Anatomy, Development, and Function of the Human Pelvis

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ABSTRACT

The pelvis is an anatomically complex and functionally informative bone that contributes directly to both human locomotion and obstetrics. Because of the pelvis' important role in obstetrics, it is one of the most sexually dimorphic bony elements of the human body. The complex intersection of pelvic dimorphism, locomotion, and obstetrics has been reenergized by exciting new research, and many papers in this special issue of the pelvis help provide clarity on the relationship between pelvic form (especially female) and locomotor function. Compared to the pelvis of our ape relatives, the human pelvis is uniquely shaped; it is superoinferiorly short and stout, and mediolaterally wide—critical adaptations for bipedalism that are already present in some form very early in the history of the hominin lineage. In this issue, 13 original research papers address the anatomy, development, variation, and function of the modern human pelvis, with implications for understanding the selection pressures that shaped and continue to shape this bone. This rich collection of scholarship moves our understanding of the pelvis forward, while raising dozens of new questions that we hope will serve as inspiration for colleagues and students (both current and future) puzzled by this fascinatingly complex bone. Anat Rec, 300:628–632, 2017. © 2017 Wiley Periodicals, Inc.

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There is perhaps no other postcranial bone that yields as much information about the biology of a living organism as the pelvis[1]. The pelvis plays important functions in (1) locomotion, as body weight is transmitted to the lower limbs through the pelvic girdle, (2) childbirth, as the human neonate must pass through the birth canal, which lies within the pelvic girdle as the baby exits the body, and (3) support of abdominal organs which are held up by both the pelvic floor musculature and the pelvis itself. As a result, the pelvis is central to a number of clinical "issues" of great significance to humans today. Of course, the basic structure of the human pelvis was inherited from our quadrupedal ancestors, but the evolution of bipedalism (about 6–7 million years ago) involved a massive reshaping of both the muscular and skeletal form of the pelvic girdle and the subsequent increase in adult and neonatal brain size (after about 2 million years ago) involved further pelvic modification.

[1]Here and elsewhere, the terms "os coxae" and "hip bones" are used rather than innominate (which literally translates to "not named" and therefore is not particularly meaningful).

As such, the pelvis has been a bone of considerable interest and that interest appears to be growing. A Pubmed search for "pelvis evolution" reveals that the average number of publications has doubled in the last ten years from the previous decade. There have been special symposia on the evolution of the pelvis at the American Association of Anatomists and the American Association of Physical Anthropologists in recent years. Some of this heightened interest is a result of new fossil pelves (or parts of pelvic bones) from Miocene apes *Pierolapithecus* and *Sivapithecus*, Plio-Pleistocene hominins *Ardipithecus* and *Australopithecus sediba*, and more

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recent finds from *Homo erectus* (Gona pelvis), *Homo naledi*, and pre-Neanderthals (Sima de los Huesos). However, much of the recent scholarship has branched beyond fossils and has investigated the integration, modularity and evolvability of the pelvis (i.e., Lewton, 2012; Grabowski, 2013), pelvic growth and development in the context of sexual dimorphism (i.e., Huseynov et al., 2016), the impact of pelvic variation on walking performance (i.e., Wall-Scheffler and Myers, 2013), form:function hypotheses in a comparative context (i.e., Hammond, 2013), and the obstetrical dilemma: a once widely accepted hypothesis about the trade-off between obstetric demands and locomotion (Trevathan, 1988; Rosenberg, 1992; Rosenberg and Trevathan, 2002) now fundamentally challenged by the work of Dunsworth et al. (2012) and Warrener et al. (2015). Furthermore, the perspective of evolutionary medicine (Trevathan, 2007) has shed light on why humans experience some of the diseases, weaknesses and injuries that we do and how the medical community might consider treatments of those "ailments" in light of that understanding.

In this issue ("The Human Pelvis: Anatomy, Development and Function"), thirteen papers are published on various aspects of the anatomy, development, variation and morphological integration of the pelvis. While these papers inform evolutionary questions, they primarily deal with modern human (or chimpanzee) pelvic functional anatomy, growth, and development. The next issue (published in May and entitled "The Human Pelvis: Evolution) will publish research aimed at understanding the evolutionary history of the human pelvis. Below, we summarize the papers in this issue in the order they appear.

To start the issue, Cara Lewis (Boston University) and colleagues provide a broad overview of basic pelvic anatomy and function in living humans. Lewis (2017, this issue) presents evidence that there are significant differences in pelvic function between males and females—a finding that is supported in detail by other scholars (Gruss et al., 2017, this issue; Wall-Scheffler and Myers, 2017, this issue; Whitcome et al. 2017, this issue) later in the issue. Finally, Lewis (2017, this issue) discusses the etiology of over and under coverage of the acetabulum and the resulting complications—femoroacetabular impingement, which causes pain and limits hip mobility—in the context of hip evolution and pelvic dimorphism, suggesting that the higher prevalence in females than in males may be a result of the evolutionary challenge of bipedalism and obstetrical adequacy in human females. How the pelvis grows and develops is the subject of the next paper by Stefaan Verbruggen and Niamh Nowlan (Imperial College, London). Verbruggen and Nowlan (2017, this issue) provide a basic review of pelvic ontogeny, but add important insight into the role that *in utero* motion may play in pelvic development. In other words, there is a cautionary tale here that just because a particular pelvic anatomy is present at birth does not necessarily make that anatomy "genetic" given the importance that fetal muscle actions *in utero* may play in stimulating bony growth and in some ways preparing the pelvis for the rigors of upright walking.

The next three papers use a three-dimensional approach to assess asymmetry (Kurki et al. 2017, this issue), and morphological integration of the pelvis during development in both humans (Mallard et al., 2017, this issue) and in chimpanzees (Huseynov et al., 2017, this issue). Asymmetry in the pelvis has not been previously studied and could conceivably have important obstetric implications. However, Helen Kurki (University of Victoria) and colleagues (Kurki et al, 2017, this issue) found very low directional asymmetry in the human pelvis and what was discovered had no regional patterning and few differences between the sexes. Previous work has found that there are reduced levels of morphological integration (and therefore high evolvability) in the human pelvis when compared to other primates (Lewton, 2012; Grabowski, 2013). How integration of the pelvis changes developmentally (if at all) remained unknown, however. Angela Mallard, a Ph.D. candidate in Benjamin Auerbach's lab at the University of Tennessee presents detailed evidence (Mallard et al. 2017, this issue) that female pelvic integration remains roughly the same throughout development—an important finding given that previous statements about the evolvability of the pelvis only examined adult specimens. She also finds evidence consistent with previous work that the individual parts of the pelvis (ilium, ischium, and pubis) are more integrated than the pelvis in its entirety. Alik Huseynov a Ph.D. student working with Marcia Ponce de Léon and Christoph Zollikofer at the University of Zürich used GM and biomedical imaging techniques to examine developmental modularity and integration in the chimpanzee pelvis. They found (Huseynov et al., 2017, this issue) that the pattern of integration in the chimpanzee pelvis changes over time and that the developmental units—ilium, ischium, and pubis—become more integrated with age, whereas the functional regions of the chimpanzee pelvis—locomotor and obstetric—become more modular. As in humans, the modularity of the chimpanzee pelvis would allow selection to target locomotor or obstetric regions of the pelvis, and might increase the evolvability of each.

But this assumption that the primary mover shaping the human pelvis has been selection—particularly selection acting on aspects of the pelvis essential to locomotor and obstetric performance—is fundamentally challenged by the work of Lia Betti (University of Roehampton). In a critique of this adaptationist approach to the pelvis, Betti (2017, this issue) provides evidence that pelvic variation in humans has been strongly influenced by neutral evolutionary processes (genetic drift and distance mediated gene flow) and that thermoregulation may be an overlooked selective pressure targeting the pelvis. This important paper demonstrates the multifactorial nature of selection on the pelvis in humans as well as other evolutionary forces that have contributed to pelvic variation.

Yet, while the obstetric pelvis has not been the only target of selection, it has been an important one. The fact that there is sexual dimorphism in the pelvis (and that it is in the opposite direction from body size dimorphism—that is females have larger dimensions for many pelvic dimensions than males, while the reverse is true for all other body dimensions) is evidence that obstetrics has played a significant role in selection on the human pelvis. Barbara Fischer (University of Oslo) and Philip Mitteroecker (University of Vienna) (2017, this issue) use a geometric morphometrics analysis of 99 human pelves to characterize dimorphism. They find almost no overlap in shape space between males and females, despite the two sexes sharing nearly the same overall pelvic size. Furthermore, while the overall proportions of the pelvis scale allometrically, obstetrically relevant anatomies (i.e., subpubic angle, sacral height, biacetabular diameter) are nonallometric. Fisher and Mitteroecker (2017, this issue) hypothesize that the development of these obstetrically relevant anatomies is likely mediated by sex hormones (consistent with Huseynov et al., 2016). So, while the pelvis overall is sexually dimorphic in humans, Hillary DelPrete (Monmouth University) asks (DelPrete, 2017, this issue) whether there is dimorphism specifically in the shape of the pelvic inlet. Many obstetric textbooks would respond "yes" and historically the inlet has been divided into categories or types including the male "android" shape and the female "gynecoid" shape. However, DelPrete (2017, this issue) shows in a sample of 400 pelves that inlet shape is not as dimorphic as typically presented, and certainly should not be treated as a categorical variable. Yet, DelPrete (2017, this issue) does find that one of her populations (Hamann–Todd) has weak, but statistically significant dimorphism in the pelvic inlet. This finding, that there are population-level differences in sexual dimorphism, is relevant to the final paper in this issue concerned with obstetrics. Jonathan Wells (University College London) argues (Wells, 2017, this issue) that the obstetrical dilemma facing more recent human populations might be worse today than it was in the past. He describes a double-edged sword in which malnutrition in socioeconomically challenged populations can alter growth and reduce both the stature and the dimensions of the pelvis in women while in these very same populations the obesity epidemic is resulting in excessively large neonates. This combination may be resulting in more difficult and dangerous birth conditions than previously faced by humans. This finding would mean that the difficulties women experience in childbirth today are probably not typical of what would have been the case in the past.

The final four papers of the issue examine the role of the pelvis during bipedal walking in humans. Jesse Christensen, a physical therapist at the University of Utah, and colleagues (Christensen et al., 2017, this issue) used gait analysis to characterize pelvic motion during obstacle avoidance in a mobile group of individuals ($n = 10$). These findings—that posterior pelvic tilt and ipsilateral pelvic hike are critically important for normal obstacle negotiation—will be an important baseline for clinicians working with populations prone to falling.

The final papers examine an issue of critical importance to our understanding of pelvic variation and dimorphism: why is female pelvis relatively wider than the male pelvis? It has been long recognized that women have on average wider hips and shorter legs than men, and it has been long thought that these differences compromise locomotion in women relative to men. Since Krogman (1951) the working hypothesis to explain these differences was that the female pelvis needed to be wide to facilitate birth, but not too wide or it would compromise bipedal mechanics and/or energetics. That is, that the pelvis in human females was seen as the result of a balance between the conflicting selective constraints of childbirth and locomotion. Washburn (1960) argued that one way to mitigate this conflict was for the human neonate to be born at a relatively earlier (and hence smaller and less developed) stage. This suggested to some that the timing of human birth was dictated by size constraints of the birth canal. A baby born too early would be at greater risks during and immediately after birth, but a baby born too late would be too large to fit through the birth canal. However, Dunsworth et al. (2012) and Warrener et al. (2015) found that the wider pelvis of human females did not increase energetic expenditure during walking at all. But, why?

In 1991, Yoel Rak hypothesized in the context of the A.L. 288-1 (Lucy) *Australopithecus afarensis* skeleton that wide hips would increase rotation in the transverse plane and would effectively increase stride length. However, up until this point, this hypothesis has not been formally tested. Three studies published in this issue address this very question (Gruss et al., 2017, this issue; Wall-Scheffler and Myers, 2017, this issue; Whitcome et al., 2017, this issue) and are stunning in how concordant the results are. Gruss (Radford University) and colleagues present their findings (Gruss et al., 2017, this issue) as a formal test of Rak's hypothesis. Indeed, they find strong evidence that individuals (whether male or female) with wider pelves take relatively longer strides. Furthermore, when taking longer strides, individuals with wider hips have less movement in the sagittal plane than those with narrower hips, reducing the energetic costs of the vertical displacement of the center of mass. Therefore, there appears to be no locomotor disadvantage to having wide flaring hips, and in fact, these wide hips confer an advantage to shorter-legged individuals, including early hominins such as the *Australopithecus afarensis* A.L. 288-1 (Lucy). Katherine Whitcome's (California Northstate University) study concurs. She and her colleagues (Whitcome et al., 2017, this issue) studied the kinematics of gait in 30 individuals and found that women have a larger component of pelvic rotation contributing to stride length than men, especially at faster walking speeds. These data are consistent with her earlier findings (Whitcome et al., 2007) that women have more oblique zygapophyses in their lumbar vertebrae and are consequently capable of more lumbopelvic rotation than men. Therefore, the energetics of walking are similar in men and women not because of identical anatomies, but because of slightly different walking kinematics. However, here and in her previous work (Wall-Scheffler, 2012; Wall-Scheffler and Myers, 2013), Cara Wall-Scheffler of Seattle Pacific University and Marcie Myers of St Catherine University (Wall-Scheffler and Myers, 2017, this issue) completely reframe the original question. Perhaps we should not be asking about (and refuting) the negative consequences of a wide pelvis, but examining instead the potential adaptive benefits of such a morphology. Consistent with the other studies in this issue, Wall-Scheffler finds that relative to their height, women walk faster than men, have a lower center of mass (increasing stability), and have a relatively longer stride length by rotating their pelvis through a greater angle. Additionally, she finds that women with a wide bitrochanteric breadth use less energy to carry loads, leading to the hypothesis that selection may have favored a mediolaterally wide pelvis, especially in women, to reduce carrying costs. The take home message from Wall-Scheffler and Myers (2017, this issue) is that the mediolaterally wide female pelvis may be an adaptation *for* locomotion, not an obstetric by-product that produces locomotor costs.

These findings raise the question of why scholars have talked of the "narrow" human pelvis as adaptively beneficial. Many authors, from Krogman (1951) on, have suggested that in humans the pelvis adapted to bipedalism by becoming "narrow" (which we interpret to mean having a relatively low transverse breadth) with the implication or explicit statement that a narrow distance between the acetabula is most biomechanically efficient for bipedal walking. In fact, while other primates have a pelvic girdle (and birth canal within it) which is relatively narrow transversely but elongated from front to back, humans have a pelvic girdle (and pelvic inlet which represents the top or start of the bony birth canal) that is relatively wide transversely but short in the anterior–posterior direction. This is true of modern as well as fossil humans. The iconic photograph that Lovejoy (1988) presented in his Scientific American article showed the pelvis of a modern human female and the reconstruction of the *Australopithecus afarensis* specimen A.L. 288-1 ("Lucy"). Both the transverse (bi-iliac) breadth and the transverse breadth of the pelvic inlet in these two specimens are similar in the modern human and the australopith in spite of the fact that the modern human was probably at least 50% taller. So early bipedal humans had a wide, not a narrow pelvis and birth canal. This suggests that a narrow pelvis is not in any way necessary for bipedal locomotion. On the contrary, the papers by Wall-Scheffler and Myers (2017, this issue), Gruss et al. (2017, this issue), and Whitcome et al. (2017, this issue) confirm that our adaptation to bipedalism makes use of our pelvic breadth in increasing our stride length, a point made earlier for australopiths by Rak (1991). All humans today and in the past have a relatively broad pelvic girdle compared to apes and evolutionary changes that have taken place within human evolution have been primarily in the anterior–posterior dimension of the pelvis rather than the transverse one.

The papers in this volume use a range of methodologies and approaches, with many different types of data to look at the morphology of the human pelvis, examining its continuities in form with other primates and mammals as well as the uniquenesses that result from our unusual bipedal form of locomotion. We hope that other students of the pelvis are as inspired as we are by this collection of scholarship to continue to investigate this fascinatingly complex bone.

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