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Vertebral Column in Land-Living Ancient and in Highly Derived Tetrapods

Holger Preuschoft*

Department of Functional Morphology, Ruhr Universität Bochum, Germany

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***Corresponding author:** Holger Preuschoft, Department of Functional Morphology, Ruhr Universität Bochum, Germany

Abstract

Approaches to body shape are reviewed in the cases of some diverse quadrupeds and of bipedal humans, and mechanical necessities are emphasized. The loading of ribs is sketched, primarily to pin down the value of their curvature. Lock-step is a unavoidable consequence of constant, fixed trunk length in quadrupeds. The mobile attachment of the shoulder to the trunk is investigated, as is the dorsa-mobile or the dorsa-stable condition of the lumbar area. The loads on the vertebral bodies ("centra") are summarized in the example of the "master cursor", the horse. While all this is relevant for quadrupeds, the situation in the bipedal humans is characterized - different from other animals (birds, bipedal dinosaurs) - by caudally increasing contribution of weight force. The often-discussed lordosis of the lumbar vertebral column, and still more so of the rarely observed "iliac neck" is a means to place the load-carrying structures close to the line of action of body weight and provides long lever arms for muscles. Accelerations applied directly to the pelvis are documented experimentally. They show that the highest forces pass without damping upward to the vertex of the head. The slender shape of the trunk is disadvantageous in static loading (e.g., lifting of heavy loads from the ground). But along with its broad shoulders and the relative breadth of the pelvis, these traits are highly advantageous in the kinetics of walking.

Keywords: Axial skeleton; Quadrupeds; Bipeds; Mechanical stress; Lordosis; Intervertebral discs; Acceleration; Walking; Architects and engineers; Locomotion; Infra- and suprahyoid muscles

Introduction

The axial skeleton is the name-giving structure in the vertebrates. It usually is taken as dictated simply by evolutionary conservatism. But its existence in a huge variety of forms is also a mechanical necessity. To understand the necessity of this trait, it makes sense to put emphasis on the external conditions to which it is subject. This approach has been elaborated in the engineering science of Technical Mechanics. A very detailed system of physical concepts has been developed, and is being used, most frequently with the aid of mathematics more than with the experimental approach so highly valued in biological and medical fields. To realize the importance of this procedure, the reader should accept that the enormous buildings which surround our daily life are the product of calculations (of architects and engineers), not of experimental work on models. Using the results obtained in other fields of science can entail considerable progress, as becomes for example evident in the work of the great orthopedist Friedrich Pauwels.

A "mechanical", or "functional" approach to the structures of living beings can done on two ways: First by looking at the (simpler) statics under which the animals live under the permanent influence of gravity, second by investigating the (more difficult) kinetics the animals have to cope with, especially in locomotion. Aquatic animals, regardless of their belonging to "fishes", or birds, or mammals are facing different problems which are not dealt with in this article but are detailed in Preuschoft [1].

Statics: Arrangement of the Structural Elements in Quadrupeds

In all four-footed animals the vertebral column serves as a compression-resistant element in the "stem" of the body, that means from skull to the tip of the tail. This holds true for most primitive forms, like newts and salamanders as well as highly derived "cursorial" animals, like cervids, most bovids and equids and some carnivores, and "graviportality" forms like hippo, rhino and elephants. The necessity of such an element becomes evident, if the bodies of the mentioned animals are simplified as heavy beams, resting on two pairs of supports: forelimbs and hindlimbs. Along with the compression-resisting element, tension-resistant elements are necessary to maintain the shape of the beam. These elements may be tendons or aponeuroses, but often they need changing lengths, or varying strengths, abilities characteristic of muscles. Usually, the head and neck, the parts constituting the "anterior" cantilever possess considerable weight. The trunk section between fore- and hindlimbs is much heavier, while the tail, as the "posterior" cantilever begins with masses of similar size as the neck but decreasing weight towards its tip.

The bending moments (=products of weight force times distance from support) occurring in the beam therefore vary from moderate values in the head, exponentially increasing values along the neck to maximal values at the shoulder. Rearward, towards the caudal end, bending moments decrease, cross the zero-line (changing their sign) and reach considerable values behind the middle of the trunk. Behind the posterior support, bending moments may again become large, if a long and heavy tail is present. If the tail is of very low weight, and slender, the bending moments remain low. In many cases, however, the hip joint is more or less flexed, so that the muscles behind must be contracted, this has a similar effect on the bending moments as a long tail has fairly high bending. What needs to be considered is the variable weight of the "beam". This is indicated in figure 1.

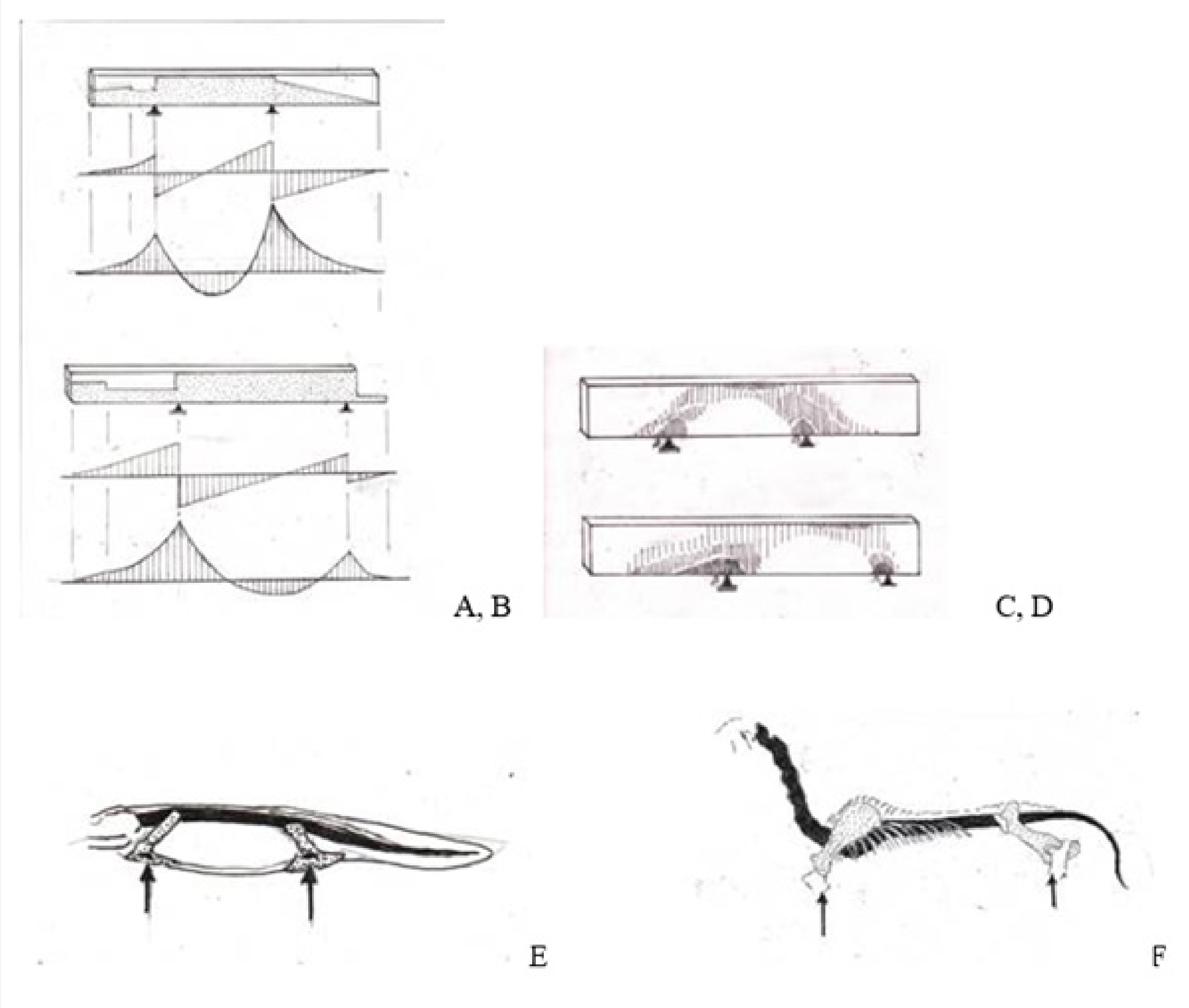

Figure 1: Beams representing "primitive" animals with long tail and short neck (a), and highly specialized (cursorial) animals with short or weightless tail and long neck carrying the heavy head (b). The parts of the animals have more or less weight, which is indicated by the stippled areas on the front aspects of the beams. Note the high load on the hindlimbs in the long-tailed form and on the front limbs in the tailless forms. The sum of both supports of course must be body weight. This distribution of weight entails different shearing forces (first hatched diagram below the beams) and different bending moments (second hatched diagram below beams) (c, d). Regardless of weight distribution, the highest compressive forces occur at the supports, and the flow of compressive forces in the beams has a dorso-caudal direction at the front support and a dorso-cranial direction at the caudal support (d, f). The first corresponds to the rearward inclined scapula, the second the forward inclined ilium.

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Corresponding to the bending moments, there occur stresses in the beam: compressive at the anterior and posterior supports, tensile at the basis of the neck and behind the hip joint. The skeletal elements of the body stem, which can resist compression are shifted ventrally in the caudal section of the neck, and dorsally along most of the trunk, while the tension-resistant elements are concentrated in the dorsal neck region. In anatomy, the muscles are usually classified as muscles either of the trunk, or those belonging to the extremities, or to the anterior digestive tract (infra- and suprahyoid muscles). This classification is well approved, but useless in our context. What we need here, is nothing than the position of tension-sustaining or tension-producing elements on the "beam", regardless of their origin: M. splenius is counted among the ("dorsal" muscles because of its innervation, m. rhomboideus belongs to the extremity, and m. trapezius is partly innervated by a cranial nerve. The infra- and suprahyoid muscles receive their nerves from the Ansa cervicalis. On the ventral side of the trunk, it is especially the m. rectus ado minis, which provides the required tension. This is experimentally controlled, mostly by EMG [2]. The muscles possess long lever arms at the basis of the neck, in the most anterior thoracal region and along the trunk, so that but moderate forces must be exerted.

It should be noted, that very high compressive stresses occur between the anterior support (forelegs) and the posterior support (hindlegs), which are inclined dorsa-caudally and dorsa-cranially. These stresses require skeletal parts to be sustained, and these parts exist in the oblique scapula and in the forwardly inclined ilum, between hip joint and Ili sacral junction (Figures 1c-1f).

The suspension of the trunk from the anterior limb is distributed over some length, that means in terms of anatomy, the insertion of the m. serratus spreads over several ribs. This has the effect of keeping local forces low, or cutting off the spike at the shoulder, visible in figure 2. Placing the foot forward, in front of the hip joint requires strong activity of the muscles, which extend the hip joint. These muscles also act on the body stem, as shown in figure 2.

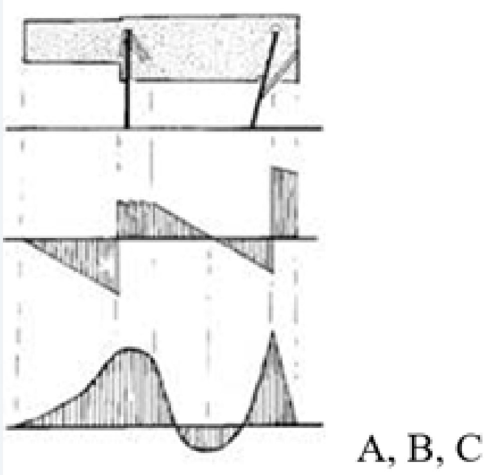

Figure 2: Beam representing a horse, supported on left side (shoulder) by muscle fibres arranged like a fan and distributing the force over some length (several ribs). The hindlimb on the right side is slightly anteverted. The muscles which balance the hip joint exert influence on the shearing forces and on bending moments.

If the beam is cut, in the anterior cantilever its anterior parts (head, or segments of the neck) will fall downward, while the more posterior elements will rest on their places. Behind the forelimbs, the anterior part will maintain its height, and the posterior part will tend to fall downward. This tendency becomes smaller along the trunk, until it assumes zero values. Behind this point, the anterior part will tend to fall downward, while the posterior part maintains its position. A maximum is reached at the hindlimbs, from where the anterior part, supported by the limbs remains and the posterior part falls downward. The force which comes into action, depends on the weights. These shearing forces are shown in the diagrams of figures 1 & 2. An effective structure to withstand them are compression-resistant ribs, in combination with tension-resistant intercostal muscles. The same construction of the thoracal wall is well suited to withstand the torsional moments, described below.

Kinetics: Vertebral Column of Quadrupeds in Locomotion

Aside from the bending moments, there occurs torsion in the trunk of a tetrapod as soon as it lifts one limb from the ground, which is necessary for any locomotion on limbs. Torsional moments consist of a part of body weight, carried by the respective limb times lever arms. In sprawling limbs, torsion therefore becomes greater than in the adducted "stilt-like "limbs of mammals. Torsional stresses concentrate near the periphery of the exposed

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body and leave its interior unstressed. This is the reason, why the large body cavity offers space for the not resistant intestines, and why the resistant elements form the trunk walls.

Highly resistant against torsion are the combination of ribs plus oblique intervertebral muscles (Figure 3 c). The farther this system is removed from the body stem´s center, the greater its strength. In animals with sprawling limbs, consequently the cross sections through the trunk are more or less circular. This trait is not marked in cursorial mammals, in which the shoulder region is narrow (Figure 3a) and so avoids great torsional moments, typical for primitive tetrapods. Nevertheless, the belly is rounded, so that parts of the body wall are widely removed from the center to provide high torsional strength. The strongly curved ribs which are seen for example in primates (Figure 3b), are suited to sustain the stresses evoked by anteverted and by abducted arms.

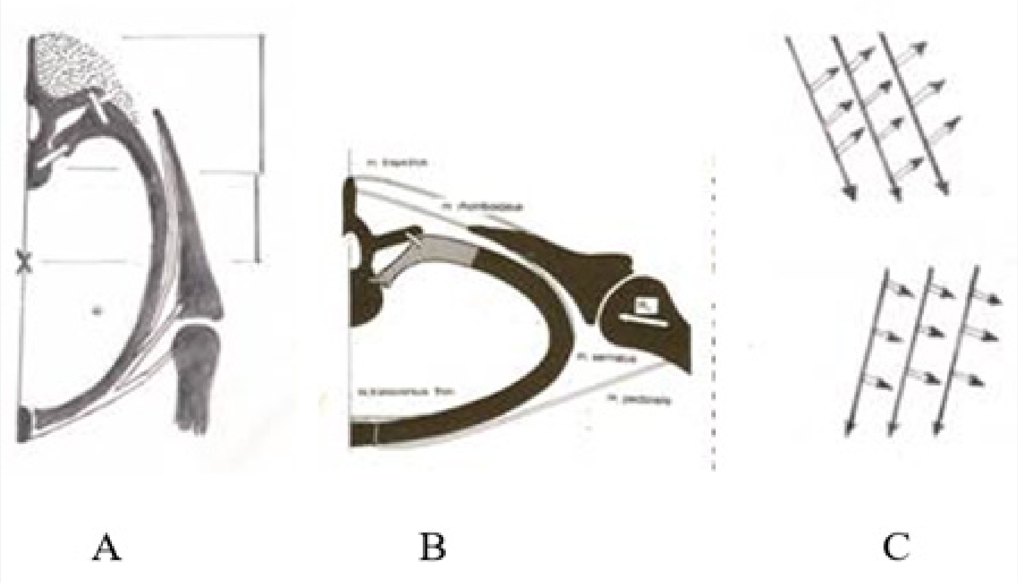

Figure 3: (a) straight ribs of a cursorial mammal in which movements are largely confined to a parasagittal plane. Note the long load arm of weight (X), and short force arm of muscles. (b) curved ribs of a primate, which often carries loads on its abducted and/or anteverted arm. The load arm of weight is short, and the force arm of the dorsal muscles is long (after Preuschoft et al.) (c) Schematical combination of compressive (black arrows) and tensile stresses (white arrows) in a twisted trunk. On top: view on left side, support on left forelimb. Below: view on right side, support on left forelimb. In walking, the patterns alternate with stance phases of limbs. The compression- resistant ribs seem to assume a position intermediate between the stress flows.

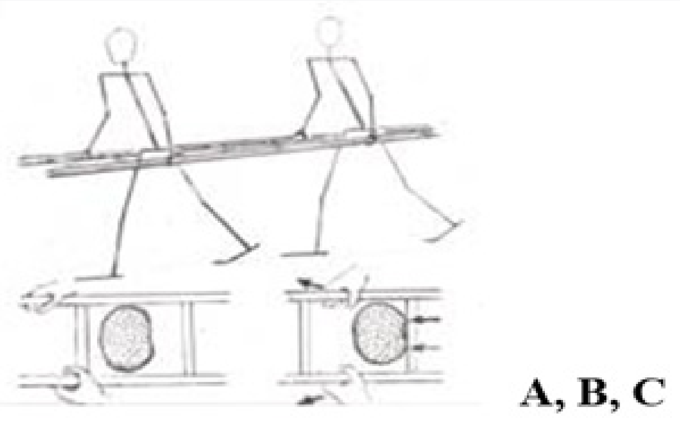

Figure 4: a) Two persons carrying a ladder, with spokes pressed from behind against their hips (c), have to walk lock- step. Free choice of step length and step frequency is possible, if one support is decoupled from the ladder by carrying it alone by the arms, without contact between hip and spoke (b).

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If the supporting fore- and hindlimbs are fixed, and the length of the vertebral column is kept constant as well, locomotion can only take place in lockstep (Figure 4). The only way out of this limitation, allowing an adaptation of step length to uneven ground, or uneven step lengths, is permitting the distance between both supports to vary. This variation can be realized either by flexion of the vertebral column (lizards and earliest tetrapod's, from the late Carboniferous) or by decoupling one pair of supports from the body stem. This is accomplished by suspending the trunk on one pair of supports alone by muscles. These permits vary the distance between fore- und hindlimbs. The anterior support and not the posterior is used because the tetrapod's from their earliest stage on depended on their ability to escape, or to rush forward towards prey. Both activities require a direct transmission of ground reaction force acting from behind, while in breaking a limited mobility between the ground contact of the forelimb and the heavy body has the appreciated effect of damping. The muscle comes down from the vertebral margin of the shoulder blade and inserts into the anterior ribs, which are most advantageous if straight and strong. Both traits indeed can be observed and discriminate anterior ribs from those of more posterior segments.

All four-footed animals are able to walk, and most of them trot. In both gaits, the body stem is kept quiet and exposed to the same loads as in static situations, the limbs function during the stance phase like "inverted pendula" and during the swing phase as "suspended pendula". The same holds true for the trot, which in addition makes use of elasticity of the long toe flexors [3]. Mammals, however, often use a new way of locomotion: the asymmetrical gaits bounding, half-bounding or galloping. Mammals have not invented these gaits, at least smaller crocodiles can use it as well (personal comm.. by Gans, 1964, and Hutchinson 2012), but mammals have made these gaits to their shape-dictating performance. The distance covered by each cycle can be increased considerably if the pelvis with the hip joint is moved forward rhythmically. The moderate excursions between adjacent vertebrae sum up to considerable excursions of the hip, which follow the cosine of the excursion angle.

All this requires flexion and extension of the vertebral column. This can take place best if the vertebrae are not connected to ribs, that means in the lumbar section (Figure 5). The longer the flexed part, the greater the gain of distance. This has two consequences: first the great length of the moved lumbar section, second shifting the most marked movement cranially. In fact, most of the flexing movement takes place immediately behind the ribcage. The short lengths of the vertebrae behind the thorax permit most pronounced excursion. In sitting cats, for example, the curvature of the back is most marked in this region.

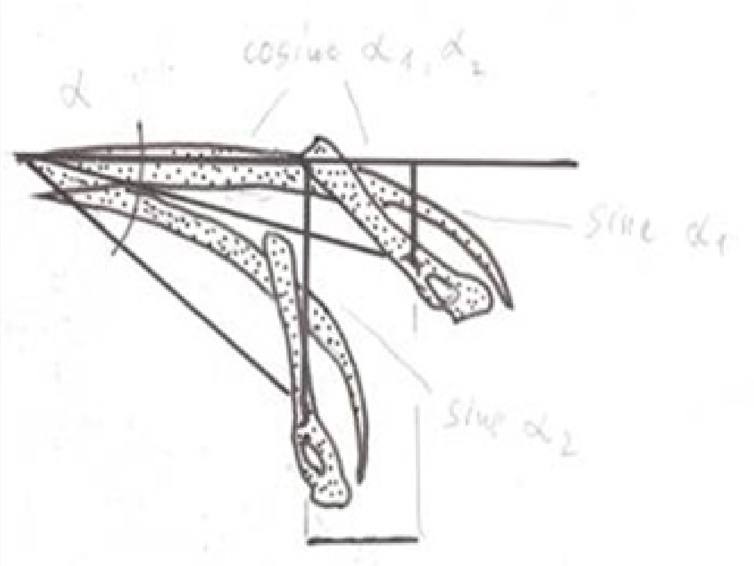

Figure 5: Movement of the hip joint during flexion of the vertebral column in a small mammal. The lift produced follows the sine, the distance d covered follows the cosine of the flexion angle α the curature is taken from Fischer [17], who has investigated the rock hyrax with x-ray movie cines Can you, please, insert the legends - at present written with pencial.

This increasing the distance covered in each cycle by flexing and extending the trunk, however, seems to be confined to smaller animals. Already Slijper [4] in his great review of vertebral column has emphasized that large animals do not move their trunk in this way. A sharp limitation was never identified between "dorsa-mobility" (Figures 5 & 6a, 6b) and "dorsa-stability" (Figure 6c), but transitory forms exist. For example, the heavy yellow-backed duiker (Cephalous sylvicultor) weighing about 200kg is clearly dormobile, like all smaller forms. Eland, gnu and large cervids like red deer or wapiti and equids (weighing 300kg and more) are dorsostabile, and smaller cervids as well as many medium-sized antelopes flex and extend their spines to some degree. An open question is why this difference occurs. The only attempt to find the solution of this riddle was made by Preuschoft & Franzen in 2011 in a study on Eocene perissodactyl from Messel.

They simplified the trunk like in figure 6 as two halves of about the same size. In this model, extension is provoked by a contraction of the dorsal muscles and flexion by the contraction of ventral muscles. The dorsal muscle group is treated here - as well as in other cases – as one heavily feathered muscle with many insertions at the dorsal processes of vertebrae. May well be that the activity of the m. iliopsoas is underestimated, but the available EMG-data of the m. rectus [2] justify our assumption. Lever arm lengths grow with size, and therefore movements become slower. They may become so slow that a flexion does not longer fit into the time span available for swinging the hindlimbs forward and so make flexion useless, even deleterious.

In the case of horses, we have observed very limited movements of the lumbar section behind the saddle and the pelvis [5]. These movements do not contribute to forward movement (Figures 5 & 6a, 6b) the length of the cosine of the angle being too long through the entire cycle. The hip, however, is moved upward rapidly, following the sine of the excursion angle (Figures 5 & 6c). This upward movement increases the field of gravitation [6] in which the hindlimbs are swung forward and so accelerates the fore swing by factor 1.7.

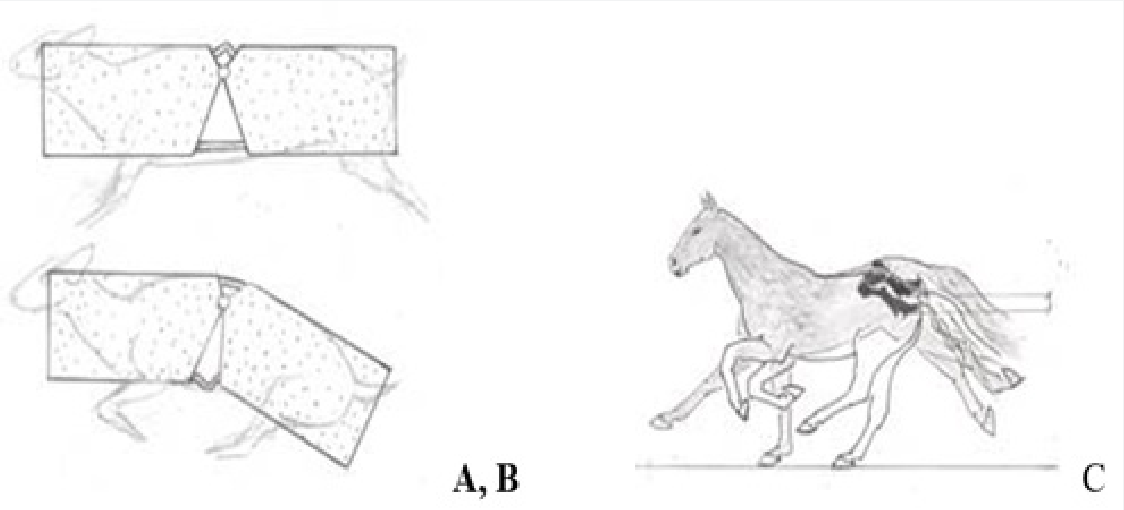

Figure 6: a, b Trunk movements in a dorsomobile animal (schematical presentation of something like a blue duiker as an example). In extension (a), the flexors of the trunk become active, while the dorsal muscle group is relaxed. In collection (b) the opposite is realised: dorsal muscles contracted, ventral m. rectus and m. psoas are relaxed. c Movement of the pelvis in a galloping horse is mainly restricted to up and down, following the sine of the angle shown in figure 5. Upward movement, however, creates a field of increased gravity, in which the foreswing of the hindlimbs is much faster than it would be otherwise. From Preuschoft [1] oder from Witte [3]?

Figure 7: Thin lines: Calculated compressive loads along the body axis of horses in various postures, relaxed or extremely challenging. Dots on top: measured cross sectional areas of vertebral bodies.

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As a well-known example of cursorial animals, I have once compared the loading of the vertebral column in horses during varying activities with the strength of the vertebral column. As a measure of strength, I used the cross sectional areas of the anterior surfaces of vertebral bodies, or “centra”. Forces distribute evenly over the resisting surface. It turned out that the so-defined strength of the vertebral column fits to the extreme loads which were investigated (Figure 7).

Statics: Body Shape in Humans

Body posture in humans differs fundamentally from that in other animals. Although it can be derived from body posture in other “higher” primates [7] and from fossil documents, the mechanical conditions are quite different from those in four-footed animals. If the body is replaced by the model of a beam, like in figure 1, this beam comprises not only head, neck, and trunk (the body stem), but the forelimb as well.

As can be seen from figure 8b, the upper part of the beam is exposed alone to compression, not bending, if the beam has a rearward kink. This kink is displaced in cranial direction in non-human primates, which possess a long, rod-like ilium. We have investigated the pronounced and permanent curvatures of Japanese monkeys which are traditionally trained for bipedal locomotion. Their lumbar lordosis is sometimes more pronounced than that in humans. In recent times gorillas are published in the press, which like and often perform bipedal walking. They seem to have the same lumbar lordosis as our Japanese monkeys. In humans, this kink is moved caudally. The lordotic curvature of the lumbar segments, which often has been observed and discussed in upright standing humans, disappears already with moderate flexion of the hip joint [8,9].

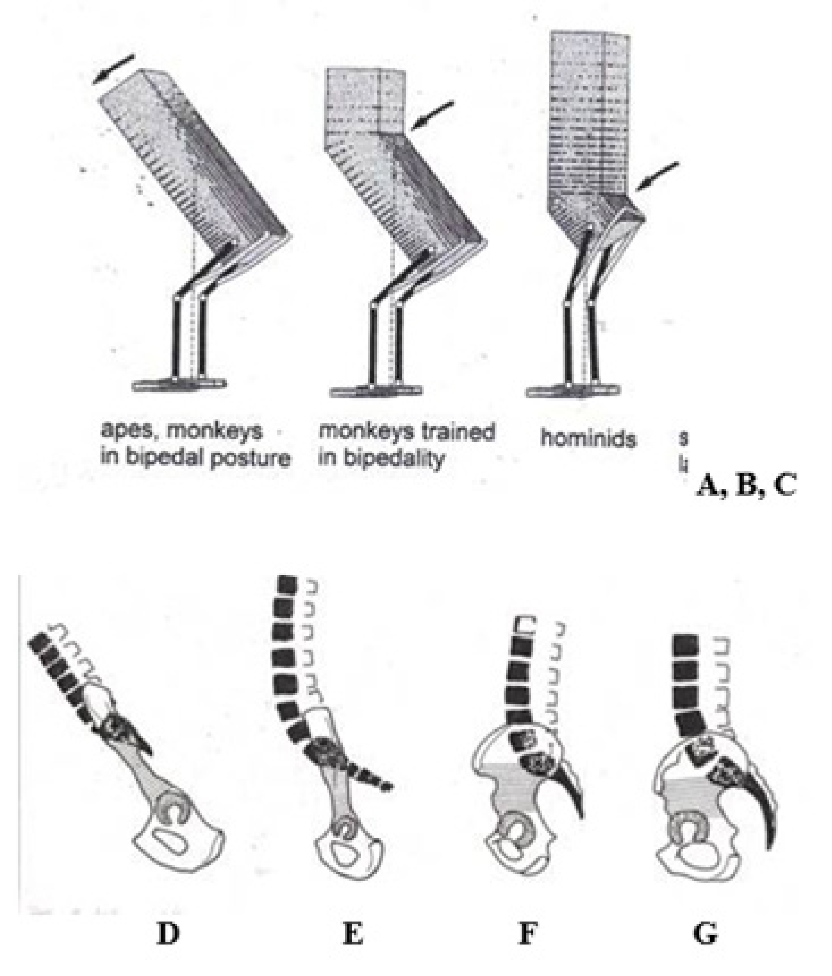

Figure 8: Body modeled as a beam in bipedal posture. a) It is exposed to bending over its entire length. That means, muscle force (longitudinal hatching) must be exerted along the entire trunk. b Existence of a lordotic “kink” shortens the length of the part exposed to bending, leaving the upright, cranial part under nothing than weight force. The more caudal this “kink”, the smaller the part which is bent. d pelvis and vertebral column in an ape (without tail); e pelvis and vertebral column in a bipedally trained monkey with lumbar lordosis and a tail; f vertebral column and pelvis of an australopithecine, and g of a member of genus Homo, with the characteristic promontorium. In all cases, the “iliac neck” is emphasised by horizontal hatching. A lordosis of the lumbar section may exist or not (see text). Modified from Preuschoft et al., 1989.

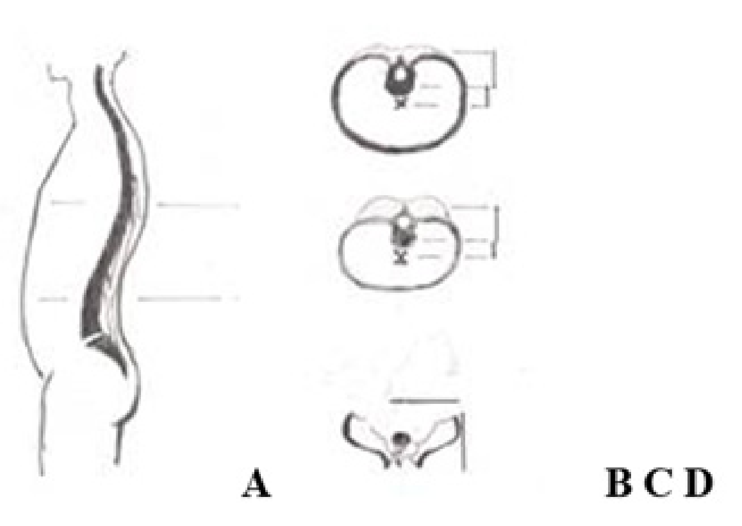

Figure 9: a Lateral view of a human trunk, showing the erector spinae-system (double lines) and the vertebral column (black). b cross section through a human body on the level of the ilium; c level of L3 or L4, showing the position of the muscles dorsal to the vertebrae, d at the level of Th 5 or Th6. Along the vertebral column, the position of the muscles is shifted far behind the centra, and the compression-resistant vertebral column is shifted in ventral direction, offering a long force arm, while the load arms of weight are short. d horizontal section through the ilium. It provides by its shape very high resistance against bending in two planes, which are indicated. For comparison with the straight ribs of a hweavy quadruped (Figure 3 a).

The "kink" is morphologically fixed/dictated by the "promontorium" and by the retroflexion and shortness of the "iliac neck", that is the part between acetabulum and a line connecting spina iliaca anterior and facies auricularis, and it includes the "ischiadic notch". This "neck" (Figures 8c - 8g) is long and rod-like in most animals, including apes, and very short in humans. In the early australopithecines, ilium shape assumes a median position between apes and Homo. The broad and short ilium with laterally flaring iliac blades instead of the long, rod-shaped form widely spread among non-human primates is a characteristic of genus Homo in contrast to the apes and to the australopithecines. Its width and orientation (Figure 9) provide high bending strength in both sagittal and coronal planes. It should be noted that the marked lordosis which develops in bipedally trained monkeys is a matter of intervertebral discs - like in the promontorium.

Interesting enough, the famous and often mentioned lordosis of the lumbar spine disappears in humans if the hip joints are somewhat flexed. Aside from the permanent built-in dorsiflexion (see above), lordosis is caused by the position of the pelvis. The crista iliaca, represented by a line connecting posterior and anterior spina iliaca points slightly forward-upward in standing. In this posture, the hip joint is not far from its limit of extension. If the hip joint is flexed, its muscles and ligaments rotate the pelvis and with it the above line more markedly forward-upward [8] (Pakusa et al. 1995). Because the movement of the pelvis is firmly connected with movement of the lumbar spine by the sacro-iliac junction, the rotating of the pelvis leads to reduction of the lumbar lordosis if the hip joints are flexed. According to our measurements [9], the lordosis is maintained during hip flexion of about 140° in not more than 15 % of healthy, young persons (>100 students of both sexes), a straight line in 17 %, but changes into a kyphosis in 68 % of the investigated persons.

Between the segments – more exactly between the centra – an equilibrium must be maintained. This exists in static situations as well as during movement, provided that the inertial forces are taken into consideration. The equilibrium is is defined by

$$F_k * h_k = F_w * h_w$$

where k stands for muscle force and w stands for weight in static situations and for weight plus inertia during movement.

A characteristic of humans is the shifting of the compression-resistant vertebral column towards the middle of the body stem. The lumbar lordosis permits the dorsal muscles to deviate in dorsal direction and to run directly, well behind the spine from the sacrum to the lower thoracal segments. In the thorax, the strongly curved ribs give the dorsal muscles a long lever arm (Figures 9a - 9c). Both traits provide long force arms for the m. erector spinae. The bowed ribs are very different from the straight ribs in narrow-chested cursorial animals, in which they are straight and very strong [1,10]. In contrast, load arms resulting from weight are short.

The m. iliocostalis, which acts in lizards and crocodiles mainly as a reinforcement of the oblique muscles of the body wall, in mammals is (in agreement with its innervation) part of the erector spinae-system. All this is quite different from the situation in

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a quadruped, in which bending moments require a dorsoventrally high cross section, and avoidance of torsional moments is favoured by a narrow shape of the anterior thorax.

The lever arms are best visible on cross sections (Figure 9). The lordosis of the lumbar section, as well as the curvature of ribs produce a long lever arm, and therefore low force, of the dorsal muscles, while the lever arm of weight is relatively short. At all places, the vertebral column is shifted ventrally, towards the middle of the cross section. Curved ribs also are of advantage in loading the arms in anteverted and in abducted postures, which are typical for non-human primates (this is detailed in Preuschoft [1] and in Preuschoft et al. [10], an example is given in (Figure 10). Curved ribs also give a part of the mass moment of inertia which helps to balance the body about a vertical axis in walking (Figure 11).

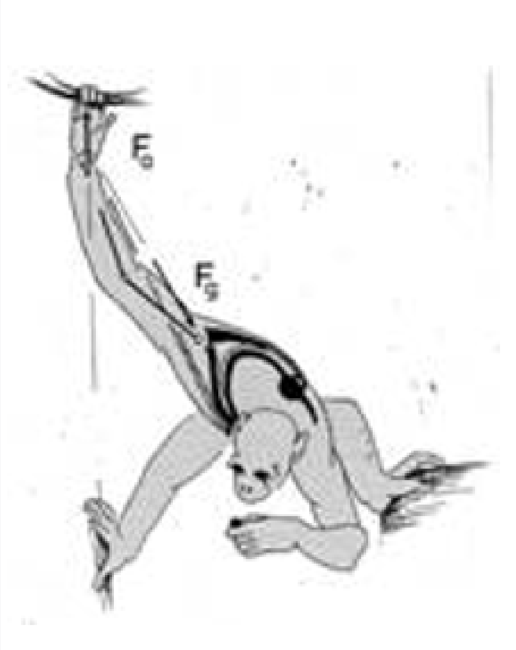

Figure 10: Example of a primate (chimpanzee) climbing with abducted and anteverted right forelimb, to illustrate the advantages of bowed ribs.

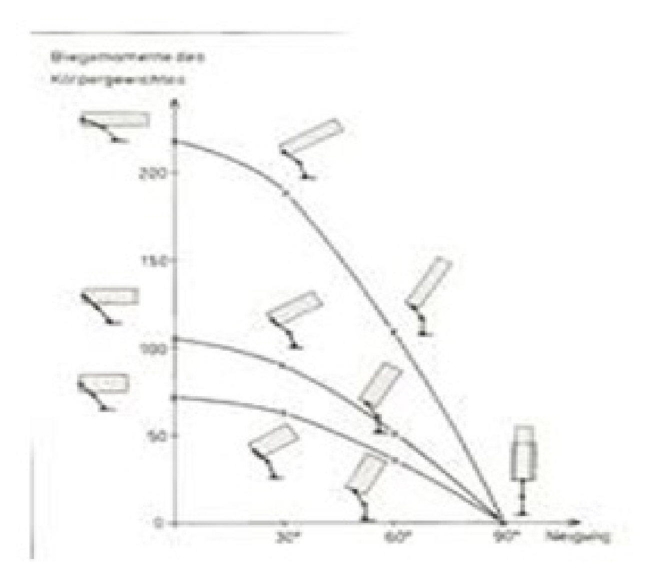

Figure 11: Inclination of body axis: decreasing inclination, vertical axis: bending moments. While the latter are zero in fully upright posture in all cases, inclination of the trunk leads to higher bending moments (that is higher muscle force) in a long and slender trunk than in a stout and compact body. Volumes (and areas in the drawing) are the same in all cases. From Jaeger [18].

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Kinetics: Human Vertebral Column in Movement

The curvatures of the human vertebral column are often seen as a means to damp forces, which act from below on the body. This interpretation is erroneous. In fact, the vertebral column is a series of blocks, or thick slices through a cylinder, one set on top of the other, regardless of a perpendicular, or a curved arrangement, which is similar to the often mentioned and well-known "lordosis" (Figures 12a & 12b). Between the vertebral bodies or "centra" there exist intervertebral discs, consisting of a semi-fluid (and therefore not compressible) "nucleus pulposus" (black), surrounded by diagonally orientated fibres, the "annulus fibrosus". This arrangement permits movement between the centra and seems to include elastic deformation. Such an elastic deformation, however, is not confirmed experimentally (Figure 13). Deformation on only one side into a wedge-like shape, however, is a necessary constituent of movements of the spine.

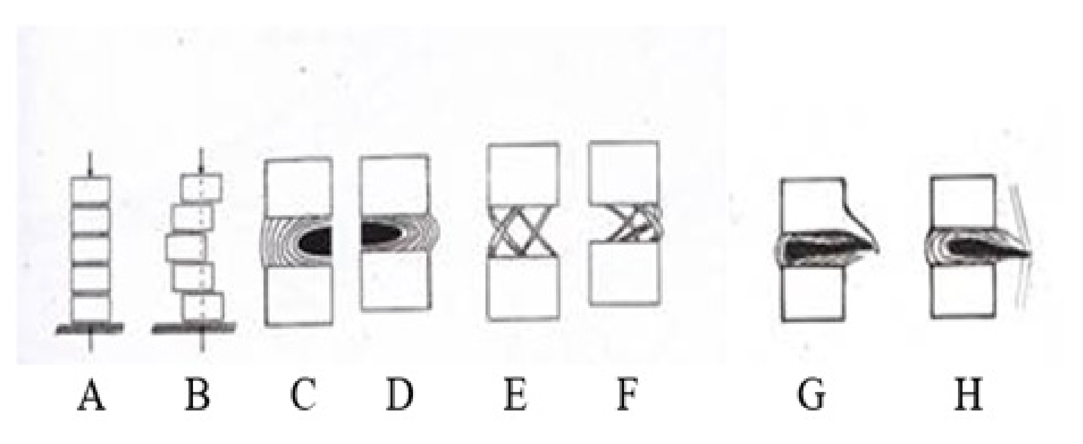

Figure 12: Models of the vertebral column as thick slices of a cylinder, set one on top of the other, forming a straight column (a), or a curved line, like the lumbar lordosis (b). Both maintain a constant length and cannot become shorter. c intervertebral disc without load; d under load, the (not compressible) nucleus becomes flattened, Because of their oblique arrangement, these annular fibres give way and bow more than before without lengthening (e, f). This happens on one side alone in movements of the spine, permitting movement. A prolaps of the nucleus after rupture of the anular fibres, can be overgrown by bony material (g). If the prolaps touches, or even squeezes a nerve (white line), this causes severe pain in the hindlimb! a-f taken from Preuschoft [1], g-h new drawings.

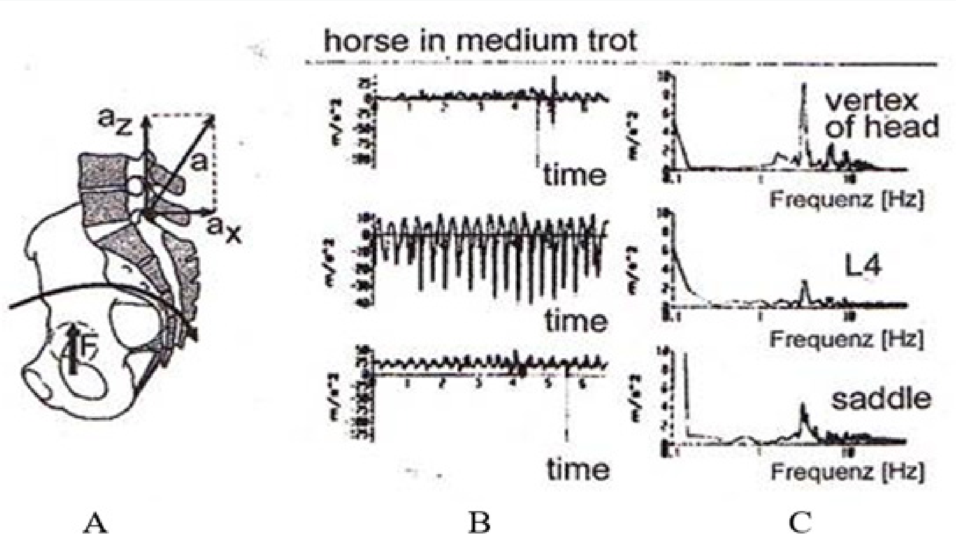

Figure 13: The movements of the pelvis and accelerations measured at the back and at the head if forces are applied directly to the axial skeleton. We used horseback riding as an example of forces applied directly into the body stem. a) Contrary to initial expectation, the pelvis is rotated backward and the vertebral column erected. b) Variation of applied forces, c frequency of impulses. Forces are passed on without damping up to the head! From Preuschoft [1].

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In order to make sure of the assumed elasticity of the vertebral spine, while excluding elastic resilience of the hindlimbs, we have placed young, healthy experimental persons (students) on a horse´s saddle and exposed them to the acceleration which occurs in riding trot. The trot was selected, because it implies the greatest and the most frequent accelerations. The forces so are applied directly to the axial skeleton, not to the hindlimbs. Accelerations were measured at the saddle, at the spinous process of L 4 and at the vertex of the head, the reactions of the body stem were controlled by the height of the spina iliaca anterior in relation to the hip joint. As figure 13 shows, the acceleration arrived full size at the head. No elastic damping at all. The same result was obtained when not horseback riding, but biking was used to provoke accelerations along the length of the body stem.

Also, very characteristic for the human vertebral column is its length (5 lumbar, 12 thoracal vertebrae) supplementing the slender form of the trunk. It implies disadvantages, that is high bending moments in forward flexed trunk postures (Figure 11). This has been classified by some orthopedists too precoxially as a “misconstruction” of the human body. Indeed, it leads to height bending moments if loads are lifted from the ground. Apes with their short, more compact trunk seem to be better. This, however, leaves out of consideration that humans are not designed (“adapted”) for lifting loads from the ground, but for long-distance walking. While in standing upright, length is no drawback, it becomes a strong disadvantage in bending forward (Figure 11). The more the trunk is approached to the horizontal, the greater the bending moments and with it grows the force required for keeping balance.

The most important argument for developing a long, slender body shape has not been found by application of statics,but needed kinetics: For walking the heavy hindlimbs must be induced to swing forward at the onset of each foreswing, and braked at its end [11-13]. The masses of the heavy hindlimbs in both cases must be accelerated. The muscles which do this task, do not only act at the hindlimb, but also at the trunk, where they create a forward and rearward nicking movement (Figure 14). This would be a vaste of energy and in addition, disturbs clear vision and hearing. It can be suppressed without expenditure of energy by a great mass moment of inertia, that is

$$mass * square\ of\ \ dis\tan ce\ from\ pivot.$$

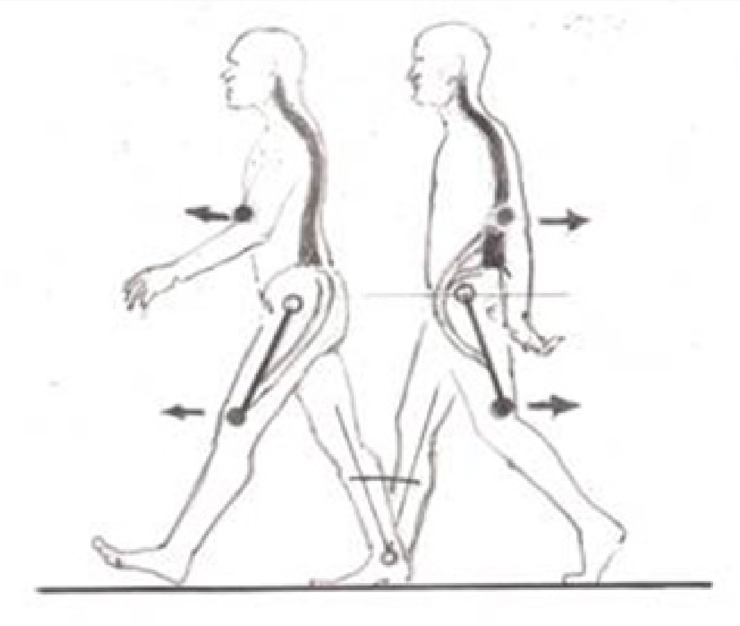

Figure 14: Walking human. Centres of mass of arms and legs are indicated by black dots, Pivots of most important movements are shown by circles. During the stance phase, the body rotates as an “inverted pendulum” about the (tibiotalar) joint closest to the ground. At the begin of the swing phase, the heavy hindlimb must be moved against its mass moment of inertia (arrows). At the end of the foreswing, it must be braked, also by muscles (white lines). In both cases, the muscles which overcome inertia also act on the body stem and induce a nicking of the trunk. This nicking is only partly suppressed by the pendulous swing of the light arms in counterphase. High resistance against nicking, however, is provided by the length of the body axis. Its big mass and the length of the spine create a high mass moment of inertia. Modified from Witte et al. [11].

Clearly, the slender trunk with long vertebral column and heavy head on top is more advantageous than a short body with a lighter(?) head on a short neck would be.

If seen from above, more details of human body shape become evident as mechanically advantageous (Figures 15a-15c): The heavy legs (each of them weighing about 14 % of whole-body mass) rotate the trunk rearward, at the same time when the light arms (each weighing 4 - 5 % of body weight) are pulling forward

– and the reverse. The arms, however, have longer lever arms than the legs. The trunk between the extremities is twisted, as is the vertebral column, and the oblique muscles of the body wall are stretched and relaxed (Figures 15c & 15d). They seem to exert forces, just because of their elasticity and so contribute to saving energy. A by-product of muscle stretching is the formation of a waist and the barrel-shaped trunk which is characteristic of Homo in contrast to the funnel-shaped ribcage of its predecessors and apes [14].

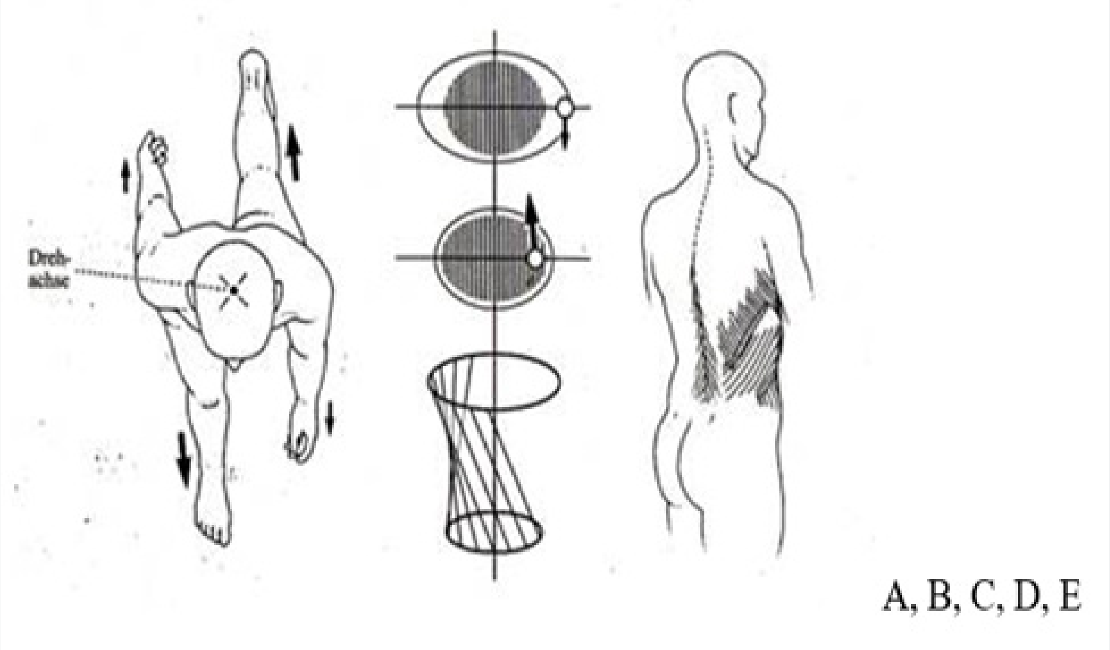

Figure 15: a) In a walking human, the heavy legs pull rearward or forward while accelerated or braked. The reverse is true for the much lighter arms. The lever arms which initiate rotation, however, are long in the arms (b) and short in the legs (c). Both forces act in counterphase and therefore expose the trunk to torsion. This torsion leads to elastic (?) stretching of the oblique trunk muscles (e) and to the famous waist below the thorax. From Witte et al. [11].

The mechanical principle is not questioned, but its biological role remains as a point of dissent: An US-American group, (Liebermann, Carrier, Bramble) emphasizes long-distance running more than walking. This, however, confines the evolutionary pressure to the presumably hunting males, while our model implies both sexes. In addition, running over hours is an ability restricted to few trained athletes, while walking over 30 km per day is a task within reach of everybody (as inquired at the Meeting in Paris, 2012) [15-21]. The tricky thing is that morphological specializations to running are the same as those to walking. So, there is no means to decide......first half of the illustrations belonging to the review.

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