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Certain medical problems resulting from evolutionary processes: bipedalism as an example

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Abstract

Humans are primates, and as such, our overall anatomy is very similar to that of other members of this biological order. Yet, there are numerous differences in certain anatomical regions of living humans when compared to our closest living relatives, the African great apes. Many of these, such as our extremely large brains compared to body size (even if all primates have relatively large brains), details in dental anatomy, and so on, appear at different times in our evolutionary past and within the tribe hominini. *However, the first, and taxonomically most significant synapomorphy of the hominin clade is a change in locomotory mode, from that of a quadruped (presumably the ancestral state in last common ancestor (LCA) of humans and apes) to biped. In this paper, a brief overview is given of the most important anatomical challenges that these novel locomotory patterns required to be enegretically efficient, as seen in the comparison between living African apes and humans. Further, an overview of the fossil record, as related to the issues raised, is given. Lastly, the importance of understanding evolutionary adaptations and changes for the medical profession is discussed.*

INTRODUCTION

Acquisition of a bipedal mode of locomotion is considered the first and most important apomorphy in hominin evolution. Anatomical structures related to this change are often used as a defining characteristics for the inclusion of a particular fossil specimen into tribe hominini (particularly when dealing with earliest supposed members of this clade). Discoveries in the last fifteen or so years have moved the earliest appearance of this novel way of locomotion (and subsequently, the beginnings of the hominin clade) to as far as 6 – 7 million years ago (although opinions vary on the degree of importance of this adaptation in earliest members of the group, and even on the taxonomy and phylogeny of these taxa, see later in the text). If the anatomy of fossils such as *Sahelanthropus*, *Orrorin*, and *Ardipithecus* indeed reflects habitual bipedalism, then we need to think about various other aspects and reasons for the first appearance of this important evolutionary novelty. By the time that the earliest members of the genus *Australopithecus* are present on the evolutionary scene, fossil data become more abundant, and all (or almost all) the necessary anatomical changes related to habitual bipedalism are well documented. Final anatomical changes in the direction of modern human anatomical form and full adaptation, not only for walking, but for efficient long-distance running are seen with the beginning of the genus *Homo* (*Homo ergaster/erectus*). That is not to say that australopithecines were not fully capable of bipedal locomotion, or not well adapted to it, but rather that their adaptation was somewhat different than ours.

There is still much debate on the dominant mode of locomotion in the ancestor of hominins, mainly because the late Miocene fossil record of Africa is very scarse. Whatever this mode was, we need to consider the benefits that the novel, bipedal mode of locomotion, provided for the early hominins. There are numerous suggestions, most related to some degree to the novel pressures of changing environment *(1),* including dietary adaptations *(2-4),* social factors and threat displays *(5-6)* and thermoregulatory and biomechanical/energetic factors *(7-15).* It is very likely all (and many other) factors played a role in the initial adaptation to bipedalism, but all need to be examined in the ecological and paleoenvironmental settings of the Middle and Late Miocene. The aims of this paper are not to discuss the reasons why and from what dominant locomotory mode bipedalism arose (however important and interesting these issues are). Rather, we provide a review of the necessary changes needed for efficient bipedalism through comparison of anatomical differences between living humans (bipeds) and our closest living relatives, the African apes (quadrupeds). Additionaly, we turn to the hominin fossil record to observe the aforementioned changes and adaptations during Pliocene and Pleistocene, when this novel mode of locomotion first arose (we also briefly discuss some of the first members of the hominin clade from the final Miocene).

A major evolutionary adaptation, bipedalism, was a starting point without which we, *Homo sapiens*, would not be here today. However, it came with a price, as much of the chronic problems of the modern humans (e.g. back and joint problems and so on) are a direct result of this novel way of locomotion. It is therefore crucial to understand the evolutionary aspects and changes in anatomy before we can succesfully approach it as a problem from the standpoint of medical profession.

ANATOMY OF BIPEDALISM

In order to understand basic anatomical requirements for habitual bipedal locomotion we need to understand the changes in anatomy from the plesiomorphic morphology (i.e. ancestral morphology of our pre-hominin ancestor). As the last common ancestor (LCA) of hominins is still unidentified with certainty, as is the dominant locomotor mode from which habitual bipedalism arose *(16-24),* a comparison of living human morphology and those of our closest living relatives (African great apes) is the best proxy to examine. Much of the differences between the LCA's anatomy and that of hominins is related to a change in locomotory mode, that is, the acqusition of bipedalism in the later group. The same is true for much of the postcranial differences between living humans and living apes. Here we list major anatomical differences between a habitual bipedal primate (as exemplified by *Homo sapiens*), and quadrupedal primate (as exemplified by the genera *Pan* and *Gorilla*).

One of the major demands of bipedal stance is to change the center of gravity in the most efficient way. In quadrupeds, the center of gravity falls somewhere between the fore- and hindlimbs. This makes maintaining balance almost effortless. However, in humans the center of gravity is located in the midline, somewhat anterior to the second sacral vertebra, and passes through an imaginary line between our feet *(25).* Maintaining of the upright position of the trunk is helped by the iliofemoral ligament (*lig. iliofemorale*), and the ligaments of the knee (*lig. cruciatum anterius* and *posterius*).

In order for a quadruped to start a forward motion, all is needed is the extention of the hindlimbs that, with a little help of gravitational forces (as the center of gravity is located in front of the hindlimbs), automatically moves the body forward. Functionality of muscles is helped by the anterior tilt of the superior part of the pelvis, as well as by the morphology of the ilium (*os ilium*), which is elongated in superioinferior dimension, compared to those of humans. In biomechanical terms, this allowes a more functional action of muscles, therefore it is less energetically demanding. Although apes are known to sometimes walk bipedally (e.g. as a threat display, when crossing creeks or carrying items), they do so with increased energetic costs, compared to their normal (quadrupedal) mode of locomotion. They exhibit a bent-hip/bent-knee gait, because they cannot position the center of gravity in the same way as modern humans *(26-27).* In order to make evolutionary (cost-benefit wise) sense, the journey from quadruped to biped requires numerous architectural changes. This is seen in various anatomical regions, including basicranium, vertebral column, pelvis, lower limbs and feet, and requires various rearrangements in musculatory system. The main muscles/muscle groups involved in bipedal locomotion include the gluteals and front and back muscle groups of the thigh. More detailed anatomical aspects related to bipedalism and musculoskeletal system can be found in Aiello and Dean *(25),* Lovejoy *(27-29),* McHenry *(30),* Cartmill and Smith *(31),* Muscolino *(32)* and references therein.

In humans, the three gluteal muscles *(m. gluteus maximus*, *medius* and *minimus*) have a major role in walking (even more so in running, jumping, etc.). The largest and strongest of these is *m. gluteus maximus*, located most superficially in the region usually referred to (politely) as our sitting area. This powerful muscle is actually about 60% larger in humans than in human-sized apes *(33-34).* Its origins are on the medial part of the ilium (*os ilium*, posterior to the posterior gluteal line) and partially on the posterolateral surface of sacrum (*os sacrum*) and the coccyx (*os coccygis).* The deeper m. gluteus maximus fibers insert on the gluteal tuberosity (the proximolateral ridge of the *linea aspera* on *os femoris*), while the remainder of

TABLE 1

Main anatomical differences between humans and African apes related to bipedalism.

Homo	Pan/Gorilla
Head	Head
anterior (central) relocation of the foramen magnum and occipital condyles	foramen magnum and occipital condyles more posteriorly located
Vertebral column	Vertebral column
S – shaped vertebral column as a result of cervical and lumbar lordosis and thoracic kyphosis	arched vertebral column, no lordosis/kyphosis present
Pelvis	Pelvis
ilium (os ilium): short and wide post acetabular extention well developed greater sciatic notch laterally oriented superior part of the bone S – shaped iliac crest (crista iliaca) developed spina iliaca anterior inferior m. iliopsoas groove present short distance from acetabulum to facies auricularis relatively large facies auricularis	ilium (os ilium): elongated and narrow no extension lacking or poorly developed notch posteriorly oriented superior part of the bone straight iliac crest (crista iliaca) poorly spina iliaca anterior inferior groove missing greater acetabulum to facies auricularis distance relatively small facies auricularis
ischium (os ischii): shorter well developed ischiac spine (spina ischiadica)	ischium (os ischii): longer poorly developed ishiac spine (spina ischiadica)
sacrum (os sacrum): relatively wide	sacrum (os sacrum): relatively narrow
Lower limbs	Lower limbs
Femur (os femoris): longer longer and inferiorly thickened femoral neck medially angled/valgus knee posteriorly elongated lateral condyle	Femur (os femoris): shorter shorter femoral neck evenly thickened relatively straight relatively circular lateral condyle
Tibia (os tibia) and patella (os patella): longer tibia more complex patellar contact surfaces	Tibia (os tibia) and patella (os patella): shorter tibia less complex patellar contact surfaces
Foot: robust calcaneus (os calcaneus) abduction of hallux less curved phalanges double arch support system	Foot: more gracile calcaneus (os calcaneus) no abduction more curved phalanges no double arch system

the muscle attaches to the iliotibial band of the *fascia lata*. *Gluteus maximus* acts as a lateral rotator, an extensor, and an abductor of the femur at the hip, but it has an important role as a principal stabilizer of the trunk *(27)*. The remaining two muscles of the group, *m. gluteus medius* and *minimus* are located deeper than *m. gluteus maximus*. Their origin is between the anterior and posterior gluteal line (*m. gluteus medius*) and between the inferior and anterior gluteal line (*m. gluteus minimus*) on the lateral surface of the ilium, while the attachment of both is located on greater trochanter (*trochanter maior*) on femur. Both muscles act as abductors of the thigh, as well as flexors and medial rotators, and to some degree as extensiors and lateral rotators of the thigh and stabilizers of the hip. Therefore they have an important role in maintaining stability of the trunk during bipedal locomotion.

M. quadriceps and *m. sartorius* are muscles that form the anterior group of the thigh muscles. Both are involved in anteflexion of the hip and flexion, or extension of the knee. *M. sartorius* also acts as lateral rotator of the thigh and originates from the anterior superior iliac spine (*spina iliaca anterior superior*) and attaches to the proximal part

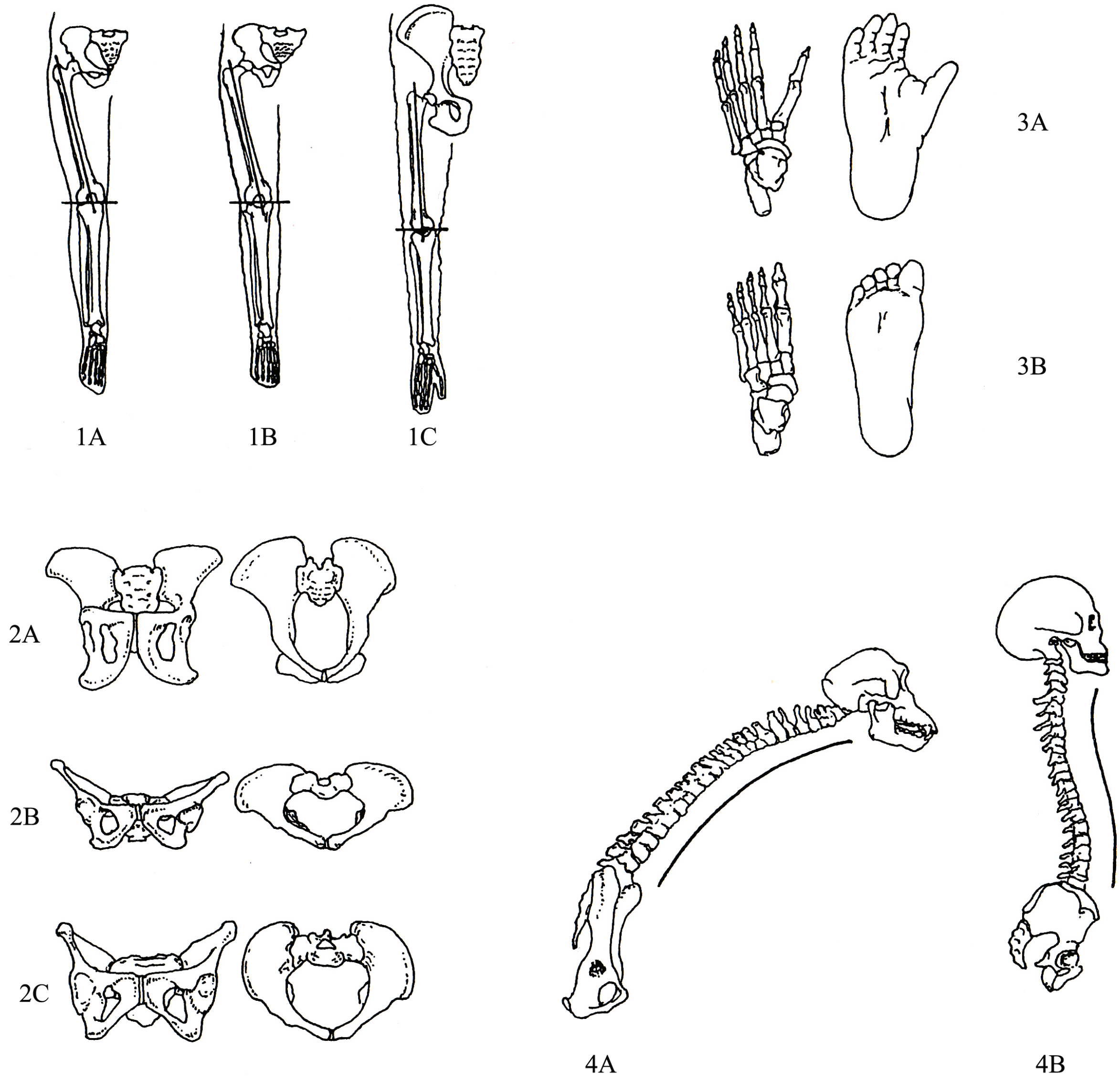

Figure 1. *Main anatomical adaptations to bipedal locomotion. Position of femora in living humans (A1), A. afarensis (1B), apes (1C); pelvic architecture in apes (2A), A. afarensis (2B) and living humans (2C); foot of a non-human primate (3A) and living human (3B); vertebral column in apes (4A) and living humans (4B). (Taken from 112, drawings by M. Galić).*

of the anteriomedial surface of the tibia (*os tibia*). *M. quadriceps* (literally, four-headed) is formed by four muscles: *m. rectus femoris*, and the three vastus muscles, *m. vastus lateralis*, *medialis* and *intermedius*. This powerful muscle group is easily palpated on the anterior surface of our thigh. The origin of *m. rectus femoris* is on anterior inferior iliac spine (*spina iliaca anterior inferior*) and partially just above the acetabulum. This muscle is involved in flexion of the thigh at the hip and extension of the knee. *M. vastus lateralis* and *m. vastus medialis* have a single origin along the *linea aspera* on femur, more precisely on the lateral lip of linea aspera and the anterior aspect of the greater trochanter and gluteal tuberosity (*m. vastus lateralis*), and the medial lip of the linea aspera and the intertrochanteric line and the medial supracondylar line of the femur (*m. vastus medialis*). *M. vastus intermedius* originates on the anterior and lateral femoral surfaces and the lateral lip of the linea aspera. The main action of the three *vasti* is the extension of the leg. All four muscles that form the *quadriceps femoris* group attach at a single site, the tibial tuberosity, on the anterior surface of the tibia (*os tibia*) via the patellar ligament.

The hamstrings, a group of muscles of the posterior thigh have an important role in flexion of the leg and the knee, and extension of the thigh at the hip, as well as in tilting the pelvis at the hip joint. Like its anterior counterpart, this muscle group consists of several muscles: *m.*

biceps femoris, *m. semitendinosus*, and *m. semimembranosus*. *M. biceps femoris* is a two-headed muscle that has its origin on the ischial tuberosity (long head) and *linea aspera* (short head). They both attach on the head of the fibula and the lateral condyle of the tibia. *M. semitendinosus* and *m. semimembranosus* both originate on the ischial tuberosity and attach on the superior part of the tibia, more precisely on its proximal anteromedial surface (*m. semitendinosus*) and on the medial condyle of the tibia (*m. semimembranosus*). The importance of these muscles in bipedal walking is clear, as they provide the initial movement, the extension of the thigh.

A brief overview of main anatomical differences between humans and African great apes in structures related to bipedalism is given in Table 1.

In order to be energetically efficient, habitual bipedalism required the reorganization of numerous anatomical areas and details. Most of these are seen in basicranium, the vertebral column, pelvis, legs, and feet (Figure 1).

Starting superiorly (cranially) the changes include the repositioning of the foramen magnum and occipital condyles more anteriorly on the base of the skull, in order to more efficiently balance the skull on the top of the vertebral column, so that the field of vision is maintained with minimum muscle action. The vertebral column had to undergo various changes, as the center of gravity (as mentioned) in quadrupeds and bipeds is rather different.

The human vertebral column is a flexible structure formed by individual (unfused in healthy humans) vertebrae. According to the anatomical region, these vertebrae are classified as cervical (7), thoracic (12), and lumbar (5). The inferior (caudal) portion of the vertebral column is formed by the immovable (fused) section, consisting of sacral vertebrae (usually 5 but can be 3 to 6), and the coccyx (the vestigial tail section that consists of 3 to 5 rudimentary vertebral parts). In quadrupedal apes, the vertebral column forms an arch that is located on the superior side of the body, therefore arching above the internal organs, which are supported by the abdominal musculature and wall. In humans, the vertebral arch is (more or less) vertical, and subsequently, the internal organs, and muscles that support the trunk and organs, are reorganized compared to that seen in our quadrupedal cousins. This is helped by the curvature of the spine, often refered to as „double S“ in form. The human vertebral column has a dorsally concave curvature (called lordosis) in cervical and lumbar regions, while the thoracic region is ventrally concave (this condition is called kyphosis). This is a result of the wedge-shaped intervertebral discs and vertebral bodies in these regions, as well as an increase of the number and average length of lumbar vertebrae from four to five in humans, which increases the length and flexibility of this region *(27, 35)*. Indeed, the modern human lower spine is much more mobile compared to that of the great apes. It has a greater overall length and shorter and broader ilia and sacrum, which must have been very important in initial acquisition of bipedality in hominins *(27)*. Combined together, these anatomical novelties increase the efficiency of trunk and head ballance and related musculature, and help with the reorganization of internal organs (the inferior portion of the internal organs now fits within the pelvic rim).

The modern human pelvis is one of the most strikingly different anatomical areas if compared to the same region in apes, as it had to undergo most changes related to locomotory pattern (Table 1). If we compare pelves of these two taxa, humans have superioinferiorly shorter and lateromedially wider pelves. Post accetabular extension is seen on ilium, and there is well developed greater sciatic notch, while the superior part of the ilium is oriented laterally and its crest is S – shaped. The anterior inferior iliac spine is well developed, and the distance between acetabulum and *facies auricularis* shortened. In addition, the ischium is shorter and has a well developed ischiac spine, and the sacrum is relatively wide. Having a wide pelvic rim allows the lower portion of internal organs to be supported by it, and lateral expansion of iliac blades helps the biomechanical properties of large gluteals to be more efficient in bipedal behavior. Specifically, the development of the iliac spines places the main muscles involved in initial phases of anterior movement (*m. sartorius* and *m. quadriceps*) to be much more efficient, as they have greater leverage and moment arms. Indeed, the whole quadriceps group functions significantly differently in bipedal and quadrupedal locomotion *(26)*. Shortening of the ilia, in combination with the superioinferiorly shortened and anteriolaterally angled ilia relocated the anterior gluteal muscles (*m. gluteus minimus* and *medius*) to a position more efficient in abduction *(28)*.

Human femora also differ from ape femora in numerous features. Alongside the lenghtening of the bone, the most important features are the elongation of the femoral neck seen in our species, that also has a different cortical bone pattern. While in most apes, cortical density is more or less equally distributed on the superior and inferior portion of the neck, in humans, the inferior portion is much denser. This is related to different loading patterns related to bipedalism *(28, 36)*. Because of the requirements of retaining the center of mass in a more or less straight line when walking (by placing each foot beneath the center of the mass during single support), human femora are angled medially (if we imagine a straight line going through medullary cavity, the line of both femora will connect to a single point somewhere below our feet – this represents a single center of gravity), and have the so-called valgus knee (angulated). This results in a bicondylar angle that in modern humans measures between 8–12° *(37)*. This angle declines with flexion, and it tends to be higher in females, which is related to sexual differences, i.e. requirements of parturition. For the same reason, the reported incidence of ankle dislocation in modern human females is higher than in males *(38)*. The human lateral condyle is elongated anterioposteriorly, compared to nearly circular cross-section in quadrupedal primates *(29)*. This increases the area of contact cartillage and reflects the increased contact (stress) length in the end phase of extension and reduces the overall stress during the toe-off and heel-strike *(29, 39)*. It needs to be noted that human patellar contact surfaces are also more complex than those of quadrupedal primates.

The human foot also had to undergo important changes in order to adapt to the requirements of walking on two limbs. Two changes that are easily observed are found in the presence of the double-arch support system (transversal and lateral) and development of plantar fascia. These structures act similar to the shock absorbers we have in our cars, as they absorb much of the impact forces generated during walking, running etc. If we would not have the arch system on our feet our joint surfaces (especially ankles, knees, acetabula, but also vertebral column and other anatomical areas that bear most of the impact force loading in bipedal hominins) would soon crush and damage.

Our calcaneus (*os calcaneus*) is very robust with a large amount of total cancellous bone volume. In fact, relative to body size, it is the largest heel bone of any mammal *(40)*. This makes sense, since this bone is the first to contact the ground during the heel-strike phase, and this robusticity helps with absorbing force. Additionally, humans (and our hominin predecessors) have the lateral plantar process, a feature not seen in other living primates *(41)*. Likewise, we have a very robust first toe (important in the toe-off phase) that is adducted (in line with the rest of the phalanges and not abducted, as in all other primates). Abduction of both hallux and pollux is a primate symplesiomorphy and adaptation to our arboreal past, while adduction of hallux is a hominin synapomorphy. Our pedal phalangeal shafts are less curved than in most primates, especially the arboreal ones. Human feet, as well as those of our hominin ancestors and relatives, lost the grasping ability. But what we gained is much more important.

Fossil record of early bipeds

After the brief discussion of main anatomical requirements of bipedalism, and comparison of living primates that have different locomotory modes (i.e. bipedal humans and quadrupedal apes), we will discuss some of the hominin taxa in order to see how these important anatomical novelties manifest in the fossil record.

The earliest anatomical changes required for efficient bipedalism have been reported in taxa as old as 6 – 7 million years. Bipedalism has been suggested for *Sahelanthropus tchadensis* fossils, discovered in Chad and dated to between 6 and 7 million years ago *(42-43)*. This was based primarily on the reconstruction of basicranial surface and the placement of the foramen magnum, supposedly more anteriorly that in quadrupeds. There are still disagreements on both degree and importance of bipedal behavior in these taxa, as well as on the phylogeny.

Likewise, the initial descriptions of fossils attributed to a novel taxon *Orrorin tugenensis* from the Miocene of Tugen Hills, Kenya *(44-45)*, suggest bipedalism, based on the attachments of *m. obturator externus* and the elongation of the femoral neck, although there are numerous plesiomorphic details still present *(46-48)*.

Ardipithecus ramidus (49) remains, dated to about 4.4 million years ago have been included in the hominin clade, although later descriptions suggest either retention of numerous arboreal adaptations (e.g. curved phalanges), changes in pelvic anatomy to basic hominin pattern and the abduction of hallux suggest bipedal behavior had an important role in this creature's lifestyle *(5, 50)*.

By about 4 million years ago, genus *Australopithecus* is well established in East and South Africa. Numerous finds (and taxa) are attributed to this genus (and its supposedly sister-taxon, *Paranthropus*). In this paper we will not discuss the taxonomic and phylogenetic issues, but concentrate on major anatomical changes related to bipedalism and treat them as two major groups, early hominins (that includes all taxa that precede the appearance of the genus *Homo*), and humans (genus *Homo*). This allows us to contentrate on adaptations and important traits, not issues related to views on phylogeny and biological classification *per se*.

Loevejoy (27:108) summarized main changes seen in the australopithecine pelvis:

The anterior gluteal muscles change their attachment position on ilium to provide pelvic stabilization during single support phase;

- the ilium is shortened in anteriosuperior dimension, lordosis is present and the center of mass is repositioned anteriorly to the hip and knee joints;
- relatively large retroarticular expansion of the ilium placed the enlarged *m. gluteus maximus* in a better position for control of the trunk extension during heel strike.

The most detailed insight into australopithecine pelvic anatomy comes from the famous 3 million year old AL 288-1 specimen („Lucy"), attributed to *A. afarensis (51-53)*, discovered in the Afar region of Ethiopia, and its half a million year later South African counterpart *A. africanus* specimen Sts-14 from Sterkfontein *(54-56)*. All the above noted characteristics of the pelvic architecture are present in AL 288-1, that also has a well developed anterior inferior iliac spine, and muscular rearrangements neccesary for effective habitual bipedalism are documented in specimen's broad and laterally flared ilia *(27)*. Most scholars agree that Lucy (and her kin) were fully bipedal, although this was achieved in somewhat anatomically different manner than in later *Homo (13, 30, 58-63)*. For example, AL 288-1 exhibits a mosaic morphology. It has significally broad ilium and superior part of the pelvis that at the same time is reduced in superoinferior aspect (caudocranially), while in the lower aspects of pelvic architecture numerous plesiomorphic details (e.g. pubic body is sagitally short and inferiorly deflected, as in chimpanzees) are present (see 27 and references therein). However, a caution is advised. Although some authors believe later anatomical changes in pelvis result from changes in lifestyle (with the emphasis on long distance running, see *64*), it is more likely that most of these actually reflect changes related to childbirth (see later in the text).

The Sts-14 specimen also clearly shows evidence of lordosis, as well as lateral flaring of the superior ilia, the aforementioned characteristic seen in these early hominins that enhances the efficiency of the associated musculature *(65-68)*. Our knowledge on the australopitecine pelvic anatomy is further enhanced with the discoveries of specimens such Stw-431 (*A. africanus*) and Stw-441/465 *(69)* from Sterkfontein, SK 50 from Swartkrans *(66, 70-72)*, and several fossils from Makapansgaat, all three in South Africa *(67-68)*. As noted, early hominin spine shows numerous features necessary for efficient bipedal locomotion, including S-shaped column and related curvatures, caudally progressive widening of lumbar vertebral laminae and the space separating their articular processes *(27)*. There is still debate on the number of lumbar vertebra in australopithecines and even in early *Homo*. Most authors suggest six segments were present (this was argued for AL 288-1, Sts-14 and Stw-432, and some other specimens, see *27, 73-76*). This, however, does not change the fact that, whether 5 or 6 lumbar segments were present, the overall vertebral morphology suggests lordosis was fully present in the lower back region of these taxa. This is in contrast with both earlier hominid condition, as well as with that seen in living apes.

Fossilized footprints discovered at the site of Laetoli, Tanzania *(77-79)* provide an important insight into adaptation to bipedal locomotion. Most important is the so-called G locality, at which footprints of three individuals have been discovered, dated to about 3.56 million years ago *(79-80)*. All necessary adaptations of the foot mentioned in the text are present, including the double-arch support system and fully adducted hallux *(81-82)*. The only hominin remains found at the site that are contemporaneous with the footprints are those of *Australopithecus afarensis*, and there is little doubt that members of this species were responsible for them. Anatomical adaptations to bipedalism are clearly seen in fossil remains of australopithecines from various sites, including Laetoli and Hadar in Ethiopia, Koobi Fora in Kenya *(83-84)*, Sterkfointein (the famous „little foot" specimen, STW 573) and Kromdraai *(85)* in South Africa, and so on (a detailed overview of the morphology of australopithecine feet can be found in 41, 86-88 and references therein). The somewhat younger foot bones from Olduvai in Tanzania (OH8), usually ascribed to *Homo habilis*, also clearly show bipedal adaptations, with the retention of certain plesiomorphic details *(89-91)*. Some authors argue that the retention of plesiomorphic details suggest arboreal behavior still had an important role in lifestyle of early hominins, such as *A. anamensis*, *A. afarensis, A. africanus*, and *H. habilis* (see references *89-98*). However, mosaic nature of evolutionary change would result in similar mixed morphology.

The later members of the gracile australopithecine clade are those of *Australopithecus garhi* in East Africa (dated to around 2.5 mya) and *Australopithecus sediba* in South Africa (dated to around 1.8 mya). Most changes described for earlier australopithecines linked to bipedal behavior are present in these two taxa. However, there are certain apomorphies present. For example, fossil lower limb remains attributed to *A. garhi* show even more humanlike dimensions, while the basic *A. afarensis*-like upper limb dimensions are retained *(99)*. Anatomical details seen in *A. sediba* suggest changes in pelvic morphology that is more similar to *Homo* (*Homo erectus/ergaster*), and for some authors this is a good ancestral species to our genus *(100)*.

The next step towards the „modernization" of anatomical features related to bipedal locomotion comes with the appearance of a more anatomically modern human form, i.e. the taxon that is more derived in overall anatomy towards the *Homo sapiens* state. If we compare the hominin fossil record between cca. 4 and 2 million years ago, this takes place at around 2 million years ago with the appearance of *Homo erectus/ergaster*, as seen in the WT 15000 specimen from Nariokotome in Kenya. In this 1.6 million year old specimen, a basic modern pattern of limbs is found *(101)*. The pelvic region also exhibits numerous changes. However, as noted by Lovejoy *(27)* most of these are not a direct consequence of adaptations to locomotor pattern, but rather to encephalization and parturition of bigger babies. Major changes in the pelvic inlet include a relatively anterioposterior increase in its saggital dimension, and an absolute increase in its coronal dimension *(27, 102-103)*. Birth in apes, early hominins, and later humans was clearly a very different process.

Benefits and drawbacks: lessons from our evolutionary past

It is clear that bipedalism was probably the most important change in human evolution, especially in the earlier phase of becoming human. However, it came with a price. There are numerous problems that living humans experience that are directly linked to our bipedal mode of locomotion.

As noted, the complete weight of the thorax, upper limbs, neck, head and anything a person is carrying is passed through our vertebral collumn first, and through our knee joint(s) (both when a person is standing still on both feet, with changing percentage of weight bearing passing to one limb, depending on the speed of movement and related factors). This is why weight-bearing caused damage in these regions is common, resulting in painful conditions and pathological changes, as well as numerous other problems resulting from vertical stance (such as hemorrhoids, constipation, incontinence etc.). The most susceptible area is the lower vertebral region, as it bears the most of the weight (likewise, most pathological conditions and slipped discs are seen between L5 and S1).

Many changes (fractures, but also pathological conditions such as osteoporosis) can be directly associated to the aforementioned enlargement in certain skeletal elements, and the overall increase in total cancellous bone volume, as this increase of the surface area can result in an accelerated rate of bone mineral loss, related to age related changes in the endocrine system *(40).* This might have not caused too many problems for our shorter-lived predecessors, but in contemporary humans, whose expected longetivity is much greater than for any other living (and fossil) primate, it does. Age related bone loss occurs regularly only in humans and is not seen in our ape cousins *(40, 104).*

One of the relatively common spinal pathologies seen in modern humans is scoliosis, almost certainly a result of skeletal modifications for acquisition of bipedalism in hominins, especially the elongation of the lumbar region. Interestingly, studies of large samples of great ape skeletons showed no evidence of this pathological change in great apes, although it was noted on the early *Homo erectus/ergaster* from Nariokotome *(27, 105).* Another pathology related to acquirement of bipedalism that is relatively common in modern humans and does not manifest in apes is spondylolysis *(27).*

In short, the biology of living humans (and any other living thing) cannot be understood without an evolutionary approach. The importance of this was best summarized by famous title of Theodosius Dobzhansky's paper: „*Nothing in biology makes sense except in the light of evolution*" *(106).* We cannot fail if we are driven by the same goal in any science that deals with living (and goes without saying, extinct, fossil etc.) organisms, as well as medicine. Medical doctors that ignore an evolutionary approach are limited to the role of mechanics, simply addressing and repairing final causes, without understanding underlying reasons and etiology of what now manifests as pathology or disease. This is relatively well understood concept, but leaves much to be desired in common medical practice. Human evolution and related topics are rarely discussed in detail in medical schools, although there are well documented instances where a certain medical problem is a direct consequence of evolutionary forces and adaptations which were beneficial at times during our evolutionary past. Well known example is the sickle-cell trait, beneficial to inhabitants of malaria ridden regions *(107-108).* Since this discovery, numerous other diseases have been considered through this evolutionary viewpoint (see *109-111* and references therein). It is at our own peril if we chose to ignore the lessons we can learn from evolutionary approach.

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