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Stw 441/465: a new fragmentary ilium of a small-bodied *Australopithecus africanus* from Sterkfontein, South Africa

In 1986 and 1987, a hominid left ilium fragment consisting of a spina iliaca anterior superior and crista iliaca was discovered during excavations at Sterkfontein, South Africa. Although the specimen is small it gives valuable hints for muscle insertions and origins at the pelvis of *Australopithecus africanus*. It indicates that the anatomy of the abdominal muscles and of the mm. glutei medius et minimus of *A. africanus* was quite different from that of the great apes and more similar to that of modern humans. This has major implications for the interpretation of the bipedalism and locomotor efficiency of the early South African hominids.

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Introduction

Pelvic remains of *Australopithecus* are relatively rare and mostly fragmentary. Until recently the best preserved pelves were those of AL 288-1 (''Lucy'', *A. afarensis*) from Hadar, Ethiopia (Johanson *et al.*, 1982), and Sts 14 (*A. africanus*) from Sterkfontein, South Africa (Robinson, 1972; Häusler & Schmid, 1995). However, for the study of the evolution of human bipedalism not only the shape of the pelvis plays a crucial part, but also the markings of muscle and ligament attachments are important. Yet on Sts 14 both the surface bone and the epiphyses of the crista iliaca as well as that of the ischium are almost entirely lacking. The structure of the well-preserved surface bone of Stw 441/465 therefore offers a substantial expansion of our knowledge of the australopithecine anatomy.

The new iliac fragment

During excavations at Sterkfontein Member 4, South Africa, conducted by the late Alun Hughes under the direction of Philip Tobias, a 38 mm-long fragment of a left hominid crista iliaca, Stw 441, was discovered in September 1986 in grid square Q46 at a depth of 20′10″–21′10″ (grid size: 1 square yard). A few months later, in February and March 1987, a piece of a left spina iliaca anterior superior (without specimen number) was excavated in the adjacent grid R46 at a depth of 20′9″–21′11″. A third iliac fragment, Stw 465, found four grids to the east (R43, 20′22″–21′11″), fits neatly between the other two fragments (Figure 1). The peculiar shape of the ilium, with a projecting spina iliaca anterior superior, is typical for an australopithecine and the association with Sterkfontein Member 4 strongly suggests attribution to *A. africanus*.

Preservation

Between the spina iliaca anterior superior fragment and the adjacent triangular fragment the ventral two thirds of the crista is flaked off over a length of about 1 cm. This leads to only a small contact area at the crista iliaca between the two fragments.

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Figure 1. Stw 441/465 in ventral (left) and dorsal aspect (right). Scale bar 5 cm.

Their relative orientation in the plane of the iliac blade is therefore subject to some uncertainty. The contact with the medial fragment (originally labelled Stw 441) is better, and about 1 cm in width. The linea epiphysis marginalis, visible on both the dorsal and ventral sides, runs smoothly across all three fragments and corroborates their close association. The cristal apophysis was thus not fully fused, corresponding to a young adult.

Association with Stw 431

At the time of discovery of the three iliac fragments Stw 441/465, the crucial Stw 431 partial skeleton of an *A. africanus* (Tobias, 1992; McHenry & Berger, 1998; Häusler, 2001; Häusler & Berger, in prep.) was found in the grid squares between these three fragments at the same excavation levels (grid squares R45 and Q45 at depths of 20′10″–28′10″). As the Stw 431 pelvis lacks the left crista iliaca, this close spatial relation suggested that Stw 441/465 might belong to the same individual. Both specimens have incompletely fused cristal apophyses, which suggests similar ages at death. The thickness of the spina iliaca anterior superior of Stw 441/465, however, is, with a maximum of 11 mm, much thinner than the 15 mm of Stw 431's right ilium (Figure 2). Although perfect symmetry is very rare in the skeleton of primates (Gaupp, 1909; Mollison, 1910; Schultz, 1930), an asymmetry of the same degree could not be found in an examination of 100 extant human and 107 great ape pelves by one of the authors (MH). In addition, the preserved pelvic elements of the partial skeleton of Stw 431, particularly the left and right acetabulum, the roots of the pubis and the other left and right ilium fragments, do not show any indication of asymmetry in size or morphology. Together with other features described below, the differences between the two ilium specimens are sufficient to attribute them to separate individuals. Stw 441/465

Figure 2. The anterolateral margin of the left ilium fragment Stw 441/465 (right) compared with the right ilium of Stw 431 (left).

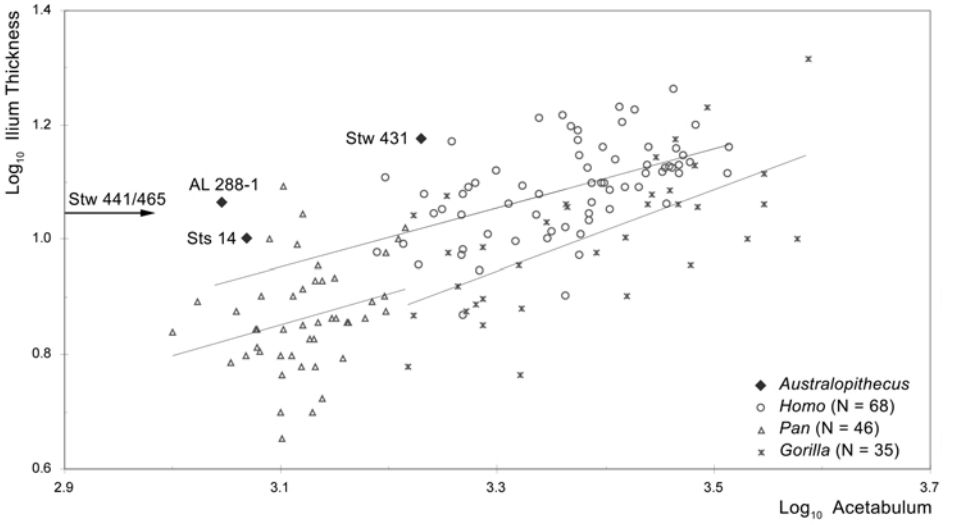

Figure 3. Scatter plot of the thickness of the ilium at the spina iliaca anterior superior *vs.* the acetabulum area (craniocaudal × transverse diameter). As acetabulum size of Stw 441/465 is unknown, the corresponding data point could lie anywhere in the direction of the arrow. The thickness of the spina iliaca anterior superior of AL-288-1 has been tentatively corrected for a longitudinal crack. The original thickness of the Sts 14 ilium was possibly greater for the crista lacks the apophysis. Least square regression lines are shown for all three extant species.

apparently stems from a smaller individual than Stw 431. It was initially thought that Stw 441/465 might be even smaller than Sts 14, which would make it one of the smallest individuals from Sterkfontein.

A plot of acetabulum size against maximum thickness of the spina iliaca shows a very weak correlation of ilium thickness with body size (represented by acetabulum size) in modern humans and great apes (Figure 3). It is thus impossible to infer from ilium thickness alone that the body size of Stw 441/465 was smaller than that of Stw 431 or that it was similar to that of Sts 14.

In contrast to the thickness, a comparison of the silhouettes of the spinae iliacae anteriores superiores indeed suggests different body sizes (Figure 4). To judge from this comparison, Stw 441/465 seems to be about 15% smaller than Stw 431 and more or less similar in size to Sts 14. The mild uncertainty about the fit between the different pieces of Stw 441/465 is of minor consequence in this respect. On the other hand, the maximal distance between the medial end of the labium externum (see below) and the spina iliaca anterior superior implies only a 5% smaller body size than Stw 431. This convincingly shows the difficulty of determining body size from small fragments.

Relative thickness of the spina iliaca anterior superior

The relative thicknesses of the spinae iliacae anteriores superiores of Stw 431, Sts 14 and AL 288-1 are in the upper range of the thickness predicted from the size of the acetabulum for humans and great apes (see Figure 3). This becomes even more distinct if the reduced major axis or major axis with their steeper slopes are used instead of the least square regression line; discussion of the different line fitting methods, however, would exceed the focus of this paper. However, if one draws a parallel to the least square regression line through the value of Sts 14, only 12 of our sample of 68 humans are above the value of Sts 14. Moreover, the

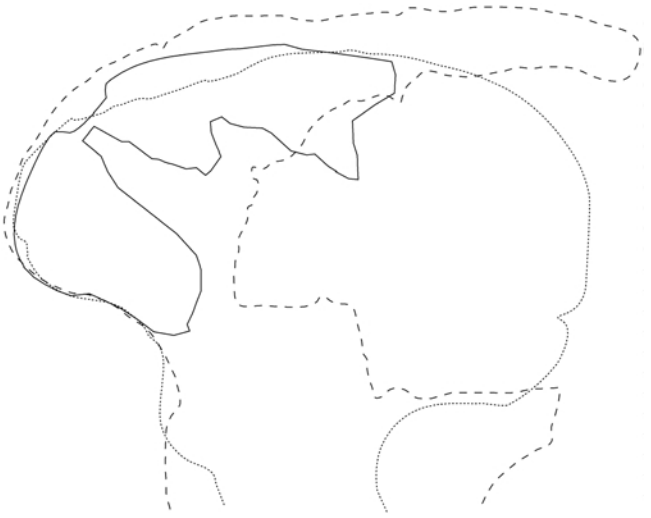

Figure 4. Comparison of the silhouettes of Stw 441/465 (solid line), Stw 431 (dashed line) and Sts 14 (dotted line). The reference region of the three profiles is the spina iliaca anterior superior and the anterior margin of the ilium. All to the same scale.

spina of Sts 14 may originally have been more robust, since the unfused apophysis of the crista iliaca is now lacking. This remarkable robusticity of all australopithecine spinae could be by chance or it could mean that during australopithecine locomotion greater forces acted on the anterior ilium than on that of humans or great apes.

Muscle and ligament attachments

The surface bone of Stw 441/465 is well preserved and allows a detailed analysis of muscle and ligament attachments. Both the spina iliaca anterior superior and the crista iliaca are more delicately built than in Stw 431, but their shape differs only slightly in the two specimens (see Figures 2 and 4). As with Stw 431, the crista iliaca bulges ventrally in the region of the spine, possibly indicating strong anterior fibres of m. iliacus (but see Ohman *et al.*, 2000). On the dorsal aspect, there is a prominent pointed tubercle just medial to the spina iliaca anterior superior (see Figure 1). It marks the end of the linea glutea anterior, which can be palpated on the medial side of this tubercle for a short stretch up to the fracture margin of the specimen (Figure 5). A comparable tubercle of the linea glutea anterior is also present in AL 288-1 (Johanson *et al.*, 1982), but is absent from Stw 431 and Sts 14. In all these australopithecines, however, the linea glutea anterior seems to be positioned close to the spina iliaca anterior superior. This indicates that the m. gluteus medius had a larger anterior portion than generally found in modern humans, but it also generates a broad area of origin for m. gluteus minimus, which thus resembles more the morphology of modern humans than that of great apes.

The front portion of the spina iliaca anterior superior is separated by a shallow, oblique furrow from the crista and is therefore conspicuous as a distinct 19 mm long knob. Such a demarcation is absent in Stw 431, Sts 14 and AL 288-1. Since the m. abdominis transversus arises from the medially adjacent labium internum, another structure must have originated from this knob. As the knob bulges ventrally over the fossa iliaca, it is possible that it is not only due to the above-mentioned m. iliacus fascia but also to the ligamentum inguinale (cf. Figure 5). At the inferolateral end of this

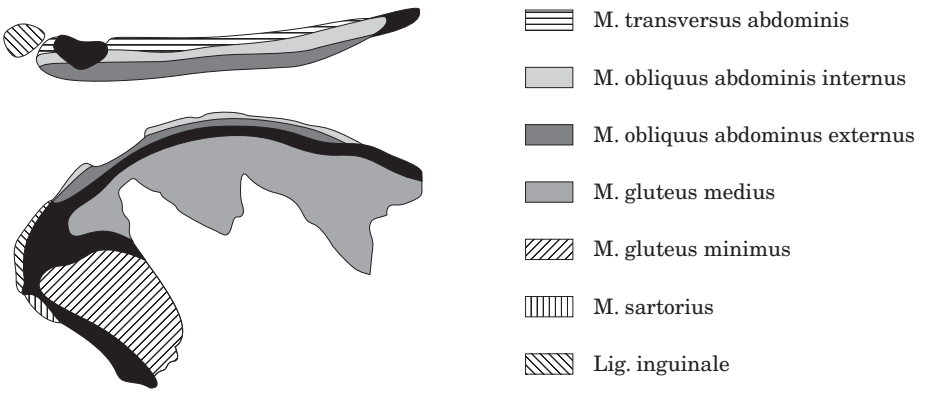

Figure 5. Proposed muscle and ligament attachment areas on the crista iliaca (top) and on the dorsal aspect of Stw 441/465 (bottom). The position of the linea glutea anterior is indicated by a dashed line.

large knob, another smaller knob can be detected. It is also absent in Stw 431 and in the other known australopithecines. This small knob could represent the origin of the ligament that unites the anterior superior with the anterior inferior iliac spine as well as the attachment of m. sartorius.

The crista iliaca of Stw 441/465 permits distinction between the muscle attachments of all three abdominal wall muscles. This is not possible in Sts 14 because the still unfused apophysis of the crista iliaca is lacking, and in AL 288-1 only a thickening of the otherwise featureless crista in the anterior region can be related to the attachment of the abdominal muscles (Johanson *et al.*, 1982). The labium internum of the Stw 441/465 crista starts just medially to the large knob and gives rise to m. transversus abdominis. In contrast to Stw 431, the internal margin of the entire preserved crista is straight and the labium internum does not bend dorsally at the medial end of the specimen. In the middle of the medial fragment of Stw 441/465, a small knob on the labium internum most probably indicates the end of the origin of m. transversus abdominis. The origin of m. obliquus abdominis internus is intermediate to the labium internum and the labium externum. The latter is the site of insertion of m. obliquus abdominis externus, beginning laterally at the height of the tubercle of the linea glutea anterior. In the middle of the medial fragment of Stw 441/465, just opposite to the small knob on the labium internum, a distinct protuberance is visible. This is possibly related to the tractus iliotibialis. On the medial side of this protuberance the external portion of the crista thins out abruptly, indicating the end of the insertion of m. obliquus abdominis externus. A comparable protuberance and such an abrupt thinning of the labium externum are both lacking from Stw 431 as well as from all other known australopithecine ilia.

Another unusual feature, not only among australopithecines but among primates generally, is the concavity of the iliac blade just below this protuberance. It is caused by an outward flaring of the external ilium cortex on the short stretch to the inferior fracture margin of the specimen. A possible explanation for this morphology could be a structure homologous to the iliac pillar of humans. The iliac pillar and tuberculum cristale are related to the attachment of the tractus iliotibialis fasciae latae and of the anterior fibres of m. gluteus medius (Dart, 1949; Mednick, 1955). In Stw 431, however, there is no indication of a tuberculum cristale or of an iliac pillar (Häusler &

Berger, in prep.). All other australopithecines also seem to lack a human-like pillar (Arsuaga, 1980). Although a pillar has been described in Sts 14, Sts 65 and in AL 288-1 (Robinson, 1972; Lovejoy *et al.*, 1973; McHenry, 1975; Johanson *et al.*, 1982), it is located near the anterior margin of the ilium at the spina iliaca anterior superior and thus cannot be compared with the iliac pillar of modern humans. Moreover, m. gluteus medius extends further laterally in australopithecines than in modern humans. It is therefore unlikely that the thickening on the Stw 441/465 crista is homologous to a proper tuberculum cristale and its significance remains unclear.

Summary and conclusion

Although the body size of Stw 441/465 cannot be determined with certainty, it apparently belonged to a small individual. It is represented only by a fragment of the ilium, yet it gives valuable hints for muscle insertions and origins at the lateral crista iliaca in *Australopithecus africanus*. It ideally corroborates the deductions for muscle attachments in *A. africanus* drawn from Stw 431, the only other specimen with a comparable, perfectly preserved bone surface (Häusler, 2001). For instance, whereas on the crista of chimpanzees the m. latissimus dorsi extends laterally to the spina iliaca anterior superior (Waterman, 1929), there is no indication of this important climbing muscle on the lateral crista iliaca of Stw 441/465. On the contrary, the whole breadth of the crista seems to have been occupied by the abdominal wall muscles, which therefore had similar attachment areas as in modern humans. Also the anatomy of the smaller gluteal muscles of *A. africanus*, with a large anterior portion of m. gluteus medius and a broad origin of m. gluteus minimum, was quite different from that of the great apes and more similar to that of modern humans. This contradicts the conclusion Berge (1994) drew from a biomechanical analysis of the guteal musculature of AL 288-1 (*A. afarensis*). According to Berge, only a pongid-like reconstruction of the gluteal musculature would be consistent with an effective bipedalism in that individual. Yet a comparison of the muscle markings on the ilium of Stw 441/465 with those of AL 288-1 suggests that the attachment areas of the smaller gluteal muscles were probably equivalent in *A. africanus* and *A. afarensis*. The comparatively large anterior portion of m. gluteus medius might be related to the laterally flaring ilium, to the absence of an iliac pillar, and to the absent ventral bending of the spina iliaca anterior superior. On the other hand, it possibly provides more favourable lever arms for the mm. glutei medius et minimus needed for lateral stabilization of the pelvis during bipedal walking. This shows clearly that *A. africanus* was well adapted for bipedalism despite having apparently more primitive body proportions than *A. afarensis* (McHenry & Berger, 1998).

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