



# The hominid ilium is shaped by a synapomorphic growth mechanism that is unique within primates

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**The human ilium is significantly shorter and broader than those of all other primates. In addition, it exhibits an anterior inferior iliac spine (AIIS) that emerges via a secondary center of ossification, which is unique to hominids (i.e., all taxa related to the human clade following their phyletic separation from the African apes). Here, we track the ontogeny of human and other primate ossa coxae. The human pattern is unique, from anlage to adulthood, and fusion of its AIIS is the capstone event in a repositioning of the anterior gluteals that maximizes control of pelvic drop during upright walking. It is therefore a hominid synapomorphy that can be used to assess the presence and age of bipedal locomotion in extinct taxa.**

*Ardipithecus* | *Australopithecus* | hominin | bipedality | human origins

Analyses of the ilium of hominids and our nearest relatives (the African apes) have been largely descriptive and have only rarely included a detailed examination of its serial development (1–3). Although evaluations of major contributing gene families have been reported, most are restricted to general factors affecting the os coxae and do not yet provide details of genomic regulation specific to primates (4, 5). In this paper, we report an analysis based on traditional anatomical observation (albeit informed by modern developmental biology), especially considering the fundamental role played by positional information (PI), the situational matrix of cooperative cell functions that guides morphogenesis (6, 7).

The iliac crests of African apes and humans are generally broader than those of their homologs in Old and New World monkeys. This likely represents an early modification of the *bauplan* of the Miocene hominoid last common ancestor (LCA) of humans and African apes (8–10). However, since that LCA, the shape and form of the iliac isthmus has been dramatically restructured only in hominids (Fig. 1 *A–D*). In each of the 3 subadults shown in Fig. 1, the auricular surface lies considerably superior to the roof of the acetabulum, a distance that is especially pronounced in the chimpanzee (11). The human specimen has lost much of its isthmus height (Fig. 2) and is much broader than its counterparts in the African apes (Fig. 3).

## Entheses versus Apophyses

The formation of most entheses (tendon–bone interfaces) does not usually also include formation of a secondary ossification center (SOC) (see detailed accounts in refs. 12–15). In the current case of the human anterior inferior iliac spine (AIIS), the reflected head of the rectus femoris muscle is an example of a non-SOC attachment (16), whereas the muscle's straight head, which originates on the superior portion of the AIIS, does include the formation of a SOC, but only in humans.

Generally, entheses can be divided into 2 main types: fibrous and fibrocartilaginous (see ref. 14). Fibrous entheses occur most often at diaphyses and metaphyses, whereas SOC's are usually attached via fibrocartilage (13, 17, 18), and these latter cases are usually referred to as apophyses and/or traction epiphyses.

Differences in tissue composition of entheses and apophyses are related to their differing roles in ontogeny. Fibrous entheses allow effective migration of attachment sites as their diaphyses undergo elongation and/or expansion (13), while epiphyses/apophyses

allow uninterrupted joint and/or muscle function by concentrating primary enlargement and shaping at more remote junctures with the diaphysis. Many apophyses, such as the greater trochanter of the femur, allow major insertion sites to remain substantially less modified during ontogeny than would be the case if growth occurred at the actual bone–tendon interface itself. In other cases, SOC's remain small and appear only briefly while growth is being terminated (e.g., lesser trochanter). The latter is true of the AIIS.

## The Formation of the AIIS Is Unique in Humans

The human AIIS collocates with a portion of the origin of both the iliofemoral ligament and the iliocapsularis muscle inferiorly, as well as the straight head of the rectus femoris superiorly (19, 20). In most primates the muscle's attachment is a typical enthesis and is commonly referred to as the rectus femoris tubercle (RFT). Many leaping primates display an unusually large RFT (21) (Fig. 1*E*), but little is known about its ontogeny. In hominids, formation of the AIIS includes a unique ossification center (1). This aspect is rarely emphasized in analyses of hominid fossil ilia because a separate apophysis is present and observable only briefly during its ontogeny. Moreover, AIIS prominence is sometimes presumed to be a downstream effect of tension from the rectus in upright walking (e.g., see ref. 22), although such an assumption now appears to be highly improbable (23, 24). Failure to recognize its importance in human evolution likely stems from the feature's transitory appearance and ossification. A review of its developmental history, however, provides a radically different understanding of its role in human evolution. Exposition of the unique development of the human ilium requires more detailed consideration of the early development of the primate acetabulum.

## Significance

**The human ilium is unusually short and broad compared with those of all other primates. Its specialized shape facilitates pelvic control during upright walking. Our ilium also exhibits a unique developmental feature: Its anterior inferior spine forms via a secondary center of ossification. We surveyed iliac development in a wide range of fetal to adult nonhuman primates, and found that such specialized anterior inferior spine formation is unique to humans and our known ancestors. Because this derived iliac structure facilitates upright walking, its presence serves as a direct indicator of the adoption of terrestrial bipedality in the fossil record and as an indicator of the minimum age of that adoption.**

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**Fig. 1.** Radiographs of subadult hominoids scaled to the same iliac transverse breadth (posterior superior spine to anterior superior spine). (A) *Pongo pygmaeus*, juvenile. (B) *Gorilla gorilla*, infant. (C) *Pan troglodytes*, infant. (D) *Homo sapiens*, 8 mo postnatal. Each lacks any fusion at its acetabular growth center. Nonhuman ages are from Cleveland Museum of Natural History (CMNH) records ("infant" designates only deciduous teeth; "juvenile" indicates mixed permanent and deciduous teeth). Human specimens shown are dental aged (26). The ilium's general form is established early in gestation and is maintained throughout ontogeny, with much of its enlargement taking place at the acetabulum (see *The Primate Acetabulum* and Figs. 2 and 3). The human isthmus is virtually truncated and is demonstrably broader than its homologs in all other primates. (E) Os coxae from a late subadult *Hapalemur griseus* displaying a tall ilium typical of nonhuman primates and a prominent RFT (arrow) common to some prosimians. (Scale bar, 1 cm.) Nonhuman primate specimens courtesy of CMNH.



### The Primate Acetabulum

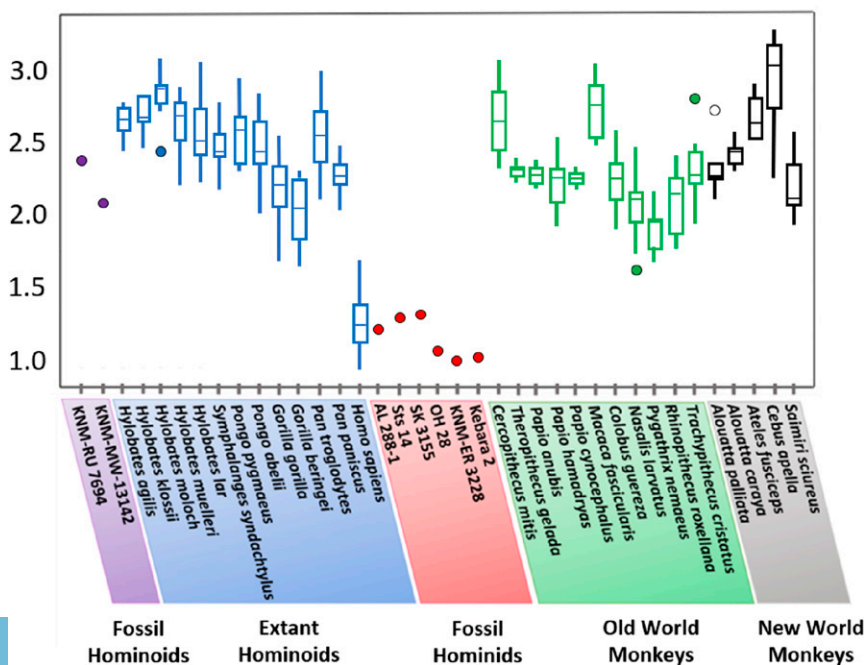
The primary focus of the growth and development of the primate os coxae is its acetabulum, which serves as the approximate point of union of the 3 separate elements of the os coxae. When viewed from a lateral perspective, the acetabulum's medial-most and deepest portion includes a structure commonly referred to as the triradiate cartilage (Fig. 4), composed of 3 triangularly shaped rays or flanges (25). The narrower end of each ray extends from a common source near the deepest part of the developing hip joint. Each ray isolates one portion of hyaline cartilage from its neighbors on either side, and each intervening hyaline segment is later replaced by a secondary bony invasion typical of those active in short bones of the skeleton (25). However, each cartilaginous ray later becomes the site for emergence of a true epiphysis—resulting from a de novo nodule of osseous tissue that appears within each ray and develops separately from its parent diaphysis (i.e., a typical SOC). In the development of the mammalian acetabulum, 3 such centers are

present—one for each of the primary bony components of the os coxae (Fig. 4).

The 3-rayed cartilaginous structure has been termed the triradiate acetabular cartilage complex (TACC) (25). Each of its hyaline cartilage components and their respective epiphyses have been termed the ischial epiphysis (for the ischium), the os acetabuli (for the pubis), and the acetabular epiphysis (for the ilium). These structures, combined with interstitial growth in the triradiate cartilage itself (and its later replacement by growth of the 3 primary bones), generate progressive expansion of the hip joint's diameter and depth (25). It should be noted, however, that the pubis contributes little to the actual shape and volume of the acetabulum (25). Of particular importance is the complex growth pattern of the acetabular epiphysis, which differs substantially in hominids compared with its simpler pattern in other primates (see below).

Our survey of the development of the acetabulum from anlage to adulthood reveals that formation of the AIIS in humans occurs in 2 distinct phases. First, a unique iliac growth front, already demonstrable in the fetus (Fig. 5A), emerges as a vertical

**Lower Ilium Height (mm) / Acetabulum Diameter (mm)**



**Fig. 2.** Relative lower ilium height among fossil and extant primates (lower ilium height divided by acetabular diameter). Data provided by Hammond and Alméjida (11).

Relative Breadth of Iliac Isthmus

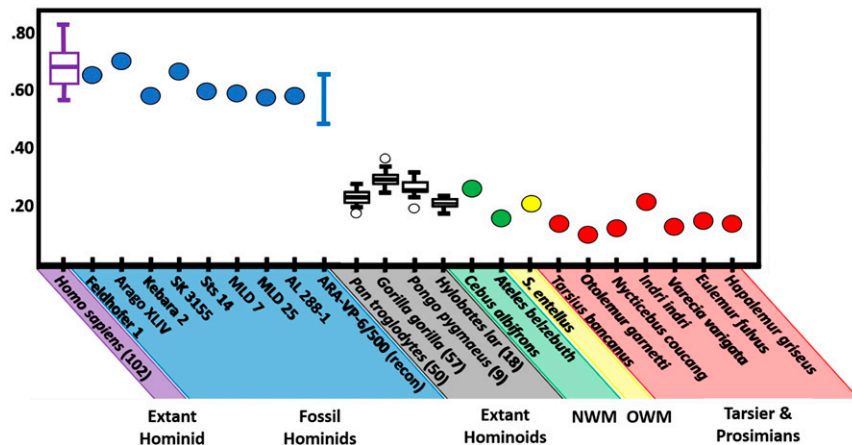


Fig. 3. Relative proportions of the iliac isthmus among fossil and extant primates (maximum isthmus breadth divided by maximum iliac height). Whiskers denote range, box length equals interquartile range, and bold bars inside each box indicate the median. Open circles signify outliers. For further definitions and data, see *SI Appendix, Table S2*.

extension of the superior portion of the acetabular physis (AP). This chondral diverticulum expands continuously superiorward to form the lower portion of an area that collocates with the attachment of the iliocapsularis muscle and the upper band of the iliofemoral ligament (19, 26). During this phase, no calcified secondary center forms. A later phase occurs more superiorly and is marked by the development of a small, isolated scalelike surface calcification that collocates with the attachment of the straight head of the rectus femoris (26). This small AIIS epiphyseal “cap,” as with most secondary centers, is characterized by an underlying billowed surface before its fusion with the diaphysis.

### The Special Mechanism of Iliac Growth in Hominids

It is not generally appreciated that even during early fetal development, the human ilium already displays rapidly forming subchondral bone in the region that is later occupied by the AP as just described (Fig. 5). A similar “field” of subchondral bone never appears in any other primate of any age (Fig. 6). This special growth shows an expanding subchondral surface that eventually terminates in one underlying the AIIS’s scalelike apophysis in late adolescence (Fig. 5F). This novel growth region can be clearly recognized in osteological specimens as a dark discoloration highlighting the calcifying cartilaginous surface that distinguishes it from other areas, which instead underlie only ordinary subperiosteal bone (Fig. 5A–E). It is present in every human subadult specimen that we have examined, and we have never encountered anything similar to it in any non-human subadult primate, whether prosimian or anthropoid (*SI Appendix, Table S1*). Its presence is clearly dictated by a fundamental change during specification of the pelvic anlage during embryonic development that must guide formation of the hominid ilium even at ~16 wk gestational age (Fig. 5A).

The AP continues as a relatively simple planar surface until approximately age 3 y in humans, after which it begins to assume a more sigmoid appearance, growing vertically until around age 5 y (Fig. 5E). The AIIS region then expands anteromedially to approximate its adult orientation (Fig. 5F). Total isolation of the AIIS subchondral portion from its “parent source,” the acetabular rim, occurs as early as 9 y (dental age, see ref. 27) in our sample, with only subperiosteal bone eventually occurring between the acetabular and AIIS portions of the now entirely isolated physis. The small ossified cap (the apophysis) appears only briefly at age 14 to 15 y and remains partially separated from the underlying ilium until final fusion, usually between 16 and 20 y of age (26, 28, 29), after which the site assumes its typical, but quite distinctive, adult configuration (Fig. 5F; see also ref. 30).

It is of special consideration that no other primate exhibits either the AIIS or any similar expansion of the acetabular growth plate, there being no separate subchondral ossification front spanning the gap between the rectus femoris insertion and acetabular rim at any point during the ontogeny of any primate specimen that we have examined (Fig. 6). Growth in the length and breadth of the primate isthmus is clearly restricted to simple accretion of bone at the AP, and all growth superior to that physis is almost certainly subperiosteal and not subchondral. Apparently, the relatively simple AP present in primates, in contrast to its homolog in humans, promotes much more rapid vertical growth throughout subadult life (Fig. 1), proportions which are maintained in the adult (Fig. 7).

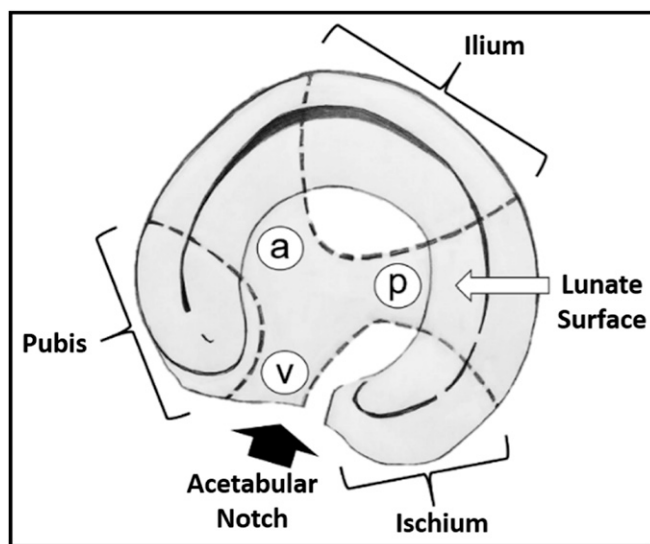
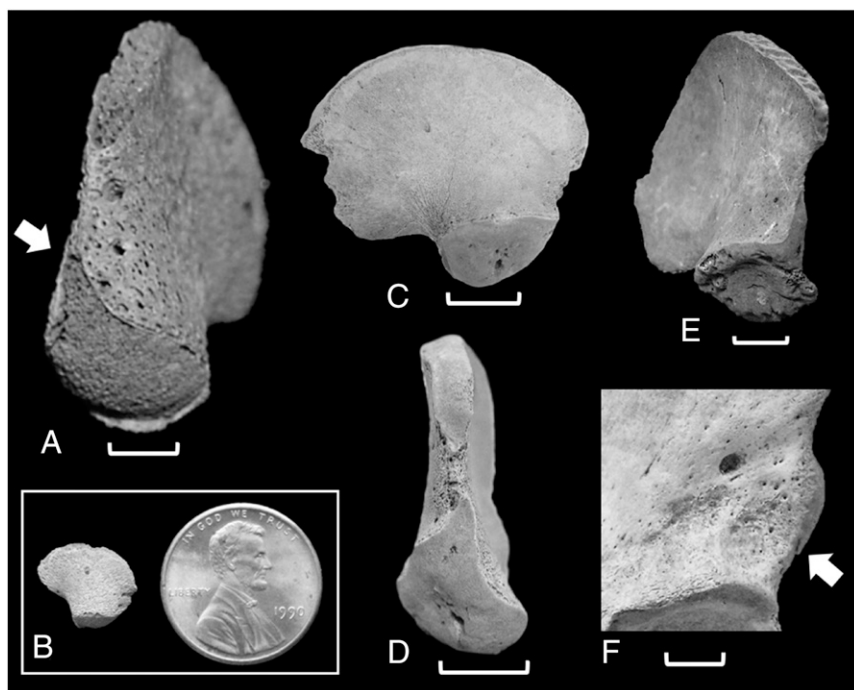


Fig. 4. Anatomical map of a lateral view of the newborn human acetabulum (consolidated and redrawn after figure 1 A–C of ref. 25). The lunate surface and acetabular notch are indicated, and the triradiate cartilage is shown as background. The cartilage’s 3 flanges, as identified by Ponseti (25), are anterior (a), posterior (p), and vertical (v). The 3 diaphyseal contributions to the developing os coxae are indicated by brackets. Each is separated from the triradiate cartilage by a growth front shown as a dashed line. Together, these structures comprise the TACC (see *The Primate Acetabulum*). Each developing cartilage model is later a host to an SOC. Each triradiate growth front then progressively expands until fusion during late adolescence. For further discussion, see *The Primate Acetabulum*. Adapted with permission from Wolters Kluwer Health, Inc.: ref. 25.



**Fig. 5.** AIIS development in *H. sapiens*. (A) Anterolateral view of ilium, fetal age ~16 wk gestation. Arrow points to the diverticulum of subchondral bone emanating from the AP. This region of the specimen is not damaged; differences in surface texture reflect subchondral versus periosteal bone formation. (B) Lateral view of same specimen with coin for visual scale. (C and D) Lateral and anterior view of ilium, 8 mo postnatal. Note expanding superiorward extension of subchondral bone from acetabular growth front. (E) Anterolateral view, 5 y. (F) Lateral AIIS, displaying near fusion (arrow), 15 y. (Scale bars in A and C–F, 1 cm). All specimens from the Libben Collection currently housed at Kent State University (44). Fetal specimens shown were aged using pelvic metrics from ref. 45. Note that the growth plate, which terminates with the appearance and fusion of the AIIS SOC, is present from anlage to maturity and that it forms as a progressively expanding subchondral diverticulum from the AP.

The expansion of the AP into the space separating the acetabulum and rectus femoris insertion is clearly coupled with the broader (but shorter) hominid isthmus. No similar area of locally specialized growth is found in any other primate. [An additional feature unique to the human ilium is its distinctive “pillar,” which has been accounted for by traditional Wolffian theory (see ref. 31). However, our knowledge of bone development and more recent examinations of human fetal ossa coxae reveal that this explanation is no longer tenable, as the pillar is already foreshadowed in the human fetal ilium (32). Its presence, as well as other uniquely human features of the ilium, are therefore more aptly assigned to differential expression of PI.] The unique growth pattern in hominids is made even more clear by simply comparing primate taxa with respect to both isthmus height and breadth treated as a ratio (Fig. 3). This ratio separates hominids from all primate quadrupeds that we have examined, whereas all fossil hominids fall well within the range of anatomically modern humans. Enlargement of the attachment areas of gluteus medius and minimus is so central to the practice of regular bipedality that the geological age of this fundamental shift can be viewed as evidence of selection on the early practice of bipedality. It is clearly a synapomorphy of the hominid clade.

We therefore hypothesize that a unique growth “apparatus,” genomically unique and expressed before anlage formation, is present in hominids whose eventual maturity is marked by fusion of an epiphysis for the AIIS. This apparatus is found only in humans and their immediate ancestors, and is absent in all other primates. In the latter, the AIIS equivalent (but not homolog) is merely a typical enthesis that serves as the simple attachment of the rectus femoris muscle and a portion of the iliofemoral ligament. In nonhuman primates, this RFT does not perform a growth function and may instead be merely an example of a tendon–skeleton junction, possibly induced by the scleraxis and bone morphogenetic protein 4 mechanism reported by Blitz et al. (33).

We conclude here that the novel (“true”) AIIS in hominids is a capstone event that marks a fundamental change in iliac growth patterning whose mechanical effect is to reposition the gluteus medius and minimus for active control of pelvic drop during the

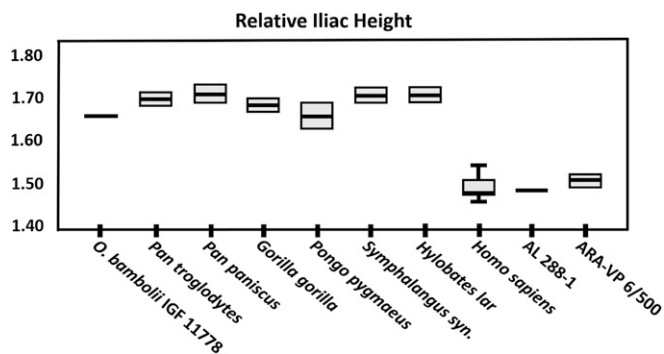
single support phase of upright walking. It therefore constitutes a hominid synapomorphy that is likely associated with earliest terrestrial upright walking.

#### The Acetabular Physis in the Hominid Fossil Record

An SOC for the AIIS has been documented in several fossil human ossa coxae (1), but the age of its first appearance is obviously of great interest. How can its ultimate geological age be determined?



**Fig. 6.** Antero-inferior morphology of the subadult ilium. (A) *H. sapiens*, 10 y. Note the superiorward, triangular expansion of the AP arising continuously from the superior acetabular rim. Only a small segment of the anterior ilium lacks a subchondral growth front, either for the crest or the AIIS epiphysis. (B) *P. troglodytes*, infant. There is no evidence of a subchondral, vertical diverticulum of the superior acetabular rim. The condition seen in *Pan* is characteristic of all nonhominid primate specimens examined. (Scale bars, 1 cm.)



**Fig. 7.** Relative iliac height. Index values (except for *H. sapiens*, AL 288-1, and ARA-VP 6/500) were collected from refs. 46 and 47. Measures for AL 288-1 and ARA-VP 6/500 were made from casts and published data (30). ARA-VP 6/500 is presented as a range between maximum and minimum estimates of possible acetabular diameter. Relative iliac height was calculated using the Jungers formula:  $\log_{10}$  (iliac height in millimeters) –  $\log_{10}$  (cube root of mass in kilograms) (see ref. 46). Body mass (BM) estimates for *H. sapiens* were calculated using regression formulas utilizing femoral head diameter (FHD) (48, 49):  $BM = (2.741 \times FHD - 54.9) \times 0.90$  [males (M)];  $BM = (2.426 \times FHD - 35.1) \times 0.90$  [females (F)]. Nonhominid sample from Jungers (46, 47): *Gorilla gorilla* ( $n = 11$ ; 7 M, 4 F); *P. troglodytes* ( $n = 9$ ; 4 M, 5 F); *Pan paniscus* ( $n = 12$ ; 6 M, 6 F); *P. pygmaeus* ( $n = 19$ ; 8 M, 11 F); *Symphalangus syndactylus* ( $n = 6$ ; 3 M, 3 F); *Hylobates lar* ( $n = 12$ ; 6 M, 6 F). *H. sapiens* specimens ( $n = 11$ ; 5 M, 6 F) are from the Libben Collection, currently housed at Kent State University. [Of additional note is that an estimated index of relative iliac height for *Oreopithecus bambolii* falls well outside the range for hominids. This finding aligns with other recent suggestions that *Oreopithecus* was likely not a biped, or at least not one in which the circumstances of origin were similar to those of hominids (50, 51)].

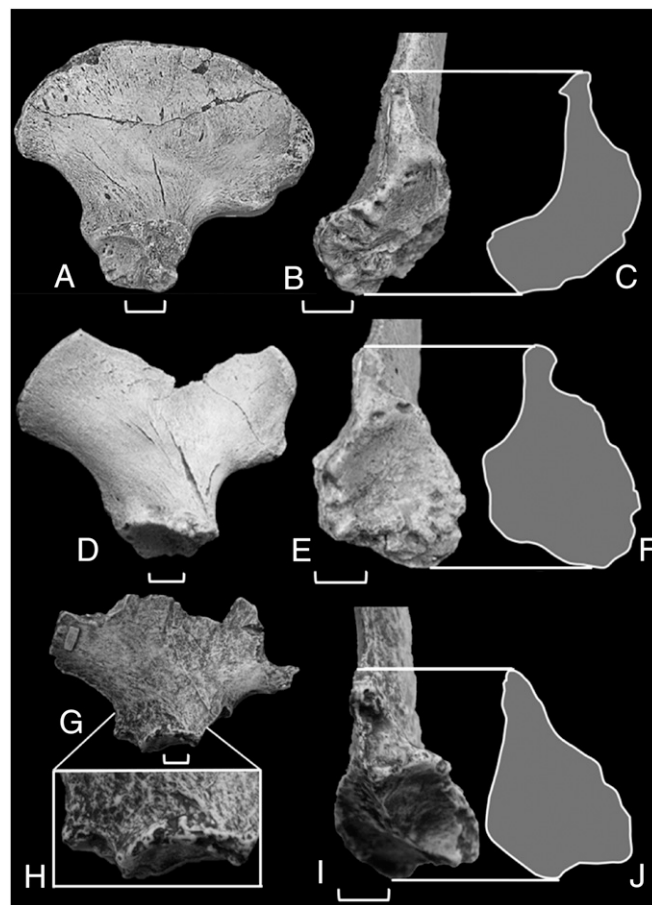
There appear to be 2 means of answering this question. One is direct. In subadult fossil specimens, an open SOC or anteriorly positioned subchondral bone plane is consistently observable when an AP is present throughout the entirety of ontogeny (see *The Primate Acetabulum*). This is the case in 2 specimens from Makapansgat (MLD 7 and MLD 25) (34) and a specimen from Kromdraai (TM 1605) (Fig. 8). Originally described as mature (35), TM 1605 nevertheless displays an open and reticulated surface typical of a subadult human AP. This feature was apparently mistaken for postmortem damage. It is of particular interest as TM 1605 likely represents a robust form of *Australopithecus* (“Paranthropus”). Thus, direct observation places the age of the human synapomorphy as being at least as old as the genus *Australopithecus* (*sensu lato*).

Although the direct method is preferable, the probability that so broad and short an isthmus emanated in earlier hominids by some other unrelated developmental mechanism, only to be later supplanted by the one currently present in *Homo sapiens* and *Australopithecus*, seems remote. Consequently, an unusually broad and short iliac isthmus is sufficient to conclude that this synapomorphy was present in any hominid ancestor, because these proportions constitute a fundamental adaptation to upright bipedal walking (i.e., control of pelvic drop during single support phase). Indeed, the data shown in Fig. 3 are sufficient to demonstrate its presence in a fossil as old as 4.4 Mya in *Ardipithecus ramidus* (36). This conclusion receives additional support from the unusual form of the adult AIIS in this and other fossil species (e.g., all members of the genus *Australopithecus*); that is, a form that largely reflects development from a distinct SOC (36).

It is worthy of note here that the presence of the AIIS epiphysis in humans might be considered an adaptation since it could be viewed as functionally enhancing the attachment of the rectus femoris and/or iliofemoral ligament. However, a separate SOC increases the likelihood of traumatic avulsion before maturity. Avulsions of pelvic apophyses (those for the AIIS and the ischial tuberosity) are seen in clinical practice (28, 37–39) and

likely occur because a developing apophyseal attachment weakens the tendon/ligament–bone interface due to the presence of growth cartilage (40). In fact, avulsion of the AIIS apophysis (i.e., attachment site of the straight head of the rectus) occurs at a greater frequency than occurs at the rectus’s enthesal origin (i.e., its reflected head) (41). Thus, the SOC, in itself, is unlikely to constitute an adaptation. Instead, its positive benefit must lie merely in its secondary role as the terminus of the AP’s unique broadening and vertical abbreviation of the hominid isthmus, which serve as the primary (i.e., true) adaptation. That is, the expansion of the isthmus is clearly a type 1 modification (7, 30), while the presence of the AIIS is merely a nonadaptive (i.e., neutral or even perhaps negative) consequence of its primary developmental process (i.e., type 2a or 2b). In the hominid lineage, the selective advantage of these modifications of the isthmus clearly outweighed the risk of avulsion fracture of the AIIS epiphysis during adolescence.

Enlargement of the attachment area of gluteus medius and minimus is central to the practice of humanlike bipedality, and the fundamental shift in the AP that is described here would appear to be direct evidence of ancient selection for upright walking. Indeed, the retention of an abductor great toe in *A. ramidus* suggests that control of pelvic drop was of greater import



**Fig. 8.** The AP on subadult australopithecine ilia. Lateral view (Left), anterior view (Center), and anterior view outline (Right) of each specimen. Note typical expansion of the anterior iliac physis from the acetabular rim in each (Center). MLD 7 *Australopithecus africanus* from Makapansgat (A–C) and MLD 25 *A. africanus* from Makapansgat (D–F) (Pennsylvania Museum casts). (G–J) TM 1605 *A. robustus* from Kromdraai (Wenner-Gren Foundation cast). The most superior portion of the AP in TM 1605 displays partial fusion. Specimen is clearly subadult, as the acetabulum is also not fused. (Scale bars, 1 cm.)

to successful upright walking (2, 36, 42), and thus is likely to be exceedingly old in the hominid clade. It also suggests a substantial period of time during which both arboreal access and terrestrial bipedality coexisted. Because the growth mechanism described here involved what are clearly extensive changes in ontogenetic patterning, it also implies that *A. ramidus* was likely more than a mere “facultative biped” as earlier accounts suggested. Indeed, upright walking perhaps significantly antedated its presence in *Ardipithecus* and *Orrorin* (43), as both of these taxa display modifications favoring control of the pelvic drop mechanism in hominids (2, 36).

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