1. Introduction
Defending the term osteoarthritis may appear unusual to many who study skeletal anatomy. Often referred to as degenerative joint disease in early studies, recognition of the hyperactive nature of the involved tissues led to discarding that designation (Moskowitz et al., 1984). In keeping with contemporary usage, our terminology will designate the condition, osteoarthritis. While the suffix "itis" is used, this is not meant to designate the presence of inflammation. While a controversy has raged whether the term osteoarthrosis is a better designation (and it probably is), contemporary usage supports use of the term osteoarthritis (Rothschild & Martin, 2006). Arthritis implies inflammation of a diarthrodial (synovial membrane-lined) joint, yet in osteoarthritis (as in the majority of the 100+ varieties of arthritis) there is negligible inflammation (Rothschild, 1982; Resnick, 2002). Any associated inflammation actually appears to be related to complications (of osteoarthritis) (Altman & Gray, 1985; Dieppe & Watt, 1985; Gibilisco et al., 1985; Lally et al., 1989; Schumacher et al., 1977). Such complications are usually crystalline in nature: Hydroxyapatite, calcium pyrophosphate, or urate (gout) crystals.

The primary sites of tissue injury in osteoarthritis are the cartilage of the joint and the subchondral bone, directly underlying and supporting it (Resnick, 2002). This gives rise to microfractures (Acheson et al., 1976; Layton et al., 1988) and proliferation of new bone at the periphery of the cartilage, forming a spur. The microfractures are accompanied by a healing process that increases the density of the bone just under the cartilage surface, resulting in subchondral sclerosis. Subchondral, in this usage, refers to that component of cortical bone located just under the articular cartilage of the metaphysis. In osteoarthritis, overgrowth of bone occurs, but not bone resorption. Those overgrowths are called osteophytes.

Although osteoarthritis was though to be common in prehistory, its identification in a 150 million years old (Jurassic) pliosaur (Jurmain, 1977) actually represents a different disorder sharing only characteristics determined by semantics (Rothschild, 1989; Rothschild & Martin, 2006). Spinal involvement with osteophyte formation, so common in dinosaurs and marine reptiles (e.g., pliosaurs) actually represents a very different phenomena (spondylosis deformans). The presence of osteophytes in osteoarthritis and spondylosis deformans defines overgrowth of joint and disc marginal bone, respectively. Although the term osteophyte is used for both, they appear to represent quite different pathophysiologies. Osteoarthritis represents a disease of diarthrodial joints (those articulating bones at which movement takes place and which are lined by a synovial membranes) (Resnick, 2002;
Rothschild, 1982; Rothschild & Martin, 2006). Spondylosis deformans involves a disc space, not a "joint." (Without a joint, it is difficult to diagnose arthritis). Spinal osteophytes are essentially an asymptomatic phenomena (Rothschild, 1989). Osteoarthritis, on the other hand, clearly is a disorder of joints characterized by morbidity (Moskowitz et al., 1984). Diarthrodial joint osteophytes, though diagnostic for osteoarthritis (Altman et al., 1986, 1990, 1991) must be distinguished from enthesiophytes. The latter represent calcification of sites of tendon, ligament or joint capsule insertion (Resnick, 2002; Rothschild & Martin, 2006). Calcific tendonitis can result from trauma, genetic, or metabolic phenomenon (Holt & Keats, 1993). While related bone divots have been considered erosions, they actually appear to represent tendon avulsions (Shaibani et al., 1993). Neither avulsions nor enthesiophytes are related to osteoarthritis.

Full loss of the cartilaginous joint surface in severe osteoarthritis allows bone to rub on bone. The articular surface becomes polished and sometimes even grooved, a process called eburnation. That process occurs whenever cartilage loss in an area is at least focally complete, independent of etiology. It is not diagnostic of osteoarthritis. Eburnation occurring in the course of another disease sometimes is referred to as secondary osteoarthritis, but that represents semantics. The disease, not osteoarthritis, caused the damage (in secondary osteoarthritis). Referring to eburnation simply as a sign of severe osteoarthritis would therefore appear misleading. Eburnation is simply evidence that cartilage destruction was so severe as to allow bone to rub on bone.

1.1 Pathophysiology of osteoarthritis

The congruence of articular surfaces is essential in reducing the frictional component of joint movement. It allows the formation of a boundary layer of surface lubrication, which is quite efficient not only in facilitating motion, but also in generating the fluid waves necessary to provide nutrition to the avascular cartilage. Impaired cartilage nutrition, secondary to loss of congruence or exposure to toxins, results in impairment of chondrocyte metabolism, which in turn leads to inefficient production of mucopolysaccharide ground substance. The ground substance is highly hygroscopic and allows the turgor necessary to maintain resilience and congruence. Because the ground substance is contained by the meshwork of collagen fibrils, any disruption of the fibrils, by trauma, inflammation, intrinsic metabolic defects, or toxic agents, will deleteriously affect the turgor and congruence of the cartilage and contribute to its destructive process. Elasticity of bone is essential in protecting cartilage. Trauma may also produce microfractures and/or remodeling resulting in less bone elasticity (Acheson et al., 1976; Layton et al., 1988). The bone is then less able to distribute the stresses of daily microtrauma, increasing their transmission to the cartilage. As the cartilage serves more for congruence and the bone for shock absorption, stiffening of the bone transfers stresses to the cartilage component, which is not designed to withstand it. Excessive weight (obesity) has been suggested as a factor in the development of osteoarthritis in humans (Goldin et al., 1976; Leach et al., 1973; Silberberg & Silberberg, 1960; Sokoloff et al., 1960; Saville & Dickson, 1968), but the opposite was found in birds (Rothschild & Panza, 2006a,b). Mechanical disadvantage (e.g., joint instability) appears to be the more important variable influencing the development of osteoarthritis (Jurmain, 1977; Rothschild & Martin, 2006). The role of joint stability is emphasized by the occurrence of osteoarthritis in 80% of humans with severe instability, versus only 30% with slight or moderate (O'Donoghue et al., 1971). The construction of the joint appears to be a major factor. Highly
stabilized joints appear to be protected (Harrison et al., 1953; Puranen et al., 1975). For example, the human ankle, when ligamentous structures are intact and joint congruity is maintained, is rarely affected by osteoarthritis, even with overuse (Cassou et al., 1981; Funk, 1976). On the other hand, the human knee, the most complicated and least constrained joint (Radin, 1978), is the most susceptible to the development of osteoarthritis.

There apparently has been selection against development of osteoarthritis, probably when the vertebrate skeleton was first developing. This selection can be observed in the properties of the anatomical and morphological features adapted to maintain the joint (e.g., articular cartilage, subchondral bone, synovial fluid, specific mechanical design). Osteoarthritis provides important (otherwise often inaccessible) clues to structure-function relationships (Jurmain, 1977; Silberberg & Silberberg, 1960; Woods, 1986, 1995). Therefore, a logical method of assessing the factors which can contribute to osteoarthritis development is to analyze the basic joint features, and to use the maintenance properties of the features as indicators of the factors of joint damage.

1.2 Biomechanics of osteoarthritis

Synovial joints are much more complex than the mechanical bearings (i.e., ball-and-socket, hinge, and cochlear joints) which are often used as explanatory analogies. As physical mechanisms, they are, however, subject to the same basic principles of static and dynamic force distribution and transmission. In order to further understand the role of these basic mechanical influences in the development of osteoarthritis, several factors must be investigated:

1. The contribution of the functional anatomy of the joint to the magnitude, rate, and duration of joint forces.
2. The effects of contact area on the distribution and transmission of those forces.
3. The resulting patterns of osteoarthritis which can develop from the interaction of functional forces and the biomechanical design of specific joints.

Although the anatomy of a quadrupedal and bipedal locomotor system is nearly identical, the morphological differences have produced a transition of mechanical function of certain muscle groups (Jenkins, 1972; Kummer, 1975; Lovejoy, 1975; Sigmon, 1975). The reorientation of the line of action of muscles (through skeletal morphology changes) suggests alterations in the concentrated areas of force transmission and the joint reaction force magnitudes between the two systems. A priori, a different topographic pattern of osteoarthritis would be anticipated among the species. Human and ape patterns are discussed below.

1.2.1 Biomechanics of the hip

In order to understand the resultant forces acting on the hip joint during the normal walking cycle, it is necessary to review the action of the musculature which produces the forces (Seedhom & Wright, 1981). The bipedal walking cycle consists of the heel-strike, foot-flat position, toe-off, and subsequent heel strike of the other foot (Fig. 1). During this cycle the limb completes a stance phase and a swing phase. The stance phase includes 60% of the walking cycle. During the stance phase (the period when the foot is in contact with the ground surface), the foot goes from heel-strike, to foot-flat, to toe-off. The swing phase includes 40% of the walking cycle. During the swing phase (the period when the limb is swinging forward), the foot goes from toe-off to heel-strike. At the end of the stance phase is
a period of double support, when both feet are in contact with the ground surface. As the rate of walking increases, this period becomes shorter in duration. As a walk changes to a run, there is no longer a period of double support (Lovejoy, 1973).

Muscular load sharing during the walking cycle, can alternatively be derived through the study of muscle groups, correlated with mathematical models of torque about the hip joint (Seireg & Arvikar, 1975; Sorbie & Zalter, 1965). The action of the musculoskeletal system in producing bipedal locomotion should, if it is to be understood thoroughly, be studied as an interacting system involving the entire postcranial organism. In view of the specific interest in joint reaction force, discussion of the action of various muscle groups will be focused on the associated joints.

During normal level walking, the forces on the hip joint have been described as quasi-static, and thus have mainly been treated as the resultants of a progression of static postures at successive intervals (Seireg & Arvikar, 1975). At faster rates of walking, other factors of dynamics (e.g., inertia forces/moments) can be calculated from the linear and angular accelerations identified for each body segment.

The hip joint reaction force has two significant peaks of magnitude. The larger peak, with a magnitude of about seven times body weight, occurs at about 55% of the cycle, just prior to toe-off. While the rate of application of this force is rapid, its actual time of application represents a period extending from 45% to 70% of the cycle. Associated with this peak force is the firing of the hip flexors, the adductors, and to a lesser extent, the gluteus maximus and hamstring group. The hip flexors, mainly the ilio-psoas and rectus femoris, fire concentrically (about 45% to 70% of the cycle), initiating swing-through and raising the thigh. The adductors, primarily the posterior group, also act as hip flexors, firing concentrically from 45% to about 75% of the cycle. The gluteus maximus fires concentrically at a low magnitude from 45% to about 70% of the cycle, and serves to prevent horizontal rotation (due to the force of toe-off by the opposite limb) of the pelvis about the stance hip. The hamstring group (which also crosses the hip joint and contributes to the hip joint reaction force) fires concentrically at low magnitude from 45% to about 70% of the cycle, also facilitating knee flexion.

The other peak hip joint reaction force, with a magnitude of about four times body weight, occurs at about 10% of the cycle, just after heel-strike. The rate of application is very rapid, with duration from 0% (heel-strike), to about 25% of the cycle. Associated with this peak force is the firing of the hamstring group, the gluteus maximus, the ilio-psoas, the abductors and the adductors. The hamstring group fires eccentrically from 90% to about 20% of the cycle (from just before heel-strike to just afterward). This action decelerates the forward swinging limb and counteracts the forward and downward momentum of the trunk and pelvis, as the body weight shifts to the other limb. In conjunction with the hamstring group, the gluteus maximus fires eccentrically, controlling the forward rotation of the trunk and pelvis about the hip joint at heel-strike. The ilio-psoas fires eccentrically at low magnitude, from 95% to about 10% of the cycle. It produces stability at the hip joint, counterbalancing the hip effect of the hamstrings (while decelerating the thigh just before heel-strike). The abductor group, a major contributor to hip joint reaction force, fires concentrically from 90% to 40% of the cycle (just before heel-strike and well into stance phase). This action counteracts the downward gravitational list of the trunk about the hip joint, limiting it to about 4 degrees (Lovejoy, 1973). The adductors fire from 90% to 20% of the cycle, and act as stabilizers of the forces of heel-strike. The anteriorly arising muscles fire eccentrically, while
the posteriorly arising muscles fire concentrically during this period. Three-dimensional representation, of the magnitude and direction of the resultant hip joint force throughout the walking cycle (Seireg & Arvikar, 1975), reveals that the force vectors transmit through the joint at a relatively concentrated area on the most superior portion of the femoral head.

1.2.1.1 Hip joint contact areas

During the walking cycle, the entire available cartilage surface on the acetabulum (with the exception of the dome) comes into contact with the femoral head (Greenwald & Haynes, 1972; Greenwald & O'Connor, 1971). However, femoral head cartilage does not share the same fate. The peripheral inferior and peri-foveal regions of femoral head cartilage come into contact with the acetabulum only during the extremes of the walking cycle. As the range of motion during walking is small (about 35-40 degrees) (Nordin & Frankel, 1980a), this area is infrequently compressed. An alternative approach to assessment of contact areas is supported by analysis of femoral trabecularization patterns. X-ray examination reveals that these trabecular "rays" pass through the femoral neck toward the anterosuperior and posterosuperior regions of the femoral head (identifying the areas of contact) (Harrison et al, 1953; Trueta, 1968).

Although the acetabulum and femoral head appear to be spherical in outline with congruent surfaces, cross-sectional examination of hip joints reveals subtle incongruencies (Day et al., 1975; Greenwald & O'Connor, 1971; Kempson et al., 1971). The acetabulum has its thickest cartilage at the periphery, becoming progressively thinner in the area of the superior dome. The femoral head has its thickest cartilage at the center, just superior to the fovea capitus, becoming progressively thinner towards the periphery (Kempson et al., 1971; Day et al., 1975). The area in the superior dome of the acetabulum has been identified as only coming into contact under extreme joint loads (Day et al., 1975; Greenwald & Haynes, 1972; Greenwald & O'Connor, 1971), a phenomena which requires (according to load-deflection curves) a load of three to four times body weight.

An advantage to this incongruity has been suggested by Bullough and associates (1973). If the methods of cartilage lubrication are contemplated, it is apparent that an area of high stress, such as the dome, is much in need of adequate amounts of synovial fluid. Suggesting that the cartilage is wetted through a sump action, they propose that a joint of perfect congruity would restrict circulation of synovial fluid within the dome area, producing malnourished cartilage.

Analyzing the hip joint reaction force, clarifies that the concentrated area of force transmission [found by Seireg & Arvikar (1975)] corresponds to the incongruent superior dome of the acetabulum. In the walking cycle, the supporting leg is in full extension at the time of the major force peak. Given that the reaction force is transmitted through a concentrated area on the most superior aspect of the femoral head, the corresponding area of force transmission on the acetabulum would be the anterior portion of the dome. The smaller peak reaction force would likewise be transmitted through the posterior portion of the dome when the leg is in flexion.

1.2.1.2 Anatomical distribution of osteoarthritis in the human hip

The highest concentration of osteoarthritis in the human femoral head is just superior to the fovea capitus (Wood, 1986), in the area of the acetabular notch (an area of habitual non-contact of articular surfaces during gait). Areas of habitual non-contact develop malnourished cartilage (with depleted mechanical properties, similar to cartilage of older
individuals) rendering such an area more susceptible to damage (Sokoloff, 1969). The area superior to the fovea is under high magnitude stress during contact, thus the resulting quantitative increase in osteoarthritis sequelae. The area of least quantifiable osteoarthritis (the upper half of the femoral head) is the area which is in constant contact with another articulating surface during gait. This supports the contention that regular, but variable pressure application maintains healthy articular cartilage in the presence of normal joint motion.

1.2.1.3 Anatomical distribution of osteoarthritis in the great ape hip

The pattern of osteoarthritis in the gorilla hip, are mild and distributed over most of the articulation, although more concentrated in the distinctly larger anterior horn area (Woods, 1986). The gorilla manifests a concentration around the periphery of the notch, which is not as pronounced in the chimpanzee. The femoral heads display a striking difference, compared to the acetabulae. Osteoarthritis in the gorilla femoral head presents as a highly concentrated band, lacking in the chimpanzee. Disregarding the dense band in the gorilla, the femoral heads of both gorillas and chimpanzees are practically void of disease. Trueta (1968) suggests that, theoretically, osteoarthritis of the hip should not be the problem for quadrupeds that it is for humans. This is based on the contention that the weight-bearing area, unlike that of humans, is continuously moved over the entire surface of the hip articulation during locomotion due to the larger range of motion.

The femoral head of a quadrupedal animal probably has more of its total surface involved as a regular contact area, and unlike that of humans, possesses healthy articular cartilage. The band of osteoarthritis in the gorilla femoral head is so common and severe, yet unseen in the chimpanzee, that a fundamental difference in anatomy and/or behavior is suggested. When the gorilla hip joint is rotated and articulated to simulate hip flexion (the common quadrupedal posture) the band lies over the acetabular notch. Two factors may be responsible. The gorilla is much less active than the chimpanzee, spending most of its time in a position of hip flexion. It is possible that the band of osteoarthritis is in a relatively malnourished cartilage area (due to lack of contact), which is therefore less able to tolerate the high stresses generated when the animal does move. The design of the acetabulum in both the gorilla and chimpanzee hip provides a distinctly larger anterior surface area, which better accommodates high magnitude joint forces. The force of forward propulsion is directed anteriorly into this enlarged dome of the acetabulum (Kummer, 1975). Secondly, the ligamentum teres of the chimpanzee runs from the fovea capitus femoris and divides in two, where it combines with the transverse acetabular ligament and inserts into the acetabular notch, just as in humans (Sonntag, 1923). However, the ligamentum teres of the gorilla runs from the fovea capitus femoris, into the acetabular notch and posteriorly along the joint capsule at the posterior horn of the acetabulum. It passes through the gemellus inferior and quadratus femoris, where it branches out and finally inserts into the innominate (Gregory, 1950). It is possible that this larger type of ligamentum teres applies pressure (i.e. mechanical force) to the joint capsule area which is not a factor in the anatomy of humans or chimpanzees. Action of the gemellus inferior and quadratus femoris could possibly aggravate condition.

1.2.2 Biomechanics of the knee

The knee is a two-joint structure consisting of the distal femur, patella and proximal tibia. The tibiofemoral articulation provides the primary motion of the joint, while the
Patellofemoral articulation serves to increase the contact area and give mechanical advantage to the quadriceps femoris muscle group. Motion in the knee joint is mainly in the sagittal plane, allowing approximately 140 degrees of flexion. However, only 67 degrees of flexion are actually utilized in the normal walking cycle (Nordin & Frankel, 1980b). The knee is actually quite a complex joint. While often thought of as a hinge joint, its motion actually encompasses a significant rotary or geocentric component. Transverse or rotary motion of up to 45 degrees of external rotation and 30 degrees of internal rotation is found in the knee. Motion in the coronal plane is restrained by ligaments and soft tissue.

The impetus of forward progression begins approximately 45% into the walking cycle (Fig. 1), just prior to toe-off, when the quadriceps group fires concentrically (producing knee extension at toe-off). Facilitation of knee extension by the tensor fasciae latae lasts until just after toe-off. Gastrocnemius firing initiates just prior to quadriceps concentric firing and lasts until toe-off. Concentric muscle contraction from 30% to 60% into the cycle produces plantar flexion of the ankle joint. As it is a two-joint muscle, it also produces knee flexion. Conjoined action of the gastrocnemius and quadriceps produces stability of the knee during the high stress periods. The action of these muscles is associated with a peak joint reaction force magnitude equivalent to three (Morrison, 1970) to seven times body weight (Seireg & Arvikar, 1975). The rate of application is moderate and the duration is from about 30% to 60% of the cycle.

A second period of peak muscular action at the knee relates to heel strike. The quadriceps femoris fires eccentrically, from approximately 95% to 20% of the cycle (just prior until just after heel-strike). At heel-strike the knee "lock" is broken. Eccentric quadriceps firing then absorbs the vertical forces attempting to buckle the knee. During this same interval (90% to 20% of the cycle), the hamstring group fires eccentrically (thus decelerating the forward moving thigh. These actions are associated with peak joint reaction force magnitude of three (Morrison, 1970) to six times body weight (Seireg & Arvikar, 1975). The rate of application is rapid, representing 90% to 20% of the cycle.

1.2.2.1 Knee joint contact areas

During bipedal progression, the knee is habitually in a more extended position, due to the narrow range of flexion and extension necessary for walking. Static analysis of the knee joint reaction force has shown that it is transmitted through the tibiofemoral articulation approximately centered up the axis of the tibial shaft (Nordin & Frankel, 1980b). The distal femoral condyles must transmit up to seven times body weight (Seireg & Arvikar, 1975), and the knee has adapted to give maximum cartilage contact to this area by flattening the condyles (Heiple & Lovejoy, 1971; Kettlekamp & Jacobs, 1972; Maquet et al., 1975; Walker & Hajek, 1972). When viewed laterally, the long axis of the condyle is about 90 degrees to the vertical shaft, indicating that the largest true contact takes place during full extension, when the contact surface is perpendicular to the stresses passing through the joint (Heiple & Lovejoy, 1971; Lovejoy, 1973).

Studies to determine actual weight bearing areas and stress distribution at different degrees of flexion have focused mainly on the role of the menisci in force transmission. The menisci are two C-shaped fibrocartilages overlying the tibial condyles and anchored firmly in the intercondylar area. Their inferior surface is flat and flush with the tibial articular surface, while their superior surface is thick at the periphery and gets increasingly thinner toward the center, exposing the more central articular cartilage. The articular cartilage of the tibial condyles is thickest at this exposed area (McLeod et al., 1977; Simon, 1970).
Poisson's principle appears directly applicable to the menisci: When an object undergoes vertical strain, it also undergoes a proportionate horizontal expansion (Shrive et al., 1978). As the spherical condyles compress the menisci, they impart vertical and horizontal components of force. Since the base of the menisci is flat, it can only resist the vertical component, leaving the horizontal component to displace the menisci outwards. The fibers of the meniscus course circumferentially around the periphery. Their tensile strength limits the amount of displacement possible, under an applied load (Shrive et al., 1978). The displacement on the medial side is also restricted by the peripheral attachment to the meniscofemoral and meniscotibial ligaments (Fukubayashi & Kurosawa, 1980). This allows a simple mechanism for increased contact area. As the menisci displace in different directions, contact is maximized throughout flexion, in spite of changes in geometry of the articulating portions of the femoral condyles. This changing condylar geometry results in a contact area during full extension distributed antero-posteriorly, compared to mediolaterally during full flexion (Shrive et al., 1978).

Throughout increasing flexion, the contact area gets increasingly smaller, and the stress therefore becomes increasingly concentrated and moves posteriorly. External and internal rotation cause the contact area to move laterally, relative to the direction of rotation (Ahmed & Burke, 1983).

During the two peak periods of joint reaction force, the knee joint is in full extension or just slightly flexed. These positions correspond with the periods when contact area is the greatest. The result is a minimization of load per unit area. Activities which place the knee into a much higher degree of flexion (e.g., climbing stairs or stooping to lift an object) produce much higher joint reaction forces (Nordin & Frankel, 1980b). The result of such activity is a very high load per unit area, transmitted at the very posterior aspect of the articulating surfaces.

During dynamic activities it has been shown that the patellofemoral joint reaction force is a consequence of the magnitude of the quadriceps muscle, which has been shown to increase as flexion increases (Nordin & Frankel, 1980b). The patellofemoral joint reaction force is only one-half body weight (Nordin & Frankel, 1980b) at the middle of stance phase. The retropatellar articular surface has three facets. Corresponding to the lateral and medial walls of the femoral surface are lateral and medial facets on the patella. The third facet runs adjacent to the most inferior aspect of the medial facet. Rarely described and difficult to observe outside of cadaveric material (although quite distinct on the macerated patellae of robust individuals), the third facet is referred to as the "odd medial facet" (Goodfellow et al., 1976). This facet does not come into contact until extreme degrees of flexion.

Patellofemoral contact areas have been identified on the basis of dye methodology (Goodfellow et al., 1976), radiographic techniques (Matthews et al., 1977), and from pressure transducer measurements in cadaveric specimens (Ahmed et al., 1983). Pressure distribution is transmitted through the vertical ridge separating the lateral and medial facets (Ahmed et al., 1983) during low degrees of flexion (from 0 to 10 degrees). From 20 to 40 degrees of flexion, the contact area was found to change to a horizontally oriented band along the inferior portion of the articulation. From 45 to 75 degrees of flexion, the contact area was a horizontal band in the central area of the articulation. From 75 to 90 degrees, the contact area was found to be a horizontal band across the superior portion of the articulation. The bands of contact area do not extend into the odd medial facet until 110 degrees of flexion is achieved (Goodfellow et al., 1976; Ahmed et al., 1983). Beyond 110 degrees of flexion, the
band begins to divide into two areas of contact: Lateral and slightly superior and on the odd medial facet. It should be noted that the knee comes into this high of a degree of flexion only during extreme activities. When the knee is in extreme flexion, the patella rotates slightly. The odd medial facet then comes into contact with the medial femoral condyle. During extreme flexion, the majority of the patella has recessed into the intercondylar notch. The quadriceps tendon then lies over the synovial membrane and joint capsule at the superior portion of the patellar surface of the femur.

1.2.2.2 Anatomical distribution of osteoarthritis in the human knee

The distal femoral concentrations conform very well to the relative joint reaction force magnitudes established for the joint. The femoral condyles show a marked osteoarthritis, compared with the patellofemoral area, in accordance with the relative joint reaction forces transmitted by each area (Woods, 1986). The posterior most portion of the femoral condyles experience the highest load per unit area and have the highest concentrations of osteoarthritis. Osteoarthritis was prominent in the areas found to transmit the highest load per unit area (the most posterior portions of each side, underlying the menisci). The patella displays greater osteoarthritis than the opposing surface on the femur, especially on the odd medial facet, in accordance with the contention that this is a site of habitual non-contact and cartilage malnutrition. Damage apparently occurs during periods of extreme flexion and high joint reaction force, when this area does come into contact.

1.2.2.3 Anatomical distribution of osteoarthritis in the great ape knee

The distal femur of gorillas and chimpanzees presents the converse concentration pattern from that noted in human knees. The patellofemoral area, especially in the chimpanzee, displays greater osteoarthritis than the tibiofemoral area (Woods, 1986). The quadriceps femoris subjects the quadrupedal patellofemoral articulation to high joint reaction forces, in spite of existing morphological differences exist between bipedal and quadrupedal knee joints. The patellofemoral joint reaction force of the gorilla and chimpanzee increases with the degree of flexion, as occurs in the human knee. During the locomotory cycle, and in common postural positions, the gorilla and chimpanzee knees are habitually flexed. Relative to the bipedal knee, the quadrupedal knee is therefore subjected to more frequent applications of a high patellofemoral joint reaction force.

Gorilla and chimpanzee femoral condyles, viewed laterally, have a distinctly rounded contour (Heiple & Lovejoy, 1971; Lovejoy, 1975; Lovejoy & Heiple, 1970). The human distal femur has an elliptical contour, providing maximum contact and minimizing loads during full extension, whereas quadrupedal tibiofemoral articulation loading occurs throughout a larger range of motion. The rounded contour in gorillas and chimpanzees results in a loading condition where high magnitude forces are not concentrated on any specific area. This may explain the contrasting reduction of tibiofemoral osteoarthritis in the gorilla and chimpanzee (relative to the human distal femur, which has a distinctly higher concentration in the tibiofemoral area than the patellofemoral area).

The gorilla distal femur does not display quite the contrast seen in chimpanzees. This may be related to the gorilla's massive size, resulting in extreme tibiofemoral articulation applied forces/surface area. The gorilla species may be nearing the size limit for this type of knee design to be effective. Considering the degree of flexion and extension involved in gorilla locomotion, they may be reaching the limits of the design capabilities of their joints for their body size. (The larger the animal, the lesser the amount of joint excursion).
The chimpanzee distal femur has a quite highly concentrated band of osteoarthritis across the most superior portion of the patellar surface. The high concentration and position of this band suggests that malnourished cartilage may also be involved. The patella retreats toward the intercondylar notch as the joint reaction force increases (when the knee is in a high degree of flexion). The superior portion of the articulation is probably only in contact during extension, predisposing to a malnourished state. The lateral condyle of the chimpanzee also has a high concentration on the most posterior portion. This is probably due to the amount of time spent in a flexed posture, when forces would be concentrated on this area.

Unlike the proximal tibia of humans, the gorilla and chimpanzee proximal tibiae do not display the posterior osteoarthritis associated with high magnitude stress application. The distribution is more generalized, as would be expected from a more distributed load application.

### 1.2.3 Biomechanics of the ankle joint

The ankle is actually composed of two joints, the tibiotalar and subtalar joints. Motion in the tibiotalar joint is primarily in the sagittal plane. Inversion and eversion occur at the subtalar joint (Alexander et al., 1982). The latter is important for ambulation on uneven ground. The total range of sagittal motion, estimated at about 45 degrees, varies greatly with age (Alexander et al., 1982). Estimates of the range of plantar flexion (20 degrees) and dorsiflexion (25 degrees) of the tibiotalar joint (Barnett & Napier, 1952; Close, 1956; Stauffer et al., 1977) have been compromised by the arbitrary division between the two, resulting in a relatively large standard deviation (Sammarco et al., 1973; Stauffer et al., 1977).

#### 1.2.3.1 Ankle joint contact areas

The weight-bearing contact area of the ankle joint is primarily tibiotalar. Ramsey and Hamilton (1976) studied the contact area of the ankle joint and found that the primary contact and weight bearing area is along the lateral side of the main talar surface, with a band of contact extending medially across the apex of the talar articulation. Damage to the ankle ligaments results in deviation of the primary contact area to the medial side of the main talar surface. A role of the fibulotalar joint in weight-bearing has been suggested (Lambert, 1971) but awaits clarification. The notably large contact area of the ankle joint makes it particularly tolerable of compressive forces (Stauffer et al., 1977). Studies of the instant centers of joint rotation (Sammarco et al., 1973) indicate that shear forces are highest during stance phase, but are not of a significant magnitude.

Plantar flexion during the stance phase of the walking cycle is the resultant of post-tibial group muscle concentric firing, representing 10% to 60% of the cycle (early foot-flat to toe-off). Maximum muscle force magnitude (five times body weight) occurs at approximately 45% into the cycle. This major peak of joint reaction force is moderate in rate of application, lasting from about 20% to 60% of the cycle.

#### 1.2.3.2 Anatomical distribution of osteoarthritis in the ankle of humans

The talus shows prominent osteoarthritis at areas where contact is irregular (Woods, 1986). The corners of the main weight-bearing portion of the articulation and the malleolar articulations are opposed by areas of the distal tibia, which are frequently irregular in shape and without a complete articular surface. The distal tibia is notably void of high concentrations of osteoarthritis, except at the anterior and posterior edges (perhaps related to ligamentous damage).
1.2.3.3 Anatomical distribution of osteoarthritis in the great ape ankle

Almost negligible osteoarthritis was found in the ankle joints of the gorilla and chimpanzee (Woods, 1986). Greater range of motion during locomotion in the apes (distributing load application over a larger area) probably explains this lesser involvement.

2. Epidemiology of osteoarthritis

2.1 Understanding the anthropologic record

The critical studies by Altman et al (1986, 1990, 1991) clearly established the importance of the osteophyte for identification of osteoarthritis. Much of the anthropology literature has lumped a variety of forms of joint pathology as osteoarthritis (Bridges, 1991; Waldron, 1991), predating their diagnoses on presumptive criteria, such as eburnation (discussed above), porosity and other joint surface disruption and any new bone formation in the vicinity of a joint. Pitting (porosity) has no correlation in clinical practice (Resnick 2002). It is not visualized on x-ray. When critically examined in knees (Rothschild, 1997), there was no correlation of porosity (pitting) with the documented unequivocal sign of osteoarthritis (diarthrodial joint osteophytes).

Comparing frequencies of osteoarthritis must be based on age and gender-based cohorts, as osteoarthritis is a phenomenon of aging (Rothschild, 1982; Resnick, 2002). It is more common in men than in women prior to age 45 and in women than in men after age 55 (Moskowitz et al., 1984). As the relationship of osteoarthritis to age appears independent of socioeconomic status, at least in the United States and Great Britain (Davis, 1988), such cohorts should be comparable. Bremner et al. (1968) suggested that osteoarthritis is found less frequently as one travels farther from the equator. Blumberg et al. (1961) reported lower frequencies in Inuit and Lawrence et al. (1963) in Finland (versus Netherlands). However, the frequency of osteoarthritis is equal in Jamaica and Great Britain (Bremner et al., 1968). Variations in race, culture, and environment, however, limit such comparisons. Prevalence and distribution of osteoarthritis vary with ethnicity and geography [Table 1 (Davis, 1988)]. Southern Chinese, South African Blacks and East Indians have a lower incidence of hip osteoarthritis than European or American Caucasians (Felson, 1988; Hoaglund et al., 1973; Mukhopadhyaya & Barooh, 1967; Solomon et al., 1975). Amerindians had earlier onset and higher frequencies of osteoarthritis than other United States populations, in contrast to Inuit, in whom the frequency was lower. Osteoarthritis should also be divided into primary and secondary. Secondary includes that due to an injury, another form of arthritis or a congenital predisposition. When osteoarthritis of the hip is common in a population, its occurrence is often considered secondary to acetabular dysplasia (Felson, 1988; Gofton, 1971; Murray, 1965; Solomon, 1976).

The genetics of osteoarthritis is beyond the scope of this discussion. Familial occurrence of distal and proximal interphalangeal joint osteoarthritis (Stecher, 1961) and role of gene polymorphism (e.g., Type III procollagen gene COL2A1) (Knowlton, et al., 1990) exemplify the challenge. COL2A1 mutation results in spondyloepiphyseal dysplasia congenital. Thus suggesting that the resultant osteoarthritis is actually not primary, but caused by the change in joint shape. How much apparent geographic variation is genetic in origin? The genetics of osteoarthritis is delegated to articles specifically addressing this developing knowledge.
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### 2.2 Joint distribution of human osteoarthritis

Hip osteoarthritis is more common in farmers than in other vocations (Peyron, 1984). Van Saase et al. (1989) suggested 2.5-4.8% of Zoetermeer men aged 45-74 had osteoarthritis of the shoulder and 10% after age 80. This contrasts with 1.4-7.7% of women in the former age group and 11.1% in the latter.

The shoulders, hips, and knees are especially affected in miners, contrasted with fingers, elbows, and knees in dockworkers (Partridge, 1968), and fingers in cotton workers (Lawrence, 1961). Hand involvement was greater in craftsmen, miners, and construction workers (Davis, 1988), and osteoarthritis of the knee in individuals involved in occupations demanding knee flexion (Anderson & Felson, 1986), but also had geographic variation, more common in Japanese and Korean than Caucasian women (Bang et al., 2011; Toba et al., 2006).

The wrist is uncommonly affected in osteoarthritis. Much of what has been called osteoarthritis of the wrist may actually be another disorder, calcium pyrophosphate deposition disease (Rothschild & Martin, 2006; Rothschild et al., 1992). Butler (1988) recorded frequencies of wrist osteoarthritis of less than 0.6% of men prior to age 60 and 1.6% after age 60 in the United States. Frequencies in women were 0.1% and 0.8%, respectively. Van Saase (1989) suggested 1% under age 44, 5% age 45-59, 10-15% in the sixties, 15-20% in the seventies, and 20-25% in the eighties, the higher frequencies representing men. However, his data fit more the age curve of wrist calcium pyrophosphate deposition disease (Rothschild et al., 1992). Kellgren & Lawrence (1958) found that 16%-27% of knee osteoarthritis was related to previous injury (Davis, 1987).
2.3 Severity of osteoarthritis in the anatomic record
The severity of osteoarthritis is determined by the amount of cartilage loss (recognized on
the basis of joint space narrowing). This measurement can only when cartilage is preserved,
ot in “bare” bones. End stage osteoarthritis often, but not invariably, results in bone
rubbing on bone. This rubbing, which represents the end stage of many forms of arthritis,
produces eburnation. It is one marker for severity, but does not always occur, even with end
stage disease. Its sensitivity has never been established for determining the frequency of end
stage of disease and its specificity for osteoarthritis has been falsified. Radiologic evidence of
joint space narrowing remains the best measure of severity.
Any discussion of severity must carry a caveat. Only a fraction of osteoarthritis is
symptomatic. Peyron (1984) reported that 2.3% of working British men and 1.3% of women
retired because of it and that in precluded working for only 3 months in 5% of individuals
aged 55-64. Additionally, there is no linear relationship be
tween structural changes and
functional limitations (Mankin & Radin, 1993).

2.4 Osteoarthritis in the zoologic/paleontologic record
It may seem paradoxical to start with the paleontologic record, but that forms the basis for
the hypothesis that osteoarthritis is actually a phenomenon of artificial environments or
mechanical disadvantage. It proved to be extremely rare in dinosaurs (Rothschild, 1990b). It
was not present in any sauropod [e.g., Camarasaurus, Apatosaurus (formally called
Brontosaurus), Diplodocus], and actually has been documented in weight-bearing bones only in
the ankles of 2 of 39 Iguanodon found in a coal mine under Brussels (Rothschild, 1991). Given
phylogenetic classification of dinosaurs, it is perhaps not surprising that osteoarthritis is
extremely rare in both fossil and extant reptiles (Rothschild, 2008, 2010) Osteoarthritis was
present in the ankles of 27% of fossil Diprotodon, the marsupial cow with a ball and socket

Fox (1939) found no osteoarthritis in 173 rodent genera, while Sokoloff (1959) described it in
the knees of laboratory mice and guinea pigs, and in the shoulders of guinea pigs. However,
comparison of captive and wild-caught guinea pigs revealed almost invariable occurrence in
the former and absence in the latter (Rothschild, 2003). Analogous to the observation in
guinea pigs, osteoarthritis is frequently reported in domestic mammals. Bovine
osteoarthritis was noted in 20% of Holstein-Friesian bulls more than 9 yrs old (Neher &
Tietz, 1959) and horses, but as only isolated occurrences in non-domestics (Rothschild &
Martin, 2006). Ten percent of large captive cats had osteoarthritis affecting shoulders,
elbows and stifles (Rothschild et al., 1998).

Examination of non-human primates revealed the same pattern, with a similar increase in
frequency with age noted in rhesus macaques in captive environments (Rothschild & Woods,
1992a,b; Rothschild et al, 1999). As the distribution of arthritis in captive animals [predominant
shoulder (33%) and elbow (47%)] was quite different from that [predominant knee (80%)] of
free-ranging individuals, this cannot be simply written off as age/survival variation.

Birds present a totally different picture. Frequency of osteoarthritis is independent of captive or
wild-caught status (Rothschild & Panza, 2004, 2005, 2006a,b). Previous reports analyzed
domestic chickens and turkeys (Poulos, 1978; Rejno & Stromberg, 1978; Sokoloff, 1959),
attributing pathology to nutritional factors (e.g., selection for weight production) and dysplasia.
However systematic examination of birds revealed species-dependent variation in frequency,
with more than 25% of some species affected (Rothschild & Panza, 2004,2005, 2006a,b).
3. Conclusions

Osteoarthritis is clearly a disease of artificial environments in mammals, the group in which humans are categorized. Comparison of wild and zoo animals show this disparity, which is not relieved by other “unnatural environments.” The conditions on Cayo Santiago are probably among the best that can be offered. Rhesus macaques have the run of an island, where the only human intervention includes observation and some provisioning. However, the hurricanes that afflict that locale reduce the canopy to one level, with greater resultant ground activity than would be found in the wild. Absence of predators on the island also minimize ground risk. Behavior changes. Conversely, birds represent a natural model for understanding the underlying causes of osteoarthritis. With frequency variation in birds being species, rather than genus-determined, perhaps greater understanding of bird behavior will provide insights to osteoarthritis that will have clinical benefit.

4. References


This volume addresses the nature of the most common form of arthritis in humans. If osteoarthritis is inevitable (only premature death prevents all of us from being afflicted), it seems essential to facilitate its recognition, prevention, options, and indications for treatment. Progress in understanding this disease has occurred with recognition that it is not simply a degenerative joint disease. Causative factors, such as joint malalignment, ligamentous abnormalities, overuse, and biomechanical and metabolic factors have been recognized as amenable to intervention; genetic factors, less so; with metabolic diseases, intermediate. Its diagnosis is based on recognition of overgrowth of bone at joint margins. This contrasts with overgrowth of bone at vertebral margins, which is not a symptomatic phenomenon and has been renamed spondylosis deformans. Osteoarthritis describes an abnormality of joints, but the severity does not necessarily produce pain. The patient and his/her symptoms need to be treated, not the x-ray.

How to reference
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