such as otters, show only occasionally opportunistic bipedal behaviours of grazing and stare-round.

Primates frequently show opportunistic bipedalism, including when in water (see photographs and movies of wading proboscis monkeys with arms up high). They could generate yet another aquatic Evolutionary Stable Strategy, balancing both known and novel aquatic adaptations in an original way. There is no need to require wetlands primates to converge exactly on cetacean, pinniped or even mustelid aquatic ESSs. Starting from primate arboreal body capability, they have new combinations of adaptive opportunities open to them, or forced on them – for instance, by the ape lack of tail – and superior vertical flexibility.

## MARINE WETLANDS ECOSYSTEMS

A generalised model of a marine wetlands ecosystem is presented in Figure 4.3. Such systems encompass salt-marsh and mangrove swamp, lagoons, rock shores, surf beaches and sand dunes, in a progression from wettest to driest. They can occur adjacent to each other, separated or intermixed in diverse ways. They are universal, distributed almost from poles to tropics. The general principles of their biology have been documented many times.

Some information is available about tropical and semi-tropical variants (Figures 4.4–4.7), including their forms extant in the Red Sea and East Africa. Bally (1986), for example, lists 1247 references to the biology of African sandy beaches, 49 from Somalia, 31 from the Red Sea, 30 from Mozambique, and lesser numbers from Kenya and Tanzania. As we know the general principles of coastline formation from geomorphology and climate, we can draw some conclusions about their Miocene–Pliocene–Pleistocene forms in the area of interest. Wetlands occur in archipelagos as well as on mainland coasts (Figure 4.6).

### **Resource content of marine ecosystems**

Salt-marshes are the high tide and brackish water component of the marine wetlands ecosystems. They comprise the edges of river channels, and soft ground with streams connecting pools of varying sizes (Ranwell, 1972). They are overgrown by various grasses and salt-tolerant plants. The vegetation is populated by many land animals, worms, birds, small mammals, but especially insects, which in wet or warm seasons may swarm in large numbers. At the seaward side of the marsh, salinity becomes noticeable, and there appear in the fauna and flora various forms of algae and a variety of molluscs and crustacea. Fish of varying size and activity inhabit the pools, streams and rivers, especially at high tide when

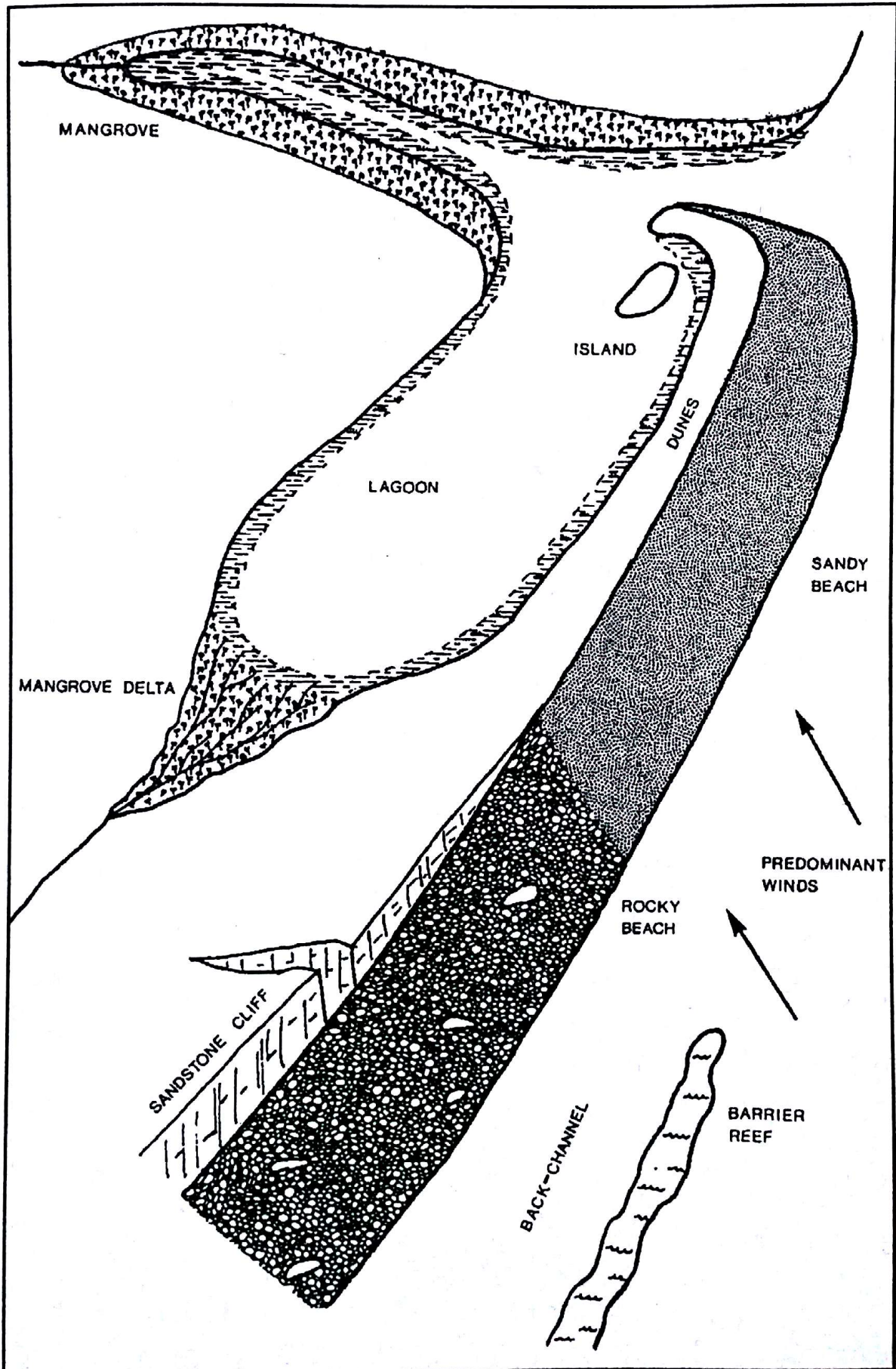


Figure 4.3 Model of marine wetlands ecosystem.



brackish water forms can swarm upstream. In tropical latitudes trees also feature. These are mangroves of several species (Figure 4.2). They greatly diversify the ecosystem and provide more niches than the salt-marshes of temperate regions, with an accompanying diversification of the microflora and especially the sedentary fauna (snails, hermit-crabs) on the trunks of trees (MacNae, 1968).

Lagoons are the lakes of marine wetlands. They occur on the landward side of barrier coral reefs as back-channels (Figure 4.4), and on the landward side of sandy depositional features (Figure 4.5) such as the spits which occur wherever the physical forces of wind, waves and an erosional feeder cliff create a longshore drift, thrusting materials across a shoreline embayment. However, any depression connected to the sea within the range of high tide will fill with brackish, salt- or hypersaline water, depending on river flow, tidal prism and air temperature. Being sheltered from direct wind and wave action, lagoons can be mud-bottomed with growth of salt-tolerant marine grasses and other plants, and a variety of marine but osmotically tolerant invertebrates and fish. Coral reef lagoons (back-channels) and atolls (Figure 4.6) tend to be well flushed and sandier-bottomed. Lagoons attract migratory water birds, often temporarily in enormous numbers, and support such mammalian herbivores as the sirenian dugongs and manatees. Invertebrates may be present in enormous numbers, the result of a few opportunistic species quickly responding to stressful changes of salinity (above 35‰) and temperature (above 25°C) (Moore, 1972). The diversity of species declines as salinities reach about 45‰ and temperatures about 30°C.

On rock shores (Figure 4.7) the stable hard surface is covered by marine algae, generally microphytic at high tide, grading to macrophytic at low tide, and with pools supporting marine grasses as well. At high tide, snail and crustacean grazers use the ephemeral unicellular or filamentous algae, often only during the cool of the night. In the pools there is an enormous diversity of attached, sedentary, and mobile invertebrates and fish herbivores and carnivores. Birds and mammals range on to the system as tides fall. At low tide the rock shore is particularly productive, with diverse algal forests of kelps and understory red, green and brown algae, and their herbivore-carnivore food chains. In the tropics these are supplanted in many places by even richer coral reefs, the upper parts of which are accessible to swimmers by shallow diving, and occasionally to waders at times of unusually low tides. There is a serious risk on rock shores, though. They can be physically dangerous, particularly during winds with an incoming tide. Wave action, and especially freak surge waves, can break unpredictably higher upshore than usual, and catch unsuspecting foragers.



Figure 4.4 Coral reef back-channel lagoon, with island.



Figure 4.5 Estuarine lagoons.



Figure 4.6 A tropical archipelago.



Figure 4.7 Chacma baboons on a surf shore with sand beach and rock habitats.

Sand beaches (Figure 4.7) are relatively unproductive in the mid-tide zone. In wet areas they support a variety of burrowing worms, molluscs and crustacea, some of which (*Donax*, the sand mussel) are visibly transient up and down the beach with the tide, and in upper levels many ocypodid and other crabs. Beaches are the main point of arrival for edible flotsam such as marine mammal carcasses. They support highly productive high-tide strand lines of algal and other debris, which in turn support enormous numbers of beach fleas and other crustaceans, readily available at night. Their disadvantage is that beaches are also vulnerable to surge waves; and a non-flying opportunist forager has to keep careful watch to start running upshore in good time. Sand dunes must be included in marine wetlands ecosystems, since they occur landward of beaches in many places. They respond vigorously to irregular rainfall by the growth of dormant plants, and can maintain oases and damp soil in the dune-slacks (depressions between the dunes).

The relative environmental risks and stresses, and the resource accessibility and adaptive demands of the various wetlands for a primate, are summarised in Table 4.2.

Finally, it should be noted that tsunamis, the so-called tidal waves, can be catastrophic over extensive areas of low-lying prograding coastline, such as is formed by millennia of longshore drift and estuarine discharge.

### **Contemporary tropical examples**

A few tropical coastlines have been comprehensively investigated, or reviewed. The most relevant to our area of interest are the shores of West Africa (Lawson, 1966), the coast of India (Natarajan, 1975), and the south Somalian coast. The West African review describes shoreline geomorphology as well as biology; the Indian review has more detailed biology of the various wetland types. The south Somalian coast investigations are described in many papers of *Monitore Zoologico Italiano*. In addition, there is a vast literature on tropical forms of most of the noted habitats: for instance, for mangroves (MacNae, 1968), for sandy beaches (McLachlan and Erasmus, 1983) and for coral reefs (Stoddart, 1969). Tropical lagoon biology is not well known. Tropical rock-shore biology closely follows similar shores in temperate zones, but is more productive and diverse (Stephenson and Stephenson, 1972).

Wetlands of the Red Sea can be used as examples in hot, dry climates. Fringing coral reefs are known to be productive, and their shallows are exposed at unusually low tides (Fishelson, 1971, 1980). Old reefs can be found above present high tides. Mangrove swamp forests occur in patches, as do salt-marshes (Kassas, 1957). Occasional seasonal convectional rainstorms flood to the sea; and run-off is absorbed in ground water to reappear at inland and shoreline oases. Even the Dead Sea has such oases. Climatic maps show relatively higher rainfall inland at

Table 4.2 Relative environmental stresses and risks, resource accessibility and adaptive demands in tropical marine wetlands

	Environmental stresses			Other risks		Adaptive demands		Potential for tool-using	
	Salinity	Insolation temperature	Waves	Competition severity	Predation risk	Nocturnal activities			
						Sleeping	Food-gathering		
Mangrove coastal forests	Least	Least	Least	Highest	Moderate	In trees	Unlikely	Moderate	Low
Lagoons -embayed -reef back-channels	High(est)	High(est)	Low	Low	Moderate	Dangerous	Possible	High	Highest
Near-shore islands	High	High	Moderate	Low	Moderate	Dangerous	Possible	Moderate	High
Rocky shore and tide-pools	High	Moderate	Low	Low	Lowest	Safest	Possible	Moderate	Moderate
Surf beaches	High	High	Highest	Low	Moderate	On cliffs (if present)	Moonlight, low tides	Low (noisy)	High (shellfish)
Sand dunes, including dune-slacks	Low	High(est)	Low	Low	High	Dangerous	Moonlight, low tides	Low (noisy)	Low

the south-east and south-west of the Red Sea (up to 150 cm per year). Monsoonal rains are features of other tropical areas, including the south Somalian coast (Vannini *et al.*, 1977).

The physical and chemical oceanography and fisheries resources of the Red Sea and off the east coast of Africa have been investigated by a variety of expeditions and coastal marine stations (Venema, 1984). Essentially, surface waters can be productive in terms of fish and shellfish. Hartnoll (1975) reports collecting over one and a half years forty-three species of ocypodid and grapsid intertidal crabs on the Tanzania coast, distributed over rocky and sandy shore and mangrove forests, and extending into fresh water.

### **Miocene–Pliocene–Pleistocene considerations**

The African Rift Valley (Figure 4.1) has been forming, possibly in one or two episodes of continental splitting (40 and 25 million years ago), since late Cretaceous–early Miocene times; then about 5 million years ago oceanic splitting of the Red Sea area started (Cochran, 1983; Girdler, 1984; Girdler and Southren, 1987). When a sea has been contained within the rift it has often approximated the present Red Sea, but has on occasions intruded inland beyond the present coastline – for example, the Afar triangle (Tazieff, 1970), containing the Danakil Depression. Island distribution would have been quite different from now. This inland sea, and the African coastline in general, has been complicated in terms of water levels (hence current flows, tides, and so on) by the sea varying  $\pm$  100–200 m from present levels (Figures 4.1 and 4.8), arising from global climate changes and glacial isostasy (Stanley, 1984). At a 200-m lower water level the Red Sea would be an inland sea subject to evaporation, supersalination and later inundation as water level rose. The Zambesi end of the rift would not have the same geomorphological and habitat diversity facilitating evolutionary isolation.

Thus, allowing for species changes through our period of interest, marine wetlands ecosystems will have occurred in the Red Sea as they do today; they would have been dynamic biological systems, with fluctuations over time scales of one day to the next, over seasons (annual wet–dry) over hundreds of years as the result of local geomorphological forces, over glacial periods, and over geological time. At any one time, biologically productive wetlands ecosystems, modified by regional climate, can be expected on appropriate coastal habitats in the Red Sea and the Danakil Depression. Under hot dry conditions, temperature and salinity stresses would constrain upper tidal wetlands to relict oases at unusually favourable sites, as occur today in Melita Bay and the Dahlak Islands of the southern Red Sea (Lewinsohn and Fishelson, 1967). When climates were cooler and wetter than today, marine wetlands would have been expected, and mangroves would have been the coastal represen-



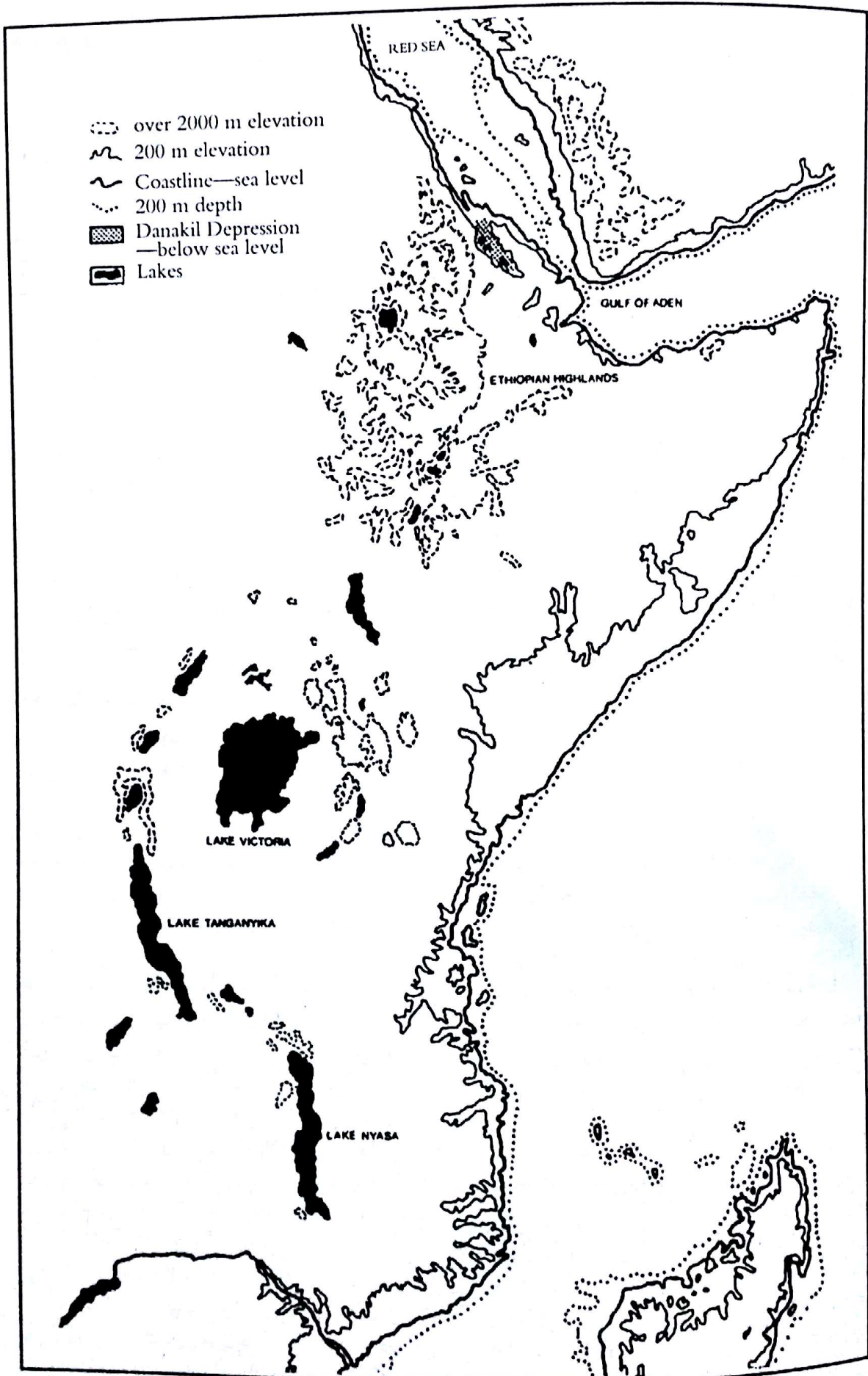


Figure 4.8 Topography of the African Rift Valley.

tative of extensive forest stretching either continuously inland or up river valleys, including the great rift, sometimes contiguous with tropical rainforests and cooler montane forest.

Under warmer and drier climates than today, drying-out, with parkland or savannah formation and possibly regional desertification, would have constrained and isolated the remaining montane and rainforests from the Rift Valley and the coast. A primate fauna is to be expected throughout these forests, whether extensive and contiguous or constrained and isolated. This would include the coastal forests, as, for example, in Borneo today, where proboscis monkey *Nasalis larvatus*, crab-eating macaque *Macaca fascicularis* and silvered leaf monkey *Presbytis cristata* coexist (Ellis, 1986). It is hard to imagine what would have prevented lower-canopy or ground apes (Dryopithecines?) being present in forests along the African rift, as the Red Sea first became a marine embayment (25 million years ago?) and then started the oceanic rifting of 5 million years ago.

## PRIMATE BEHAVIOUR

An ethogram (an inventory of the behaviour of a species (Tinbergen, 1969)) for a primate would be a long list, with many categories and lengthy descriptions of variable behaviours. Nevertheless, we should attempt to compile an ethogram when hypothesising ancestral species. It is a salutary experience, forcing one to consider the whole animal as an integrated behavioural-anatomical-physiological system in a realistic habitat. This section presents comments on a few primate behaviours which appear relevant to preparing an ethogram for a human ancestor.

### **Swimming**

At least six species of primates have been recorded as swimming when free-ranging (Table 4.3). A further twelve have been recorded swimming or wading in zoos. All four primate major taxa are represented: prosimians, platyrrhine and catarrhine monkeys and apes. Three of the four ape species groups have been recorded as swimming or wading in zoos (Figure 4.9), and the pygmy chimpanzee *Pan troglodytes pygmaeus* in the wild also (Nishida, 1980; Uhara, 1976). From information obtained from primate keepers, it appears that many, if not most, primates can learn to swim during infancy. In the wild they would learn to do so from peers and seniors, with the first of the stock doing so fortuitously, surviving, benefiting either by food, escape or comfort (cooling), and responding similarly again when the situation was repeated. Once established as part of the culture of an ape or monkey stock, swimming would be perpetuated down the generations, as with the Koshima stock of Japanese macaques *Macaca fuscata* (Napier and Napier, 1985).

Table 4.3 Swimming and other water activities of primates  
(extended from Ellis, 1987)

Species	Species that swim in		Species that wade/play in zoos or wild	Other littoral wetlands species	Comments and references
	wild	zoos			
<b>Prosimians</b>					
Gentle grey lemur ( <i>Hapalemur griseus</i> )	X				Lake Alaotra troop swim (Kavanagh, 1983)
<b>New World monkeys</b>					
Spider-monkey ( <i>Ateles geafroyi</i> )		X			(Chaffee)
Dusky titi ( <i>Callicebus moloch</i> )				X	Swamp and riverine forest (Kavanagh, 1983)
White-faced capuchin ( <i>Cebus capucinus</i> )				X	Shoreline occupants harvest oysters (Kavanagh, 1983)
<b>Old World monkeys</b>					
Cercopithecinae					
Allen's swamp monkey ( <i>Allenopithecus nigroviridis</i> )	X	X			Has foot-webbing (Gilbow, 1985; Forney, 1985; Wolfheim, 1983)
White-collared mangabey ( <i>Cercocebus torquatus</i> )				X	Can occur in swamps (Grizimeck, 1972). The most ground-dwelling of several rain-forest mangabey species (Napier and Napier, 1985)
Mandrill ( <i>Mandrillus sphinx</i> )		X			(Bourne)
Mona monkey ( <i>Cercopithecus mona</i> )		X			(Kagan)
DeBrazza's monkey ( <i>Cercopithecus neglectus</i> )		X			(Bourne)
Japanese macaque ( <i>Macaca fuscata</i> )	X	X			(Kagan, Bourne; Kavanagh, 1983)
Crab-eating/long-tailed macaque ( <i>Macaca fascicularis</i> )		X			(Shumaker, Ruhe)

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Species	Species that swim in		Species that wade/play in zoos or wild	Other littoral wetlands species	Comments and references
	wild	zoos			
Rhesus monkey ( <i>Macaca mulatta</i> )	X	X			(Lindberg, 1971; O'Neill)
Celebes-crested macaque ( <i>Macaca nigra</i> )			X		(Shumaker, Kagan, Ruhe)
Barbary macaque ( <i>Macaca sylvanus</i> )			X		(Shumaker)
Talapoin ( <i>Miopithecus talapoin</i> )	X				(Kavanagh, 1983)
Yellow baboon ( <i>Papio cynocephalus</i> )				X	(Messeri, 1978)
Chacma baboon ( <i>Papio ursinus</i> )				X	Cape stock beach-dwelling (Ellis, 1985; Davidge, 1976)
Baboon (unidentified)			X		(Ruhe)
Colobinae					
Proboscis monkey ( <i>Nasalis larvatus</i> )	X	X			(Ellis, 1987; Hutchins)
Dusky leaf monkey ( <i>Presbytis obscurus</i> )				X (rarely)	(Kagan)
Silvered leaf monkey ( <i>Presbytis cristata</i> )				X	Inhabit coastal forests (Kavanagh, 1983)
Olive Colobus ( <i>Procolobus verus</i> )				X	Low-stratum riverine forests (Napier and Napier, 1985)
<b>Apes</b>					
Gorilla ( <i>Gorilla gorilla</i> )			X		(Brown <i>et al.</i> , 1982; Golding, 1972)
Chimpanzee ( <i>Pan troglodytes</i> )				X	(Uhara, 1976; Nishida, 1980)
Orang-utan ( <i>Pongo pygmaeus</i> )				X	(Ellis, 1987)

Respondents providing information referenced above:

Bourne, D., Toronto Zoo; Chaffee, P., Fresno Zoo; Dotts, C., San Diego Zoo; Hutchins, M., Bronx Zoo; Kagan, R., Dallas Zoo; Lindberg, D.G., San Diego Zoo; Marsh, L., University of California, Davis; O'Neill, P., National Institute of Health, Dickerson, MD; Ruhe, L., Baby Zoo, San Jose; Shumaker, R.W., National Zoological Park, Washington, DC; Tong, M., Houston Zoo.

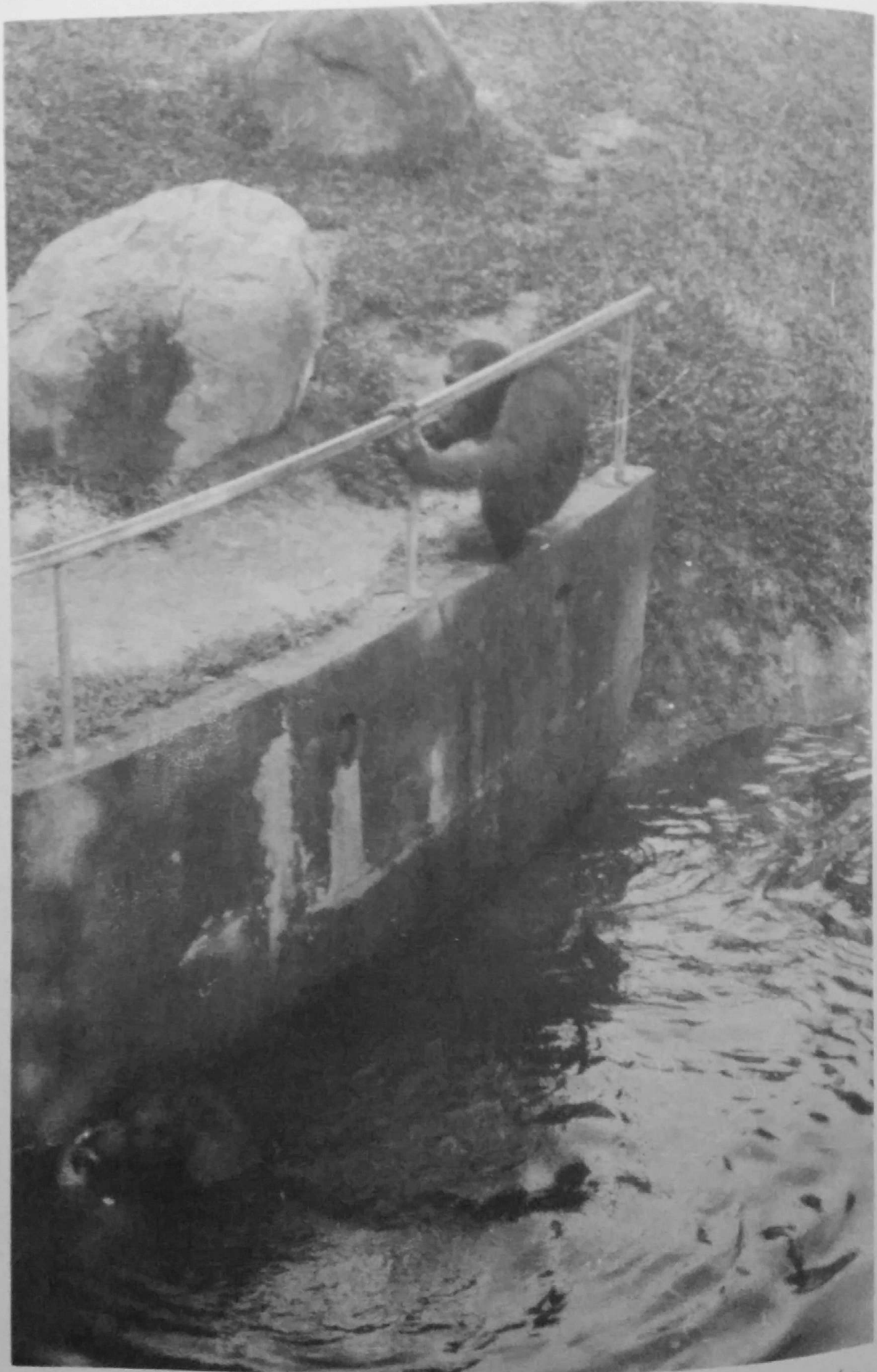


Figure 4.9 Orang-utan wading in the moat at the Singapore Zoo (reprinted from Ellis, 1987).

The comment is often made that apes and monkeys cannot swim and are afraid of the water, and 'that is why zoos have moats around monkey compounds'. However, zoos that use moats have to check carefully that their expensive apparently non-swimming apes and monkeys really cannot or will not swim. Young apes and monkeys are like young children. Given the right instruction or peer models, they will quickly learn, particularly from a socialising attendant who likes to swim with them (Ellis, 1987; see also Wind, chapter 17, this volume). Indeed, zoos with moats had better not teach their curious, attention-seeking young monkeys and apes how to swim. Or their moats will no longer work, as was found with two gorillas at the University of Ibadan Zoo (Golding, 1972): 'Both animals soon learned to run across the compound and either leap diagonally into the water in a tremendous belly-flop or twist about at the last minute and plunge in backwards . . . the male was able to launch himself with a kick from the mud bottom, travelling several feet in a horizontal "breast stroke" position.'

### **Coastal monkeys and home ranging**

Three species of catarrhines have coastal stocks. They all show pronounced home-ranging behaviour: that is, they routinely patrol daily a limited range of their shoreline habitat. The species are the proboscis monkey *Nasalis larvatus* (Ellis, 1986; and Figure 4.2), the chacma baboon *Papio ursinus* (Davidge, 1976; and Figure 4.7) and the yellow baboon *Papio cynocephalus* (Messerli, 1978).

The limit to shoreline stock vagility appears to be set by a critical path of safe roosting places. Proboscis monkeys select high riverine trees, from which they can escape (their main predator is the clouded leopard) by dropping into the water below. The two coastal baboon stocks sleep on predator-inhibiting cliffs. The daily patrols, although circumscribed by the roughly twelve-hour light-dark cycle, vary from day to day opportunistically according to food availability, need to drink (for the baboons) and proximity of the nearest roosting place.

### **Social (kin) grouping**

Table 4.4 summarises levels of social organisation in terms of numbers of individuals commonly grouping together and kin relationships within the groups. The term 'solitaries' may be misleading. It can mean a scale of individual territoriality beyond easy recognition by an observer, with the animals (such as orang-utans) knowing who their neighbours are, and with males maintaining a larger territory than females, and encompassing theirs.

An important pattern in the tabulated information is that the different types of social grouping occur in the four major primate taxa. In other words, type of social group is a flexible behavioural property which can

change easily over evolutionary distance (as well as historically in human society). An ancestor to chimpanzee, gorilla and human need not have had a social organisation similar to any one of the three extant species. Martin and May (1981), using arguments based on ape and human genitals, suggest that an early ancestor had single male breeding groups. Nevertheless, social group flexibility in primates is so great that other ancestral stages could have had substantially different forms of social grouping.

Table 4.4 Group organisation of primates (modified from Chalmers, 1979, and Ellis, 1985)

<i>Group type</i>	<i>Group size</i>	<i>Home-range size (hectares)</i>
Solitaires Several lemurs and lorises	1	c.1 or less
Orang-utan Male especially Female with young to 4-5 years Juveniles may group		
Monogamous family groups – Breeding male, female and young	2+	4-50
Indri, some monkeys Gibbon, siamang		
One-male, several-female groups	10-20	10-5000
Many monkeys Gorilla (may tolerate some mature males) Hamadryas and gelada baboons (groups may aggregate)		
Multi-male, multi-female groups	10-100	1-2500
Some lemurs Many monkeys, including macaques and baboons Chimpanzee – frequent subgrouping, between kin and 'friends'		

### **Dispersal phases – young adults?**

Goodall (1986) has shown that female chimpanzees tend to wander as they mature sexually, and subsequently settle in one troop or another. Strum (1975) and Ransom (1981) have shown that male baboons can bully, bluff or wheedle their way into a new troop. The consequence of these dispersals is to reduce the risk of inbreeding. It is to be noticed that although the dispersing sex differs between the two species, the common pattern is that dispersal is by young adults. An implication of this pattern is that species vagility (hence gene spread) is quite limited compared to potential gene spread by, for example, a wandering sexually active male consorting with stranger females over many years and long distances.

### **Day–night cycles**

The majority of primates have a wake–sleep cycle closely related to the day–night light–dark cycle. They roost at dusk and rise at dawn. Table 4.5 presents some data that I recently obtained at a twenty-seven-cage arena in the San Diego Zoo. The various species settled down for the night by preliminary quiet sitting, then progressed to sleeping over about two hours before and after dusk. They started to rise about an hour before dawn. The times seem to be similar in the wild. A few species, while still tied to the day–night cycle, reverse it (the lorises and the Douroucouli, *Aotus trivirgatus*) (Kavanagh, 1983), waking at dusk, being nocturnally active and roosting at dawn. At least one diurnal lemur is an exception – for example, *L. fulvus* (Harrington, 1975) – and can be active at night (Schilling, 1979) as well as during the day.

The issue is significant, since the twenty-four-hour activity pattern of one primate species, ourselves, can break the usual environmental constraints. We can stay awake after dusk for culturally determined activities, and rouse ourselves for prolonged activities at night: for instance, the graveyard shift in a factory, and the first mate's midnight–4 a.m. watch at sea. This potential (for opportunist nocturnal foraging) would not have been unimportant to an omnivorous human ancestor: for example, during seasons of nocturnally swarming insects, at times of full moon illumination, and at the coast during night-time low spring tides.

### **Communication**

Primates communicate by a mixture of scents, badges and displays, and by calls including extended songs in canopy species (indri, howler monkeys and siamangs). Scents, particularly, are a feature of ground-dwelling forms. Complex sound communication is a feature of oceanic and aerial mammals. Both Cetacea and Chiroptera use high-frequency direction-finding sonar in their open habitats, unencumbered by



Table 4.5 Observations on primate roosting and waking in a 27-cage arena at the San Diego Zoo, 8-9 April 1987

Cage no.	14:00 hrs					18:00hrs					19:00 hrs					20:00 hrs					05:00 hrs					06:00 hrs					
	10	40	DATA	NO	DATA	13	20	30	40	50	00	10	20	30	40	50	00	10	20	30	40	50	01	10	20	30	40	50	00	10	20
	Sunset															Sunrise															
<i>Allopihceus nigrovindis</i>											S	S	R																		
<i>Presbytis francoisi</i>																R	R														
<i>Presbytis entellus</i>											S																				
<i>Alouatta pigra</i>																															
<i>Alouatta seniculus sara</i>						S																									
<i>Macaca niger</i>																															
<i>Mandrillus leucophaeus</i>																															
<i>Pithecia pithecia</i>																															
<i>Callicebus moloch</i>																															
<i>Clonacophilus cercebus</i>																															
<i>torquatus</i>																															
<i>torquatus</i>																															
<i>Cercopithecus cephus</i>																															
<i>Lemur catta</i>																															
<i>Varecia variegata</i>																															
<i>Cercopithecus talapoin</i>																															
<i>Macaca silenus</i>																															
<i>Cercopithecus hamlyni</i>																															
<i>Cercopithecus diana rolouay</i>																															

Key R = all roosting  
 S = some roosting  
 Blanks = cage occupants active  
 ? = uncertain  
 ----- all roosting  
 ----- some roosting

complex three-dimensional fine-habitat structures, such as tree and algal forests. The sonar of the Cetacea also produces complex vocalisations, apparently meaningful between individuals.

There is another potential use of sound by aquatic species, employed by the young of the sea-otter. This is the property of distant transmission through reflectivity of the water surface. The infant sea-otter will utter a piercing scream after being left by its parent for more than a few minutes of a feeding dive, and the call travels very effectively, particularly when the surface is calm. On a calm day in coastal waters the conversation of boaters can be clearly understood kilometres distant. Lagoon living, particularly, would provide both selective pressure and calm-water habitat for evolving complex vocalisations effective over long distances. The new complexity would add to demands on the brain.

### **Feeding and omnivorousness**

Apes and monkeys are dextrous enough to use fine probes for termiting (Goodall, 1986), and to wash food in water (Napier and Napier, 1985). Many are insectivorous and nut-cracking. Some chimpanzees catch and eat living small mammals. At least some of these behaviours may be learned. A coastal ape would have no difficulty in using such learned abilities to catch and break into the sedentary and sessile animals that are there on shore, in pools, lagoons and wetlands in enormous numbers, especially at low tide. In learning to adapt the abilities to new foods in a wet habitat, new and complex selective pressures would be put on the brain.

## **SOME RELEVANT ECO-ETHOLOGICAL AND EVOLUTIONARY CONCEPTS**

### **Behavioural integration and optimisation**

An animal's behaviour and anatomy is a system: an ethosystem. The system is integrated so that the animal survives and breeds, even though it may perform some actions that seem risky, and lack some structures that seem useful. Krebs and Davies (1981) have called this 'optimality'; 'trade-offs between costs and benefits will give the maximum net benefit to the individual'.

An example relevant to hominid evolution comes from the loss of the tail by the ape stock. The best-known benefit to primates of being tailed arises from the prehensile form: that is, where the tail is a grasping device supplementing the four limbs for moving through the forest canopy. Gibbons and orangs have to do without a tail, and have adapted to canopy living by brachiation (gibbons) and slow movement (orang). Catarrhine monkeys and prosimians derive other benefits from the tail, even though it is not prehensile. It can be a touch sensor, which can be

used in the trees and on the ground, providing information from behind and to the side. In addition, it is often used in social displays, as a contact device when sleeping and resting, and in balancing.

Apes have lost the tail, along with its considerable survival advantages. Presumably, at some stage in the catarrhine–hominoid split, apes were in an adaptive situation where the benefits of a tail became too costly for survival. A selective explanation is needed, since the tailless ape on the ground was eventually able to compete with the tailed baboons already there, and establish itself in spite of the baboons very successfully occupying the parkland niche. Lack of a tail, plus other ape characters, could well be important to the human stock in coexisting with baboons.

The tail might have been lost in the following way. An isolated ancestral monkey stock came to spend increasingly more time on the ground than in the lower canopy, such that the tail was less needed as a touch sensor. The animals were exposed continuously to a range of daytime visually-hunting ground predators that could detect them by their movements, including tail waving. The optimum balance had changed, and long-tailed specimens were at a disadvantage. Such a scenario for one character is too simple, and needs expanding, so that all the anatomical–behavioural–physiological differences between apes and catarrhine monkeys (Andrews, 1981, 1985) are explained in terms of benefits and costs. Also, the various characters must have a net benefit during all life stages, for infants and juveniles, and for females as well as mature males.

### **Evolutionary theory**

Primates, like any other clade, evolve either by straight-line evolution (anagenesis) or by line-splitting (cladogenesis). If anagenesis occurred, an ape could have evolved to human by adapting to a reducing forest drying out to parkland and savannah. There are problems with this, in that gene flow would continue over a wide area between the grassland and remaining forest stocks (sympatry). The alternative of cladogenesis means that ape stocks evolving to chimpanzees, gorillas and humans were isolated one from another. Appropriate forest clusters would have occurred during a Pliocene drying: for example, as mountain-mist forests, river-valley and coastal forests. Elevations over 2000 m in Africa are shown in Figures 4.1 and 4.8. Mountains group in patches over several hundred kilometres in East Africa, and the southern patches are several hundred kilometres from the coast.

Any scenario for human evolution must pinpoint the area and explain human descent in terms of biologically and geographically appropriate anagenesis/cladogenesis and sympatry/allopatry.

There is a great range of theoretical biological concepts which must be considered in developing theories of human evolution and lines of

descent. The concepts of Hennigian cladistics (e.g., Wiley, 1981; Ciochon, 1982), molecular biology (e.g., Sarich, 1971), punctuation and stasis (e.g., Eldredge and Gould, 1972) and molecular drive (e.g., Dover, 1986) are all highly relevant, and should be brought together into human evolutionary theory.

## AN ALTERNATIVE TO THE SAVANNAH THEORY

Table 4.1 lists some difficulties in evolving humans on the savannah. These difficulties can be avoided if the clade spent an evolutionarily significant period of time in a habitat where characters changed in such a way that on later entry to riverine savannah the ape-human stock had a set of characters allowing it to feed omnivorously, to survive predators there day and night, and to do so more efficiently than the baboons already present. The situation is summarised in Figure 4.10 and Table 4.6. We need a habitat other than a forest-savannah boundary ecotone for the separation of ape and human stocks.

Table 4.7 shows that many human characters can be arranged in sets ordered by different levels of functioning in an aquatic habitat.

To explore an aquatic descent scenario in some detail, we must use the concept of the ethogram, hierarchically arranged (Ellis, 1985). The upper-level categories used here are: habitat and its use, food-gathering, avoidance of and escape from predators, sleeping, social grouping and organisation, comfort behaviours and juvenile behaviours.

The scenario starts with a generalised ape convergent with coastal monkeys now extant. It is hard to see what could have stopped lower-canopy and ground apes from inhabiting the African Rift Valley, and the forested coasts of East Africa and the Red Sea by 5 million years ago, after separation of catarrhines and hominoids 20 million years before. The second stage of the scenario explores how an aquatic ape could have been viable as a localised rapidly evolving form. This would be sometime during the oceanic rifting, sea-level changes, archipelago appearance and drowning, supersalination and inundations, starting about 5 million years ago. It would represent the extreme aquatic stage and form of a clinally varying Rift Valley ape. It would be localised at the geomorphologically dynamic Red Sea end of the rift, not the Zambezi end. The third stage explores whether transition to *Australopithecus* or *Homo* or both, inland, is a viable process. This last stage must be developed, as the Aquatic Ape Theory can only be convincing if it can bring back inland up the Rift Valley (at least once) the hominid stock in a way strictly conforming to biological-evolutionary forces. In so doing, the aquatic ape ancestral species must become extinct.

Table 4.6 An alternative theory for human evolution

- 
- 1 An ape stock was isolated in a habitat unusual for a primate
  - 2 The stock, by adapting to that habitat, evolved characters which were functional there
  - 3 Loss of the habitat or population pressure due to successful adaptation forced the stock towards riverine savannah
  - 4 The stock survived in riverine savannah, since a subset of the new unusual primate characters allowed them to out-compete the baboons already there and to avoid predators
- 

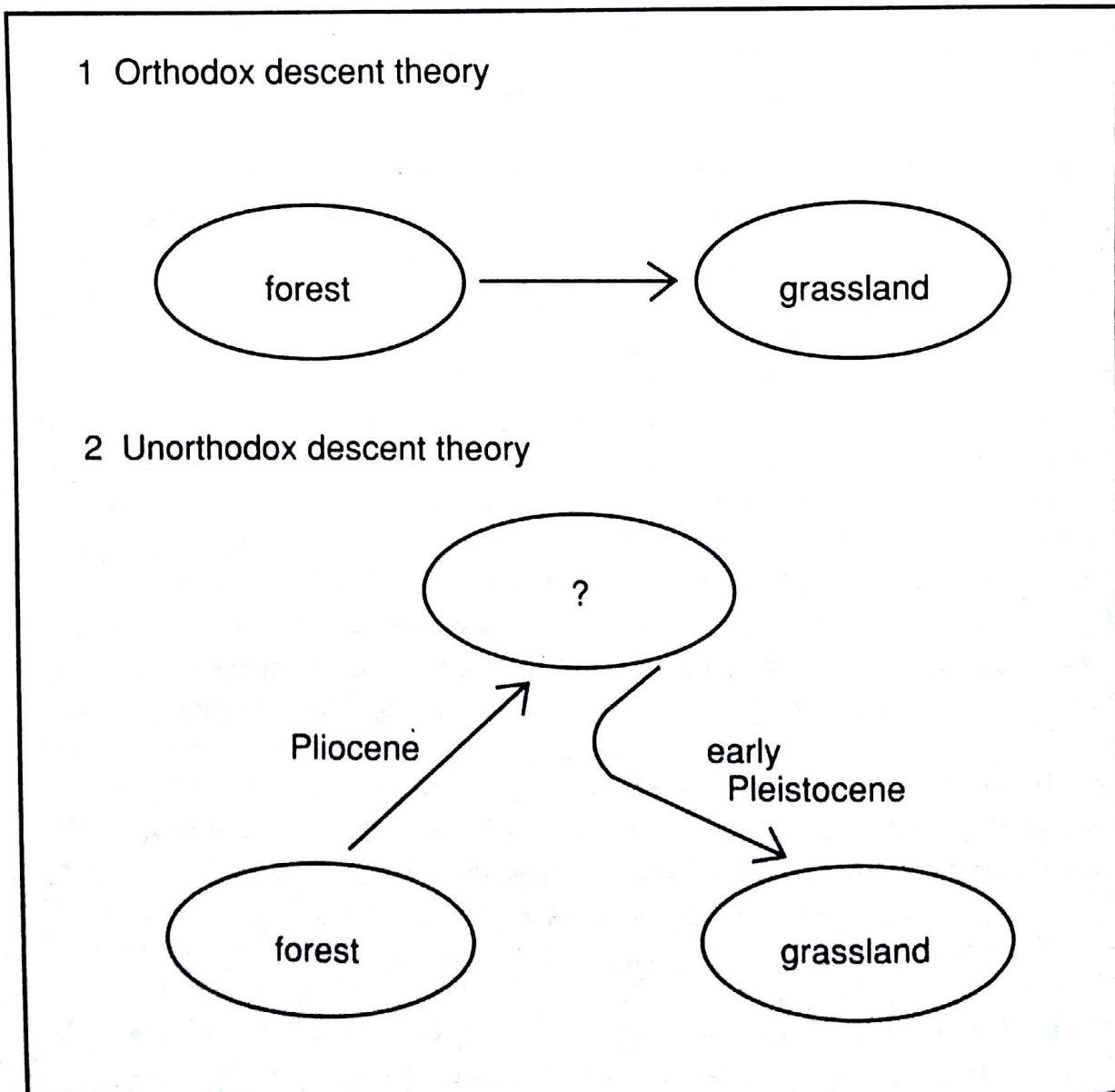


Figure 4.10 Models of direct and indirect habitat-shift descent theories for humans.

Table 4.7 Some human characters, arranged in four sets with comments on aquatic adaptiveness

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*Set 1*

Hairlessness, or almost  
Subcutaneous fat, or blubber  
Dilute urine  
Salty tears  
The diving reflex  
Ventre-ventral mating  
Floating infants, able to breathe

These characters are commonly found in various combinations in aquatic mammals of different evolutionary origins, but rarely in terrestrial, and particularly not dry savannah, mammals

*Set 2*

Sheltered nostrils  
Head hair, with rest of body almost hairless (see Set 4)

These characters would be adaptive in an aquatic ecosystem

*Set 3*

Upright stance  
Fine hand-grasping ability  
Communication by diverse calls, not by badge-displays and pheromones  
Enlarged and complex brain

These characters would be adaptive in an aquatic ecosystem, and would also be preadaptive to riverine savannah, thus allowing humans to enter the ecosystem, out-compete baboons and minimise predation

*Set 4*

Feet not grasping  
Black skin, with pubic and underarm hair  
Capable of nocturnal as well as daylight activity

These characters are unique for a primate, and require adaptive explanations. They could be adaptive to an aquatic habitat

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**Coastal and riverine forest ape stock: Stage 1**

Effective present-day utilisation of habitat by coastal and riverine-parkland monkeys derives from home-range opportunism, with troops returning daily from roosting sites to remembered feeding grounds, exploring as they go. Baboons penetrate far on to low ground-cover habitat (including maritime dunes) and even shoreline. An omnivorous coastal primate – that is, a baboon-sized, nut- and beetle-cracking insectivore–frugivore (Kay, 1984) – would find no shortage of foods on shore, in marshes and in tide-pools, on dunes (nesting birds) and beaches (breeding turtles) and in eruptions of foliage, fruits, insects, and so on at various times (Davidge, 1976). Even folivorous primates, such as the proboscis monkey, are well provided for. Tool use for termiting, clam-breaking and so on would be possible. Occasional small flotsam would be eaten, or larger fresh corpses torn apart.

The apes, however, would need to be fairly large, especially the males, and socially organised and aggressive for group defence against predators. Sleeping quarters would be either (remembered) suitable stands of trees high over water, or cliffs, or both. Only a few such sleeping quarters would be needed within the home range of a particular troop, but they would need to be spaced conveniently, and this factor would be the critical path limiting range size and resources availability. The social organisation would be based on large-troop self-defence, so would probably be a multi-male harem, resembling one or other of the two extant baboon strategies, with expendable young males functioning as sentinels. Young male dispersal would reduce inbreeding of such a kin group. Grooming would be an important social bonding device, and the productive ecosystem would allow plenty of time for it. Juveniles would have familiarised themselves with wading and swimming. Water entry for travel and feeding would follow, even by heavy adults, and especially in emergencies.

At this stage, the ape stock would be limited to the Rift Valley and coastal wetlands forests and open spaces by the postulated African Pliocene desertification. Thus stocks would be scattered over some 5000 km or more along the rift and the coasts of the Red Sea, if not more widely along the coasts of East Africa. Low-vagility-induced social grouping and limited juvenile wandering would generate clinal differences, possibly extensive enough to qualify as subspeciation, with those stocks most dependent on aquatic food and safety starting the appropriate anatomical and cultural changes, leading the clade to a uniquely primate set of aquatic adaptations – Stage 2.

**An aquatic ape: Stage 2**

The extreme aquatic habitat is now island and coastal open ground of marsh, lagoons, reef back-channels, beaches, rocky shores and dunes and restricted forest around the Red Sea, as water levels, temperatures and

salinities fluctuate relative to the continuous or disjunct Gulf of Aden and Mediterranean Sea. Home ranging, including on to land, would continue. Night feeding opportunities would be taken at full moon and low spring tides. Stone-pounding to crack oysters, mussels, crabs and so on would occur (Figure 4.11). Sharp stones would be used to cut into freshly beached corpses. Much time would be spent exploiting lagoon and reef back-channel ecosystems with their marine grasses, invertebrate and fish faunas. Individuals would reach under water and make shallow dives for food. They would range these sheltered sea-water highways by wading and swimming. Ranging might be restricted to certain times of day and be undertaken cautiously, especially in turbid water, because of predation at certain sites by sharks and crocodiles (Figure 4.12). Escape from land-based predators, when the apes were on shore, would be by running back to water and swimming away.

Sleeping would be on islets (a significantly new resource, for nocturnal safety) or cliffs, or (less frequently) up trees, with safe locations remembered by troop elders. Social groups would be smaller and less rank-structured than in the earlier coastal apes, as a result of greater availability of safe habitat (lagoons and islets). Open-ground social defence by large and powerful individuals would be less necessary. Many social activities, including grooming, resting and playing, and ventro-ventral mating, could occur in the water. Calls would travel long distances over calm water without distortion, and with reduced visual and chemical signalling, calls would become more complicated and meaningful.

Infants would float instinctively, the right way up, and adults would also float, especially in hypersaline sea water. The nose would have developed, and so would other anatomical and physiological adaptations to prolonged aquatic wading and swimming – for instance, bipedalism, an appropriate diving reflex, hair loss and subcutaneous fat (Morgan, 1972, 1982, this volume, chapter 2; Verhaegen, 1985, this volume, chapter 5), in part by neotenic mechanisms.

Some troops would be more land-based than others, reflecting learned differences in resource exploitation. (The aquatic ape was really a wading ape.) The changing archipelagos of the rifting Red Sea, however, would keep gene pools mixing between island and mainland, in spite of a low vagility between separated, largely swimming, troops. At this stage in the actively rifting African valley, the continentally moving section was subject to catastrophic habitat destruction by volcanoes, lava and fire. The oceanic rift of the Red Sea and Danakil Depression would be safer. At some stage the clade was reduced to one or more highly aquatic stocks in which novel adaptive features appeared, making up a unique primate aquatic ESS.



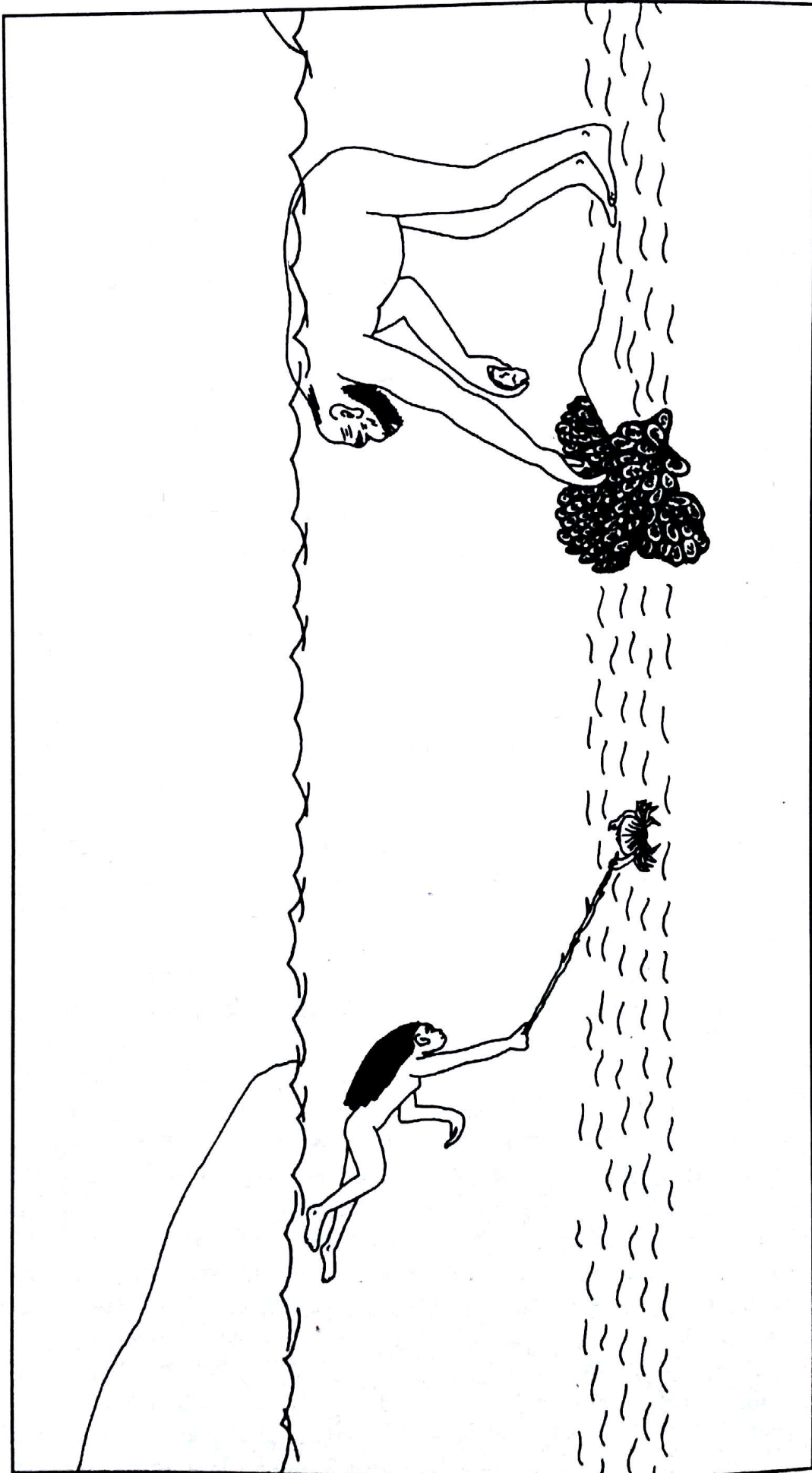


Figure 4.11 Active aquatic apes in a shallow lagoon.

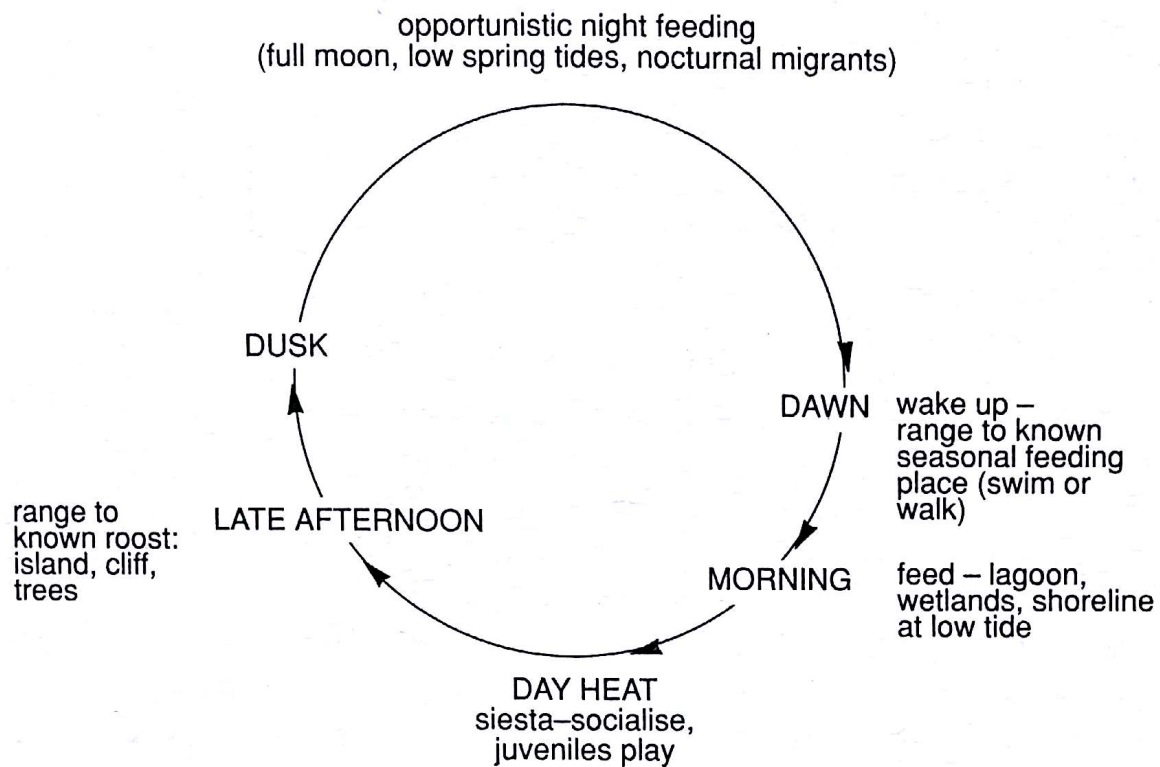


Figure 4.12 The daily cycle of an aquatic ape.

### **The return inland: Stage 3**

The more land-based troops, now bipedal, gradually spread along Rift Valley riverine parkland during one or more cooler, less catastrophic, periods. This spread is the product of troop-splitting and the wandering of young adults, penetrating into a habitat now empty of competing ancestors. Baboons would be present, but can be out-competed. The spread inland is driven by population pressure. This arises from great success in exploiting the limited but productive wetlands habitat of the rift, and a climate providing riverine parkland for range expansion. Possibly it arises also from constraints to the aquatic ape heartland habitat by climatic or water-level changes, or both – for instance, a drying-out Danakil Depression. These hominids are either still largely herbivorous or omnivorous, depending on what stage in the aquatic ape clade the range expansion occurred, and whether it occurred more than once.

The Behrenmeyer sketch in Lewin (1984) shows some of the important habitat features. However, lake and river foraging is limited, due to underwater predators and large, intolerant species such as hippopotamuses. Aquatic foraging is limited to safe pools and shallow wading-gathering places. Anti-predator social defence on land is supported by rock-throwing, shouting, and waving and hammering.

branches. Sleeping spots are safe islets, narrow river spits, ox-bows, and so on. Trees can still be used. Perhaps thorn-barricading has already been learned. Social grouping is less intense now, with some separation into transient subgroups.

If omnivorous, males – largely young adults but led by a troop-dominant or high-ranking subordinate – periodically range grassland (but not penetrating far into the relatively dry and dangerous savannah) as hunting and scavenging parties. The troop, led by the most assertive and intelligent males or females, supported by the benevolent dominant, mostly range near the home base, gathering small foods and scouting for new sources, especially during new growth seasons. Both hunting and gathering groups carry food and materials back to the home base. Inactives (elders, infants, injured) may remain in the home safe spot during the daily ranging.

Monogamy occurs, not necessarily exclusively, as a consequence of a particularly complicated optimality balance between greater intelligence and the amount to learn (especially in developing language), some Darwinian selection by females for the mix of hominid qualities, and simple environmental management through tools and weapons, rendering the world a less dangerous place and thus allowing smaller groups. Meanwhile, juveniles are the academics and inventors of the troops, exploring and inventing from the examples of elders, so that new routes and practices work their way into the troops' repertoires of behaviours.

The aquatic ape is now poised as a proto-hominid for radiation into *Australopithecus* and *Homo*, along and near the African Rift Valley.

Extinguishing the aquatic ape is the part of the scenario that offers the most options. Restriction to limited habitat in the Red Sea through climatic change – for example, to the Danakil Depression only – could have been part of the population pressure dispersing fringe populations progressively inland. One or other form of coastal unsuitability could have occurred, such as cooling of sea water, or heating, super-salination and drying-out. If this did indeed happen, the aquatic ape disappeared anagenetically, and we are effectively the aquatic ape ourselves.

A second option is the elimination of the limited-distribution aquatic ape by catastrophic change, such as a tsunami caused by one or other of possibly several inundations of a Red Sea evaporated below the levels of an interglacial Gulf of Aden or the Mediterranean Sea.

A third option is that the aquatic ape was a victim of Pleistocene extinctions (Martin and Wright, 1967), as hominid descendants arrived at the coast and either out-competed or preyed on their ancestor; or that it succumbed to glacially induced climatic changes.

## CONCLUSION

Responses to the question that forms the title of this chapter are as follows:

- (1) In terms of marine ecology, the tropical coastal environment provides productive ecosystems exploitable by a range of extant monkeys. There is no evident reason to believe that an ape could not converge to successful adaptation there, nor that coastal ecosystems were unsuited for such convergent apes during similar, warmer or cooler, Pliocene and Pleistocene periods. The oceanically rifting Red Sea provides a uniquely suitable timing (starting about 5 million years ago) and location (mainland coast and archipelagos, open embayments and enclosed sea, at various times).
- (2) In terms of primate behaviour, a number of species occupy a limited range of coastal ecosystems, with the critical path to the system presented by protective sleeping sites. Extant species resolve the problem by home ranging from a few remembered roosting places to opportunistically available and remembered foraging grounds, supplemented by a variety of predator-escape strategies, such as climbing trees and cliffs, and group defence. The aquatic ape clade could have resolved its predator avoidance and escape problems in similar primate ways, supplemented by water escape, nocturnal roosting on islands, and avoidance of remembered dangerous sites with underwater predators.
- (3) An aquatic ape is a viable creature in terms of marine ecology and primate behaviour, and the hypothesis of its existence is testable by appropriate fossil search, as previously suggested by LaLumiere (1981). To a biologist there is no problem in evolving an aquatic ape: the biological problems come in clading it to humans and in later making it extinct.

The characters in Table 4.7 meet the need for a balanced and integrated behavioural set (an ethosystem), producing a viable animal in an aquatic habitat. What is more, it is a set of characters with potential for more efficient utilisation of riverine savannah than by the baboons already there. The combination of dexterity, intelligence and complex vocalisations is the preadaptation. The characters in Table 4.7 show that the primate line of descent, although including characters in the several acknowledged aquatic clades, nevertheless developed its own unique set, functional for an opportunistically upright, tailless, socialising, tropical, insectivorous-herbivorous ape living in and beside shallow water.

Savannah Theory protagonists also should, for comparison, produce a balanced eco-ethological adaptive descent scenario for primate ancestors

at the right time (late Miocene and Pliocene) and in the right place. Most authors avoid the critical time punctuated in at 4–5 million years ago, although Kortlandt (1972) showed what was needed almost twenty years ago.

#### ACKNOWLEDGEMENTS

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ACTIVATED V PROTECTED PEARL REEF  
 AAT - marine ecosystem (oligohaline)  
 ~ left valley (blue sign. theory)  
 ~ main channel - wellhead adaption  
 MARINE ECOSYSTEMS IN COASTAL POPLAR  
 HAVE RHYTHM - CIRCADIAN RHYTHM.  
 APES CAME DOWN FROM THE TREES.  
 OUT INTO THE SANDWALS.  
 diff. levels - 4.  
 p39 "an aquatic ape - marine adapted"  
 fact.  
 GEOMORPH - Red Sea