Neonatal Shoulder Width Suggests a Semirotational, Oblique Birth Mechanism in *Australopithecus afarensis*

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ABSTRACT

Birth mechanics in early hominins are often reconstructed based on cephalopelvic proportions, with little attention paid to neonatal shoulders. Here, we find that neonatal biacromial breadth can be estimated from adult clavicular length ($R^2 = 0.80$) in primates. Using this relationship and clavicular length from adult *Australopithecus afarensis*, we estimate biacromial breadth in neonatal australopiths. Combined with neonatal head dimensions, we reconstruct birth in *A. afarensis* (A.L. 288-1 or Lucy) and find that the most likely mechanism of birth in this early hominin was a semi-rotational oblique birth in which the head engaged and passed through the inlet transversely, but then rotated so that the head and shoulders remained perpendicular and progressed through the midplane and outlet oblique to the main axis of the female pelvis. Any other mechanism of birth, including asynclitic birth, would have resulted in either the head or the shoulders orthogonal to the short anteroposterior dimension of the A.L. 288-1 pelvis, making birth untenable. There is a tight fit between the infant and all planes of the birth canal, perhaps suggesting a difficult labor in australopiths. However, the rotational birth mechanism of large-brained humans today was likely not characteristic of *A. afarensis*. Thus, the evolution of rotational birth, usually associated with encephalization, may have occurred in two stages: the first appeared with the origin of the australopiths with their platypelloid pelves adapted for bipedalism and their broad-shouldered neonates; the second which resulted in the modern mechanism of rotational birth may be associated with increasing brain size in the genus *Homo*. Anat Rec, 300:890–899, 2017. © 2017 Wiley Periodicals, Inc.

Key words: birth; *Australopithecus*; neonatal

INTRODUCTION

"and even if my head would go through," thought poor Alice, "it would be of very little use without my shoulders." Lewis Carroll, *Alice's Adventures in Wonderland*.

While the mechanism of birth can be variable in both humans (Walrath, 2003) and in nonhuman primates

(Elder and Yerkes, 1936; Stoller, 1995; Hirata et al., 2011; Trevathan, 2015), humans, in general, give birth in a unique way (Trevathan, 1987; Rosenberg, 1992; Rosenberg and Trevathan, 1995). In nonhuman primates, the female pelvis is anteroposteriorly expanded and accordingly, the neonate enters the pelvic inlet sagittally, with the longest (occipitofrontal) dimensions of the cranium aligned with the AP axis of the pelvis. Although some form of rotation in chimpanzees and some monkeys has been documented (Elder and Yerkes, 1936; Stoller, 1995; Hirata et al., 2011; Trevathan, 2015), it is thought that most births in nonhuman primates proceed in this sagittal, nonrotational orientation such that the infant is born with the front of the head facing anteriorly, allowing the mother to safely assist with her own delivery (Rosenberg, 1992).

In bipedal hominins, there has been a reduction in the distance between the sacroiliac joint and the acetabulum (Berge et al., 1984; Tague and Lovejoy, 1986) resulting in an anteroposteriorly shortened pelvic inlet. The neonatal head generally cannot engage with the inlet in a sagittal orientation and instead enters the birth canal with the long occipitofrontal axis of the cranium flexed and either obliquely or transversely oriented. Given the platypelloid shape of *Australopithecus* female pelves, it is likely that this derived transverse entry of the neonatal head into the birth canal has been occurring for at least the last 3 million years (Berge et al., 1984; Tague and Lovejoy, 1986; Claxton et al., 2016).

In modern humans, the pelvic midplane is shaped differently than the pelvic inlet, being transversely reduced and relatively anteroposteriorly expanded. This changing dimension results in the neonatal head internally rotating as it progresses through the midplane and outlet. Furthermore, the back of the neonatal head (the broadest dimension of the skull) typically aligns with the front of the mother's pelvis (usually broadest at the midplane). It has previously been argued that this tendency for the human baby to emerge facing away from the mother—a position obstetricians call occiput anterior—provides an advantage to having companionship or at least minimal assistance during birth (Trevathan, 1987, 1988, 1996; Rosenberg and Trevathan, 2001)

However, owing to a lack of complete, undistorted, female fossil hominin pelves, it has been difficult to determine when the human-like rotational birth became the most frequent mechanism of delivery. Some have suggested that internal rotation of the neonate and occiput anterior presentation was already happening in the australopiths (Berge et al., 1984; Häusler and Schmid, 1995; Berge and Goularas, 2010). Others have posited that rotation is not necessary in small-brained australopiths (Tague and Lovejoy, 1986; Lovejoy, 1988; Tague, 1991; Abitbol, 1996) and that only with the encephalization characteristic of early *Homo* did rotational births became the norm (Ruff, 1991; Ruff, 1995; Weiner et al., 2008; Ruff, 2010). Late Pleistocene fossils indicate to some that Neanderthals shared with modern humans a rotational mechanism of birth (Trevathan, 1987; Trevathan, 1988; Rosenberg, 1992; Arsuaga et al., 1999; Trevathan and Rosenberg, 2000; Ponce de León et al., 2008; Franciscus, 2009). Still others have argued that even Neanderthals lacked rotational births and that the modern human mechanism of parturition is quite recent and restricted to anatomically modern *Homo sapiens* (Weaver and Hublin, 2009).

In a study of the obstetric pelvis of *Australopithecus afarensis*, Tague and Lovejoy (1986) used the dimensions of Lovejoy's reconstruction of A.L. 288-1 to propose a unique, transverse, nonrotational method of birth in *A. afarensis*. Because the A.L. 288-1 pelvis remains platypelloid (transversely wide) throughout the entire length of the birth canal, they hypothesized that the occipitofrontal axis of the neonatal head would have aligned with the transversely wide pelvic dimensions and been born in an "asynclitic" manner (Tague and Lovejoy, 1986). Häusler and Schmid (1995) presented a slightly different reconstruction of the A.L. 288-1 pelvis and proposed that the *A. afarensis* hypodigm is a mixture of two species and that the obstetric pelvis of the A.L. 288-1 individual was not spacious enough to have successfully given birth—effectively making "Lucy" a male. An academic exchange followed that addressed not only the mechanics of birth in *A. afarensis* but the sex of the A.L. 288-1 specimen (Häusler and Schmid, 1995; Wood and Quinney, 1996; Tague and Lovejoy, 1998; Berge and Goularas, 2010).

However, what is too often forgotten in efforts to reconstruct birth in extinct hominins is that fetal rotation in humans today involves both the neonatal head and the neonatal shoulders (Trevathan, 1987; Rosenberg and Trevathan, 1995; Trevathan and Rosenberg, 2000). The longest axis of the shoulders (biacromial breadth) is perpendicular to the longest axis of the head and in modern humans, the shoulders typically follow the same path and series of rotations as the head. Humans and apes (and likely, early hominins) have broad, rigid shoulders. Thus although the size of the brain may not have required rotational birth [indeed Tague and Lovejoy (1986) argued that the head *could not* have rotated], it has been hypothesized that the broad shoulders of an *A. afarensis* neonate could not have passed through the A.L. 288-1 pelvic inlet (with its short AP dimension) without some rotation (Trevathan and Rosenberg, 2000; Wittman and Wall, 2007).

When shoulders become arrested in the birth canal in humans today it is recognized clinically as shoulder dystocia (Beer, 2003). This condition can lead to birth injuries to the infant, (e.g., permanent damage in the form of brachial plexus injury, resulting in paralysis or palsy) or prolonged labor, leading to higher risk for maternal complications such as hemorrhage. Although the incidence of clinically recognized shoulder dystocia that constitutes a medical emergency is low (0.2–3.0% of all births [Ouzounian and Goodwin, 2010]), it is not uncommon for shoulders to be briefly arrested during fetal rotation and descent. Today, when shoulders fail to rotate, an attendant may be able to manipulate the emerging head, apply suprapubic pressure, or alter the mother's position, all of which may dislodge the shoulders. Given the potential for complications arising from broad shoulders passing through a platypelloid birth canal, and the advantages of having some form of assistance at birth in those cases, it is important to characterize not just cephalopelvic disproportion in *Australopithecus*, but also the relative size of the neonatal shoulders, in efforts to reconstruct birth mechanics and obstetric practices in our ancestors.

TABLE 1. Adult clavicular length and neonatal biacromial breadth in primates

Species	Adult		Neonate	
	N	Clavicular length (mm)	N	Biacromial breadth (mm)
Homo sapiens	198	149.2 ± 9.0	2604	119.6[a]
Pan troglodytes	25	125.5 ± 10.0	9	84.9
Gorilla gorilla	23	152.8 ± 20.6	4	92.0
Pongo pygmaeus	6	164.7 ± 22.7	4	81.8
Hylobates lar	85	87.2 ± 5.1	6	51.2
Nasalis larvatus	7	75.9 ± 6.1	1	59.0
Macaca spp.	12	57.6 ± 6.6	28	49.2
Ateles geoffroyi	1	57.0	8	50.4

[a]Neonatal biacromial breadth reported here is a weighted average of data reported in Schultz (1949) ($n = 10$), Tanner et al. (1956) ($n = 80$), Kaarma et al. (1997) ($n = 292$), and Verspyck et al. (1999) ($n = 2222$).

Here, we test models of birth mechanics in *A. afarensis* by calculating biacromial breadth in neonatal *A. afarensis* and simulating birth in this species using both reconstructions of A.L. 288-1 (Tague and Lovejoy, 1986; Häusler and Schmid, 1995).

MATERIALS AND METHODS

Obstetric dimensions of the A.L. 288-1 pelvis were obtained from both reconstructions of this fossil (Tague and Lovejoy, 1986; Häusler and Schmid, 1995). The relevant dimensions are the anteroposterior depth and mediolateral width of the pelvic inlet, midplane, and outlet (Table 2).

In addition to the standard AP and ML dimensions of the A.L. 288-1 pelvis, we calculated the oblique dimensions of the standard planes of the pelvis. The oblique dimensions are the conjugate diagonal distances across the pelvis and are relevant if the orthogonally positioned head and shoulders of a neonate cannot both pass through the birth canal. The oblique dimensions were calculated using the equation:

$$\text{Oblique diameter} = \sqrt{a^2 + b^2}, \text{ where}$$

$$a = \text{anteroposterior depth of pelvis}/\sqrt{2} \text{ and}$$

$$b = \text{mediolateral width of pelvis}\sqrt{2}$$

The linear dimensions of the neonatal head of an *Australopithecus afarensis* were modeled in two ways. First, it was assumed that *A. afarensis* had neonatal cranial dimensions identical to a newborn chimpanzee: biparietal (BP) 7.1 cm; occipitofrontal (OF) 8.3 cm (Tague and Lovejoy, 1986 from Schultz, 1949). Second, because the average adult cranial capacity in *A. afarensis* (~450 cm³) is roughly 20% larger than the average cranial capacity in modern chimpanzees (DeSilva, 2011) and because neonatal brain size scales with adult brain size in catarrhines (DeSilva and Lesnik, 2008), we find it reasonable that *A. afarensis* neonates may have had slightly larger brains at birth than do modern chimpanzees. Therefore, neonatal brain volume was calculated from the DeSilva and Lesnik (2008) ordinary least squares equation:

$$\log (\text{neonatal cranial capacity})$$
$$= 0.77 * \log (\text{adult cranial capacity}) + 0.19$$

Adult cranial capacity in *A. afarensis* averages 442.8 ± 74.5 cm³ based on five adult crania (Holloway et al., 2004; Kimbel and Rak, 2010). The 95% CI of the resulting neonatal cranial capacity is 168.6 cm³, which is only slightly larger than the average brain size in neonatal chimpanzees (DeSilva and Lesnik, 2006). This value differs slightly from the 173.8 cm³ reported in DeSilva and Lesnik (2008) because of the inclusion of a new *A. afarensis* skull A.L. 822-1 by Kimbel and Rak (2010). This neonatal cranial volume was converted to linear dimensions of a neonatal cranium following Claxton et al. (2016) by modeling the maximum dimensions of a neonatal skull as an ellipse using the equation:

$$\text{Volume of neonatal cranium} = (\pi/6) * a * b * c, \text{ where}$$

$a = $ biparietal breadth of cranium, $b = $ occipitofrontal length of cranium, and $c = $ height of cranium.

The relationship between these neonatal cranial dimensions are known in humans and in chimpanzees (Tague and Lovejoy, 1986; Simpson et al., 2008) and average to:

$$\text{Occipitofrontal length of cranium} = 1.22 * \text{biparietal breadth}$$

$$\text{Height of neonatal cranium} = 0.65 * \text{biparietal breadth}$$

The resulting equation becomes:

$$\text{Volume of neonatal cranium} = (\pi/6) * a * (1.22 * a)$$
$$* (0.65 * a), \text{ or :}$$
$$\text{Volume of neonatal cranium} = a^3 * 0.415$$

Solving for the dimension of the cranium (a) rearranges the equation to:

$$a \text{ (biparietal breadth)} = \sqrt[3]{\text{volume of cranium}/0.415}$$

Given the relationship noted above between biparietal breadth, occipitofrontal length and cranial height, once biparietal breadth is calculated, the other dimensions can be as well.

Neonatal shoulder width (biacromial breadth) in extant primates was obtained from the literature

TABLE 2. Obstetric dimensions in *Australopithecus afarensis*

	Inlet			Midplane			Outlet		
A.L. 288-1 reconstruction	ML	AP	Oblique	ML	AP	Oblique	ML	AP	Oblique
Tague and Lovejoy (1986)	13.2	7.6	10.8	10.1	7.2	8.8	9.6	7.1	8.4
Häusler and Schmid (1995)	12.5	7.8	10.4	9.5	8.6	9.0	8.7	8.8	8.8

TABLE 3. Neonatal cranial and biacromial dimensions in humans, chimpanzees, and *Australopithecus*

	Australopithecus afarensis	*Pan troglodytes*	*Homo sapiens*
Occipitofrontal length of neonatal head	~9.0 cm	8.3 cm[a]	12.4 cm[a]
Biparietal breadth of neonatal head	~7.4 cm	7.1 cm[a]	9.9 cm[a]
Neonatal biacromial breadth	~8.7 cm (range 8.0–9.4)	8.5 cm	11.8 cm

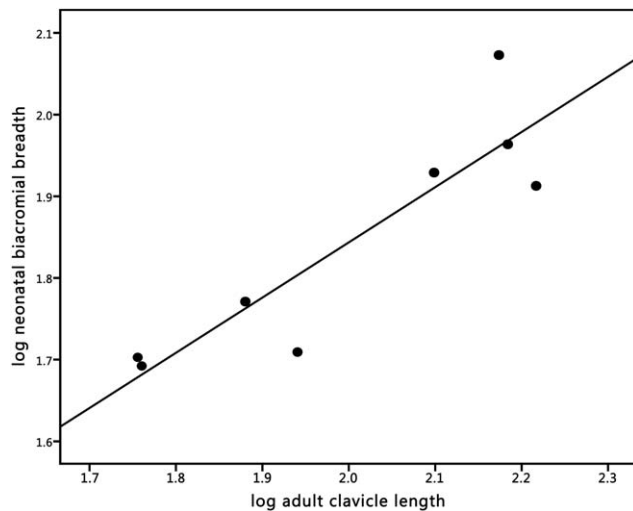[a]Data from Schultz (1949) via Tague and Lovejoy (1986).

Fig. 1. Adult clavicular length predicts neonatal biacromial breadth in primates (R^2 = 0.80). The OLS regression equation is: $y = 0.68x + 0.49$. The RMA regression equation is: $y = 0.76x + 0.32$. In this study, the OLS equation was used to predict biacromial breadth in neonatal australopiths.

(Schultz, 1949). These data are difficult to obtain and are known from only 8 primate species: *Homo sapiens*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*, *Hylobates lar*, *Macaca mulatta*, *Nasalis larvatus*, and *Ateles geoffroyi*. Adult clavicular lengths were measured on extant primates at the Harvard Museum of Comparative Zoology and the American Museum of Natural History (Table 1). These data were supplemented with published measurements (Schultz, 1930; Tanner et al., 1956; Rodman, 1979; Bass, 1995; Kaarma et al., 1997; Verspyck et al., 1999). Neonatal biacromial breadth from *Macaca mulatta* (Schultz, 1949) was compared with adult clavicular length from *Macaca nemestrina* (Rodman, 1979) given the nearly identical body size of both species (Smith and Jungers, 1995). The utility of the adult clavicular length in predicting neonatal biacromial breadth was assessed with both reduced major axis (RMA) regression and with ordinary least squares (OLS).

Neonatal shoulder width in *A. afarensis* was calculated by applying adult clavicular length to the OLS equation describing the relationship between adult clavicular length and neonatal biacromial breadth in extant primates. In *A. afarensis*, the adult clavicular length from the large male skeleton KSD-VP-1/1 is between 156.4 and 157.2 mm (Haile-Selassie et al., 2010; Melillo, 2016). It may be inappropriate to use such a large male clavicle to simulate birth constraints in the small female pelvis from A.L. 288-1. Therefore, we included two additional specimens. First, a smaller partial clavicle from *Au. afarensis*, A.L. 333 ×-6/9, is estimated to have been 134.0 mm long (Melillo, 2016). Additionally, using sex differences in clavicular length in *Gorilla* (n = 10 females; n = 13 males) we applied a *Gorilla*-like clavicular dimorphism to *A. afarensis* (assuming KSD-VP-1/1 is a typical male), yielding an estimated clavicular length in the small Lucy-like females of 123.2 mm, similar to the average clavicular length in chimpanzees (125.5 mm). This is not to say that dimorphism was *Gorilla*-like in *A. afarensis*, but instead this approach was used as an extreme to calculate the minimum likely biacromial breadth in a neonatal australopith. The average of the smaller-bodied presumably female *A. afarensis* clavicle, the 333 clavicle, and the large-bodied male *A. afarensis* clavicle was used to calculate the average neonatal biacromial breadth in a full-term *A. afarensis* infant.

RESULTS

Using the dimensions of the A.L. 288-1 pelvis as reconstructed by Tague and Lovejoy (1986), the oblique length of the pelvic inlet is 10.8 cm, the midplane 8.8 cm, and the outlet 8.4 cm, consistent with the funneling morphology found by others (Berge et al., 1984; Tague and Lovejoy, 1986; Häusler and Schmid, 1995; Table 2). Using the Häusler and Schmid (1995) reconstruction results in oblique dimensions of 10.4 cm (inlet), 9.0 cm (midplane), and 8.8 cm (outlet) as shown in Table 2.

From a predicted neonatal cranial volume of 168.6 cm³, an *A. afarensis* newborn would have had on average cranial dimensions of 7.4 cm biparietal and 9.0 cm occipitofrontal. This is slightly larger than the 7.1 cm BP and 8.3 cm OF dimensions of a modern chimpanzee neonate (Table 3).

Adult clavicular length is a strong predictor (R^2 = 0.80) of neonatal biacromial breadth in primates (Fig. 1).
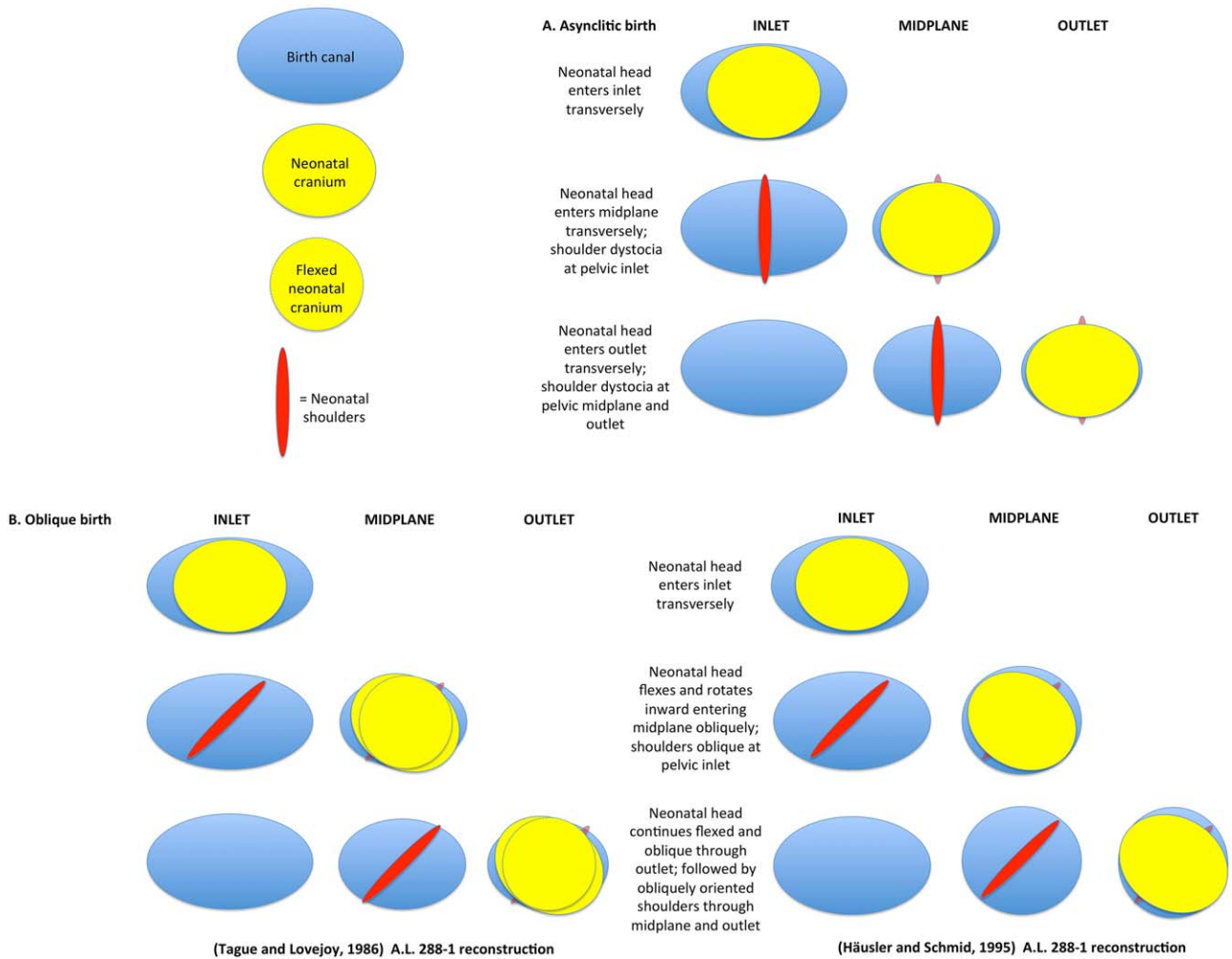
Fig. 2. Birth scenarios in A.L. 288-1. (A) The asynclitic mechanism of birth proposed by Tague and Lovejoy (1986) explains how the neonatal head passes through the platypelloid pelvis of an *A. afarensis*, but would not permit passage of the shoulders. (B) Using the Tague and Lovejoy (1986) dimensions of the A.L. 288-1 reconstruction, internal rotation of the neonate at the midplane and an oblique orientation of the shoulders and a flexed head would be required for birth. Note the tight fit between the neonatal cranium and the pelvic midplane and outlet. (C) Using the Häusler and Schmid (1995) reconstruction, birth of an *A. afarensis* neonate is slightly easier, but only via internal rotation at the midplane and an oblique orientation of both the head and the shoulders.

The ordinary least squares regression is: $y = 0.68x + 0.49$

The reduced major axis regression (RMA) equation is: $y = 0.76x + 0.32$

where $y = \log$ (neonatal biacromial breadth) and $x = \log$ (adult clavicular length).

Application of this regression equation to *A. afarensis* adult clavicles yields a neonatal biacromial breadth of approximately 8.7 cm (average of 8.0 cm using the A.L. 288-1 estimate, 8.5 cm from A.L. 333x-6/9, and 9.4 cm using the KSD-VP-1/1 clavicular length) as shown in Table 3.

The use of these dimensions for reconstructing birth mechanics in *A. afarensis* is presented in "Discussion" below.

DISCUSSION

Using these dimensions, we can test the asynclitic hypothesis of birth in *A. afarensis* (Tague and Lovejoy, 1986) and reexamine the mechanism by which this species may have delivered its offspring. The head dimensions of a neonatal *A. afarensis* (estimated to be 7.4 cm BP and 9.0 cm OF) would likely have entered the platypelloid inlet of A.L. 288-1 transversely, as others have proposed (Berge et al., 1984; Tague and Lovejoy, 1986). This is true whether the Tague and Lovejoy (1986) or Häusler and Schmid (1995) reconstruction is used, given similarities in both of their inlet measurements (Fig. 2). Furthermore, the neonatal head appears to have been able to continue transversely into the midplane given the platypelloid shape of the A.L. 288-1 midplane. However, while the neonatal cranium was reaching the midplane, the neonatal shoulders would be approaching the inlet. We can infer this because the approximate distance between the pelvic inlet and the ischial spines in A.L. 288-1 (~5 cm) is roughly the same as the cranial height of a neonatal *A. afarensis* (see "Materials and Methods": cranial height = biparietal diameter × 0.65 = 4.8 cm), though we do not consider
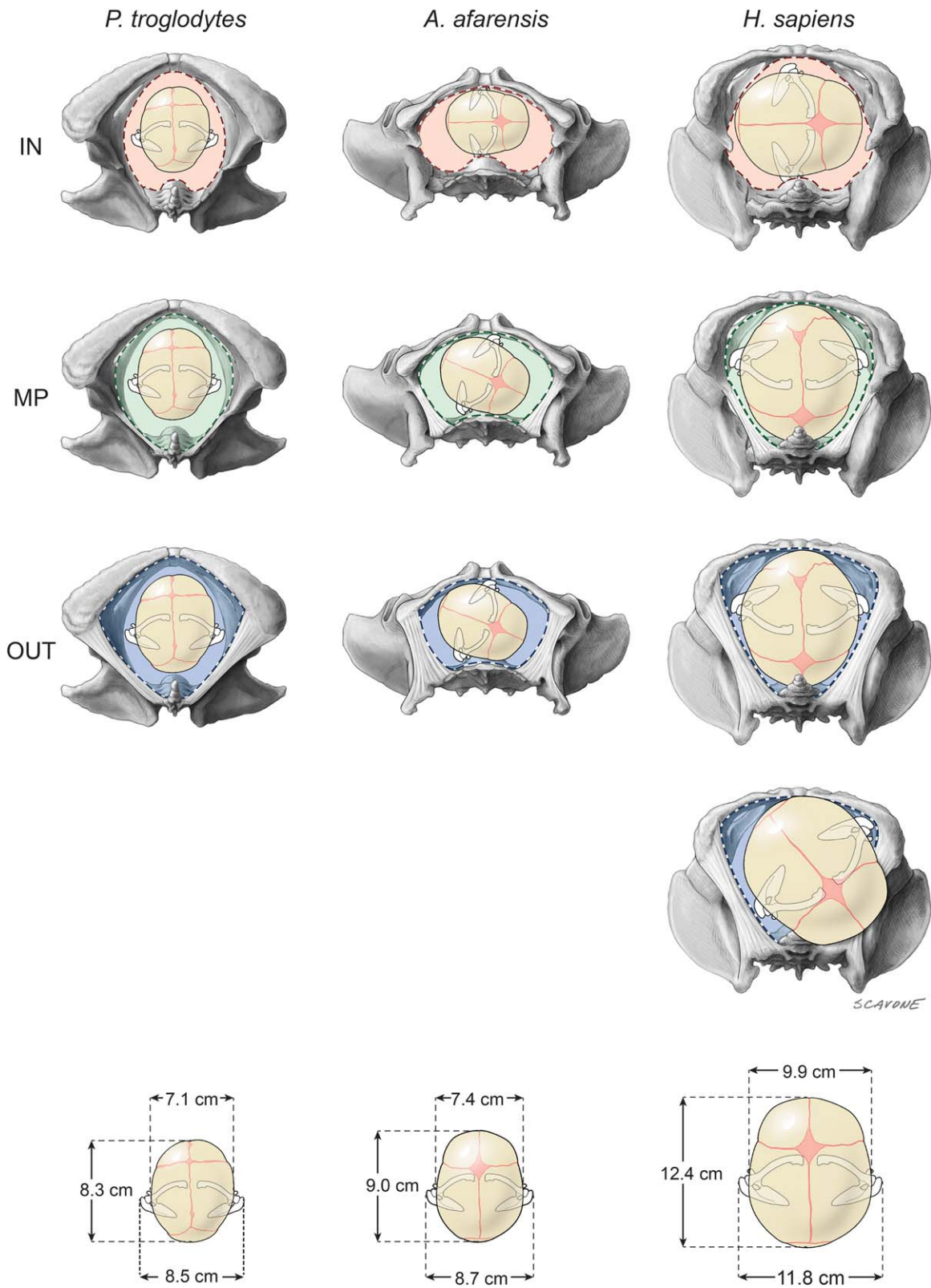
Fig. 3.

the length of the neonatal neck and assume a somewhat flexed neonatal head. The estimated biacromial breadth of a neonatal *A. afarensis* (8.7 cm; range 8.0–9.4 cm) exceeds the inlet anteroposterior dimension of the A.L. 288-1 pelvis (7.6–7.8 cm). If birth proceeded in this manner, shoulder dystocia could have resulted, increasing the likelihood of injury to the infant, fetal or maternal death, or both (Trevathan, 1988). In fact, shoulder dystocia is most commonly a problem in platypelloid shaped pelves (Rosenberg and Trevathan, 1995), the precise shape of the A.L. 288-1 pelvis. Even if the minimum biacromial breadth (8.0 cm) is applied to this hypothetical birth scenario, the neonatal shoulders would still have been larger than the anteroposterior dimensions of the inlet. Certainly, compression of the shoulders and relaxation of the pelvic ligaments could have resulted in enough sacral mobility to increase the AP dimension enough to have squeezed the shoulders through the AP dimensions while the head continued transversely. However, the AP dimensions get even smaller (7.2 mm midplane; 7.1 mm outlet) in the Tague and Lovejoy (1986) reconstruction, making shoulder dystocia more and more likely throughout the birth process, and making this birth mechanism more and more dangerous (Fig. 2). We suggest that there is a simpler solution to this obstetric challenge.

While it is likely that the neonatal cranium entered the pelvic inlet transversely, spiral contractions of the uterus (explained in Berge and Goularas, 2010) may have internally rotated the neonate through the inlet, allowing the neonatal head to engage with the midplane obliquely. The oblique dimensions of the midplane (8.8–9.0 cm) are sufficient to pass a slightly flexed neonatal cranium (9.0 mm OF; less if presenting the suboccipital-bregmatic (SOBR) axis in a flexed position). Meanwhile, the oblique dimensions of the inlet (10.4–10.8) are sufficiently large to fit the shoulders even if the very largest biacromial estimate from a neonate (9.4 cm) is used.

Given that the oblique dimensions remain larger than the AP dimensions in all reconstructions of the A.L. 288-1 pelvis, we propose that this oblique, semirotational neonatal position was maintained through the remainder of the birthing process (Fig. 3). The female *A. afarensis* pelvis funnels, making the fit between neonate and the birth canal tighter and likely resulting in a more difficult delivery. We therefore agree with others that birth in australopiths was challenging (Berge et al., 1984; Häusler and Schmid, 1995; Wells et al., 2012; Claxton et al., 2016) and not "quick and easy" (Leutenegger, 1972, p. 569). Whether semirotation of the neonate into an oblique position, combined with a strenuous birth

would have encouraged other (presumably female) *A. afarensis* to assist during birth—a contemporary human universal (Trevathan, 1987; Rosenberg and Trevathan, 1995; Rosenberg and Trevathan, 2001; Trevathan, 2015)—remains unclear. However, given the potential for complications arising from broad shoulders passing through a platypelloid birth canal, we suggest that the advantages of having some form of assistance at birth may have been present in the australopiths.

Regardless of whether birth was a social event in australopiths, these data on shoulder dimensions make an asynclitic method of birth in *A. afarensis* unlikely. Additionally, the dimensions of the A.L. 288-1 pelvis—particularly in the AP dimension—make it unlikely to us that full human-like rotational birth occurred in *A. afarensis* either. This is because either the longest dimension of the head (occipitofrontal) or the orthogonally oriented shoulders would have contended with the anteroposteriorly narrow midplane or outlet if full human-like rotation occurred. Given that the oblique dimensions are wider than the anteroposterior dimensions, following Joulin's Law (1864), we instead find it most likely that the neonate passed through the dimensions of least resistance for both the head and the shoulders—the oblique dimension.

It still remains unclear whether the upper thorax of *A. afarensis* was more human-like (mediolaterally broad and barrel shaped) or ape-like (funnel shaped). Recent evidence has pointed toward a thorax and shoulder girdle that was mediolaterally wide and in many ways more human-like than ape-like (Haile-Selassie et al., 2010; Melillo, 2016; Latimer et al., 2016); whereas others have reconstructed the thorax as more funnel shaped (Schmid, 1991) and there is evidence for a more *Gorilla*-like shoulder in at least juvenile *A. afarensis* (Green and Alemseged, 2012). Critical to our analysis is the observation that that the shoulder dimensions in neonatal *A. afarensis* remain problematic for birth in the AP plane even if we substitute the biacromial breadth of a neonatal chimpanzee (8.5 cm). If—as many have suggested (e.g., Haile-Selassie et al., 2010)—the upper thorax in *A. afarensis* was more human-like, then the biacromial breadth of a neonatal chimpanzee would likely underestimate *A. afarensis* newborn shoulder width, exacerbating the problem we have outlined here.

Therefore, the evolution of the modern human birth mechanism requiring a series of rotations may have occurred in two stages. The first was associated with rotation of the shoulders as the infant head emerged from the birth canal so that the broad shoulders could pass through the broad transverse dimension of the pelvic inlet and midplane. We propose that this first

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Fig. 3. Hypothesized mechanism of birth in *Australopithecus afarensis* compared with birth in *Pan troglodytes* and *Homo sapiens*. From top to bottom, the illustrated sequences follow birth from the inlet, through the midplane, and the outlet. The bottom row provides measurements of the neonatal cranium and biacromial breadth used in this study. In chimpanzees, the neonatal head is oriented sagitally and typically, but not always, the orientation is occiput posterior. The shoulders are orthogonally positioned and there is sufficient space of the maternal pelvis both anteroposteriorly and mediolaterally. In humans (far right) the neonatal head enters the inlet obliquely or transversely.

At the midplane, the head internally rotates such that it is in occiput anterior position as it proceeds through the outlet. The fourth illustration shows the final maneuver required to deliver the wide shoulders in humans. As in humans, *Australopithecus* neonates engaged the inlet with the head positioned transversely. However, when the head reached the midplane, the shoulders would engage with the anteroposteriorly narrow inlet and partial rotation would be required to fit both the head and the shoulders through the midplane and the outlet. Figure © Scavone, after Tague and Lovejoy (1986).

rotation appeared with the origin of the australopiths with their platypelloid pelves for bipedalism and their relatively large-bodied (DeSilva, 2011) and broad-shouldered neonates, but long before encephalization in the hominin lineage. It is not possible to pinpoint exactly when the second stage evolved. It could have evolved within the australopith lineage itself since some have found evidence of human-like rotational birth in *A. africanus* (Berge et al., 1984; Häusler and Schmid, 1995; Berge and Goularas, 2010). Furthermore, different australopiths may have delivered in different ways given the substantial intrageneric postcranial variation that has been discovered in *Australopithecus* (Robinson, 1972; Harcourt-Smith and Aiello, 2004; Kibii et al., 2011; DeSilva et al., 2013; Haile-Selassie et al., 2012; Prang, 2015). Alternatively, it could be that human-like rotational birth did not evolve until the encephalization that characterized early *Homo* (Ruff, 1995; Tague and Lovejoy, 1986). Likely, by the time of the archaic *Homo sapiens*, seen in female fossil specimens from Jinniushan (Rosenberg et al., 2006), Tabun (Ponce de León et al., 2008), and the male from Sima de los Huesos (Arsuaga et al., 1999), the shape of the birth canal and sexual dimorphism in the pelvis had assumed modern configurations. Thus, the modern human mechanism of birth did not evolve as a monolithic unit; rather, like virtually all human characteristics, it evolved in a mosaic pattern.

Finally, we emphasize that whether the Tague and Lovejoy (1986) or Häusler and Schmid (1995) reconstruction is utilized, the limiting obstetric dimension in the A.L. 288-1 pelvis is the anteroposterior depth. Similarly, the limiting obstetric dimensions in the *A. africanus* Sts 14 (Berge and Goularas, 2010) and the MH2 *A. sediba* (Kibii et al., 2011) pelves are in the sagittal anteroposterior plane. In fact, australopith pelves are excessively wide mediolaterally, wider than they need to be to facilitate birth (Tague and Lovejoy, 1986). Berge and Goularas (2010) have argued that a mediolaterally wide pelvis is the primitive condition in the first hominins, likely a locomotor adaptation to increase the mechanical advantage of the lesser gluteals, which prevent pelvic tilt during the single-legged stance phase of bipedal gait (Lovejoy, 1988, 2005). While this particular bipedal adaptation does not compromise birth, given the ample mediolateral dimensions of the obstetric pelvis in all female australopiths, it likely meant that australopiths had to give birth in a manner that was different from the primitive condition. Furthermore, recent work finds no relationship between relative pelvic width and locomotor efficiency (Dunsworth et al., 2012; Warrener et al., 2015). If true, these findings call into question some predictions of the so-called "obstetrical dilemma[1]"—the hypothesis that there has been an evolutionary tradeoff between the competing demands of childbirth and locomotion in human evolution (Washburn, 1960).

Given the platypelloid shape of the australopith birth canal, we suggest that the anteroposterior dimension requires more careful consideration. The shortening of the lower iliac height via a reduction in the distance between the sacroiliac joint and the acetabulum has been recognized for years as a bipedal adaptation that lowers the center of mass and reduces the moment caused by the body weight around the hip joint (Straus, 1929; Schultz, 1930; Berge et al., 1984; Tague and Lovejoy, 1986). In addition to the mediolateral reduction of the pelvic midplane, it is this anteroposterior shortening of the pelvic inlet in particular that can introduce obstetric difficulties. Given the difficulties of human birth, some authors have wondered why the mediolateral dimensions of the pelvis do not increase (Dunsworth and Eccleston, 2015), especially given the apparent absence of locomotor consequences (Dunsworth et al., 2012; Warrener et al., 2015; but see Ruff 2017, this issue). However, we suggest that one may (and should) equally wonder why the anteroposterior dimensions of the pelvis have not increased. It is here where locomotor consequences of pelvic shape variation may exist, and where Washburn's (1960) obstetrical dilemma—positing a trade-off between locomotion and obstetrics—may still have explanatory power.

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[1]Here, we are solely describing the evolutionary trade-off between locomotor efficiency and/or minimization of lower limb injury and obstetric challenges. We are not using the "obstetrical dilemma" to characterize gestation length or the timing of birth. This aspect of Washburn's obstetrical dilemma has, in our opinion, been effectively refuted by Dunsworth et al. (2012).

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