Bipedalism and Human Birth: The Obstetrical Dilemma Revisited

KAREN ROSENBERG AND WENDA TREVATHAN

. . . . adaptation to bipedal locomotion decreased the size of the bony birth-canal at the same time that the exigencies of tool use selected for larger brains. This obstetrical dilemma was solved by delivery of the fetus at a much earlier stage of development. (Washburn[1])

. . . . there can be no doubt that many of the obstetrical problems of Mrs. H. Sapiens are due to the combination of a narrower pelvis and a bigger head in the species. (Krogman[2])

Although Washburn described it as as a "dilemma" and Krogman called it a "scar of human evolution," both authors recognized that the unique way that humans give birth is the result of a set of constraints imposed by several exclusively human attributes: bipedalism, a large brain, and "secondary altriciality," or the delivery of the infant in a helpless state. Although human birth has long been seen as a single compromise between locomotion and brain size, we now know that the particularly complex series of twists and turns that human babies make in the process of emerging from their mothers' birth canals is the result of a history of continual compromises, adapting first to one constraint and then to another.

BIRTH IN NONHUMAN PRIMATES

Contrary to popular perceptions, humans are not the only animals that have difficulty during childbirth. One important characteristic of primates as a group is a large head and brain relative to body size (i.e., a high encephalization quotient). For most primates this means that their infants, at birth, have heads that are close to the size of the maternal birth canal through which they must pass. This is especially true of monkeys, lesser apes, and humans. Schultz[3,4] depicted this relationship in a classic figure, redrawn here as Figure 1, showing the size of the maternal pelvic inlet and the infant cranium in *Ateles, Nasalis, Macaca, Hylobates,* the great apes, and humans. The close correspondence between the size of the maternal pelvis and the size of neonatal cranium is obvious for monkeys, gibbons, and humans, whereas chimpanzees, gorillas, and orangutans appear to have spacious birth canals, probably as a result of their large bodies. As one would expect from examining these drawings, birth is reported to be difficult for the smaller-bodied primates (monkeys and gibbons), as well as for humans,[5-9] but somewhat easier for the larger-bodied (great) apes. [10]

Although observations of wild animals giving birth are rare, we know that neonatal death resulting from cephalopelvic disproportion, when a fetal head is too large to pass through the mothers birth canal, is not uncommon in species such as marmosets, squirrel monkeys,[11] baboon[8] and macaques. [12] Cephalopelvic disproportion is also, of course, a relatively frequent cause of death for human infants and can be the cause of death for their mothers.[13] Because the cephalopelvic constraints in monkeys are greater than those in great apes, the comparisons made herein between nonhuman primates and humans will use monkeys, rather than the phylogetically closer great apes, to represent nonhumans.

It is not only the size of the pelvic aperture that is important to the birth process, but also its shape. The birth canal can be seen as a passageway with an entrance (the inlet) and an exit (the outlet) and a space between (the midplane) through which the infant must pass. For most primate species, the entrance (see Table l), the exit, and the passageway between them are longer in the sagittal dimension than in the transverse dimension. The neonatal cranium is largest in the sagittal dimension in all primate species, including humans. Furthermore, the back of the infant cranium is broadest, so that it fits best against the broader back of the monkey pelvis.

Until recent work by Stoller,[14] it had been assumed that in monkeys the sagittal dimension of the infant cranium lines up with the sagittal dimension of the pelvis, the infant facing the ventral side of the mothers body (Fig. 2) and passing straight through the birth canal without rotating. The infant is born in a position obstetricians describe as occiput posterior. Based

Karen Rosenberg is Associate Professor of Anthropology at the University of Delaware. She is a paleoanthropologist who has worked on fossils in Europe, the Near East and Eastern Asia. Her research interests are in the origin of modern humans and the evolution of modern human childbirth. Wenda Trevathan is Associate Professor of Anthropology at New Mexico State University. Her major research interests are the evolution of human female reproductive behavior, including sexuality, pregnancy, childbirth, and menopause. Her major publications include Human Birth; *An Evolutionary Perspective* and articles on menstrual synchrony, sexuality, and evolutionary medicine.
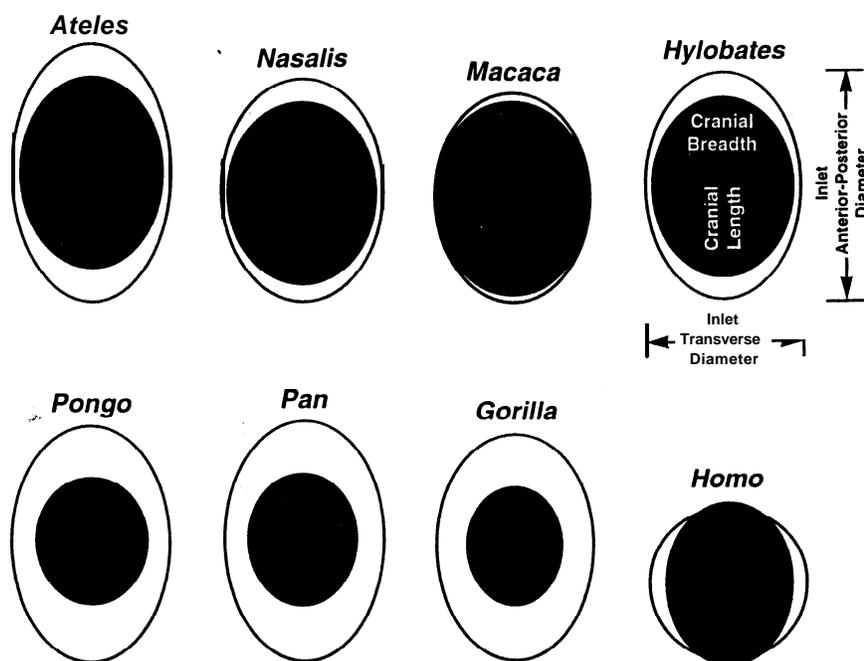
Email: KRR@UDEL.EDU

Figure 1. A redrawing of Schultz' classic diagram relating the size of the maternal pelvic inlet and the size of the neonatal head in different primate species. Maternal pelvic and infant cranial outlines are diagrammatic, but scaled so that the transverse diameter of all maternal pelvic inlets are constant and all dimensions are correctly scaled relative to one another. For each species, the outlined oval represents the average maternal pelvic inlet, the black oval represents the average infant's cranium. Note that in the monkeys and gibbon, the dimensions of the infant cranium are only slightly smaller than the dimensions of the mother's pelvis. In great apes, the pelvic inlet is relatively spacious. In humans, the infant cranium is actually longer than the anterior-posterior dimension of the pelvic inlet, requiring the head to enter the inlet facing sideways.

on observations that included radiographs of laboratory animals during parturition, Stoller[14] has shown that squirrel monkey and baboon infants may rotate during birth, albeit in a different way than human infants do. In the four baboons *(Papio anubis)* and seven squirrel monkeys *(Saimiri sciuretrs)* Stoller studied, the fetuses entered the birth canal in various positions, but then rotated to exit face first (mentum anterior), facing the maternal pubic bones and with their heads in an extended position.

Monkey mothers usually deliver in a squatting position. As the infant is born, the mother typically reaches down to guide it out of the birth canal and toward her nipples, and may wipe mucus from the baby's mouth and nose to assist its breathing.[10] Other animals may observe the birth process from a distance but do not assist the mother or infant. The newborns of most monkey species have sufficiently. developed motor skills that an infant can assist in its own delivery once its hands are free.

Monkeys and apes generally give birth wherever and whenever other group members and predators are least likely to be present. Laboring mothers typically seek seclusion, often among trees, which provide protection from terrestrial predators. Diurnal species generally give birth at night; nocturnal species tend to give birth during the day.[15] For nonhuman primates, birth generally is a solitary event.

BIRTH IN MODERN HUMANS

Although, as shown in Figure 1, the close correspondence between the infant cranium and maternal pelvis in monkeys is also characteristic of humans, the orientation of the pelvic diameters differs. In monkey pelves, both the inlet and the outlet are greatest in the sagittal dimension. In contrast, the human birth canal is "twisted" in the middle so that the greatest breadth at the inlet is in the transverse dimension, while the outlet is largest in the sagittal dimension. In other words, the long axes of the inlet

and outlet lie perpendicular to each other in humans, whereas in other primates they are parallel to each other.

The human infants head, like the monkey's, is greatest in the sagittal dimension. The extremely close correspondence between the fetal head and the maternal pelvic dimensions requires that these dimensions line up so that the head enters in the transverse plane (facing to the side) (Fig. 2), but then rotates to emerge in the sagittal plane, usually facing to the back in a position obstetricians refer to as occiput anterior (Fig. 3). The head must rotate again after it passes through the outlet so that the shoulders, which, as in the great apes, are fairly broad and rigid, can follow the head through the maximum diameters of the birth canal.

In addition to the differences in cross-sectional shape, human and nonhuman primate pelvic morpholo-

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gies differ in another way The broadest part of the monkey pelvis is at the back, whereas the human pelvis is also spacious in the front. As with monkeys, the human infant's occiput is the largest, most rigid part of its head. Thus, rather than lining up with the back of its head against the maternal sacrum as monkeys do, the human infant more commonly lies so that its occiput is against the pubic bones, and toward the front of the pelvis as it exits the birth canal, its convex frontal bone passing along the concave anterior surface of the sacrum. The smallest diameter of the human fetal head is the sub-occipito-bregmatic diameter (from the back of the head to the top of the head). In order to make this minimum cross-sectional diameter pass through the plane of the maxi-

TABLE 1. Average transverse diameter of female pelvic inlet, newborn cranial breadth, and relative breadth of newborn cranium for primate species (from Leutenegger[11])

	Adult females		Newborns		
Species	N	Transverse Diameter of Inlet (mm)	N	Cranial Breadth (mm)	Relative Cranial Breadth[1]
Callithrix jacchus	15	17.2	4	18.0	104.5
Saimiri sciureus	7	23.1	3	28.0	121.1
Cebus capucinus	4	35.1	2	43.0	118.2
Alouatta villosa	2	47.0	1	38.0	80.8
Lagothrix lagothricha	4	44.3	1	48.0	108.3
Ateles geoffroyi	7	54.4	8	52.2	95.9
Macaca mulatta	41	50.9	28	50.7	99.6
Nasalis larvatus	15	51.8	1	49.0	94.6
Hylobates lar	87	55.9	6	52.7	94.3
Pongo pygmaeus	26	102.5	4	74.9	73.1
Pun troglodytes	29	98.0	9	71.0	72.4
Gorilla gorilla	10	122.6	4	79.0	64.4
Homo sapiens	10	121.6	10	123.8[2]	101.8

[1] Relative cranial breadth is newborn cranial breadth as a percentage of the transverse diameter of the maternal pelvis. Index Is calculated for the means of each species.

[2] Cranial length rather than breadth is included here, since that is the dimension that passes through the transverse diameter of the inlet in humans,

mum diameter of the outlet, the fetal head must be in an occiput anterior presentation as it exits the birth canal. This means that the head not only rotates from its original sideways facing orientation as it passes through the birth canal, but emerges facing in the opposite direction from the mother.

In summary, the mechanism of birth in nonhuman primates differs from that most common in humans in two fundamental ways. The orientation of the fetal head as it enters the birth canal is different, that of nonhuman primates usually facing forward or backward and that of humans facing sideways. The change in orientation of the fetal head as it passes through the birth canal is also different, that of nonhuman primates rotating to a variable degree but emerging facing forward with the head flexed and that of humans rotating to exit facing backward with the head extended.

These two distinctions account for significant differences in maternal behavior at birth. For humans, birth is a social activity. Unlike nonhuman primates, which seek solitude at this

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time, human mothers actively seek assistance in childbirth.[16] We suggest that this distinction is related to the mechanical differences in the birth process, which are the result of the previously discussed anatomical differences. Like nonhuman primate mothers, human mothers often squat during delivery, although they also assume a wide range of other postures. Because the human fetus emerges from the birth canal facing in the opposite direction from its mother, it is difficult for the mother, whatever her position, to reach down, as nonhuman primate mothers often do, to clear a breathing passage for the infant or remove the umbilical cord from around its neck. If a human mother tries to assist in delivery by guiding the infant from the birth canal, she risks pulling it against the body's angle of flexion, possibly damaging the infants spinal cord, brachial nerves, and muscles.[16]

The adaptation that humans have made to this situation is to seek assistance during birth. Today, virtually all women in all societies seek assistance at delivery from relatives, midwives, or obstetricians. In a survey of 296 cultural groups in which attendance at childbirth has been described, ethnographers for 24 such groups noted that
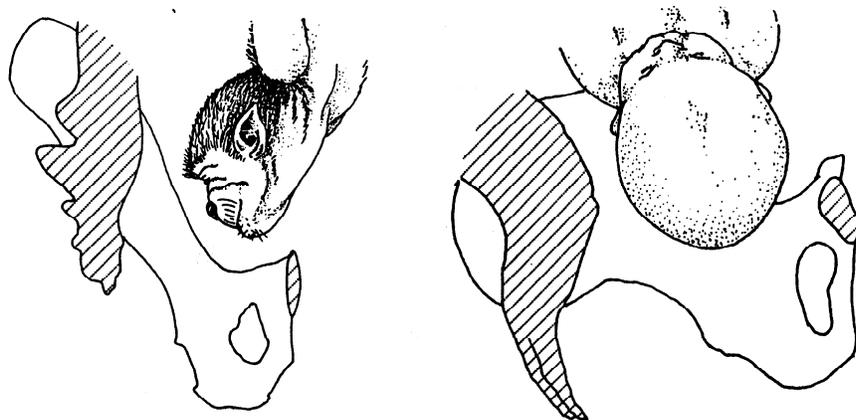
Figure 2. Comparison of the entry of the fetal head (seen in lateral view) into the birth canal in a baboon (left) and a human (right). The figure on the left was drawn from a radiograph taken of *Papio anubis* by Melissa Stoller.[8,14] The traditional understanding of monkey birth mechanics was that because the longest axis of the neonatal head and the longest axis of the maternal pelvic inlet are in the sagittal dimension, the fetal head enters the birth canal with its sagittal axis aligned with the mother's sagittal axis. The infant is positioned with its occiput against the internal surface of the maternal sacrum and remains in that orientation as it passes through to the outlet. Stoller's recent work on nonhuman primate birth[8,14] has shown that the neonatal head may enter the pelvic inlet in other positions, such as the one shown here, but that it exits the birth canal face first, facing the front of the mother's body. in humans,[10] because the longest axis of the neonatal head is the sagittal dimension and the longest axis of the maternal pelvic inlet is the transverse dimension, the fetal head enters the birth canal with its sagittal axis aligned with the mother's transverse axis (Le., facing to the side). Because the birth canal is not a straight tube of unchanging shape, the human fetus must rotate as it passes through (See Fig. 3). (Note that these drawings are not scaled correctly relative to one another.)

delivery may, under certain circumstances, take place unattended. For example, first births may be attended and subsequent ones unattended, or attendance may occur only at births involving complications. Even among the !Kung, a woman who gives birth alone arouses interest and concern,[17] suggesting that solitary birth is not as routine as some ethnographers have reported. Howell[18] reported that although giving birth alone is the cultural ideal for !Kung women, most have their mothers, sisters, or other women with them. So, while there are rare exceptions,[19] it is a phenomenon that comes close to being a "cultural universal." At some point in the evolutionary past of humans, the benefits of having assistance during birth outweighed the costs, so that the species-typical pattern of "obligate midwifery" emerged. Human birth is a social, rather than a solitary event.

WHEN DID THE HUMAN PATTERN OF BIRTH EMERGE?

In contrast to our understanding of human evolution fifty years ago, we now know that bipedalism is independent of encephalization and sec-

ondary altriciality in the human evolutionary record. Although all of these human characteristics affect the birth process, their influence is sequential rather than a single compromise to conflicting constraints.[20]

The series of rotations that the human infant must undergo during birth is related to the locomotor pattern, bipedalism, as well as to another characteristic aspect of human morphology, a relatively large brain. The close relationship between the size and shape of the maternal birth canal and the size and shape of the infant skull means that in humans the mechanism of birth can be inferred from the morphology of the bony birth canal.[21] Fortunately, some aspects of this morphology are preserved in the fossil record.

Our knowledge of the pelvic anatomy of the earliest bipeds comes principally from two australopithecine specimens, both sexed as female: Sts 14[22-24] from Sterkfontein, South Africa, and A.L. 288-1[25] (Lucy) from Hadar, Ethiopia. Although controversy surrounds the fine details of the locomotor system of these earliest hominids,[26,27] it is clear that their
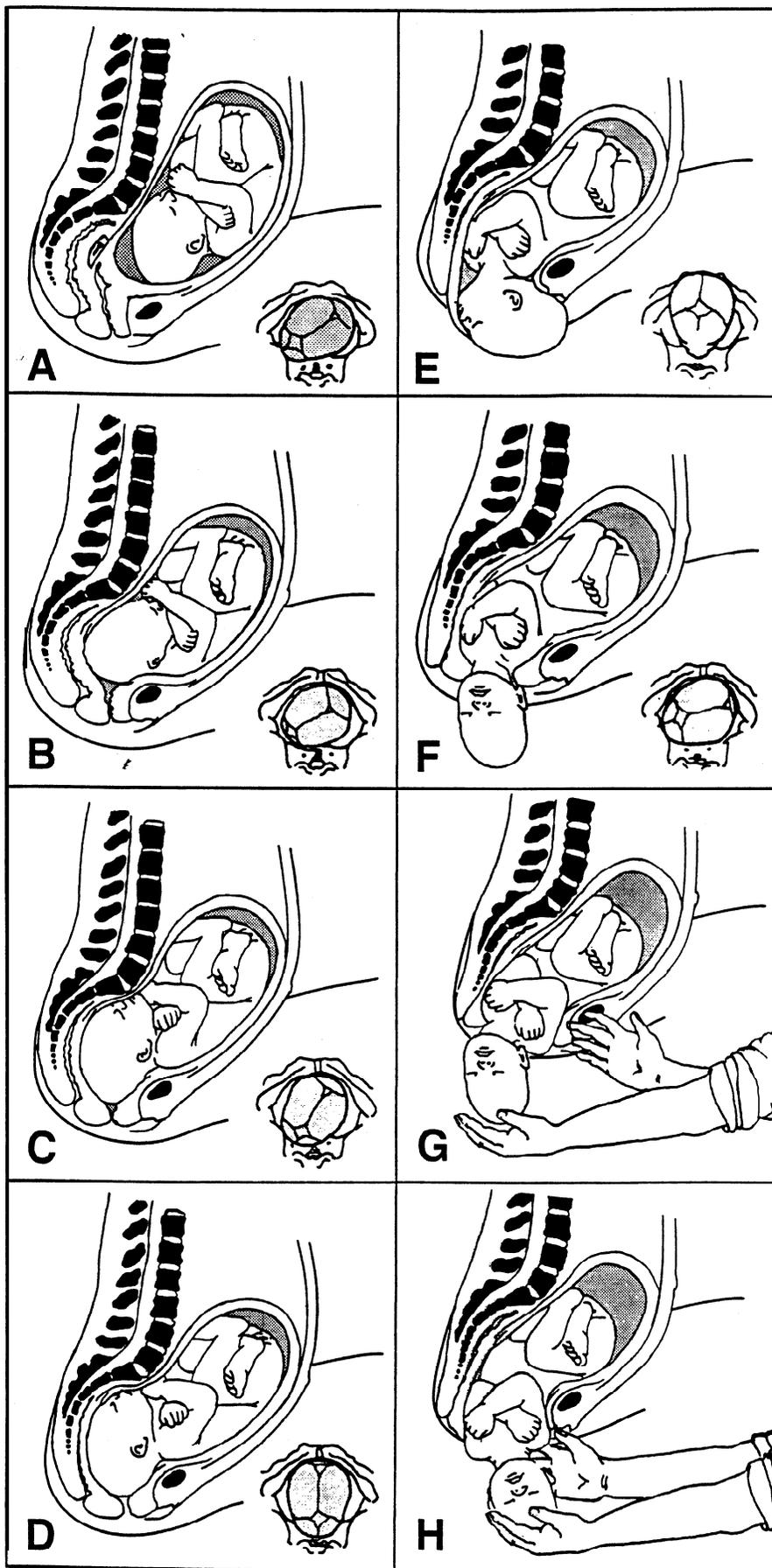
anatomy represents a significant departure from the pattern in apes and that they were bipedal (Fig. 4). The pelvis of both australopithecine specimens includes a birth canal that is extremely wide (i.e., platypelloid), both absolutely and relative to stature. Tague and Lovejoy showed that in contrast to the twisted birth canal' of modern humans, the australopithecine birth canal maintains the same shape throughout its passage from inlet to outlet. This makes it similar to the straight passageway of the nonhuman primate birth canal, but with the significant difference in the orientation of its longest diameter.

An important point is that the modifications in morphology visible in the bony fossil remains and footprints of

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early hominids occurred primarily because of locomotor rather than obstetrical demands. However, these locomotor changes had important consequences with regard to the way that early hominids gave birth.

Studies of the birth process in australopithecines yeilded diverse conclusions: that the process was "quick and easy"; that it was similar to the modem human process in degree of difficulty[28] or in "mechanism of birth"[29,30]; or that it was unlike the process in any living human or nonhuman primates. Tague and Lovejoy[21] assumed that australopithecine infants had cranial dimensions similar to those of a modern chimpanzee infant[3 1,32] and that "the shape of the maternal pelvis directs that pattern of

Figure 3. The passage of the human fetus through the maternal birth canal. Each box shows a sagittal section through the maternal body of a woman squatting during labor. The maternal pubic bone, sacrum, and vertebrae are shown in black (other parts of the bony skeleton are not visible in this midline view), In the lower right corner of each box is a "midwife's- eye" view of the fetus as it rotates within and emerges from the birth canal.

birth." Using the morphology of known australopithecines, they inferred a mechanism of birth. The australopithecine infant cranium would have been too long to enter the pelvic inlet if it were oriented in the same direction as a nonhuman primate (i.e., facing either forward or backward, but with its sagittal axis aligned with. the sagittal axis of the mothers body). At the inlet, then, the australopithecine infant cranium would have had a human-like orientation. Tague and Lovejoy suggested, however, that because the australopithecine birth canal had a constant shape throughout, there would have been no "bony resistance to fetal descent" and the infant would have moved through the passageway in this sideways facing orientation. Although they suggested that birth may have been "slow and difficult," rotation within the birth canal would have been unnecessary, given the size of the infant head, and impossible, given the platypelloid[16] shape of each pelvic plane.

This proposed mechanism of birth for australopithecines is unlike that known for any living animal and represents a mosaic of features, including some aspects of modern human birth, such as the orientation of the infant's head in the pelvic inlet; coupled with a lack of rotation as the fetus passes through the birth canal. This unique mechanism was not, as implied by the Washburn quote at the start of this paper, a product of either encephalization or secondary altriciality, for these human adaptations had not yet evolved. Instead, the australopithecine mechanism resulted from obstetrical modifications necessary in a small-brained hominid that had undergone massive alterations in pelvic morphology as a result of the shift to terrestrial bipedalism.

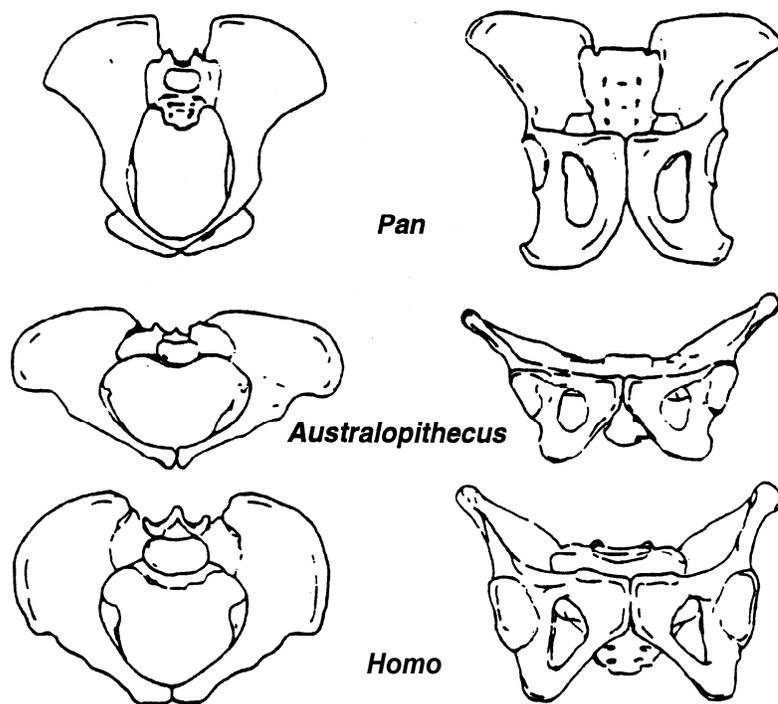Fetal rotation in modern human

Figure 4, A chimpanzee (top), australopithecine (the reconstructed pelvis of A.L. 288-l) (middle), and the pelvis of a modern human female (bottom) in approximately superior (left) and anterior (right) views. Note the shape of the pelvic inlet in the superior views. The chimpanzee inlet is long in the sagittal plane whereas both hominid inlets are broad transversely (though the modern human is also more spacious in the sagittal plane than is the australopithecine). Redrawn from Tague and Lovejoy and Rosenberg.[20]

ways, our species is typical of precocial mammals in having small litters, a long gestation, hemochorial placentas, and large brains, and thus probably evolved from prehominid ancestors that gave birth to more precocial young. However, modern human young typically are altricial, being extremely undeveloped at birth as compared with infants of other primate species. This observation has led to speculation about the gestation length that would have been characteristic of past hominids. Some authors[34-36] have suggested that in the past gestation was longer, either absolutely, or relatively, than it is at pre-

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births, however, is not simply a mechanism to accommodate a large cranium. An additional characteristic that may have had an impact on birth in hominids may have been important first in australopithecines. Hominoids as a group have broad, rigid shoulders, which are associated with their locomotor adaptations. In modern humans, shoulder dystocia, or obstruction of an infant's shoulders, is associated with increased mortality for both mothers and infants, especially when the pelvis is platypelloid. Although this does not present a problem to the large-bodied great apes because of their spacious birth canals, it may have been source of difficulty and, hence, selection, in early hominids. It is possible that after the australopithecine fetal head passed through the pelvic outlet without rotating within it, it had to rotate so that the wide shoulders at a ninety-degree angle to the long axis of the head, could also pass through the pelvic passageway. This hypothesis remains untested, but we suggest that shoulder size may have been an important constraint during hominid

birth and, along with increased infant cranial size, may have been among the causes of selection for the more rounded pelvis of later hominids.

Recently, based on their reconstructions of A.L. 288-l and STS 14, Häusler and Schmid[33] have proposed that birth in *Australopithecus* may have involved rotation of the fetus in a manner similar to modern human birth. In addition, these authors offer the provocative hypothesis that A.L. 288-l may have been male. (Because of the small size of the specimen, that suggestion would require the presence of two australopithecine species at Hadar.) Ruff[40] has pointed out that, regardless of the sex of A.L. 288-1, Häusler and Schmid's estimates of the birth canal size and shape in australopithecines are, in fact, consistent with a nonrotational birth mechanism, at least as far as the head is concerned, though not necessarily the shoulders.

BIRTH AND ENCEPHALIZATION

Humans are often described as being secondarily altricial. In many

sent. The human 38-week gestation is not very different from the gestation periods of our close relatives, the great apes-35-39 weeks for orangutans, 32 weeks for chimpanzees, and 37 weeks for gorillas-and probably is close to the length of primitive hominoid gestation. However, humans are born at a stage of development at which they are more helpless than the neonates of our relatives. Montagu[37] referred to the period immediately after the birth of human infants as "exterogestation," suggesting that the human neonate continues for some time to function more as a fetus than an infant. Clearly, the extreme helplessness of human newborns has important behavioral implications for such areas as parental
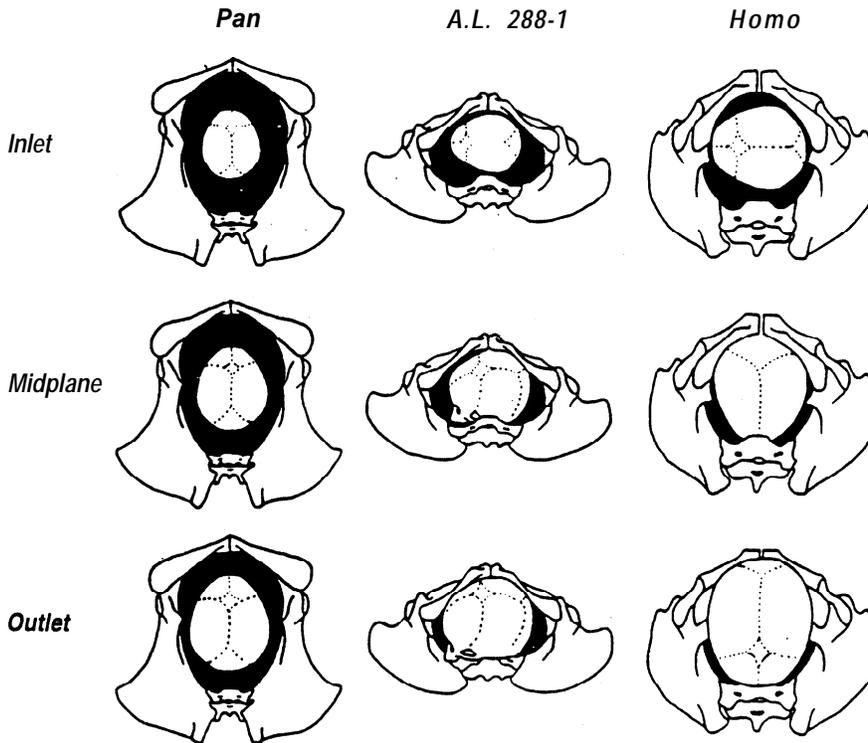
Pan	A.L. 288-1	Homo
Inlet		
Midplane		
Outlet		

Figure 5. Comparisons of the mechanisms of birth in Pan, *Australopithecus afarensis* and modern Homo. This diagram shows the "midwife's-eye" view of a neonatal head passing through the birth canal. In each drawing, the maternal pelvis and fetal head are shown in inferior view, with the sacrum at the bottom of the picture and the pubic symphysis at the top. This view corresponds to the drawing in the lower right hand corner of each box in Figure 3. Redrawn from Tague and Lovejoy.[21]

behavior and social relationships.

When did secondary altriciality evolve in humans? Martin[38] proposed that approximately 1.5 mya, the pelvic size placed a limit on prenatal brain growth. Until that time, brain size could have increased simply by increasing the fetal rate of growth rather than by altering the postnatal rate. Two changes could have allowed encephalization to continue: for human infants to become secondarily altricial (that is, to have a smaller percentage of adult brain size at birth), or for birth to occur at a relatively earlier time in fetal development. The only other possibility would have been alteration of the shape of the pelvis and change in the mechanism of birth.

Unfortunately, no complete pelvic apertures of early Homo are available. Based on the fragmentary adolescent male skeleton WT 15000 from Kenya, dated at 1.5 mya, Walker and Ruff[39] estimated the pelvic capacity of an adult female *Homo erectus* and sug-

gested that it could accommodate a modern fetus at 32 to 33 weeks of gestation. They concluded that in order to achieve adult *Homo erectus* cranial capacity, this species must have been characterized by a modern human-like pattern of growth in which rapid brain growth continues after birth rather than an -ape-like pattern of growth in which the timing of birth corresponds to a decline in the rate of brain growth. This would mean that *Homo erectus* birth was nonrotational, as in australopithecines, but that secondary altriciality was present.

Ruff[40] has recently suggested, based on biomechanical concomitants of pelvic expansion in the femur, that early *Homo*, like *Australopithecus*, had a wide, platypelloid pelvis and a nonrotational birth mechanism like that proposed for australopithecines. He further suggests that the increases in cranial capacity above the average of 900 cc reached in *Homo* by l-l.5 mya became possible only when a rotational mechanism of birth had

evolved. This would mean that secondary altriciality evolved in humans some time after 1.5 mya. If this is correct, *Homo habilis*, with an adult cranial capacity of approximately 700 cc, was the last hominid to deliver infants with the typical mammalian pattern in which half of brain growth has been completed. If, as suggested earlier, shoulder dystocia was a significant source of selection in australopithecines, necessitating rotation of the head after its passage through the bony birth canal, this would have been true of *Homo erectus* as well. Hence these early hominids may have had a rotational form of birth. This rotation may have been different from that in modern humans, however, in that it would have been necessary to accommodate only the broad shoulders of *Australopithecus* and early *Homo* rather than both the large head and broad shoulders of the modern human fetus.

SPECULATION ABOUT BIRTH IN ARCHAIC HOMO, INCLUDING NEANDERTALS

In Neandertals and other archaic humans, the anterior portion of the pelvis generally is elongated.[41] Moreover, this portion of the pelvis is expanded in modern females relative to males. Several hypotheses about the functional significance of this morphology suggested that archaic and modern humans differ in such aspects of reproductive biology as gestation length,[34] accelerated fetal growth,[42] and maternal-fetal size relationships.[43] It is clear now that female archaic humans fall within the modern female human range for pubis length and size of the birth canal relative to body size. It can be thus concluded that these archaic humans probably gave birth much as modern humans do, not only with respect to the mechanism of birth (i.e., rotation of the fetus as it passes through the birth canal and emergence of the infant from the birth canal in the occiput anterior position), but also in the behavior associated with birth (i.e., obligate midwifery[10]). Differences between male archaic humans (Neandertals) and modern males exist, but remain unexplained, although hypotheses focusing on locomotor differences have been proposed.[44]

A corollary issue that arises from discussion of the evolution of human birth is the question of when the modern human pattern of pelvic sexual dimorphism arose.[45] Modern human sex differences in the pelvis are a reflection of differing balances of the selective constraints on males and females imposed by locomotion and birth. It seems probable that, like the modern pattern of birth, the evolution of pelvic sexual dimorphism took place in a mosaic fashion.

One result of the anatomical changes in the pelvis and concomitant changes in the way human babies are born is that birth has been transformed from the solitary event that it is for nonhuman primates and other mammals into a social and cultural event. This is a result of the fact that the human infant emerges from the birth canal facing away from the mother, which, as noted previously, hinders her ability to help her child. The presence of another individual who can assist in the final stage of delivery reduces the risk of mortality for the infant and probably for the mother as well. Thus, as the modem process of birth evolved, selection began to favor hominid females who sought the assistance of others during birth. Although the proximate causes of seeking companionship during birth include pain, fear, other emotional stress, or conformity to cultural norms, the ultimate cause of this behavior may be that it reduces mortality. The evolutionary process has resulted in heightened emotional needs during labor, which lead women to seek companionship at this time. This suggests that the desire for supportive, familiar people at birth is deeply rooted in human evolutionary history

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