Gestation and the evolution of vertical stance bipedal humans

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Abstract
During mammalian gestation a change in maternal stance alters the velocities of maternal blood flows and results in a changed rate of delivery and distribution of nutrients required to form the bone and tissue in various parts of a developing foetus. The latter in turn results in change in the extent and position of tissue and bone formation in the foetus. It is shown that such changes would, over many generations, alter the physical characteristics of the ancestor offspring under conditions where the pregnant maternal ancestor normally exhibiting horizontal stance was constrained to adopt a vertical stance for all or most of the gestation period. This behaviour produced the physical characteristics seen in humans and other Hominidae primates, including the vertical stance and bipedalism of the former accompanied by increase in skull and brain size. The manner in which difficulties of giving birth as the change from horizontal stance to vertical stance proceeded from generation to generation, limited survival is discussed andreasons for the adoption of this behaviour are proposed. The induction of evolutionary change and the operation of natural selection through alterations in the characteristics of embryo/foetus of an animal, induced by physical, chemical, mechanical or behavioural means, is shown to be feasible. The changes are not related to the Lamarckian principle of inheritance of acquired characteristics as the changes described occurred before birth and are not related to any physical or mental characteristics already present in or acquired during the lifetime of the breeding pair.

Keywords: blood velocities; stance; evolution

Introduction

The evolution of the vertical stance and bipedalism in humans has been the subject of numerous hypotheses (1-13). All animals classed as primates are considered to be linearly descended from animals whose fossilised remains exhibit similarities of skeleton structure (14-18). Such fossils lead to the conclusion that all primates evolved from small, terrestrial and nocturnal archaic insectivores known as prosimians which existed from fifty-eight million years ago to sixty-five million years ago. From fossil evidence animals considered to be the direct ancestor to primates are the proconsulids which appeared 24 million years B.P. This conclusion is not universally accepted (19). Although the skeletal relationship above is obvious it is not necessarily true and has never been proven absolutely. In the work below the linking of the origin of Hominidae primates to past animals with particular skeleton characteristics is not invoked. When Darwin advanced his Theory of Evolution he specifically invoked breeding, for example of pigeons and other animals, as part of the process of evolutionary change (20). Breeding involves gestation and no consideration has been given to changes which could have occurred in the embryo and foetus of the animal from which the Hominidae primates evolved and which lead to evolutionary change, including the origin of vertical stance and bipedalism in humans. There are several mammals alive at present where a large part of the lifetime is spent in water and birth occurs on land. Examples of this are the seal, the otter and the hippopotamus. In the first two instances the source of food is in water and in the third the source of food is on land. In all of these cases the offspring are born on land with a limited capability of operating in water and have to learn by trial and error to deal with this medium. In the case of the hippopotamus birth sometimes occurs in shallow water. With the exception of the human primate there are no known mammals alive at present where the lifetime is spent on land, where the sources of food are available on both land and in water and where birth can take place both on land and in water. Any human offspring born in water is perfectly capable of operating in this medium. Fossilisation of past animal bones is aided by burial in silt associated with river beds and most skeletons of early humans occur in terrain which in the distant past was associated with such conditions These characteristics support the selection of a semi aquatic mammal attracted to or adapting to one on more food sources on land as the ancestor of Hominidae primates. For the purposes of the following hypothesis the ancestor animal of Hominidae is taken to have been mammalian, exhibited a four footed, equal leg length, horizontal body stance with associated skeleton and a multitoothed skull. It is further assumed that the body mass of the adult primate ancestor was approximately the same as present day humans and that gestation lasted for approximately the same period of time. The groups of prehistoric animals which most match the physical characteristics given above are represented by early Sirenians such as *Prorastomus sirenoides*, which was alive 40 million years ago and considered to have been predominantly terrestrial and herbivorous or Desmostylians an extinct order of marine mammals which existed from about 30.8 million years ago to about 7.25 million years ago. This animal is considered to have been predominantly aquatic with possibly a mixed herbivorous and crustacean diet (21,22). These dates are compatible with the proconsulids having evolved from such ancestors. The work below proposes and explains the changes which could have occurred on the developing foetus of the ancestor animal during gestation as a result of the adoption of vertical stance by the maternal animal. This behaviour had the result of evolution of vertical stance and bipedalism in humans and other specific characteristics associated with the process of birth in humans.

Alterations in foetal development with change in stance

Stance is defined as the angle of the backbone relative to horizontal ground decided by the limb length involved and does not include short term changes in this angle involved in food gathering and rest periods. The stance of a maternal animal on level ground can be with the backbone parallel to the ground, the backbone at an angle to the ground, with head at the highest or lowest point, or with the backbone vertical to the ground. Change of stance in the instance of the ancestor defined above means from the normal horizontal stance to vertical stance. The forms of placenta vary among mammals and the form associated with primates is known as discoid and comprises a single placenta which is discoid in shape. The placenta form associated with the ancestor of primates could have been any of the other forms (diffuse, cotyledonary, zonary) and the changes described below gave rise to the placental form now present in humans and other present day related primates. The human embryo/foetus is initially aligned with the backbone approximately horizontal to the ground. This position is also the case for present day animals with a four footed stance such as the horse. It is assumed that this was the case for the ancestor animal of the Hominidae. The position of the embryo and foetus in the mammalian amniotic sac in present times is decided by the buoyancy. Within the amniotic fluid the force of buoyancy acts upwards against the weight of embryo and the subsequent foetus acting downwards. The buoyancy force F = -rVg, where r is the density of the amniotic fluid, V is the volume of amniotic fluid displaced by either of these bodies and g is the acceleration of gravity. The force arises from the difference in pressure exerted on the top and bottom of an object. For a floating object the upper surface is at atmospheric pressure and the bottom surface is at a higher pressure.

This is the result of the fact that the lower surface is in contact with the fluid at a particular depth of fluid and pressure increases with depth. For a completely submerged object where the surface is no longer at atmospheric pressure the bottom surface is still at a higher pressure because this surface is deeper in the fluid. In both cases the difference in pressure results in a net upward force (the buoyant force) on the object. This is the principle of Archimedes. Although varying pressure is applied to the amniotic fluid during gestation any pressure applied to an enclosed fluid is transmitted undiminished to every part of the fluid and the walls of the container (Pascal's Law). Under external pressure change the values of the pressure at the different depths are changed. However the pressure difference will remain. As the value of V increases during gestation the value of the buoyancy force increases maintaining the position of the foetus approximately central in the volume of amniotic fluid. The embryo and foetus are bodies of uniform density in the early stages of development. Under these conditions a short term change in maternal stance (resting, food gathering) does not affect the buoyancy orientation of the foetus as the embryo and early foetus suspended in the amniotic fluid adjusts to the change. If otherwise, short term alterations in the maternal stance of present day mammals would give rise to continuous changes in the physical characteristics of each succeeding generation as described below.

Blood flow in mammals is driven by the pumping action of the heart. If a closed pump system, such as blood flow, is changed from operating in a horizontal position to operation in a vertical position there will be changes in the velocity of flow of the fluid in the tubes of the system. This arises from the Bernoulli principle which is a statement of the conservation of energy, namely, that kinetic energy plus potential energy plus the internal energy of the fluid is constant. Expressed mathematically:

$$1/2mv^2 + mgh + \int Vdp = K$$

Where m is mass, v is the velocity of flow, g is the value of the acceleration of gravity, h is the height of the tube being considered above a selected level, V is the specific volume (the volume of a substance per unit mass that is the reciprocal of the density), p is the pressure exerted by the internal molecular relationships of the fluid and K is a constant. This formula is valid for any non viscous compressible fluid (gas) in steady motion and the same constant holds for the entire fluid. Blood is not a non viscous fluid and is to all intents and purposes an incompressible fluid. However the formula is taken to give a good approximation to the flow conditions in blood. The potential energy is higher the higher the fluid is above some selected level in the surroundings, kinetic energy is higher the higher the velocity of the fluid in the circulation. As the fluid approaches highest point in the circulation the kinetic energy is decreasing to a minimum value and the potential energy is increasing to a maximum value. The reverse is the case at the lowest point of the circulation. Under these conditions physical laws have the result that the velocity of blood flow in any part of a mammalian body varies. It is lowest approaching the highest point above ground level and increases leaving this point. It is highest approaching the lowest point in the body and decreases leaving this point. Blood fluid velocities in the horizontal direction are uniform (23). A change of stance of an animal from horizontal to vertical results in the horizontal blood flows becoming vertical and the vertical blood flows becoming horizontal with consequent change in flow rate. In a mammalian metabolism the maternal blood circulation transports the compounds required to form the bone and tissue of the foetus although there is no direct mixing between the maternal blood flow and the blood flow which forms in the developing offspring. The rate of supply of these compounds (gms per minute) to the foetus is directly dependent on velocity of blood flow in maternal circulation and this velocity is directly linked to maternal stance. Application of the physics of fluid flow demonstrate that the rate of formation of bone and tissue is highest where blood flow velocity is slowest (23). In the case of a mammal with backbone parallel to level ground the placental artery and vein supplying blood to and removing blood from the placenta are presently also orientated essentially parallel to level ground. This is taken to have been the case in the ancestor animal. The rate of formation of bone and tissue and the mass of these formed in specific regions, for example the head and fore limbs or the pelvis and rear limbs of the forming foetus, are determined by the rate of supply of the required compounds by the maternal blood circulation and the directions of blood flow (horizontally or vertically) in the forming embryo/foetus. The rates of blood flow in the embryo/foetus immersed in the amniotic fluid are subject to the same changes with respect to change in orientation as is the case for the blood flow of the maternal animal since the Bernoulli principle applies and is independent of the external pressure to which the blood system is subject. This remains the case even if the foetal blood flow comprises one or more linked circulation from a single heart (23). The head and forelimb regions of an embryo are the first to form meaning that a greater proportion of the supply of relevant compounds is used in the head and fore limb region initially. A reduced supply resulting from change of stance means that less bone and tissue forms in the pelvis and rear limbs than was the case for horizontal stance. These changes also result in the loss of any tail. The developing foetus does not remain a body of uniform density in present times as the result of varying density of body components. The density of the amniotic fluid varies in the range 1.010 to 1.025 gms per ml. (24). The densities of some of the foetal components in grams per millilitre are, bone 1.08, brain matter 1.04, muscle tissue 1.04, nerve tissue 1.04, cartilage 1.100 grams per millilitre. These density differences of body components are taken to have existed for the ancestor. As a result of these differences the developing foetus tends to adopt a buoyancy orientation in which the higher density parts are directed downwards and the lower density parts are directed upwards. For example for the human foetus the face and limbs are directed upwards. As gestation proceeds the higher density skull of the human embryo tends to point downwards. This means that the direction of blood flow in the foetal circulation changes and the rate of supply of the required nutrients to the head and forelimb region is further enhanced. These changes are proposed as first having occurred as the result of the adoption of partial or full vertical stance by the female ancestor for the greater part or all of the gestation period. The effects of change in rate of supply of nutrient to the embryo/foetus on the extent of bone formation in the skull of various embryo/foetuses as the result of the changes above are shown diagrammatically in Figures 1 to 4. Considerable evidence exists of the development of physical and other foetal abnormalities resulting from changes in maternal and foetal blood flow (25). A progressive change of maternal stance towards the vertical resulted in a redistribution of bone formation in the skull of the offspring of the ancestor animal such that the length of the jaw contracted and a greater amount of bone formed in the facial region and frontal region of the skull. This is origin of the form of the jaw characteristic of the gorilla or chimpanzee (prognathism). Further increases in the angle of stance lead to less bone deposition in the facial region and an increase in bone deposition at the top and back of the skull. An animal with a maternal stance greater than that of the gorilla, for example 50° to the horizontal, would have fewer skull and facial characteristics of the gorilla such as prognathism and more characteristics of the human such as smaller teeth. An animal with an angle of stance of 70° degrees to the horizontal would have facial characteristics of humans with some characteristics of apes, for example more pronounced or heavier jaw bones. The initial change resulting from increased bone formation at the rear of the skull and the consequent change in the foetal buoyancy was a change orientation in the from face and limbs down, characteristic of mammals with a horizontal maternal stance, to face and limbs up characteristic of humans. Increase in the angle of the maternal stance also resulted in change in the ratio of bone and tissue in the skull (Figure 1) giving an increase in the mass of tissue within the skull which forms the brain resulting in increased brain size. These changes are supported by the observed characteristics of fossils. One fossilised skull coded KNM-ER1805 from Kenya (26) has mixed facial characteristics and this animal therefore used a stance where the backbone was at a greater angle than is the case for present day non-human Hominidae primates and more like present day humans. The form of the facial characteristics also lead to the adoption of a particular diet. The animal represented by KNM-ER1805 would have been less able to survive on an entirely vegetable diet which included tough fibre due to reduced dentition and would have been constrained to attempt an animal diet. The flattened face and small teeth of the recently discovered fossils classified as *Kenyanthropus platyops* also indicate that the stance of this animal was near vertical on the basis of the above model (27). In addition the above model indicates that the evolving animals would developed a tendency to exhibit more extensive head and shoulder development over that of pelvis and rear limbs. This is a characteristic of Hominidae primates alive at present. Differences have been observed in the distribution of bone in the skull (28,29,30) supporting the changes in deposition of bone induced by change in foetal blood flow rates induced by change of maternal stance. Comparison of thickness of the occipital plate for modern humans and one fossil [*H.Ergaster/erectus* 1.25 Myr B.P., (28)] have been made. These measurements demonstrate a similarity between modern humans and this fossil and imply that the latter possessed a vertical stance in common with present day humans.

Figure 1

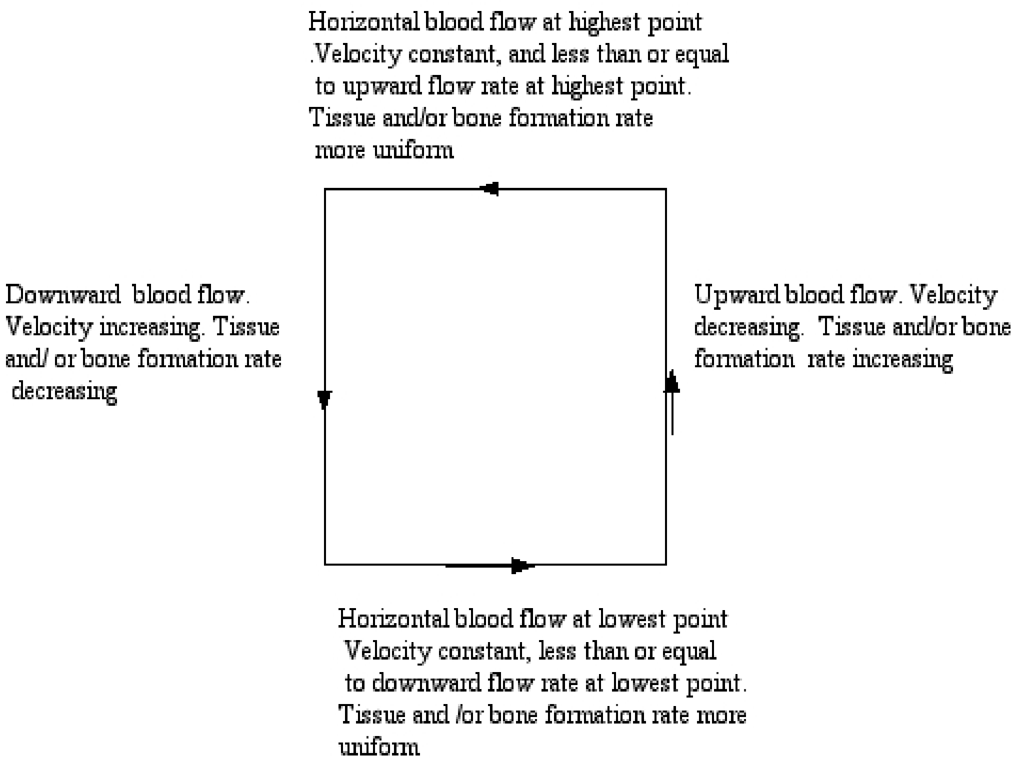
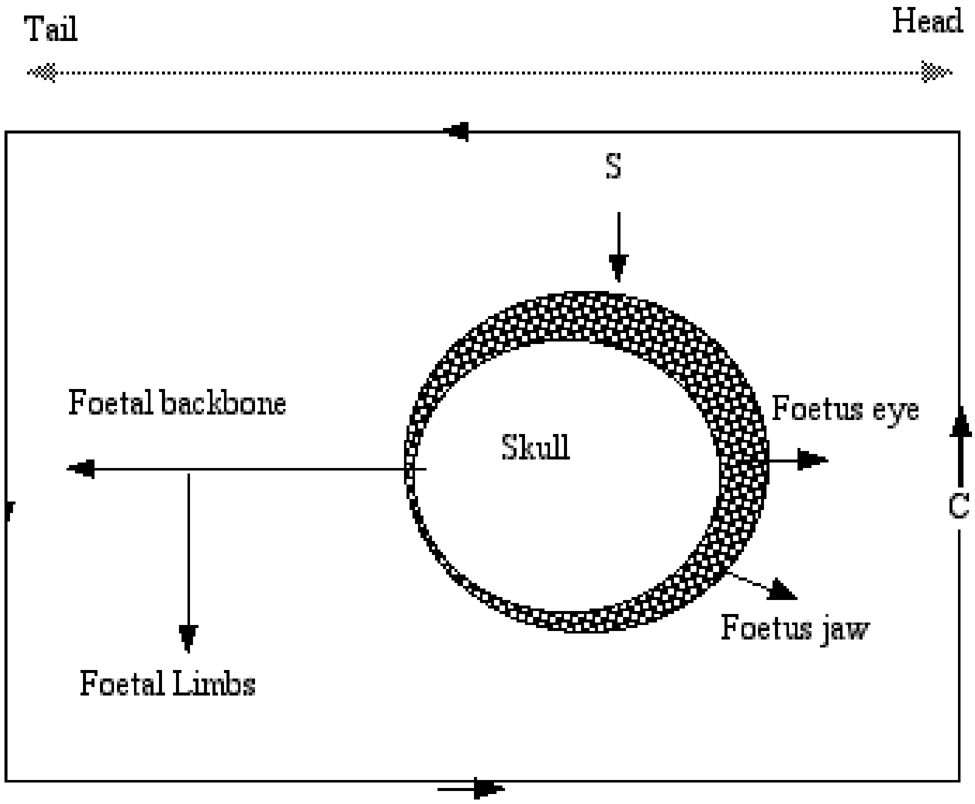


Figure 1 Directional blood flow velocities and regions of greatest bone and tissue formation (general case)

Figure 2

Angle of maternal backbone in relation to flow directions in Figure 1



Horizontal stance of primate ancestor. Bone formation heaviest at top and front of skull (S)

Designates bone deposit

C designates concentration of nutrient in foetus blood flow.

Figure 2 The blood flow velocities and regions of greatest bone formation of skull in embryo/foetus of primate ancestor; horizontal maternal stance

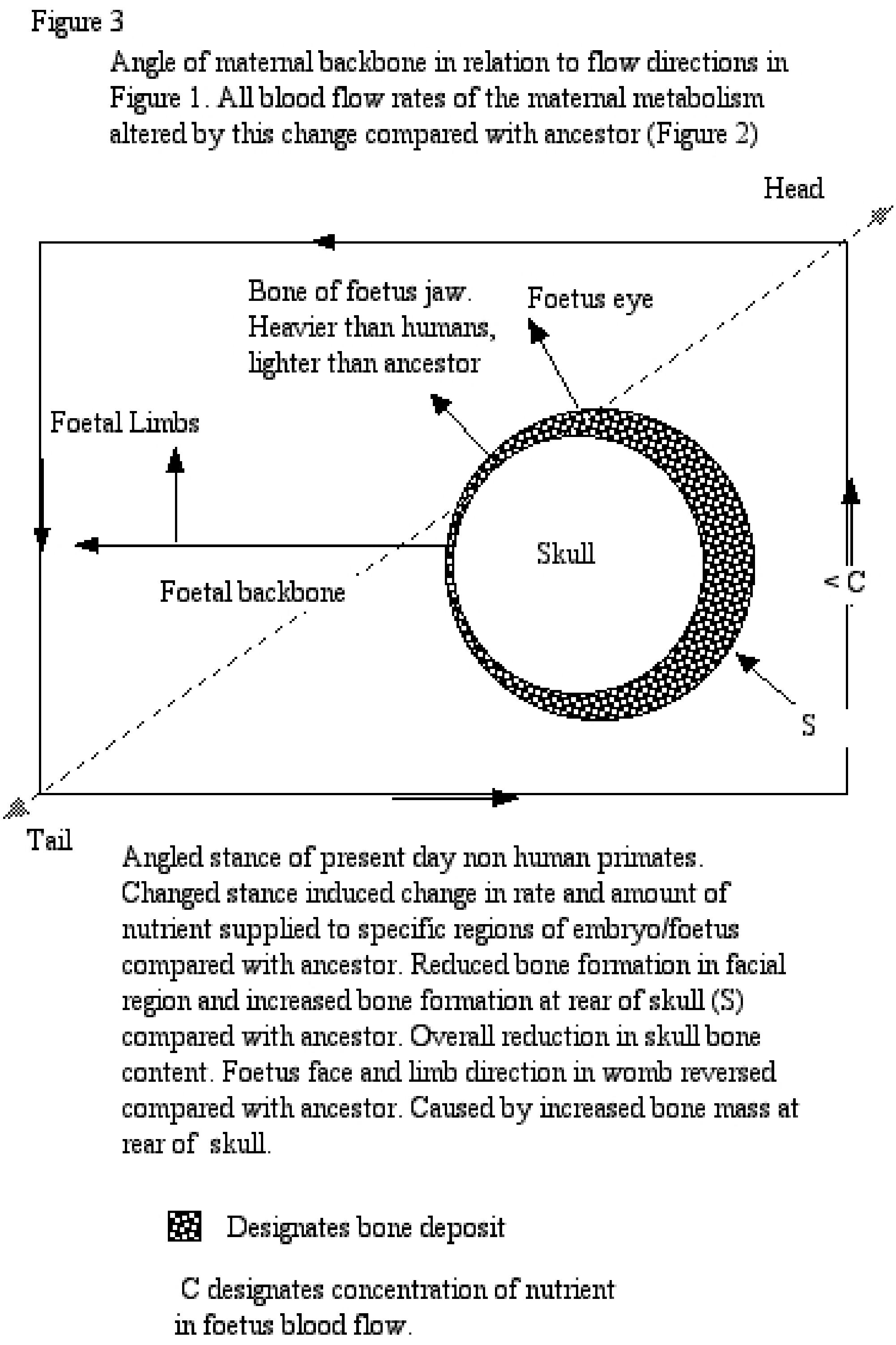
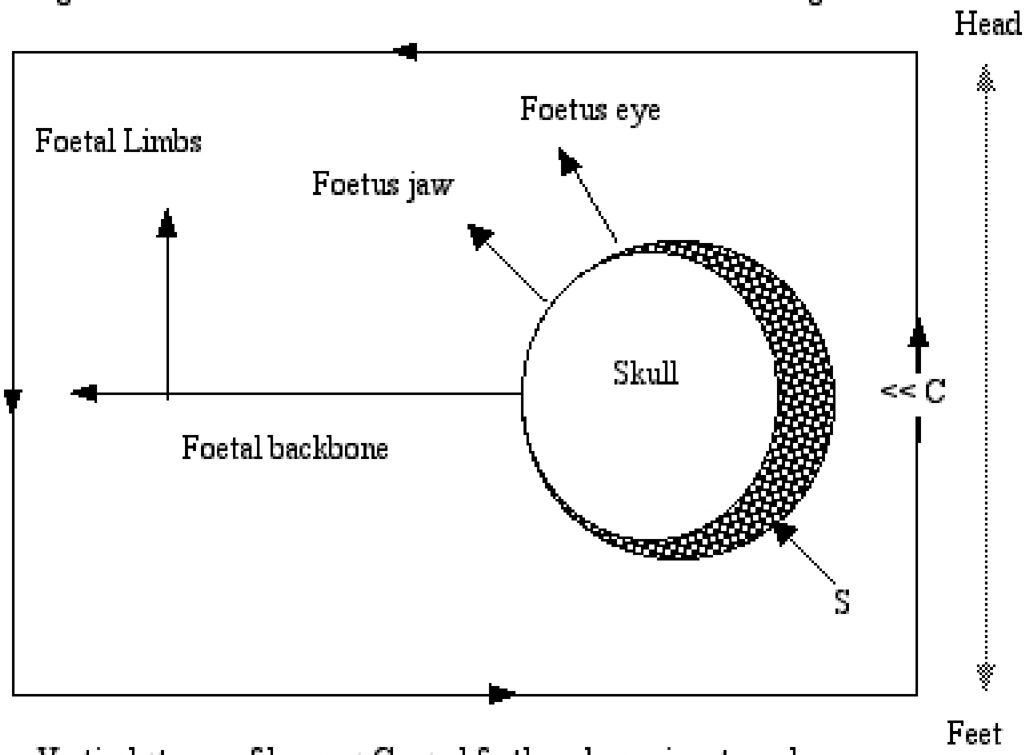


Figure 3 The blood flow velocities and regions of greatest bone formation of skull in embryo/foetus; the case for nonhuman primates; angled maternal stance

Figure 4

Angle of maternal backbone in relation to flow directions in Figure 1



Vertical stance of humans.Caused further change in rate and amount of nutrient supplied to specific regions of embryo/foetus compared with with horizontal stance of ancestor Overall reduction of skull bone formation. Bone formation heaviest at top and back of skull (S) lightest at jaw. The internal volume of the skull increases as the result of decrease in skull thickness compared to that of the ancestor giving an increase of brain tissue mass.

▩ Designates bone deposit

C designates concentration of nutrient in foetus blood flow.

Figure 4 The blood flow velocities and regions of greatest bone and tissue formation of skull in embryo/foetus; the case for humans; vertical maternal stance

The effects of the change in maternal stance on birth

It is axiomatic that survival and multiplication of any mammalian species must involve the process of giving birth in that birth difficulties reduce both of these factors. Several researchers have considered the reproductive process in early humans (31-34). Study of the available fossilised Australopithecine pelvic bones and the possible mode of giving birth by these animals has been discussed (32,35) with the conclusion that the process would have been difficult. At present the final position of the foetus for non-human Hominidae primates is inverted and facing away from the maternal backbone. At birth the offspring can climb out of the birth canal (36.). In some instances the mother may reach down and pull the infant from the birth canal. This action does not injure the offspring as it is compatible with the normal bending of the spine. Although the usual birth position of the inverted foetus of humans is facing towards the maternal backbone, various other birth positions are displayed. Emergence in the former position results in any maternal assistance to birth tending to pull the infant backward with the resultant risk of spinal injury. A reason advanced for the prevalence of the former position is the shape of the maternal birth canal (widest in front) and of the foetal head (widest in back) that causes the infant to emerge facing away from the mother (37). These differences of birth position displayed by human primates are also the result of the adoption of vertical stance. The more rapid increase in the density of the skull and forelimb bone and tissue mass in comparison to other body features also gave rise to the rotation of the foetus prior to birth which is also characteristic of Hominidae. The foetal position described (buoyancy position) above is maintained in humans until a short time before birth when the foetus rotates to a position in which the head and shoulders are lower than the pelvis and rear limbs. This rotation is generally interpreted as foetal movement of adaptation to the available space in the maternal pelvis on the basis that a foetus is known to exhibit independent movement through muscular activity. It is also considered that bone shape, tissue and muscle of the maternal pelvis are involved in the rotation (37,38). While the foetus is buoyant the muscular activity would not be effective in altering the foetal orientation in the amniotic fluid. The alternative is that as the foetus develops the parts of the body which are the most dense change. The final birth position is then determined by the density distribution of the foetus at the time of birth as required by the buoyancy equation above. Under these conditions rotation can occur without the intervention of any of the available muscle systems while the foetus is buoyant. These changes are the result of change in stance proposed. In present times the occurrence the breech birth position in humans where the density changes described have not taken place supports the proposals above even though in this case there is apparently no significant change in maternal stance. Walking in an upright position causes an oscillating motion of the maternal body about the vertical axis through the backbone. This induces an oscillating motion in the amniotic fluid which will be translated into an oscillating motion of the buoyant foetus about the same vertical axis. As a consequence the foetus experiences a rotation force. If the value of this force about the vertical axis was identical in both clockwise and anticlockwise directions the foetus would experience no overall change in body axis direction. However the extent of twisting of the maternal body in a clockwise direction will not always be identical to that in an anticlockwise direction. This difference means that the foetus will experience a resultant turning force in one particular direction around the vertical axis and experience a change in direction of the body axis. The effect of this movement is that the body axis direction of the buoyant foetus, particularly in the head down position can be in any one of the 360° of direction around the vertical axis (head to feet) of the maternal body as observed. The position of the foetus observed at birth represents the last position of the buoyant foetus with respect to rotation around the above axis before rotation into the birth position. This variation of facial direction in the birth position is not general for non-human primates. In this case the animals do not adopt a permanently vertical stance and the oscillating force is reduced to a pendulum action also induced by gait. As the transformation towards vertical stance continued giving birth by the females of animals with a stance greater than 50° would have encountered the difficulties such as breach birth and incomplete foetal rotation into the vertical position. These factors affected the reproduction success of ancestor animals undergoing the change from horizontal to vertical stance and hence the population size.

Adoption of vertical stance during gestation

One reason for the adoption of a partial or full vertical stance during gestation was that this stance was the most comfortable for the females involved and that any other body arrangement involved some degree of pain or physical discomfort. Such a situation would occur where the downward descent of the uterus from the earliest stages of gestation resulted in contact of the lower abdomen with the ground or interfered with the functioning of the rear limbs as would happen in a mammal with short straight limbs and a four foot stance operating on land. Such a development would also have interfered with activities such as feeding and escape from predators. It is noticeable that the latter of these activities is also limited during the advanced stage of gestation in present day human females. Under these circumstances the female would have tended to relieve the resulting discomfort of, for example, dragging the lower abdomen over the ground by raising the body from contact straight limbs of equal length and a four foot stance this would have had a limited effect while on land. Alternatively returning to a water environment for all or a large fraction of the gestation period would have been more effective. It is possible that the ancestor animal had limited defences against attack by predators and used return to water as a primary escape route. The return to water resulted in a considerable fraction of gestation being spent in a vertical position with the nose and mouth at the surface in order to acquire sufficient air for both mother and offspring. In addition the increasing weight and bulk of the offspring makes this position inevitable in order to avoid drowning and facilitates extended periods of rest. Seals and other mammals avoid this condition by giving birth on land and female seals are observed to spend extended rest periods on land. These conditions are met by the ancestor animal clinging to submerged vertical rock faces and birth taking place in water. When physical mobility on the land became restricted and the female primate ancestor became isolated from the food source on land, the rock vegetation and rock living water life forms became the source of sustenance for the females indicating the evolution of the omnivorous diet of humans.

Discussion

When Darwin advanced the concept of evolution by natural selection no indication was given of the means whereby this change became effective. The present hypothesis of the evolution of one form of a living being into a form with different characteristics such as change in skeleton, stance and body weight is based on the hypothesis which defines the order of the linked purine and pyrimidine compounds (bases) forming particular lengths of the molecule of DNA, which is present in all cell nuclei, as genes (39-41). A gene is advanced as a unit which conveys information concerning a particular characteristic of a lifeform from generation to generation. In particular this hypothesis proposes that particular sequences comprising three bases (codons) of the base sequence composing genes controls the sequence of different amino acids which are linked to form proteins. Under these conditions the type and quantity of a given protein is transmitted through the generations giving rise to repetition of the body characteristics which involve particular proteins. Genes within a cell (DNA) are located in chromosomes and any alterations in genes leading to changes in the nature of the proteins and other chemical compounds formed by the cell is proposed as occurring through random changes in the base sequence of any given gene which take place at cell division (meiosis). This mechanism allows a link of natural selection to the classification of lifeforms (taxonomy, cladistics). However the formation of a peptide bond giving rise to a protein is a chemical reaction involving reacting compounds, amino acid concentration in cells, reaction rates, reaction temperatures, the intake or emission of heat and other forms of radiation and the production of water. This information cannot be influenced or derived from the DNA molecules and means that this hypothesis of evolution is not in keeping with the known laws of chemical combination. The operation of natural selection through alterations in the characteristics of any lifeform induced by physical, chemical, mechanical or behavioural means is considered less likely, particularly as such changes are not readily linked to classifications. However as demonstrated above changes which occur during gestation are equally likely to result in evolutionary effects. The changes induced by the change in the rate of supply of the chemical compounds required to construct various parts of the mammalian body would also affect the rate of supply of chemical compounds required to form the bases of DNA leading to the differences in the molecule presently observed to occur between Hominidae. On this basis the changes described lead to evolutionary change and alterations in DNA and not alterations in DNA leading to evolutionary change. The animal from which the Hominidae evolved was not the ancestor of all present day animals classed as primates, for example tarsiers, lemurs and others. This leads to the conclusion that the ancestors of these animals have yet to be defined. These considerations also eliminate the need to define and explain changes in the nature of the environment and animal foraging and other behaviour which resulted in the increase in physical size from lemur to gorilla. It is possible to test the suggestion that ancestors of Hominidae were Sirenians by comparison of the DNA Sirenians alive at present with that of members of Hominidae although this would not eliminate the Desmostylians as possible ancestor animals. Any ancestral animal which originally had a horizontal stance and in which the females were induced by the physical changes of gestation to adopt a vertical or near vertical position for most if not all of the period of gestation would produce continuous change of foetal characteristics through generations and would given rise to a series of animals with stances at every angle from horizontal to vertical. These changes are not related to the Lamarckian principle of inheritance of acquired characteristics. This principle involves changes in physical characteristics acquired during the period from birth to breeding age in both male and female of any species. The changes described above occurred before birth and are not related to any physical or mental characteristics already present in the breeding pair. The origin of the pre-birth changes occurred as the result of members of the ancestor species of Hominidae primates with a horizontal stance on land retreating to a water environment during gestation and adopting a vertical stance in this medium. However foetal physical changes and birth difficulties which became associated with successive generations the female offspring born from mothers with this behaviour only allowed for a poor reproduction rate until the change to vertical stance and permanent bipedal motion was complete. Many variations of the animals undergoing these changes would not have survived. This is in keeping with the principle of natural selection advanced by Darwin. The process gave rise to a clade (Hominidae) in keeping with present day classifications of lifeforms. Within the population of any generation of offspring undergoing the changes described there would have been animals with variations in characteristics such as the nature of face, head and front limb development. The conclusions above are supported by the fossilised remains of a variety of early primates resembling Hominidae and which lived in parts of East Africa four to six million years BP (42,43). When the angle of stance reached a particular value resulting in relief from gestation discomfort on land there would have been no further incentive to adopt a stance closer to the vertical. Some of the facial features, formed as described by change in stance, such as nostril position, discouraged return to water. These characteristics depended on the exact nature of maternal behaviour during gestation. Animals in this latter group were the ancestors of the non-human Hominidae primates (gorillas, chimpanzees and orang-utans) which either left or were driven from the regions of origin. Those remaining members of this now varied population of animals, derived from one or more members of the ancestral species, all with degrees of the same behaviour during gestation and whose evolving characteristics or place of origin encouraged continued return of the female to water for gestation, became the ancestors of humans and progressed to vertical stance and bipedalism.

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