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Evolution of human posture and bipedal locomotion within a provisional time frame of harsh climate changes

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Abstract

In this review paper several emerging issues related to development of human posture and locomotion are arranged in a provisional time frame.

Accumulated evidences show that the Eurasian climate was often cold and arid with abundant dust in the atmosphere during the last 500 Ky. These dusty periods of cold, aridity and low insolation lasted from 360 to 340 Kya, 270 to 255 Kya, 170 to 130 Kya, 80 to 60 and finally 40 to 10 Kya. They coincide with migrations of Neanderthals and H. sapiens out of Africa, suggesting that harsh climates might have been important factors in forcing global migrations of our ancestors.

When reaching the middle Eurasian latitudes, with reduced sun exposure due to dusty atmosphere and no sea food, our ancestors developed a deficit of vitamin D with compromised locomotion of young individuals due to rickets. This problem of bone maturation made a strong selection pressure toward lighter skin pigmentation.

New evidences suggest that skin pigmentation genes in our genome came from the Neanderthals. They have survived several dusty periods, under the selection pressure of becoming pale skinned during their more than 400 Ky in Eurasia.

On the other hand, H. sapiens came much later from Africa. Long-legged modern men could easily chase smaller preys, while groups of slower Neanderthals proambushed larger preys. Fossil evidence suggests that both hominid species lived in the same areas for thousands of years, until the final survivors turned out to be mixed individuals, possibly of Caucasian phenotype although with pale skin genes inherited from their Neanderthal ancestors.

1. INTRODUCTION

When considering human evolution, we often take our bipedalism as granted, although the combination of upright body posture and free hands is sometimes regarded as a prerequisite of making and using tools. This approach has developed in a misconception that the human hand has created the mankind (1), although it is quite undisputable that brain development was the crucial factor in deciding what to do with our hands.

So, instead of being a unique human feature, human hands are quite similar to our terrestrial and arboreal relatives. Beside our hands, we

should separately consider upright position, bipedal walk and standing. Many adaptations to the upright position are already present in modern arboreal primates, so it can be assumed that we share these adaptations with them for more than 5 Myr. They include the integration of senses with the instantaneous body posture, increased mobility of joints, particularly in extremities, grasping movements of hands and also of their feet or even their long curved tails in some fully arboreal species.

It is more complex if we consider human feet. It probably took more than 5 Myr to make our hind limbs able to support the whole body weight while standing and also to allow running and swimming. In this gradual process, hind limbs of our ancestors improved their stamina, endurance and physical strength, but also reduced their motility, changed shapes of many bones in our legs, until our bipedality has become a more natural mode of locomotion, and possibly the most economical one.

Recent data suggest that the probable role of our gait and locomotion in human evolution was more complex and much slower than anticipated. In his last book D.F. Horrobin has written his opinion on several theories of early hominid development (2), with a focus on their almost deliberate simplicity. Various modern human traits are often interpreted as features that have occurred virtually instantaneously in one, more or less isolated hominid population, over less than one hundred generations. This „*deux ex machina*” approach is among their main weaknesses.

Instead of that, contemporary fossil data prove that human evolution probably took more than 5 Myr. This slow transition of our ancestors through many climate changes incorporated several periods of isolation of small hominid groups. Probably more than once, severe „bottleneck” situations were resolved by very few surviving individuals and the whole process of „tempering” the mankind has started again. Likewise, development of bipedalism probably took millions of years to become the dominant and perhaps even more to remain as the only adult mode of human locomotion, beside swimming.

Complex changes in posture and locomotion did not occur without important physiological adaptations of several organs, tissues and regulatory systems. When the average lifespan among our ancestors has sufficiently increased, the health toll of bipedalism has become obvious through various health issues, common in elderly individuals.

In this short review we will try to address some important issues related to our development of posture and locomotion, arranged in a provisional time frame.

2. BASIC ASSUMPTIONS BEHIND THE PROPOSED TIME-FRAME

If we want to make a provisional time frame of events that changed our locomotion during human evolution, accepting few assumptions is important:

Diversification of a certain group of individuals into a separate species requires time of many generations during which some form of sequestration is needed to prevent interbreeding with other individuals that still belong to the initial pool. Beside sequestration, a persistent selection pressure is needed that favors the selection of an alternative phenotype that will lead to a new species. This means that isolated fringe habitats with some unique survival pressures are probably the best cradles for individuals adapted to unusual conditions. In cases of a climate catastrophe, although individuals with a dominant phenotype might all perish, the world can be repopulated from fringe habitat individuals, if their phenotype can cope with the new climate (3).

When comparing functions of some organs or tissues, the reductionist approach to analyze a certain isolated feature is not adequate. All known tissue/organ features and interactions must be taken into consideration to explain why some tissue/organ has hypertrophied or disappeared.

For instance, fur and subcutaneous adipose tissue both provide thermal insulation important for mammals in temperate climates. The main difference between them is that the adipose tissue is a huge energetic reserve that helps animals to survive even long periods without food.

The same holistic approach is suitable for physiological systems. Our ancestors acquired an unusual feature. Ovarian cycles have become dependent on the body fat reserve, clearly suggesting that for many generations short periods of abundant food were regularly intervening with longer periods of food scarcity (4).

3. A PROVISIONAL TIME FRAME OF HUMAN LOCOMOTION EVOLUTION

Let us see relations used for making the possible sequence of events in Table 1.

Bipedalism is not necessarily linked to the occurrence of body nakedness. Instead of that, human posture, leg anatomy and preferential bipedality probably took very long time, while our ancestors were still fur covered.

The main difference among extant and extinct primates and humanoids is probably in diverse capabilities of their brains. It may have all started due to essential polyunsaturated fatty acids (PUFA), important in brain development. These types of fat are scarce in savannah sources and abundant in food taken from water organisms (5). So if our ancestors had to wade through water in search of food rich in essential fatty acids, their locomotion would slowly change toward making them more bipedal than their contemporary arboreal relatives. It is here important to note that individuals with larger deposits of subcutaneous fat had an additional advantage of

TABLE 1

A provisional time frame of the human locomotion development linked to atmospheric dust exposure (grey table fields) and vitamin D availability (based on textbook sources and cited references).

Time before present (Mya)	African population					
	Climate / migrations	Hominid	Bipedalism	Subcutaneous fat	Nakedness	Skin pigmentation
7-3.8	Warm	S. tchadensis A. anamensis	partial bipedalism, arboreal mobility	as in other	fur covered	on exposed areas without fur
3.7-2.6	Colder and arid	A. afarensis	improved bipedalism, possibly due to wading through water	increased	follicle directions adapted to water flow	in African hominids, exposed skin progressively darkens as a protective measure against UV
	biseasonal climate with a short wet and a long dry season				fur gradually disappears as super uous thermal insulation	
2.58-1.8	cold drought	H. habilis	dominant bipedalism	abundant fat reserves allow pregnancy and survival during periods of food scarcity	nakedness, clothes of animal skin for protection	pale skin in Eurasian hominids as an adaptation to low vitamin D production, dark pigmentation remains in African hominids
1.8-0.5	climate driven migrations to China, Indonesia	H. erectus				
0.400	dust 360-340 Kya migration to Europe	H. rhodesiensis	bipedalic locomotion	abundant fat reserves allow pregnancy and survival during periods of food scarcity	nakedness, clothes of animal skin for protection	pale skin in Eurasian hominids as an adaptation to low vitamin D production, dark pigmentation remains in African hominids
0.250	dust 270 to 255 Kya migration to Europe	H. neanderthalis				
0.19-0.16	dust 170-130 Kya spread in Africa	H. sapiens	bipedalic locomotion	abundant fat reserves allow pregnancy and survival during periods of food scarcity	nakedness, clothes of animal skin for protection	pale skin in Eurasian hominids as an adaptation to low vitamin D production, dark pigmentation remains in African hominids
0.100	migration to Israel					
0.070	migration to Israel, Asia	80-60 Kya	H. neanderthalis	abundant fat reserves allow pregnancy and survival during periods of food scarcity	nakedness, clothes of animal skin for protection	pale skin in Eurasian hominids as an adaptation to low vitamin D production, dark pigmentation remains in African hominids
0.045	migration to Eurasia	40-10 Kya	H. sapiens			
0.040	migration to Oceania, Australia					

increased body buoyancy, allowing them to float and swim better in cases of danger.

Brain expansion fueled by PUFA abundance in an aquatic habitat made them more vulnerable when more arid climates prevailed in Africa some 3 Mya. It seems quite possible that the survivors lived near remaining sweet water lakes surrounded by semidesert that isolated them from forest ancestors of other primates.

Perhaps the first adaptation to this water-centered habitat was altered orientation of human body hair follicles that resemble water flow around the body of a swimmer (6).

Further deterioration of the climate toward a two-seasonal annual cycle possibly resulted in North African Monsoons, one of components of the Sahara pump theory (7). During a short wet monsoon period food was abundant, while during six or more months of dry season, the food was very scarce. This immense survival pressure forced the remaining human ancestors to store as much fat as possible if food was available. Subcutaneous fat deposits helped them survive the season of hunger. This meant that ovulatory cycles of our female ancestors were

allowed only when the body fat reserves were sufficiently high (8).

With increased subcutaneous fat reserves that acted also as thermal insulation, fur has become superfluous. The body hair gradually vanished until our ancestors became naked in most of body parts covered by subcutaneous tunica adiposa.

The most convincing link between human locomotion and sun exposure was proposed by Nina G. Jablonski and George Chaplin (9, 10). They have postulated that skin pigmentation possibly increased after our African ancestors have lost their body hair. This new dark skin protected folate in the blood stream from harmful African UV exposure that was particularly important during pregnancy. Pale skin was then interpreted as a later adaptation to reduced sun exposure when our ancestors moved to continental Eurasia. Insufficient vitamin D formation in the skin due to norther latitudes might compromise bone growth and locomotion of young adults.

These premises implicate that dark skin had to occur early in our African ancestors, not long after they had become naked. On the other hand, pale skin occurred

much later, when still naked African exiles inhabited colder Eurasian areas without sufficient dietary vitamin D. Those who migrated along sea coasts could remain with darker skin, due to the vitamin D content in sea food.

An important fact is that during human evolution, the climate was often cold and arid with abundant dust in the atmosphere (11, 12, 13, 14). Probable causes for this long lasting dustiness included glacial erosion, scarce vegetation, aridity with little precipitation and strong winds.

Heavy dust exposure lasting for thousands of years formed the European loess ridges aligned with the prevailing winds during the last glacial period (15, 16).

Estimated periods of atmospheric dust lasted from 360 to 340 Kya, 270 to 255 Kya, 170 to 130 Kya, 80 to 60 and finally 40 to 10 Kya. During the Last Glacial Maximum (LGM) (26.5 to 19 Kya), levels of dust in ice cores were 20 to 25 times greater than the present dust levels (11, 12, 13). Heavy dust exposure started more than 40 Kya and ended less than 10 Kya.

Several periods of cold, aridity and low insolation coincide with migrations of Neanderthals and *H. sapiens* out of Africa (Table 1), suggesting that the harsh climate might have been important in forcing our ancestors to migrate. During long periods of drought, water sources were scarce and the lack of drinkable water might have forced them to follow animals, leave the Eurasian coast and move to the south edge of the glacier belt. Here, at middle Eurasian latitudes, with reduced sun exposure due to dusty atmosphere and no sea food, the deficit of vitamin D has probably become evident in bone maturation of their offspring. Compromised locomotion due to rickets made a strong selection pressure toward lighter skin pigmentation that eventually resulted in the occurrence of Caucasian phenotype.

The question of sun exposure and hominid locomotion has become more complex when new evidences suggested that skin pigmentation genes in our genome came from the Neanderthals (17, 18). These hominids have survived more than 400.000 years in Eurasia and it seems probably that during that long period, they have been under the selection pressure of becoming pale skinned.

It is known that Virchow considered the first Neanderthal bones to show signs of rickets (19), and although vitamin D deficiency signs are present in some of their fossils, their unique skeletal anatomy was considered as an elaborate evolutionary adaptation to living in cold and sloped habitats. Beside the deformed occipital bone, the femoral shafts of Neanderthal are anteroposteriorly bowed, making their legs short (20). This unique leg anatomy possibly allowed Neanderthals to better move on slopes, although they might have been slower in moving on flat surfaces. Since the Neanderthals have survived several long arid and dusty periods, perhaps even their leg

anatomy is an adaptation to walking toward the base of glaciers, probably the most reliable sources of fresh water in that harsh climate.

If this was the case, survival risks pushed toward short childhood and early skeletal and muscle development, resulting in strong bodies with shorter limbs. The survival chances during several cold, arid and dusty periods of Eurasian climate favored pale skinned, strong and stable individuals, able to climb over piles of crashed rocks to get near water or food.

It must be kept in mind that our *H. sapiens* ancestors came much later from Africa, also during the one of last glaciations. Long-legged modern men could easily chase smaller preys, while groups of slower Neanderthals probably ambushed larger preys. Fossil evidence suggests that both hominid species lived in the same areas for thousands of years, until the final survivors turned out to be individuals of mixed heritage that probably got their pale skin genes from Neanderthal ancestors.

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