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The paranasal sinuses and other enigmas: an aquatic evolutionary theory

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Abstract

The functional role of the paranasal sinuses in man has long been in dispute and as yet no satisfactory explanation has been offered for these 'unwanted' spaces. An answer may be found by study of the comparative evolutionary development of the sinuses in man and other higher primates.

Several unique physical characteristics of man not seen elsewhere in the ape family, or indeed in other terrestrial mammals, including some relating to the upper aerodigestive tract, are not satisfactorily explained by the traditionally held theory of evolutionary development of early man directly from the arboreal ape.

It is argued that these developmental differences are much more logically explained by a period of aquatic adaptation at a crucial period in the evolution of pre-hominid man. A new theory is proposed which might explain the importance of the sinus air cavities as buoyancy aids for protection of the upper airway tract in such an aquatic environment.

Further evidence is offered relating to a pathological condition of the external ear canal which supports this theory that man at some stage in his early development acquired an affinity for an aquatic environment.

Explanation of these unique hominid characteristics in terms of an aquatic evolutionary theory may help to resolve some of the enigmatic inconsistencies between man and other higher primates, and may account for man's eventual emergence as the dominant extant species, and perhaps an explanation for the 'missing link'.

Introduction

> 'Remnants of the past that don't make sense in present terms—the useless, the odd, the peculiar, the incongruous—are the signs of history.'
>
> Stephen Jay Gould

The Greek physician Galen (130–201 AD) is credited with the original description of skull porosity, but it was Leonardo da Vinci who clearly demonstrated for the first time the existence of the paranasal sinuses in his publication 'Two views of the skull' (*circa* 1489). Direct reference to the sinuses was made later by Vesalius in his treatise 'De Humani Corporis Fabrica' published in 1543. However, the functional role of the paranasal sinuses in higher primates and in particular, man, has remained a mystery despite the formulation of many theories since the time of the Renaissance to explain their anatomical or physiological significance.

The eminent otolaryngologist, Sir Victor Negus, who devoted much of his life to the study of the comparative anatomy and development of the upper aerodigestive tract, discounted these theories but was unable to offer any possible alternative (1958). More recently in his essay on evolution of the sinuses, Blaney (1990) concludes that no plausible argument has yet been proposed which offers a satisfactory explanation for their existence. Takahashi (1983) also acknowledges the significance of these air spaces as one of the most difficult problems in human evolution.

Although many of these theories of paranasal sinus function may have seemed superficially plausible at the time of their conception in the context of the anatomical and physiological development of modern *Homo sapiens*, they do not fully address the reality of the evolutionary process in terms of time and functional necessity. Not unreasonably, they are also based on the traditionally accepted theory of evolution of early man (the savannah ape) from the arboreal ape, which only recently has been called into question (Hardy, 1960; Morgan, 1982).

The essential point is that evolutionary adaptations take place in response to things that *have happened,* not things which are predestined to happen (Morgan, 1990). Evolution does not aspire to the development of 'unwanted spaces' any more than to the development of bipedalism or loss of body hair, unless these characteristics provide a definite evolutionary advantage conducive to survival.

That man possesses a large volume of empty paranasal sinus cavities, including an extensive labyrinth of ethmoid cells not found in any other species, must have an important evolutionary significance. There must have been some logical explanation for the expansion of the sinuses in early anthropoid man and development of additional ethmoid cells which offered a definite survival advantage over other ape species.

It can certainly be argued that this legacy left to modern man has proved much more of a liability than an asset as no other species has the misfortune to suffer from sinusitis or other allied upper respiratory problems. This cannot simply be due to the presence of ethmoid sinuses, and two other contributory characteristics, both also unique to man, are of equal relevance as aetiological factors.

The first of these is man's upright posture which has a distinct disadvantage in providing inadequate drainage of the sinuses, which previously had evolved quite satisfactorily in quadruped mammals over many millions of years. The second contributory factor is that man is the only terrestrial mammal not to be an obligatory nose breather. In all land mammals except man, the larynx is in contact with the soft palate, and the normal airway, from the nasal cavity to the trachea, is thus protected from possible aspiration of liquid and food, which pass around the larynx directly into the pyriform fossae.

The descent of the human larynx allows the possibility of free mouth breathing and with this comes the unique ability to speak. Despite this obvious advantage, the cost of breathing through our mouths when we are speaking or exerting ourselves, or through necessity because of nasal obstruction from a deviated septum, for example, is significant. With it comes the loss of the important physiological advantages of nasal breathing such as olfaction, humidification, disinfection and temperature control of inspired air.

These factors, predisposing to the development of upper respiratory infections are unique consequences of the various modifications of the upper aerodigestive tract in man. The only animals to suffer similar problems are breeds like Pekinese dogs in which selective breeding has artificially reduced the length and efficiency of the nasal passages (Morgan, 1990).

Since these modifications to the upper aerodigestive tract in man seem to have occurred at more or less the same time in his evolution, it is perhaps more relevant to consider them together rather than in isolation. There are also other important features about the human nose, particularly relating to its shape and structure, which are quite different from those of all other ape species.

These changes could not have evolved for any trivial reason and must represent some significant developmental adaptation that occurred in the vital period of ape/man transition which did not happen to other members of the ape family who evolved over millions of years with very little change into modern apes and chimpanzees. In a broader context, we cannot ignore other unique human features such as bipedalism, loss of body hair, presence of subcutaneous fat and differences in sweat and tear production, which evolved over the same transition period.

There is certainly no doubt about the validity of Darwin's theory of evolution of man and ape from a common ancestor, but the widely accepted concept that early man evolved directly from apes who came down from the trees and ventured on to the savannah offers no convincing argument to explain all the evolutionary adaptations that have occurred in man, and why there are gorillas, chimpanzees and humans and not simply three different species of African ape.

Before considering what appears to be a more logical explanation of these changes, it is pertinent to discuss what is known about the comparative evolutionary development of the sinuses and current theories of paranasal sinus function.

Evolution and comparative anatomy of the human paranasal sinuses

> 'Anatomy is to physiology as geography to history: it describes the theatre of events'.
>
> Jean Fernel (1497–1558)

Study of the evolutionary development of the paranasal sinuses is difficult to consider as a whole since their functions are widely different. The maxillary sinuses are distinct in origin, and while the frontal and sphenoidal air spaces can be grouped together, the ethmoid sinuses are only present in man, although they are found in rudimentary form in some other higher primates. However, certain facts are acknowledged about the functional role of the paranasal sinuses in the arboreal ape such as Ramapithecus and in other species during the immediate prehominid era (10–20 million years before present (mybp)).

Maxillary sinus

The maxillary sinus shows considerable variation in size and is particularly well developed in the higher primates, notably man, and some ungulates. In the chimpanzee it extends across the floor of the nasal cavity to communicate with its opposite sinus and also with the few ethmoid sinuses present.

To some extent, the size of the maxillary sinus depends on the length of the upper jaw which primarily was evolved for the purpose of seizing and devouring prey. As pointed out by Wood-Jones (1916), the length of the snout varies inversely according to the ability of prehension with the forelimbs. Animals which can grasp food, whether fruit or nuts, as in the case of monkeys or squirrels, or animal prey (*e.g.* the cat tribe), usually have a short snout. Others which have to crop herbage, such as ungulates, some rodents and marsupials (*e.g.* kangaroos) or predators that can seize prey with their jaws (*e.g.* dogs, bears and racoons) in general have a long and protruding snout (Negus, 1958). In many of the carniverous animals with long snouts the additional space in the upper jaw is occupied by important olfactory maxillo-turbinals.

Frontal and sphenoidal sinuses

The frontal and sphenoidal sinuses are present in many different species but are particularly well developed in keen scented animals such as the carnivores. Extension of the olfactory mucosa from the nasal cavity into adjacent cavities is seen in members of the cat and dog tribe where there is excavation of the sphenoid and frontal bones (Negus, 1958). Some herbiverous animals also have a large olfactory area in the nasal cavity with specialized mucosa covering five or more ethmoturbinal bodies.

In both groups of animals the ethmo-turbinals have a similar arrangement within the nasal cavity and the remaining space is occupied by the maxillo-turbinals which are the main source of moisture for humidification of the inspired air, essential for olfaction. The result is that in keen-scented animals, the nasal fossae are filled with ethmo-turbinals and maxillo-turbinals, with little or no free space.

In primates, however, there is a wide difference in the extent of these sinus cavities. The majority have no frontal or sphenoid sinuses, but in the gorilla and man these spaces are often well developed without any obvious reason, for their olfactory area is very restricted and they have a feeble sense of smell (Negus, 1958).

Ethmoid sinuses

The reduction of the olfactory area in higher primates has resulted in regression of the olfactory turbinals which instead are replaced by additional air spaces—the ethmoid sinuses. According to Cave and Haines (1940), the chimpanzee has a small anterior ethmoid cell opening into the frontal sinus, and a posterior cell, whereas the gorilla has an anterior and two posterior cells.

In man, however, there is unique development of large and numerous ethmoid sinuses, communication with the nasal fossae by narrow ostia, despite the absence of any olfactory or other apparent role. In addition, the sinus openings are well protected from the nasal airstream by single scroll-like turbinates which project downwards to cover the ostia, forming narrow valve-like communications.

The extensive system of empty ethmoid cavities found only in man form a honeycombed labyrinth situated between the upper part of the nasal cavity and the orbit, resulting in characteristic widening of the intercanthal distance. There may be as few as three or as many as 18 on each side, their number varying inversely to their individual size. The pyramidal shaped labyrinth has an average length of 4–5 cm, a height of 2.5–3 cm, a width anteriorly of 0.5 cm widening to 1.5 cm posteriorly, giving an overall volume of up to 30 cc (Mosher, 1929).

In the context of higher primate evolution, the emergence of early man with his short snout but extensive framework of large empty paranasal cavities, despite a rudimentary olfactory or prehensile requirement, poses an apparently unanswered question: 'what was the purpose of these empty sinuses and why did man develop a profusion of additional ethmoid spaces not present in any other animal?'

Theories of paranasal sinus function

The hypothetical role of the paranasal sinuses has been the subject of much speculation but little empirical research or investigation over the last few centuries. Several well known theories have been proposed but later discounted for lack of substantial evidence or conclusive observations.

1. Resonance theory. Bartholinus (1660) originally proposed that the sinuses were important in phonation by aiding resonance of the voice. As Blaney (1990) points out, this theory has been discounted because the size of the sinuses bears little relation to the strength of the voice. Animals such as the giraffe and rabbit, despite having large sinuses, have a weak or shrill irresonant voice (Negus, 1958), whereas others, for example, the lion, although possessing small sinuses, can produce an unmistakable loud roar (Proetz, 1953).
2. Mucus secretion theory. In 1763, Haller suggested that the sinuses played an important role in moistening the olfactory mucosa but this theory has been discounted because of a comparative lack of mucus glands in the paranasal sinus lining (Skillern, 1920; Negus, 1958; Mygind and Winther, 1987).
3. Olfactory theory. This theory was first proposed in 1830 by Cloquet who assumed quite erroneously that the large sinus cavities in man were lined with olfactory epithelium. As with other animals which have a poor sense of smell, the olfactory mucosa in man is confined to a limited area in the roof of the nasal cavity and the sinuses are lined with respiratory epithelium (Rhŷs Evans, 1987).
4. Thermal insulation theory. First suggested in 1953 by Proetz who likened the paranasal sinuses to 'an air-jacket about the nasal fossae closely resembling the water jacket of a combustion engine', this theory has been discredited for several reasons. In species which require the greatest degree of warming the air for increasing humidification, the heating apparatus takes the form of an elaborately branching maxillo-turbinal body inside the nasal cavity.

   Heat exchange of the inspired air is much more efficiently carried out with this extensive system of superficial vascular spaces in contact with the nasal air stream than with large sinus cavities situated adjacent to, but separate from, the nasal fossae. Furthermore, the presence of only one small ostium, or occasionally two, precludes the possibility of adequate circulation of air into the sinuses (Negus, 1958).

   In addition to the humidification theory, it has also been suggested that the paranasal sinuses help with insulation of the base of the brain, but the apparently anomalous presence of large frontal sinuses in the African Negro (Brothwell *et al.,* 1968; Wolfowitz, 1974) and frequent absence in Eskimos (Koertvelyessy, 1972; Tillier, 1975), would seem contradictory to this theory.

   Neanderthal man also possessed large frontal sinuses which according to Coon (1962) were adapted to insulate and protect the brain from the cold but as Tillier (1975) points out, this theory cannot be extended to other hominids since the frontal sinus and supraorbital size relationship is unique (Blaney, 1990). Quite apart from this, Neanderthal man was mainly accustomed to a temperate climate with little need for partial cerebral insulation.
5. Lightening the skull. Another suggested role of the paranasal sinuses is to lighten the skull, particularly its anterior half, in order reduce the work of the neck musculature (Skillern, 1920). Unlike other primates such as the gorilla, orang, chimpanzee and gibbon, man is unique in maintaining his upright posture. In these other species the skull is held in a forward inclined position requiring strong neck muscles capable of supporting the head under all conditions (Fig. 1). Only in man is the head balanced on occipital condyles situated in the middle of the skull base rather than at its posterior extremity, as in most four footed animals (Wood-Jones, 1916).

   'If sinuses served no other useful purpose than the supposed reduction in weight', writes Negus (1958), 'the obvious alternative would be the apposition of the two tables of bone which form their walls'. He goes on to say that 'this would be a simple matter in the frontal and sphenoid regions' and elimination of the necessity for maxillary sinuses could be evolved, as in the baboon, by incurving of the cheeks.
6. Facial growth theory. Proetz (1922) originally considered the presence of nasal sinuses to be directly related to the development of the face and that 'we are not called upon to attribute to these cavities any further functional activity'. He concludes that 'the face parts develop because the individual has need of them: larger, stronger jaws, increased breathing space. The sinuses, which, after all, are nothing but unoccupied spaces, result incidentally'.

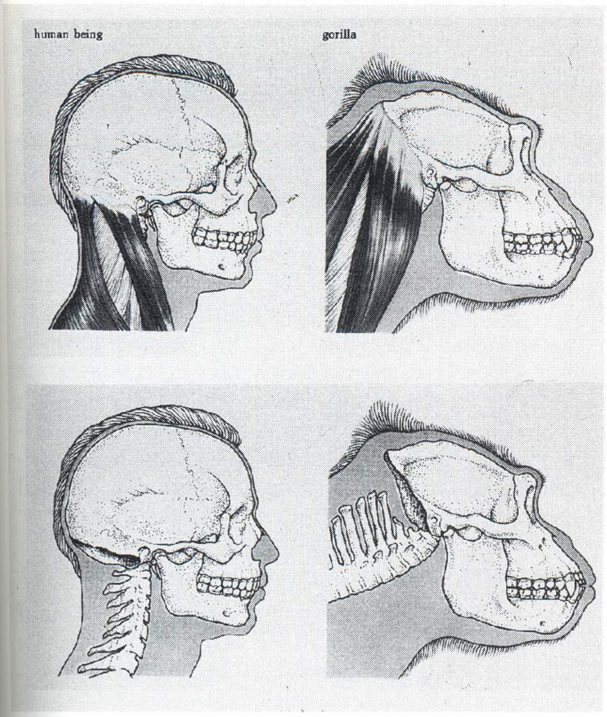

FIG. 1

Cervico-occipital articulation in man and gorilla, showing difference in sternomastoid and trapezius musculature and spinal orientation. (By courtesy of the Natural History Museum, London.)

More recent authors have stressed the importance of craniofacial development and increase in the angle between the forehead and frontal cranial base in dictating sinus morphology (Takahashi, 1983; Shea, 1985; Blaney, 1990). But these arguments do not explain the evolutionary necessity for the presence of large empty spaces in the facial skeleton adjacent to the nasal cavity in man when compared to parallel development in other species.

Although this theory may be tenuously applied to the maxillary and ethmoid sinuses, there does not appear to be any reason to regard the presence of the sphenoidal sinus as connected with growth of the face, since it does not form part of the facial structure. Similarly the wide variation in the size of the frontal sinuses without obvious change in the shape of the facial contour seems to render this argument invalid.

Certain conclusions about the functional importance of the paranasal sinuses may therefore be derived from a general survey of their comparative anatomy and evolutionary development. Expansion of the nasal fossae and adjacent sinuses was almost universally apparent only for purposes of extension of the olfactory mucosa in carnivora and other keen-scented animals, apart from the higher primates and perhaps one other exception—the excavated sinuses and hollow horns of some ungulates.

Other functions ascribed to the sinuses in man such as vocal resonance, humidification, heat exchange, thermal insulation and craniofacial development may be discounted for the various reasons described. Since these theories, based on traditional evolutionary ideas of ape/man transition, are not wholly convincing, we are still left with the same unanswered question about the functional role of the sinuses and why they developed to such an extent in man. If, however, we introduce the concept of aquatic adaptation as proposed by Hardy (1960) and Morgan (1982), many of the puzzling evolutionary changes seem to have a more logical explanation.

Paranasal sinus function—a buoyancy theory

> 'We must, however, acknowledge, as it seems to me, that man with all his noble qualities still bears in his bodily frame, the indelible stamp of his lowly origin'.
> Charles Darwin (1809–92)

As we shall see later, the theory proposed by Skillern (1920), that expansion of the sinuses in man was for the purpose of lightening the skull, may be nearer the truth. The counter-arguments to this theory pointed out by Negus (1958) and others are perfectly valid when taken in context of the accepted savannah theory of ape/man evolution. If simply lightening of the anterior part of the skull was needed for reducing work of the neck musculature, this could equally be achieved by reduction in sinus size and apposition of their walls.

If, however, we argue that the anterior part of the skull not only needed to be light, but also buoyant, the presence of air in the cavities would be essential, and development of larger and more numerous sinuses (*e.g.* ethmoid cells) would be even more advantageous. From purely a physical and anatomical point of view, this would seem to be the simplest and most logical explanation.

This hypothesis would obviously have no relevance if one continued to accept the traditional savannah ape theory of evolution. It is, however, consistent with the aquatic theory (Hardy, 1960; Morgan, 1982), which proposes that certain early hominids, ancestral to *Homo sapiens,* spent a period of several million years in an aquatic environment before returning to their terrestrial existence. In this situation, additional buoyancy of the facial structures would certainly be advantageous to an aquatic ape living in a marine environment, in helping to keep the airway opening above water, relieving workload of the cervical muscles and assisting forward migration of the cervico-occipital articulation.

Other aquatic species have evolved structural buoyancy to suit their individual needs. Those non-air breathing animals which live an entirely submarine existence, such as fish, require mainly negative buoyancy, which is controlled in many species by a swim bladder, but others which need to surface for breathing have additional buoyancy. Aquatic mammals such as cetacea (whales and porpoises) have developed a layer of subcutaneous fat which provides buoyancy as well as streamlining and insulation. This layer of subcutaneous fat is also a unique feature which distinguishes man from all other primates. If we regard *Homo sapiens* as a terrestrial mammal, this distribution of fat is highly uncharacteristic, but as an ex-marine mammal this feature would be conforming to type.

Maintenance of the airway is essential in air-breathing animals. In whales and other cetacea the nostril or blowhole has migrated well on to the dorsum of the head which allows the snout to remain submerged on the surface while the animal is still breathing. In the reptile family the long characteristic boatshaped snout of the crocodile gives additional buoyancy for the airway which is also vital for maintaining its acute sense of smell.

The presence of air sacs or cavities is one of the most efficient means of assisting buoyancy as seen in some surface insects. In frogs and toads the air sacs provide buoyancy for the head while the animal is partially submerged to help keep the nasal opening above water. It is therefore not unreasonable to suggest that in primates, who already have rudimentary sinuses, expansion of the cavities and development of additional ethmoid spaces could not have evolved in man for the same purpose.

The nasal valve

One other essential characteristic of air-breathing marine animals is the ability to close off their airway when submerged, which can be done either by a valvular mechanism to close the nostril (newt, crocodile, cetacea, salamanders, sea elephants, sea lions, seals and polar bears), or the laryngeal aperture (penguins). This provides protection for the airway and allows the animal to catch or eat prey whilst under water. Of tailless amphibia, the frog has a specialized pad on the anterior angle of the lower jaw which is thrust upwards when submerged to close the external nares (Young, 1950). The ability to close off the nostrils is not exclusively aquatic since the camel can also achieve this in order to keep out sand.

The mechanism of closure of the nostril is by two sets of opposing muscles, the dilator and constrictor naris situated on the dorsum of the nasal aperture. It is perhaps curious that although humans are not able to completely close off their nostrils, they are unlike any other higher primate in possessing similar muscles around the external nares which can be used for flaring the nostrils. The only difference between man and the seal in this respect is that when the muscles are relaxed, the seal's nostrils are completely closed, whereas ours are not (Morgan, 1982).

The external nose

The shape of the human nose has intrigued scientists and anatomists for centuries, but no logical explanation has been offered to account for its elongated form and the unique differences which distinguish it from those of other higher primates.

The prominent cartilaginous portion of the nose has made it vulnerable to trauma causing deviations and fractures, but functionally it may have evolved to allow closure of the external nasal valve. It has also been suggested by Morgan (1982) that its protective hooded shape may be important when diving and swimming in deflecting water from the nasal opening, preventing inundation of the airway (Fig. 2). Certainly the caudally directed opening in man differs significantly from the wide ventral aperture seen in other higher primates. The only other primate to possess a prominent nose of any proportion is the semi-aquatic proboscis monkey (Fig. 3).

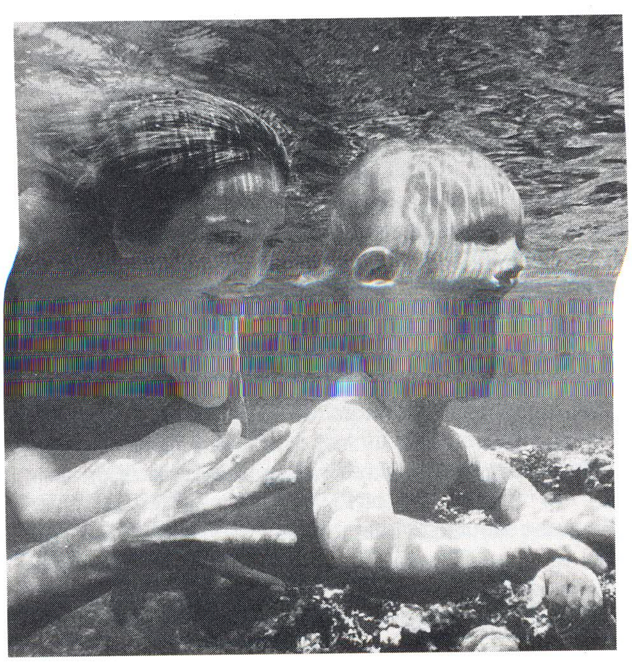

FIG. 2

The elongated nasal skeleton protects the nasal opening when swimming.

Thomson and Dudley Buxton (1923) have studied the configuration of the nose in modern man in relation to race and climate and found that the wide platyrrhine nose is associated with a hot, moist climate and the narrow leptorhine with cold, dry conditions. The breadth of the pyriform aperture, however, has no correlation with racial differences (Negus, 1958).

Other hominid evolutionary adaptations

In his opening introductory paragraph to 'The Origin of Species', Darwin states: 'until recently the great majority of naturalists believed that species were immutable productions, and had been separately created. Some few naturalists, on the other hand, have believed that species undergo modification, and that the existing forms of life are the descendants by true generation of pre-existing forms'.

The process of natural selection applies equally to man,

FIG. 3

The proboscis monkey—the only other aquatic primate—has a nose of enormous proportion. (By courtesy of Camera Press, Ltd).

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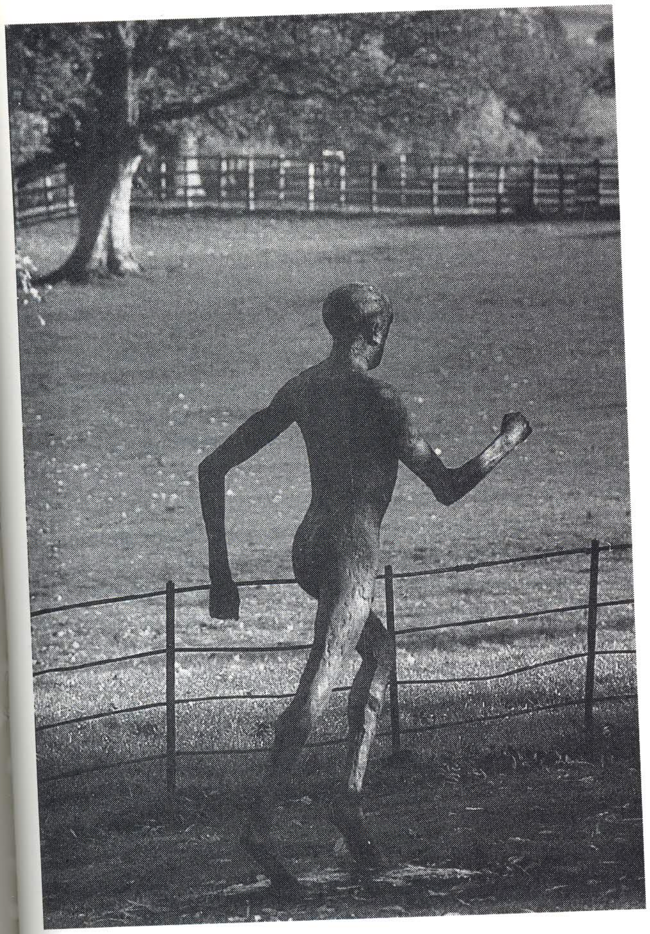


FIG. 4
Man is the only primate or terrestial mammal to have adopted a bipedal mode of locomotion.

and the various unique modifications evolved in early hominids during the ape/man transition must have had some important evolutionary significance. These adaptive changes are questioned in the light of traditionally held beliefs of anthropoid evolution, and an alternative theory of aquatic adaptation is suggested which may provide a more logical explanation.

1. Bipedalism

The most striking feature that distinguishes man from all other primates and terrestrial mammals is his upright mode of locomotion (Fig. 4). What may seem quite natural to us has only been made possible through adaptation over millions of years, but for the savannah ape the initial impetus which promoted this dramatic evolutionary change is difficult to explain.

The only other quadrupeds which can move faster on two legs than on four, albeit by hopping, are those which have large heavy counterbalancing tails such as kangaroos and wallabies. Apes and chimpanzees can travel for short distances on two legs, usually when holding something in their hand, but it is characteristically in a diagonal direction using their other hand for stabilization. One other primate which can walk on two legs for an appreciable distance is the proboscis monkey when wading in shallow waters.

Other land-dwelling primates (macaques) and rodents (beaver) which live near the shore, may adopt an upright posture when wading into the water in search of food, sometimes using their forelimbs to carry objects. According to Hardy's original hypothesis (1960), the initial impulse towards bipedalism came when the ancestral primate waded into the sea. Additional buoyancy in the water would have reduced pressure on the spine and assisted rotation of the pelvis to bring the spine and hind limbs into alignment.

One other creature to have undergone similar adaptation is the penguin, which unlike any other bird, has a perpendicular stance, just as ours is dissimilar to any other mammal. This posture is maintained whether the animal is swimming, floating or on dry land, and after a few million years would have achieved a degree of stability which could be retained permanently, irrespective of the environment.

2. Loss of body hair

Another unique characteristic which distinguishes man from other higher primates is his relative hairlessness. Why did he lose his furry coat, which for a terrestrial mammal made him less adaptable for regulation of body heat, since a hairy skin is much more efficient for keeping the body warm in the cold and keeping cool when it is hot?

Man in fact does have an equal distribution of hair follicles per unit surface area when compared to the chimpanzee, but the hairs are short, thin and largely vestigial—but for what reason? Perhaps, as Sokalov explains in his book 'Mammal Skin' (1982), the answer is that 'in water, fur provides poor insulation and becomes atrophied'. Such a naked ape is unique and the only other hairless mammals dwell either in the sea (whales and porpoises) or underground (the naked mole rat).

3. Subcutaneous fat

The presence of a layer of subcutaneous fat is another remarkable feature of human skin which is unique among primates. This is far more characteristic of aquatic mammalian species for which it provides buoyancy, streamlining and an effective form of insulation (Fig. 5). Fat stores in terrestrial mammals are located mainly in the mesenteries and around the kidneys; subcutaneous deposits are minimal since these do have a distinct disadvantage in terms of optimum mobility and weight distribution.

4. Sweat and tear production

The proliferation of lipid secreting sebaceous glands in human skin is undeniably unique among terrestrial primates but common in aquatic species where it serves the useful purpose of waterproofing. Moreover, the presence of eccrine glands producing a hypotonic saline solution is important in thermoregulation in man, but in terrestrial animals they do not function in a similar fashion, since loss of vital salt and water would be potentially fatal. It is quite possible that at some stage in our evolution, ancestral man developed this capacity for excreting excessive salt through the skin as well as through the kidneys, particularly if he lived in a marine environment.

One other method of excretion of excessive salt, found in marine reptiles and in some marine mammals, is

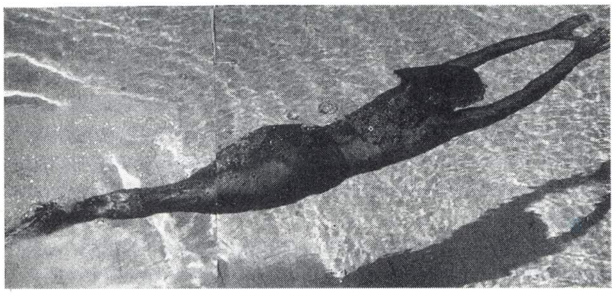


FIG. 5

For a terrestial mammal, how could its graceful, streamlined shape have been acquired in any other way than in an aquatic environment?

through the production of tears. Although nearly all land mammals possess lacrimal glands, man is the only weeping primate, a phenomenon which is difficult to explain purely on a quantative basis.

Tears produced in response to emotional stimuli are quite different in their chemical composition to reflexive ones and Frey (1985) has suggested that the lacrimal glands in these situations possibly function to eliminate excess stress-related chemicals, thus bringing emotional relief. Morgan (1990) also postulates that the well known globus sensation associated with the emotional weeping response may well be a primitive protective cricopharyngeal contraction reflex preventing swallowing of undesired chemical excretions.

A theory of evolution

> 'There are 193 living species of monkeys and apes. One hundred and ninety-two of them are covered with hair. The exception is a naked ape self named *Homo sapiens*'
>
> Desmond Morris (1928–)

The publication of 'Origin of Species' by Charles Darwin in 1859 was followed in 1871 by his book 'The Descent of Man' which expounded his theory of evolution of man and apes from a common ancestor. There is little dispute today about the validity of this theory, although there is much argument about the manner in which the remarkable differences between the higher apes and man were evolved.

'Considering the very close genetic relationship that has been established by comparison of biochemical properties of blood proteins, protein structure and DNA and immunological responses', writes Elaine Morgan (1982), 'the differences between a man and a chimpanzee are more astonishing than the resemblances. They include structural differences in the skeleton, the muscles, the skin and the brain, differences in posture associated with a unique method of locomotion, differences in social organization, and finally the acquisition of speech and tool-using, together with the dramatic increase in intellectual ability which has led scientists to name their own species, *Homo sapiens sapiens*—wise wise man'.

There is little doubt that the three main higher primate species: the gorilla, the chimpanzee and prehominid ape evolved from the common ancestral African ape (Fig. 6). But what were the circumstances which dictated such a divergent evolutionary path for man during which he acquired unique adaptations such as bipedalism, loss of body hair, subcutaneous fat, an excess of sweat and sebaceous glands, changes in sexual and social habits, as well as modifications to the upper aerodigestive tract, which set him so much apart from the other apes?

A theatre of change

> 'When it is not necessary to change, it is necessary not to change'
>
> Lucius Cary, Viscount Falkland (1610–43)

It is difficult to explain many of these enigmatic human characteristics in terms of traditionally held beliefs of prehominid evolution. Some other vital factor or circumstances must have played a role in motivating these unique adaptations which are clearly more advantageous in setting man apart from his primate cousins on a path of evolution leading ultimately to the emergence of *Homo sapiens*.

The crucial period of time during which these remarkable divergent evolutionary changes were taking place in the higher primates was the late Miocene/early Pliocene epoch which commenced about 9 million years ago and lasted roughly 5 million years (Fig. 7). Fossil remains of ape-like prehominid primates during the preceding Miocene period are abundant both in Africa and Asia, and one bearing early changes in jaw structure thought to be possibly precedent to the hominid ape was Ramapithecus, discovered by G. E. Lewis in India in 1930 and later by Leakey in Africa.

During this time, large populations of ape-like creatures flourished in temperate forest expanses widely distributed throughout Asia, Africa, and Europe. A dramatic climatic change, however, was to alter the geological and ecological structure in many of these regions, and in one place in particular, in the Afar region of East Africa, these environmental changes may have been significant in altering the destiny of primate evolution.

The onset of what was known as the Pliocene drought resulted in decimination of the forest habitat of these apes and created a changing environment when adaptation was essential for survival. At the same time, continental shift of the East African plate caused inundation of a large low-lying area with formation of an extensive inland sea (Fig. 8). This sea eventually dried up after several million years leaving only deep deposits of salt as evidence of its former existence.

Fossil evidence has shown that the majority of ape-like species evolved with few changes during the Pliocene period, but remains discovered in the Olduvai gorge in East Africa from about three and a half million years ago indicated that a dramatic evolutionary step had occurred in one particular branch of the ape family. Australopithecus, as he was called (meaning southern ape), was different from all other apes in that he walked upright on two legs instead of four.

One of the most remarkable finds in this region was 'Lucy' whose almost complete skeleton was discovered by Donald Johanson. 'In 1973' he writes 'I found a humanlike knee joint that proved beyond doubt that our ancestors walked erect close to three and a half million years ago—long before they developed the big brains that had once been thought to be the hallmark of humanity' (Johanson and Shreeve, 1989).

Similar discoveries of hominoid fossils in this area have proved beyond reasonable doubt that at some time

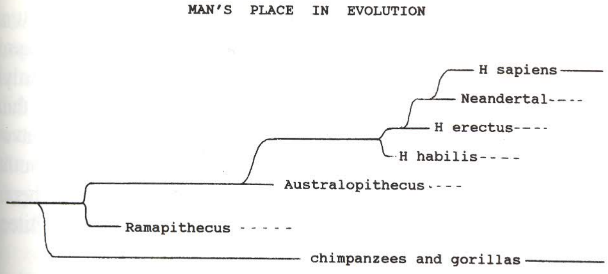


FIG. 6

Man's place in evolution. There is little doubt that the three main higher primate species: the gorilla, the chimpanzee and prehominid ape were evolved from the common ancestral African ape.

between six or seven million years ago and three and one half million years ago, probably somewhere in North East Africa in the Afar region near the Red Sea, certain anthropoids stood up and began walking erect (Morgan, 1990). 'Something must have happened', she adds, 'which meant that the near universal mammalian mode of locomotion (walking on four legs) rather suddenly ceased to be efficient for them. They switched to a mode that was not merely different, but unique among mammals' (Fig. 7).

Other proof that divergence of evolution between man and apes from common ancestors took place about this time has come from molecular biological studies, and in particular DNA hybridization (Sarich and Wilson, 1967).

The Savannah Theory

The traditionally held Darwinian 'Savannah' theory postulates that gradual evolution of ancestral man from the arboreal ape occurred because of climatic and behavioural changes. Loss of their forest habitat with corresponding extension of grassy plains or savannahs resulted in movement of prehominoid apes from the tree habitat on to the plains.

Other ape species who remained in the forests ultimately developed into gorillas and chimpanzees with few morphological or physiological changes during this period. Parallel behaviour changes developed mainly as a result of dietary requirements. No longer able to depend on lush vegetation in the forest, the Savannah apes gradually evolved an omnivorous diet scavenging for small game to satisfy their needs, later evolving into hunters.

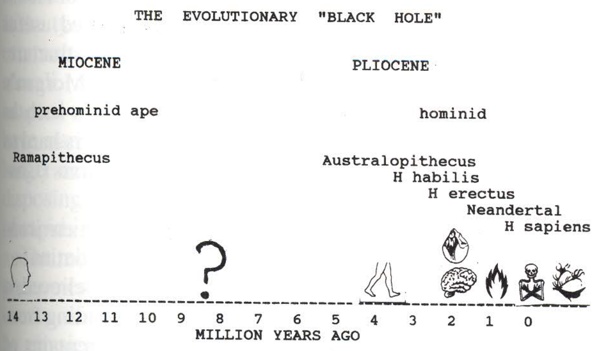


FIG. 7

The Evolutionary 'Black Hole'. Change in jaw structure in the Ramapithecus ape was an early hominoid feature. But at some time between 6–7 mybp and 3.5 mybp 'something must have happened, which meant that the near universal mammalian mode of locomotion (walking on four legs), rather suddenly ceased to be efficient for them' (Elaine Morgan, 1990). The acquisition of large brains, use of tools and fire, ceremonial burials and artform came much later.

According to this theory, the one crucial development of bipedalism in the Savannah ape evolved because of the alleged advantage of standing upright on two legs and being able to see further over the plains and high grass in search of prey. Later, the advantage of having two hands free to carry weapons enabled his development as a hunter in pursuit of game (Morgan, 1982). One other complex and less tenable theory proposed by Lovejoy (1990) is that bipedalism actually evolved in these apes when still forest dwellers for various social and sexual reasons.

The Aquatic Theory

> 'Nothing of him that doth fade
> But doth suffer a sea change
> Into something rich and strange'
> William Shakespeare (1564–1616)

In April, 1960, an article appeared in the New Scientist by Sir Alister Hardy suggesting an alternative theory of evolution which seemed to explain many of the dramatic changes that occurred during Man's development from the arboreal ape.

He proposed that as a result of the changing environment at the onset of the Pliocene drought with reduction of the forest habitat and vegetation, certain anthropods were driven by competition from life in the trees to assume a new habitat on the shores of inland waters where they

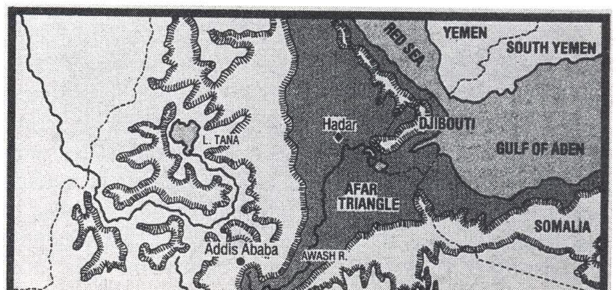


FIG. 8

The Afar Peninsula during the late Miocene Period (By courtesy of Donald C. Johanson and Maitland Edey).

became adept at hunting for food, shell fish and sea urchins in the shallow coastal waters. The conincidental inundation of the Afar region in East Africa would have provided an ideal environment for these changes.

Initially wading on all fours, these aquatic apes gradually assumed a more upright posture enabling them to extend their territory into deeper water, also allowing them to escape more easily from predators, later developing the ability to swim and dive.

Because of the additional buoyancy, stability on two legs would have been much easier to acquire in the water environment than on the savannah, as exemplified by the only other primate to have ventured into the sea. The proboscis monkey (Fig. 3) lives in the mangrove swamps in the coastal waters of Borneo, and among other features, the male of the species is characterized by his enormous nose. Although retaining a mainly terrestrial quadruped gait similar to other apes living in trees, he can adopt a bipedal mode when wading in the shallows in order to keep his head above water. In certain instances he has even been noted to use this mode of movement for walking on dry land.

The compelling argument proposed by Hardy that ancestral Man spent a period of aquatic adaptation is not unique in evolutionary history. On the contrary, this process is well recognized and several species of birds, reptiles and mammals are known to have abandoned their terrestrial existence to become adapted and modified to an aquatic life.

An early example is a member of the dinosaur family (ichthyosaur) which took to the water, evolving flippers instead of legs before becoming extinct. Among mammals, members of the cetacean family (the whales, dolphins and porpoises) successfully adapted to an aquatic existence, as did some of the hoofed mammals related to the elephant (the sea cows and manatee). Others include aquatic birds (penguins), aquatic carnivores (sea lion, seal, otter), aquatic rodents (beaver, water vole), aquatic reptiles (crocodile, sea snake) and aquatic insectivores (water shrew, desman).

There is, therefore, no reason to suppose that a similar transformation did not occur among the primate order. The aquatic theory postulates that one such species of ape did embark on this course and that adaptation to this new environment resulted in the emergence of a bipedal age, ancestral to Australopithecus and eventually *Homo erectus*.

It has been argued that such rapid evolution could not have been possible over a period of 3 to 4 million years, but evidence suggests that when the Afar was invaded by marine waters about 6.7 million years ago (Barberi *et al.*, 1972a, b) in the late Miocene period, certain mountainous regions may have become isolated from the mainland. One such area known as Danakil Island may have been the site where a group of apes along with other animals was trapped, on a biological island where evolutionary adaptations are known to occur much more rapidly (Morgan, 1982). Increasing desiccation and loss of the forest habitat on the island may have provided an ideal environment where certain families of apes living near the coastal waters were forced to adapt to a more aquatic existence in search of food by wading into the shallow waters. Under these unusual conditions rapid evolution of the hairless, bipedal Australopithecus apes described by Hardy and Morgan may have taken place.

Episodic volcanic activity in the Afar triangle is known to have taken place since the early Miocene Period (Gass, 1974) and bridging of the Danikil Strait would certainly have allowed migration of apes and other animals from the island back to the mainland. Among them would have been hominoid Australopithecines who ventured south along the Afar Gulf towards the Hadar settlement where fossils were eventually found (Johanson and White, 1979).

Other Australopithecines may have remained on the island to continue their evolution, crossing to the mainland about 1.75 mybp, to the Koobi Fora and Olduvai Gorge where the remains of *Homo habilis* were found (Leakey, 1979; Morgan, 1982). According to Morgan (1982), further development continued on Danakil Island with emergence of *Homo erectus* (about 1 mybp), until the final desiccation of the Danakil Depression about 30,000 years ago (Bonatti *et al.*, 1971; Tazieff, 1972).

The aquatic theory postulates that when these upright, hairless Australopithecines re-emerged back on to the savannah, they brought with them various adaptations acquired during this aquatic period which were retained and which provided distinct advantages over other ape species. Their stable bipedal gait permitted more freedom of the forelimbs once they were back on land to enable them to hold and carry objects and weapons which was distinctly favourable in their emergence as dominant hunters in this new terrestrial environment.

What is the evidence?

Whatever is the truth about evolutionary development of early man from the arboreal ape, suppositions must be based on established scientific facts, although the final explanation of the sequence of events may not be readily apparent. The aquatic theory does seem to provide a more logical and consistent answer to many of the enigmatic inconsistencies between higher primates and man, and is frequently supported by parallel development in other species.

Fossils provide the only 'hard evidence' of evolutionary changes and have proved beyond doubt that bipedalism was the first crucial adaptation in early hominid evolution (Johanson and Edey, 1981). Recent detailed studies of early skulls and post-cranial remains of *Homo erectus* by Rightmire (1990) have also provided useful information about comparative changes in bone structure. Although much of the evidence for Elaine Morgan's aquatic theory relates to soft tissue adaptations such as changes in skin structure, where specific dating is hard to establish, it is based on sound scientific deductions (Charlton, 1991).

Preservation of skeletal remains in a marine environment is extremely unpredicable because of continuous wave erosion, and if the aquatic theory is to be believed, it is not surprising that no early hominid fossils dating from this period have been found. However, those remains of primitive Australopithecines which have been identified, have all been in the vicinity of coastal areas or inland waters in the region of the Afar peninsula and Olduvai Gorge, a fact which protagonists of the savannah theory claim is coincidental.

There may nevertheless be some tangile evidence of the aquatic theory, which so far has been overlooked by anthropologists and scientists, which might provide important evidence that early man did venture into the sea in search of prey, and that unlike his ape predecessors, he did spend a large proportion of his time swimming in the water. This evidence is crucial to the argument supporting the aquatic theory and may be relatively easy to prove or disprove, given adequate fossil remains of early anthropoid man. It relates to the presence of ear canal exostoses.

External auditory canal exostoses

Bony swellings of the external ear canal occur with varying frequency and are of two distinct types. Osteomata usually arise in the outer part of the canal and have a pedunculated or lobular appearance. They are composed of dense ivory bone are considered true pathological benign tumours of bone. There may be a hereditary factor in their aetiology, since Roche (1964) has found an incidence of 27.9 per cent in Australian aborigines. Hrdlicka (1935) has also described a particularly high incidence in Peruvian and American Indian populations.

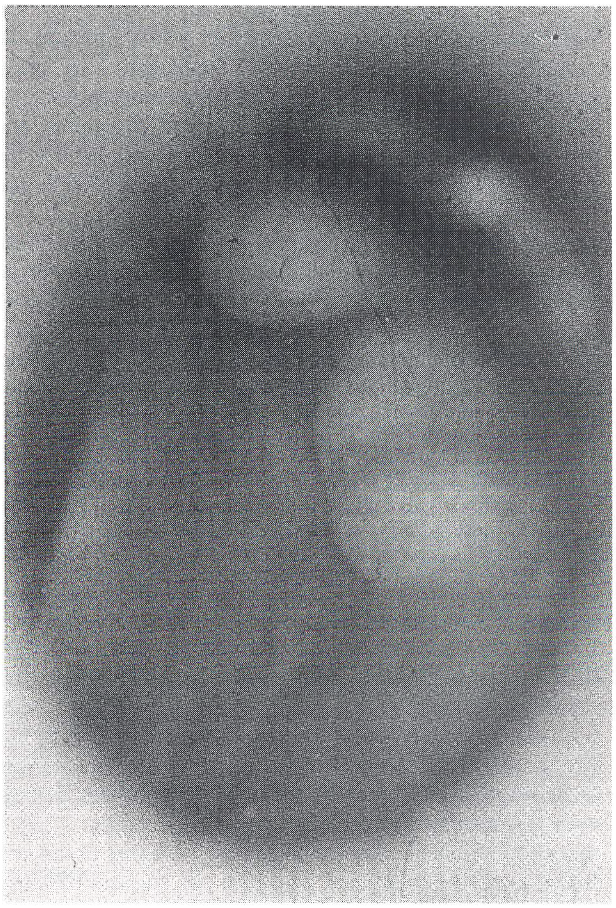
True exostoses of the ear canal arise in the deep part of the meatus, close to, but not involving the annulus of the tympanic membrane. There is usually one situated on the lower anterior wall and one in a similar position posteriorly, and sometimes a third arising from the roof (Fig. 9b). Progressive growth may gradually reduce the size of the deep meatus to a pinhole, causing deafness and often secondary otitis externa. Smaller exostoses of similar aetiology may also be found arising near the annulus (Fig. 9a). The relevance of this condition is in its pathogenesis, for it occurs exclusively as a direct result of exposure to relatively cold water in swimmers.

An experimental study in Guinea pigs reported by Fowler and Osmun (1942) demonstrated fibrous profileration of the subcutaneous tissue in the deep meatus with new bone formation. Repeated exposure to cold water in the canal stimulates the periosteum to produce a layered formation of periosteal bone, suggesting a periodic growth pattern. With further growth, it undergoes remodelling to produce lamellar bone.

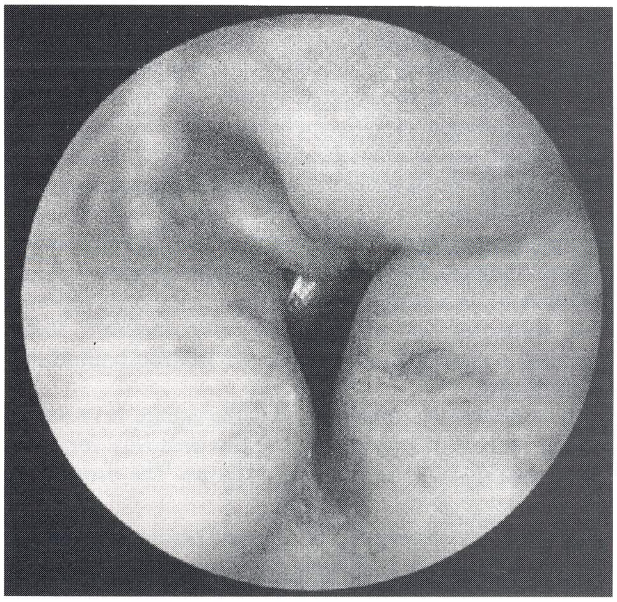
No adequate explanation has been given for this condition, but I believe that this process may represent an adaptive response to an aquatic environment. Land based animals which depend on air mediated sound transmission at the tympanic membrane usually have a widely patent external ear canal for maximum reception of auditory stimuli. Marine mammals, on the other hand, have adapted to sound transmission in an aquatic medium and have narrow or vestigial canals. A wide meatus is no longer needed and may also be a dangerous liability predisposing to rupture of the tympanic membrane because of rapid increase in external pressure when diving.

The relationship between swimming and exostoses is a phenomenon well known to otolaryngologists, but the relevance of their pathogenesis has been largely overlooked by physical anthropologists and archeologists who have considered both types of ear swellings as one of a range of discrete cranial traits helpful in determining ethnic affinities and population movements (Mann, 1986). Korner (1904) was the first to note the difference in incidence of exostoses between coastal and inland populations in Germany, and suggested salt water as a cause.

In 1935, Belgraver found an overall incidence in his clinic patients of 2.02 per cent but in members of swimming clubs the incidence was as high as 42.8 per cent and virtually all instructors were found to possess exostoses. Other studies by van Gilse (1938), Harrison (1962) and Mann (1986) have produced similar results, the last study



(a)



(b)

Fig. 9

Exostoses of the external auditory meatus. 9a. Small exostoses arising near the annulus. 9b. Large exostoses of the deep meatus. (9a by courtesy of T. R. Bull.)

by Mann showing an incidence of 64 per cent in people swimming at least three times a week. In all of these papers, the most important and consistent finding was that no person was found with exostoses who was not a frequent swimmer.

Other factors such as age, sex, racial variations and water temperature are also important in determining the incidence of exostoses. In warmer climates they are found less frequently; comparative population studies are few, but one by Kellock and Parsons (1970) in Polynesians and Melanesians, where the average temperature of the sea differed by 4°C, showed an incidence of 5.3 per cent and 1.3 per cent respectively.

Hrdlicka (1935) observed that exostoses were far more common in males, and this has been confirmed in other series, presumably reflecting a greater affinity for swimming in this sex, certainly in the earlier studies this century. The incidence also increases with age due to longer duration of exposure to water. Racial variations suggest a genetic component, but this most probably is explained by environmental, temperature or cultural differences, which determine swimming habits in different communities.

The presence of exostoses in skulls of four different archeological population groups ranging from 300–5000 BC has also been studied by Mann (1986), who found a variable incidence of 0–7.5 per cent (Table I). There appeared to be an increasing incidence over the centuries and the groups from Gizeh (300–600 BC) and Qau (1500 BC) seemed to have a similar incidence to series from this century, indicating similar swimming habits. Other authors, including Adis-Castro and Neumann (1948) and Gregg and McGrew (1970), have also described cases in archeological populations, but have not associated these with swimming habits. Ortner and Putschar (1981) describe 'numerous examples of ear exostoses in the collections of the National Museum of Natural History, USA', but the two examples illustrated in their publication are clearly osteomata, arising in the outer part of the canal, rather than true exostoses.

Studies of prehistoric skulls are clearly more difficult to interpret because of increased fragmentation and erosion, but Rightmire's recent publication (1990) on the evolution of *Homo erectus* includes comparative examinations of fossil skulls from the early Pleistocene period (1–2 mybp). He describes several variations or abnormalities of the temporal bone and external auditory canal, including one from Lake Ndutu in the Olduvai Gorge, where 'the plate surrounding the auditory porus is clearly thickened'. Whether or not this thickening does represent the formation of exostoses clearly requires further detailed examination to determine its true pathological significance.

It is obviously important to differentiate between the social aspects of swimming and the necessity for swimming and diving for hunting purposes. The presence of exostoses in modern and more recent archeological populations reflects the former social aspect, but if their occurrence is verified in primitive hominids such as *Homo erectus* or Australopithecus, this surely must provide substantial evidence that early man spent considerable periods of time in the water, for hunting rather than social reasons.

TABLE I

INCIDENCE OF EXOSTOSES IN ARCHEOLOGICAL POPULATIONS (MANN, 1986)

Location	Date	No. of skulls	Exostoses	%
Naqada	5000 BC	315	None	0
Qau	1500 BC	142	3	2.14
Kerma	1500 BC	147	None	0
Gizeh	600–300 BC	293	22	7.5

It is well known that apes and other higher primates, with the exception of the Proboscis monkey, have an abhorrence for water, and not surprisingly, exostoses have not been described in these species. If we do accept the aquatic theory of hominid evolution, vital supporting evidence may possibly be found by careful search for the presence of exostoses in primitive hominid skulls. Although no fossils from the crucial late Miocene/early Pliocene epoch have yet been identified, the finding of hominid skulls with exostoses from this period would certainly justify the existence and belief in the reality of 'The aquatic ape.' Could this also provide an explanation and proof of 'The missing link'?

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