THE EVOLUTION OF THE HUMAN ILIUM

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SEVEN FIGURES

INTRODUCTION

The australopithecines of South Africa are commonly regarded as bipeds. If the Meganthropus jaw-fragment from Java is included in this group, the case may be made that these forms lived throughout the Old World tropics. At least some of them appear to be of Villafranchian age (Oakley, ’54), and so may be representative of the kinds of animals that are directly ancestral to man. If this view of human evolution is considered reasonable, or at least possible, then the evolution of bipedal locomotion seems to have preceded other uniquely human attributes. It appears quite probable that our ancestors walked first, and subsequently became large-brained, tool-using humans.

The reason for asserting the priority of bipedal locomotion rests primarily on the ilia of the australopithecines. The Sterkfontein, Makapansgat, and Swartkrans ilia appear so human that many anthropologists regard them as indicating bipedal locomotion, thus differentiating the australopithecines from the apes (Dart, ’48; Broom, ’50a, ’50b; Heberer, ’51; Clark, ’55a). Zuckerman (’54) seems alone in his view that the australopithecines might be ancestral to the great apes.

Prior to the discovery of the australopithecines, many investigators had called attention to the unique features of the human pelvis, emphasizing the shortening, bending back, and widening of the ilium as essential features for bipedal locomotion of the human sort. However, these studies, based on the anatomy of living apes and men, could give no knowledge
of the actual stages through which a generalized quadrupedal pelvis might have passed in evolving into a bipedal one. Clark ('55a) has rightly stressed that the australopithecines, in a general way, confirm the expectations of students of comparative primate anatomy. Although this is true, no one anticipated a rather long, ape-like ischium combined with a short, wide ilium. Furthermore, no one suspected that the backward bending and widening of the ilium preceded the development of an S-shaped iliac crest, definition of two gluteal planes, and strong development of the iliac tubercle.

Although agreeing with those who maintain that the australopithecine ilium indicates bipedal locomotion and affinity with man, one wonders about the functional significance of the differences between the australopithecine ilium and that of man. Were the australopithecines fully erect? Are the curved iliac crest, tubercle, and gluteal planes significant for bipedal locomotion? If so, how might this significance be analyzed?

The pelves of the australopithecines have already been compared to that of man with regard to general shape (Dart, '49; Broom and Robinson, '50, '52), by outline (Clark, '55b), and biometrically (Zuckerman, cited '54, but data unpublished). Additional knowledge may be gained by an analysis of the internal structure of the pelvis in apes and man, and by relating the differences of internal thickness and organization to muscle action and locomotion. This paper is a preliminary attempt at analyzing the inner form of the innominate bones of man and chimpanzee in a way which will help in the interpretation of the fossil australopithecines. If the function of the iliac tubercle can be determined, then its presence in man and absence in chimpanzee, should be understandable in terms of each animal's way of life. If the significance of the presence and absence of this structure can be understood in living forms, then it should be possible to make much better inferences about the meaning of the intermediate condition seen in the fossils.
With this purpose in mind, the innominate bones of man and chimpanzee were compared with regard to their internal organization as shown by the distribution of thick and thin bone and their split-line pattern. In this paper, the bony pattern is related to muscle function and, in turn, to locomotion. Finally, the understanding of the mechanism of balance, which resulted from this analysis, is applied to the problem of the interpretation of the locomotion of the australopithecines. The suggestion is that their adaptation to the human type of bipedal locomotion was not complete, that they were forms in transition, and that the change in locomotion from ape to man may have taken place during the Villafranchian period.

MATERIALS AND METHODS

Split-line preparations were made of 4 chimpanzee and 8 human innominate bones. This technique, first described by Benninghoff ('25) and improved by Seipel ('48) and Tappen ('54), consists in placing bone in a ten per cent solution of HC1 until the bone is soft enough to allow easy penetration of a teasing needle. The puncture results in a split, which may be lengthened by carefully guiding the needle in the direction of natural splitting. Properly decalcified bone will only split in one direction, and the pattern cannot be altered in artificial directions. The splits are marked by india ink. This may be done by dipping the needle in the ink prior to making the split, or the ink may be added afterward. The prepared bones are best preserved dry, since they tend to discolor and are apt to mold if stored in fluid.

Decalcification occurs more rapidly in thin regions. Since chimpanzee innominate bones vary greatly in thickness, the thin parts of the bones may be completely destroyed before the thickest parts are sufficiently decalcified. Therefore, the illustrations of the split-line patterns are composites of the pattern seen at successive stages. Although the human innominate bone is also of variable thickness it may, with care, be decalcified and mapped in one operation.
No attempt was made to analyze small individual differences in this study. This paper deals with the major patterns which are characteristics of the species and lie far beyond the range of individual variation.

**Observations**

*Areas of thick and thin bone.* Figures 1 and 2 show the distribution of thick and thin bone in the innominate bones of chimpanzee and man. In the chimpanzee, the thick bone forms a column from the posterior superior spine of the ilium to the tuberosity of the ischium. The ala of the ilium is much thinner, although there is a slightly thickened portion near the anterior margin of the bone. In man, the region from the sacro-iliac articulation to the acetabulum is also thick, but the external table of the bone leading from
the iliac tubercle to the region of the acetabulum is more markedly thickened. This column of bone demarcates the two gluteal planes of the human bone and adds to the curvature of the iliac crest.

Both animals have a thickened region connecting the sacro-iliac articulation to the margin of the acetabulum. The difference lies in the extreme thickening in the outer table from the tubercle to the acetabulum in man. These differences were first noticed because of the retardation of decalcification of the thick areas, and were later checked by sectioning the bones.

*Split-line pattern.* The split-line patterns of the chimpanzee bone are shown in figures 3 and 5. The pattern on the inner and outer surfaces are nearly identical. This indicates that the internal organization of the bone is similar on both surfaces. In man, figures 4 and 6, the patterns on the two surfaces are quite different. The pattern on the inner surface closely corresponds to that of the chimpanzee, but on the outer surface several differences are noted when the two animals are compared. In chimpanzee, the major tracts of split-lines are oriented from the sacro-iliac articulation to the ischial tuberosity and from the superior margin of the acetabulum to the iliac crest. This same orientation holds for the inner surface of the human bone.

On the gluteal surface (outer) of the human ilium, *three* distinct tracts of split-lines are discernible. The first is oriented between the anterior superior spine and the superior margin of the acetabulum. The second runs from the sacro-iliac articulation around the greater sciatic notch to the ischial tuberosity. The third and unique tract of split-lines, begins immediately inferior to the iliac tubercle and runs downward to the posterior margin of the acetabulum.

This column of split-lines running from the tubercle to the acetabulum corresponds to the thickened bone which lies in exactly the same region of the ilium. Whether examined by split-line or by thickness, the same structural pattern is apparent.
Split-line patterns of chimpanzee and human innominate bones.

Fig. 3 Chimpanzee iliac (inner) surface.
Fig. 4 Human iliac surface.
Fig. 5 Chimpanzee gluteal (outer) surface.
Fig. 6 Human gluteal surface. Note over-all similarity of two surface mappings in chimpanzee and marked differences in man.
Muscles. The thickened outer table of bone which lies between the sacro-iliac articulation and the acetabulum, with the corresponding tract of split-lines, common to both man and chimpanzee, obviously serves the function of connecting the lower extremity and the sacrum. However, the thickened column of bone with its characteristic tract of split-lines, which runs from the tubercle to the acetabulum, in man only, is not related to weight-bearing nor to abdominal musculature. It is related to the musculature of the hip.

In man, the gluteus maximus muscle is a large muscle arising from the posterior superior margin of the ilium and lateral extent of the sacrum and inserting into the iliotibial band of the fascia lata and into the gluteal tuberosity between the vastus lateralis and adductor magnus muscles on the lateral aspect of the thigh.

In the chimpanzee, the gluteus maximus muscle is small and has no origin from the ilium. It lies primarily lateral to the greater trochanter of the thigh and is, in the main, an abductor of the leg as are the other two gluteal muscles of the chimpanzee. All three gluteal muscles act primarily as abductors of the chimpanzee thigh. In man, on the other hand, the bending back and shortening of the ilium results in an altered position, and thus, action of the major gluteal muscle. The gluteus maximus muscle lies behind the femur and no longer acts primarily as an abductor, but rather as an extensor (Washburn, '50, '53). The gluteus medius and gluteus minimus muscles are still lateral to the thigh; the more vertical fibers of these two fan-shaped muscles run directly downward from the region inferior to the iliac tubercle to the greater trochanter of the femur.

These two human muscles have the function of all of the gluteal muscles of the chimpanzee, abduction and rotation of the thigh. They are the muscles which play the major role in shifting the body weight from one foot to the other in walking and in standing erect. These muscles are crucial for balance. Figure 7 shows the bone-muscle relationships of the human gluteal area. The importance of the two gluteal
Fig. 7 Diagram of the action of gluteus medius and gluteus minimus in human locomotion. The body weight is supported on the right foot. The left leg and foot are raised preparatory to stepping off on the left foot. The contracture of the right gluteal musculature prevents the body from slumping toward the unsupported side.

muscles in aligning the trunk above the supporting leg and foot and in maintaining balance is readily apparent.

DISCUSSION

The changes that took place during the evolution of the human pelvis are far more complicated than is gathered from an examination of the external form and shape of the bones. The internal structure of the bones has changed as well, as
shown by the distribution of thick and thin regions and the split-line tracts. All these changes are related to changed patterns of behavior.

An examination of figure 7 shows the relationship of the gluteus medius and minimus muscles to the structures under consideration. It is seen that a line projected downward through the tubercle would pass through or close to the greater trochanter of the femur. Elftman ('54) in his discussion of the functional structure of the lower limb stresses that one of the key functions of the hip musculature is control of the lateral stability of the body. An individual standing on one foot, about to step off on the other, must align the parts of his body so that the center of gravity of the whole is above the area of support provided by the foot. Because of the lateral projection of the hip joint in relation to the mid-line of the body, the trunk and opposite unsupported leg have a tendency to slump toward the unsupported side. Contraction of the gluteus medius and minimus muscles on the supported side, counteract this tendency and maintain the erectness of the body as weight is shifted from one foot to the other in normal walking. The development of the iliac tubercle and pillar is directly related to this balance of the body.

Sections through the bone in this region have shown that it is an area of strong, heavily reinforced bone, directly related to the muscles used for balance in standing and bipedal locomotion. The chimpanzee, an essentially quadrupedal animal on the ground, lacks these structures for balance.

The pattern of behavioral change associated with bipedal locomotion explains the differences in the development of the iliac-tubercle, -pillar, -crest and in the split-line orientations characteristic of the human innominate bone. The pelvis of the australopithecines show that selection effected various parts of the pelvis at different times. It now seems clear that the widening, shortening, and bending back of the ilium came first; changes in the structure of the ilium in the region of the tubercle and pillar were secondary, yet probably prior to modifications in the ischial ramus and tuberosity. It is
still not quite clear why the human type of ischial ramus and tuberosity is advantageous for a biped. Waterman ('27) states that a short lever arm insures better precision of action, and Clark ('55a) suggests that the high position of the ischial tuberosity enhances the extensor action of the hamstring muscles in full extension of the hip.

This study suggests that the australopithecines, lacking a well-developed iliac tubercle and pillar, could not balance as well as man. The inference is that they were still in the process of adapting to the orthograde progression and what is seen in these fossils is neither the stable condition of the great apes (whose locomotor adaptation appears to have been essentially the same for millions of years, Clark, ibid.), nor that of man whose posture and progression may have been stabilized in its present form by the middle of the Pleistocene. The australopithecines may represent a transitional stage of bipedal adaptation that never reached its culmination. Or, they may represent a stage that developed into man.

Many anthropologists believe that man's locomotor adaptation preceded the enlargement of the brain and modification of the face. This belief rests on the evidence that the femora associated with Java Man (Weidenreich, '38), Peking Man (ibid.), Rhodesian Man (Morant, '28), and the tibia from Ngandong (Weidenreich, '38), are all more anatomically modern than their skulls. It is easy to separate the skulls of a Java or Peking Man from the early representatives of anatomically modern man, but their limb bones are within the range of variation of living populations. (It is true that the limb bones of the Classic Neandertals, with their large articular surfaces and short radii and tibiae, are peculiar [Weidenreich, '43], but these are probably racial features and do not offer any clue to the anatomic conditions of more remote ancestral forms [Howell, '53].)

Unfortunately, no pelves are known from the middle Pleistocene, but judging from the early femoral evidence and from the fact that the pelves associated with the Mt. Carmel population (McCown and Keith, '39) are essentially human in
their details, there seems little reason to suppose that the pelvess of middle Pleistocene men were any different, or to doubt that the locomotor adaptation had already occurred prior to the changes in the brain and face.

If it is believed that man was differentiated from the apes first in his way of locomotion, it is not contradictory to assert that a form is a part of the hominid radiation, and still may be ape-like in the majority of its features. If bipedal locomotion marks the beginning of peculiarly human evolution, then the origin of man will be reflected first in the pelvis. The combination of features seen in the australopithecines may be very close to such a hypothetical animal, ape-like in brain size and much of their anatomy, but already starting to move bipedally on the ground.

At this postulated stage of hominid evolution, it would be quite difficult to separate the diverging pelvic types since the first stage of pelvic change is marked by the progressive shortening and bending back of the ilium, accompanied by changes in the musculature permitting bipedal locomotion. The second stage of modification would be characterized by the beginnings of the iliac tubercle and pillar permitting an improvement in balance. Finally, the gradual shortening of the ischium and modification of its tuberosity would result in the unique human pelvis.

This sequence of change would represent the pelvic adaptations for bipedal locomotion, but there would also be concomitant modifications of other parts of the body in response to this changed behavioral complex. It cannot be expected that selective pressures operating on other functional units of the body would remain the same during, or after, this major adaptation. With the attainment of erect posture, the use of tools became a possibility and this changed the whole subsequent course of human evolution.

The techniques utilized in this study offer a method of checking the conclusion that the australopithecines were adapting to bipedal progression. The morphological details of the human ilium that are all important for balance, the
iliac tubercle and pillar, may be discernible in these fossils. A familiarity with the split-line technique and its results often enables the investigator to recognize the patterns of organization in unprepared bones. For example, some untreated bones show unmistakable splits and cracks that follow the general pattern of internal organization. The australopithecine innominate bones may show these patterns. Also, the marked thickening in the outer table of the ilium, through the region of the tubercle and pillar, may be detectable in the Swartkrans innominate bone which is broken off across this region; and x-ray would show the thickness of the fossil bones. An examination of the fossils themselves is necessary, however, since casts and pictures fail to reproduce sufficient detail. The present study would have been aided immeasurably by study of the actual fossils.

In spite of this limitation, this paper focuses attention on the importance of a functional analysis and the utilization of a combination of experimental and comparative techniques. Even when there are many more primate fossils, the full story of human evolution will only be elucidated by the use of a wide variety of techniques. Changes in the thickness of bone and in its internal organization offer clues to past behavioral adaptations which are as important as changes in general form.

**SUMMARY**

1. Benninghoff split-line preparations were done on 4 chimpanzee and 8 human innominate bones.
2. Comparisons of the split-line patterns and areas of thick and thin bone characteristic of man and chimpanzee, demonstrated the relationship of internal structure to behavioral patterns.
3. The relationship of the iliac tubercle and pillar to the balance of a biped was functionally analyzed. The implication of this relationship was drawn for the australopithecine mode of locomotor adaptation.
4. Methods for checking the postulated stage of the fossil adaptation were given.
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LITERATURE CITED


Human organs, much like the human heart, have changed and evolved over the history of time. The human brain is no exception to this natural phenomena. Based on Charles Darwin's idea of Natural Selection, species that had larger brains capable of complex functioning seemed to be a favorable adaptation. The ability to take in and understand new situations proved invaluable to the survival of Homo sapiens. This crucial step was necessary for brain evolution since the modern human brain requires a constant source of energy to keep functioning at the rate it does. 2 million to 800,000 Years Ago. Species of this time period began moving to different places across the Earth. As they moved, they encountered new environments and climates. Human evolution is the lengthy process of change by which people originated from apelike ancestors. Scientific evidence shows that the physical and behavioral traits shared by all people originated from apelike ancestors and evolved over a period of approximately six million years. One of the earliest defining human traits, bipedalism -- the ability to walk on two legs -- evolved over 4 million years ago. Scientists also debate over how to identify and classify particular species of early humans, and about what factors influenced the evolution and extinction of each species. Early humans first migrated out of Africa into Asia probably between 2 million and 1.8 million years ago. They entered Europe somewhat later, between 1.5 million and 1 million years.