Evolution of the human pelvis and obstructed labor: New explanations of an old obstetrical dilemma

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Abstract

Without cesarean delivery, obstructed labor due to a disproportion of the fetus and the maternal birth canal can result in maternal and fetal injuries or even death. The precise frequency of obstructed labor is difficult to estimate because of the widespread use of cesarean delivery for indications other than proven cephalopelvic disproportion, but it has been estimated that at least one million mothers per year are affected by this disorder worldwide. Why is the fit between the fetus and the maternal pelvis so tight? Why did evolution not lead to a greater safety margin, as in other primates? Here, we review current research and suggest new hypotheses on the evolution of human childbirth and pelvic morphology. In 1960, Washburn suggested that this "obstetrical dilemma" arose because the human pelvis is an evolutionary compromise between two functions, bipedal gait and childbirth. However, recent biomechanical and kinematic studies indicate that pelvic width does not considerably affect the efficiency of bipedal gait and thus is unlikely to have constrained the evolution of a wider birth canal. Instead, bipedalism may have primarily constrained the flexibility of the pubic symphysis during pregnancy, which opens much wider

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in most mammals with larger fetuses than in humans. We argue that the birth canal is mainly constrained by the trade-off between two pregnancy-related functions: while a narrow pelvis is disadvantageous for childbirth, it offers better support for the weight exerted by the viscera and the large human fetus during the long gestation period. We discuss the implications of this hypothesis for understanding pelvic floor dysfunction. Furthermore, we propose that selection for a narrow pelvis has also acted in males due to the role of pelvic floor musculature in erectile function. Finally, we review the cliff-edge model of obstetric selection to explain why evolution cannot completely eliminate cephalopelvic disproportion. This model also predicts that the regular application of life-saving cesarean has evolutionary increased rates of cephalopelvic disproportion already. We address how evolutionary models contribute to understanding and decision-making in obstetrics and gynecology as well as in devising health care policies.

Keywords

Cephalopelvic disproportion and obstructed labor

Human childbirth is substantially more difficult than that of most other primate species, owing primarily to the close match between the maternal birth canal and the fetal head[1] (Figure 1). As a consequence of this close fit, even small variation of maternal and fetal dimensions in human populations leads to a considerable rate of cephalo-pelvic disproportion (CPD) and obstructed labor. Where cesarean delivery is not easily available, particularly in developing regions of the Global South (Africa, S Asia and Latin America), obstructed and prolonged labor are frequent causes of maternal morbidity and mortality. Complications can be short-term, such as uterine rupture and chorioamnionitis, or long-term, such as fistulas and incontinence[2–6]. Despite rich epidemiological data on obstructed labor and caesarean delivery, precise frequency of CPD is difficult to estimate. Current methods of pelvimetry are unreliable predictors of anatomical disproportion[7]. Apart from an arrest of descent, which is often a sign of CPD[8], cesarean deliveries are frequently performed for other indications, some of which take place before an arrest due to CPD would manifest, including fetal distress, failed induction, arrest of dilatation, repeat cesarean delivery, and maternal request[9,10]. With this complexity in mind, reported CPD rates range from 1% to 8% of childbirths across different geographic regions[11] (Source: WHO 2003). Hence, even the most conservative estimate entails about 40,000 affected births in the US and about 1.3 million worldwide every year. It is intriguing that childbirth – a process so fundamental to our species' existence – exhibits such significant complication rates.

Human anatomical traits have been subject to natural selection for millions of years, and are therefore often considered to be the best fit available for a given function. Hence, evolutionary anthropologists have long asked the questions: Why is the human fetus so

tightly matched to the maternal birth canal and thus so prone to birth complications? Why is there not a greater "safety margin," as in most other primate species (Figure 1)? These long-standing evolutionary puzzles, which are of immediate relevance to obstetrics, gynecology, and public health, have received renewed attention in recent years. Here we review current theoretical and empirical research on the evolution of human pelvic form and childbirth. As several recent reviews highlighted the manifold social, cultural, psychological, and legal components underlying obstructed labor and surgical delivery[12–19], we focus here on biological aspects and their evolution since the split of the human lineage from the great apes.

The conflicting effects of bipedalism and encephalization on pelvic architecture

Bipedalism (see Glossary) evolved in the human lineage 5–7 million years (myr) ago and coincided with a major remodeling of the pelvis. Approximately 2 myr later, it was followed by the massive increase in brain size in the fully bipedal genus *Homo*, accompanied by an increase in the size of the fetal head[20].

Studying pelvic evolution throughout this time is difficult for several reasons. First, the pelvis is prone to fragmentation and thus poorly represented in the paleontological record[21]. Second, the pelvis is a highly integrated structure, in which selection on any one part results in changes to many others in order to preserve anatomical and functional integrity[22,23]. Finally, the human pelvis encountered multiple episodes of different selection pressures, each one leaving traces in the shape of the pelvis that are contingent on previous changes; this challenges the separate reconstruction of these selective forces[24].

Despite these limitations, there is no doubt that the evolution of bipedalism coincided with major anatomical restructurings of the primate pelvis, as can be seen by comparing pelves of early bipedal hominids, such as australopithecines, to human-like apes (Figure 2). These modifications include the shortening and widening of the illium, the alignment of the sacrum and the pubic symphysis in a dorso-ventral plane, the broadening of the sacrum, the development of more prominent ischial spines, and a reduction of the distance between the hip joints and the vertebral column. Many of these pelvic changes relate to the muscular requirements for efficient upright locomotion and balance of the upright body as well as for support of the viscera. Pelvic changes during the transition to bipedalism also sculpted a very specific birth canal. In australopithecines, the birth canal is mediolaterally broad both at the level of the inlet and at lower levels[25]. Obstetric aspects likely played a minor role in the evolution of the australopithecine pelvis as their skull was relatively small[24].

Several myr after bipedalism evolved, the pelvis encountered a new evolutionary challenge in the genus *Homo*: the gradual increase of relative brain size (encephalization, see Glossary) and, hence, also of fetal size. Evolutionary effects of encephalization on the pelvis usually are inferred from comparisons of modern humans with early representatives of the genus *Homo*, mostly *Homo erectus*. Even though the cranium of *H. erectus* is already substantially larger than that of *Australopithecus*, pelvic differences between australopithecines and *H. erectus* are likely confounded by cooccurring ecological and

behavioral changes that are independent of encephalization, such as changes in body size, ranging behavior, and thermoregulation[24]. It is currently unknown when the increase in brain size started to affect pelvic form, but it is clear that this process continued after the *last common ancestor* (see Glossary) with *H. erectus*.

Relative to modern humans, *H. erectus* has flaring illiac blades and a medio-laterally broad (platypelloid) birth canal (Figure 2). The prevailing view is that birth-related pelvic changes within the human lineage accounted for the anterio-posterior broadening of the birth canal. Compared to *H. erectus*, the modern human pelvis is medio-laterally narrower, but this narrowing is relatively recent and appears to have occurred *after* the adaptation to changed obstetric demands. Finally, modern humans also became taller, which adds another source of strain to the pelvis by increasing the requirements for locomotory musculature and support of the inner organs.

Despite the common evolutionary history and functional demands, pelvic shape varies considerably within and across modern human populations (for the classic types see[26,27]; Figure 3). Studying this variation, along with its functional consequences and complications, can help to determine the manifold roles of the pelvis in locomotion, pelvic floor support, and childbirth[28], as detailed below.

The concept of an obstetrical dilemma

In 1960, Sherwood L. Washburn introduced the term "obstetrical dilemma" in a review of the effect of tool use on human evolution[29]. Washburn proposed that bipedalism, while freeing hands for tool use, also resulted in the selection for a larger brain because of the increasing tool use. Eventually, this led to conflicting selection pressures on the pelvis: concurrent with the evolution of bipedalism, the size of the birth canal had been reduced relative to that of other primates, but the subsequent increase in brain size required a large birth canal. Such an opposition of selective forces is able to bring net evolutionary change in a trait to a halt; hence the term "obstetrical dilemma." Washburn proposed that advantages gained by increased pelvic width are outweighed by biomechanical disadvantages for bipedal gait. For example, individuals with a wide pelvis would have an easier labor and delivery process; however, they would be less successful in gathering food and providing for offspring. Moreover, he reemphasized an idea suggested earlier by Portmann, that the problem of large fetuses was partially ameliorated in human evolution by giving birth at an earlier – more altricial – developmental stage, at which cranial size is smaller[30,31]. Whereas primates, in general, are born at an advanced (precocious) developmental stage relative to, e.g., mice, this trend secondarily reversed in the human lineage (secondary altriciality, see Glossary). Hence, human neonates are more developed than those of truly altricial animals, but less developed than those of other primates.

Washburn's proposal has been highly influential and gained wide acceptance in the anthropological community. The details of this idea, however, have undergone further scrutiny. For simplicity, we will refer to generally "wide/broad" and "narrow" pelves in the discussion below, referring to a composite of multiple characteristics, including the width of

birth canal, that make the female pelvis more or less suitable for childbirth (see Figure 4). More specific terms will be used when referring to detailed assessments of pelvic shape.

Clearly, a broader birth canal is beneficial for childbirth. This female-specific selection for childbirth is manifested in the strong sexual dimorphism of pelvic anatomy, specifically in the size and shape of the pelvic outlet (Figure 4). In fact, the pelvis is the most dimorphic element of the human skeleton (e.g.,[32]). The source of selection for a narrow pelvis, however, is less clear. Washburn proposed that further widening the pelvis would impede bipedal gait, but recent biomechanical studies did not support this hypothesis (Figure 5). Warrener et al. showed that females and males do not differ in efficiency in either walking or running on a treadmill (Figure 5)[33,34]. The kinematic study of Whitcome and collegaues[35] showed that during walking at higher speed females translate more of the pelvic rotation into strides than males, which leads to similar efficiency of locomotion despite wider hips. Thus, instead of decreasing efficiency, a wide pelvis contributes to stride length and, particularly in individuals with shorter legs, may even be beneficial for walking[36].

These findings do not contradict the assumption that human pelvic architecture evolved in response to bipedal gait; they only show that, in modern humans, pelvic width does not considerably affect walking efficiency. This implies that walking efficiency is unlikely to be the cause for the evolutionary retention of our modern narrow pelvis; a broader pelvis, which would clearly ease childbirth, must have other functional disadvantages than only locomotion.

The importance of the pelvic floor

In primates, the pelvic floor musculature evolved primarily for moving the tail[37], whereas in upright humans, the muscles and fasciae of the pelvic diaphragm create a horizontal pelvic floor that supports the abdominopelvic organs. It has thus been suggested that maintaining a relatively small pelvic outlet enhances this support function[37]. Furthermore, the ischial spines, which severely narrow the birth canal in modern humans, serve as attachments of the muscles and fasciae of the pelvic floor (Figure 6). These spines are considerably smaller and located more dorsally in quadrupeds, in which the pelvic floor is a vertical structure, and the weight of the fetus rests predominantly on the backbone[37]. Similarly, the sacral bone protrudes anteriorly into the birth canal in modern humans, whereas it is much shorter and posteriorly oriented in apes. After the evolution of bipedalism, the importance of pelvic support further intensified with the increase of fetal weight in the genus *Homo*. Indeed, the ischial spines are less prominent in early hominoids (such as *H. erectus*, Figure 6) than they are in the modern human pelvis[37], and the modern narrow pelvis likely provides more support for the pelvic floor than the broader archaic one. This evidence suggests that a broad pelvis is more suitable for childbirth but less suitable for carrying the heavy fetus throughout a long pregnancy.

Evolutionarily, this situation intensifies the obstetric dilemma, because both carrying and childbirth are part of the same process – pregnancy (Figure 7). If gait was the major selective force for a narrow pelvis, walking efficiency might have been compensated independently by changes in leg musculature or behavior. But if pelvic floor support was the crucial driver

for a narrow pelvis, such a compensation would not be possible: an evolutionary change that affects one function – either carrying or delivering the fetus – would always affect the other function, too.

Pelvic floor disorders and the obstetrical dilemma

Pelvic floor disorders (PFD) are common complications associated with pregnancy in general and obstructed labor in particular. The pelvic floor is a complex structure comprised of ligaments, muscles, and fascia, arranged in several layers[38]. The term "pelvic floor disorders" refers to a wide range of complications, affecting different parts of pelvic floor architecture and reflecting disruptions of distinct functions[39]. One group of PFD arises at birth as a direct consequence of injuries to the muscles of the lower part of the pelvic floor, such as fistulas, uterine rupture, and injury to the sphincter muscles[40]. These injuries are frequent outcomes of prolonged labor due to CPD and thus reflect disadvantages of a narrow birth canal, specifically for *passing* the large fetus during parturition. According to the pelvic floor hypothesis, another group of disorders is expected to originate from strain to the muscles and connective tissue while *carrying* the heavy fetus. This strain is more likely to result in complications such as late-onset weakness of ligaments, associated with pelvic floor prolapse and incontinence, as a long-term consequence of multiple pregnancies (although acute injury can also cause these disorders). The strain due to carrying is exacerbated when the bony pelvis offers little support and the pelvic floor is weak. Thus, both a wide pelvis during carrying the fetus as well as a narrow pelvis during birthing can result in the same general group of disorders (PFD).

Studies addressing the association between PFD and pelvic anatomy often pool different PFD to obtain sufficient sample size, but this challenges the detection of associations between specific complications and specific pelvic features. Nonetheless, several studies detected associations of PFD with both a narrow and a wide bony pelvis. For example, in a study on 59 women with PFD and 39 controls, Handa and colleagues[41] found that the transverse diameter of the pelvic inlet is greater in women with pelvic floor disorders than in those without. Interestingly, they also showed that prolapse is associated with a narrow obstetrical conjugate (the shortest pelvic diameter of the birth canal, see Glossary), presumably due to a predisposition to injury. Similarly, in a study on 34 patients and 34 controls, Sze et al.[42] found that women with vaginal prolapse have a wider transverse diameter of the pelvic inlet than the control group. Two other large studies reported associations of a broad birth canal with urinary incontinence. Stav and coauthors[26] found that women with wide transverse and anterio-posterior inlet diameters as well as with a wider pelvic outlet diameter are more frequently affected by incontinence than women with a narrower inlet. Similarly, Berger et al.[43] reported that stress urinary incontinence is associated with a wide subpubic angle and a wide pelvic outlet (large interspinous and intertuberous diameters)[43,44]. Because of the relatively small effect sizes, large samples may be critical, as some smaller studies did not find differences in bony dimensions[45,46]. But even weak statistical associations between pelvic shape and pelvic floor function, which may be of limited clinical relevance today, can drive evolution: any consistent association between a morphological trait and survival rate or reproductive success imposes a selective pressure on this trait.

To understand the conflicting selection pressures acting on pregnancy, it will be important for future studies to distinguish between the different disorders and their associations with specific pelvic traits. Such studies may help to predict the risk of certain PFD based on pelvic anatomy and to develop preventive strategies for women with wider a pelvis, such as strengthening specific aspects of the pelvic floor, introducing external support for carrying, or encouraging behavioral changes that ameliorate unnecessary strain.

The human pubic symphysis is particularly inflexible

Softening and widening of the pubic symphysis as well as relaxation of the sacroiliac joints during pregnancy widens the birth canal and thus eases childbirth; it may appear as a human-specific adaptation to the tight feto-pelvic fit. However, in several other mammals with relatively large neonates, flexibility of the pubic symphysis is much larger than in humans[47]. In guinea pigs, for instance, the mean diameter of the fetal head is 20 mm, whereas the pelvic canal in early pregnancy is just 11 mm wide. To accommodate the fetal head, the pubic bones separate up to 23 mm during late pregnancy in response to estrogen and relaxin, and a ligament appears in the middle of the joint[48,49]. This flexibility is crucial, as calcification of the symphysis, which occurs if the first pregnancy is delayed, frequently leads to CPD in guinea pigs[50]. The emergence of an interpubic gap, bridged by a flexible ligament, is a prerequisite for successful delivery also in other species, including mice, bats, deer mice, and macaques[49,51]. In mice, for instance, the gap measures 4–10 mm at delivery[52], whereas in humans the mean increase of the interpubic gap is only 3 mm[53,54]. In other mammals, by contrast, e.g. in many odd- and even-toed ungulates and in big cats, the pubic symphysis is completely fused by ossification[47,49].

Why is the flexibility of the pubic symphysis so variable across mammals, and why is it so *in*flexible in humans despite the difficult childbirth? A widened pubic symphysis increases the birth canal, and thus also the vulnerability of the pelvic floor. Most species with a wide pubic gap are either very small and hence experience little pressure on the pelvic floor, engage in postures that reduce force on the pelvis and the pelvic floor (e.g., roosting head down in bats), or they reduce the pressure of the viscera and the fetus on the pelvic floor by living in water. An ossified symphysis, by contrast, allows for a higher net force applied by the muscles to the rest of the body and thus may facilitate more energetically efficient locomotion[47]. Apart from many fast running species, pubic flexibility is also strongly reduced in other large-bodied bipedal species, such as kangaroos.

In humans, a wide symphysis during pregnancy and birth is associated with severe pelvic girdle pain[55,56], which is common among athletes and patients with traumatic pelvic injuries[53,57]. It is aggravated by weight-bearing and associated with difficulty in walking[58]. Evolutionarily, the larger birth canal that would result from increased symphysial flexibility apparently was outweighed by the increased risk of injuries to the pelvis and the pelvic floor. Grunstra and colleagues[47] even hypothesized that bipedal locomotion in humans has not primarily constrained pelvic width – as classically suggested – but the flexibility of the symphysis.

Selection for a narrow pelvis may act via males: a role in erectile function

Not only the obstetric demands, but also the additional strain exerted on the pelvic floor by the heavy fetus, are specific to females. The evolutionary trade-off thus differs between the sexes and gave rise to the sexual dimorphism in pelvic morphology and pelvic canal size observable today. Similar dimorphism patterns are also seen in other primate species with a large fetal head relative to the size of the pelvic canal (cephalo-pelvic index, see Glossary), such as in lar gibbons, rhesus macaques, and squirrel monkeys, suggesting that pelvic dimorphism is, at least in part, a consequence of fetal size[59,60].

It is important to consider the specific conditions required for sexual dimorphism to arise in the evolution of traits that are present in both sexes. Divergent evolution (see Glossary) of such traits requires opposing selection pressures in the two sexes; selection acting in only one sex is not sufficient because the developmental genes and processes underlying a trait, in this case the pelvis, are mostly the same whether they find themselves in a male or a female organism ("genetic correlation between the sexes", see Glossary). This means that selection for a broader pelvis in females must have been counteracted by selection for a narrow pelvis in males. If there is no selection in males *against* the female adaptation, selection in females will also change – at least to a great extent – male shape, and no dimorphism will arise.

The fact that pelvic sexual dimorphism has nevertheless evolved implies that *there has been selection opposing the widening of the pelvis in males.* Studying the male pelvis may thus provide insights into the advantages of a narrower pelvis independent of disadvantages due to birthing complications[25]. Two relevant selection regimes are plausible: males can either share the same selective pressure for a narrow pelvis with females (as was suggested for gait or for visceral support) but lack the pressure for widening. Alternatively, selection in males may be for a male-specific function, perhaps also indirectly affecting the pelvis in females via a correlated effect.

If pelvic width is associated with pelvic floor strength in males, as is the case in females, male-specific pelvic floor disorders may offer interesting insights. In addition to general effects such as pelvic pain and sphincter dysfunction, one of the disorders associated with a weak pelvic floor in males is erectile dysfunction (ED)[61]. The pelvic floor contributes to erectile function by the muscles that form the penile basis, in particular the ischiocavernosus and bulbocavernosus muscle (Figure 8). These muscles act as part of the complex involuntary muscular interplay establishing and maintaining the pressure during erection and ejaculation. The stability of these muscles may have become particularly important for erection in the human lineage because human males have evolved relatively large penises without a penile bone – a situation uncommon among primates[62]. A summary of US epidemiological studies, including the large Massachusetts Male Aging Study[63–65], reports severe erectile dysfunction in 10% of men aged 40–70, with another 25% experiencing intermittent erectile difficulties, and 17% minimal difficulties (http://www.bumc.bu.edu/sexualmedicine/physicianinformation/epidemiology-of-ed/). The prevalence of erectile dysfunction increases steeply with age, but even 5–10% of men below 40 are affected. Vascular diseases and aging are the most important proximate factors underlying erectile dysfunction, but it is unclear to what extent they are conditional on

pelvic floor strength, which has long been associated with male and female reproductive functioning[66,67]. Recent studies reported that improving pelvic floor strength considerably alleviated erectile problems in a substantial percentage of men[61], even though direct estimates of how frequently a weak pelvic floor is the main cause of erectile dysfunction are, to our knowledge, lacking. For example, a study on 55 men showed large improvement of erectile function after six months of exercise of the pelvic floor musculature, with 40% regaining normal erectile function and further 35.5% improving[68]. Large randomized trials similarly revealed considerable positive effects of exercise on erectile dysfunction [69–71].

In short, indirect evidence indicates that the strength of the pelvic floor affects erectile function and thus, likely, male reproduction. Furthermore, the fact that the evolutionary widening of the female pelvis did not "spill over" to widen the male pelvis, implies a selective advantage of a narrow pelvis in men. The missing information to link these two lines of evidence is whether the pelvic width is indeed associated with pelvic floor strength in males. Data in women suggest that this is the case, but we are not aware of studies that have addressed this question in men.

One way to address this question would be an individual-based study examining the association between pelvic measurements and erectile dysfunction. Such data may be readily available to urologists. An alternative, but less direct way would be a comparison of sex-specific pelvic morphology with the prevalence of erectile dysfunction across different populations. Literature suggests that inter-population variation in pelvic shape and erectile dysfunction prevalence is large[72–76]; a study combining these data, accounting for confounding factors such as overall health status, may be able to address the influence of pelvic morphology on erectile dysfunction.

The cliff-edge model

Despite the multiple sources of selection for a narrow pelvis in females and males, it still appears puzzling that a population's fitness loss resulting from maternal and fetal mortality has been evolutionarily outweighed by the – presumably small – advantages for locomotion and pelvic floor stability. The recently developed *cliff-edge model* of obstetrical selection[77–79] revealed why natural selection, however strong, is not able to fully optimize the match between fetal and maternal dimensions, thus avoiding CPD.

The cliff-edge model is based on an idealized variable D (disproportion), which represents the difference between the size of the fetus and that of the maternal birth canal. When the fetus is smaller than the birth canal and encounters no obstruction, D is negative, whereas when the size of the fetus exceeds that of the birth canal, thus leading to obstructed labor, D is positive (Figure 9A). In order to study the evolutionary dynamics of feto-pelvic disproportion, as expressed by D, an "evolutionary fitness" value is assigned to each value of D (y- and x-axes in Figure 9A, respectively). In evolutionary theory, fitness refers to the average number of offspring of individuals with a particular genotype or phenotype (in this case D). The offspring number is affected both by survival rate and fecundity; what do we know about survival and fecundity with respect to childbirth that enables us to attribute fitness to values of D? Clearly, without cesarean delivery, individuals with $D > 0$ do not

survive, so their fitness equals zero. Epidemiological data document that larger neonates have higher survival rates[80,81] and thus higher fitness than smaller neonates. Furthermore, mothers with a wide pelvis have higher rates of PFD, which can lead to serious infections and social ostracization, as is common in sub-Saharan Africa[40,82,83]. These relationships translate into the blue line in Figure 9A: fitness increases approximately linearly as a function of D, as long as the fetus is smaller than the birth canal. When fetal size exceeds the size of the birth canal ($D>0$), survival and thus fitness drop sharply in the absence of medical care. This highly asymmetric fitness curve resembles a cliff edge (hence the name of the model).

The association of fitness with D imposes natural selection on the corresponding fetal and maternal dimensions. Only heritable traits can evolve by natural selection, and indeed, a number of studies reported considerable heritability (see Glossary) for fetal size and pelvic dimensions[84–87]. Hence, the disproportion D is expected to respond to selection and increase in the population. In other words, the population becomes enriched for those trait values that confer high fitness so that the trait distribution gradually approximates the fitness curve. In the case of our trait D, one would expect many pregnancies to be just below 0, that is, with fetuses that are as large as possible while still being able to be born.

Yet here lies the inherent limitation of evolving biological systems: many phenotypic traits in a population, including fetal size and pelvic dimensions, have approximately symmetrical ("normal") distributions and thus cannot match the asymmetrical fitness curve specific of obstetrics. Symmetrical distributions arise because most traits are affected by many genes with small additive effects along with symmetrically distributed environmental influences. This mismatch limits the adaptive evolution of cephalo-pelvic fit: evolution by natural selection maximizes *average* fitness in the population (i.e., the average number of offspring per individual), which results in an average value of D below the value with maximal individual fitness (at $D=0$) a certain proportion with $D<0$, and a certain proportion of cases exhibiting CPD ($D>0$; Figure 9A). The persistent rates of CPD in human populations therefore do not suggest that natural selection has not worked, but rather that evolution is limited by the inherent biology of human reproductive traits. The model also shows that because of the cliff-edged fitness function, only weak selection towards larger D is necessary to explain the observed rates of CPD[83]. In other words, against the common intuition, only weak fitness advantages for large newborns, or for a narrow female pelvis, or both, are necessary to evolve the relatively high CPD rates.

The heritability of fetal and pelvic dimensions implies that women born by the Cesarean due to CPD are more likely to experience CPD when giving birth to their own offspring, compared with women who were born without CPD. Large multigenerational studies on well-documented populations (Scandinavia, US) have found extensive evidence for inheritance of CPD[88–91], primarily via the maternal genome. Despite different time periods, geographical regions, and methodical details, these studies report relatively homogenous odds ratios for CPD ranging from 1.55 to 2.06, which likely are underestimates (non-anatomical reasons for obstructed labor are not or only weakly heritable but may be misdiagnosed as CPD). The expected odds ratio inferred from the cliff edge model is

at 2.77[79] (using an estimated heritability of 0.5 for D), a value remarkably close to the empirical observations, which supports the cliff edge model and its assumptions.

Future dynamics of cephalopelvic disproportion

Based on the cliff-edge model, we predicted that CPD rates would increase – and may continue to increase – as a consequence of cesarean delivery (Fig. 9B). The regular and safe use of cesarean delivery in cases of CPD removes the fitness threshold at D=0; if the fetus is larger than the birth canal, fitness no longer drops to zero, it may even continue to increase with increasing D. Thus, cesarean delivery has changed the selective pressure on maternal and fetal dimensions. As a consequence, evolutionary dynamics will move the population distribution towards greater D, leading to increasing rates of CPD (Fig. 9B). In other words, the evolved equilibrium between the opposed selective forces of childbirth, pelvic floor stability, and infant survival has been disrupted by surgical delivery, giving rise to a new evolutionary trend. Assuming an average heritability of 0.5 for fetal and maternal traits, as well as a duration of two generations since caesarean deliveries have been regularly and safely performed, we estimated that the original frequency of CPD would increase by about 10–20% (depending on assumptions about male fitness and the genetic correlation between sexes), which is roughly half a percentage point of CPD incidence. Note, however, that only cesarean deliveries due to CPD are contributing to this effect, not those performed for other indications[9,92].

This rough estimate is based on several assumptions (such as the representation of feto-pelvic disproportion by a single quantity). Nonetheless, it shows that evolution by natural selection, triggered through medical intervention, can affect human anatomy over decades, and not only within thousands or millions of years[93]. Yet, the model does not specify whether the increased rate of CPD results primarily from a change in fetal or maternal dimensions. Historical data on pelvic dimensions are, to our knowledge, not available, and changes in neonatal dimensions are mainly driven by changes in nutrition and obstetric practices[78,92]. In fact, the average neonatal weight has been decreasing in several industrialized countries because of shorter gestation length and a higher frequency of preterm birth, often due to medically-indicated preterm birth, coupled with a higher survival rate due to advances in neonatal care.

It is worthwhile to note that Berg-Lekås et al.[90] reported an increase of primiparous dystocia from 2.2% to 12.5% between the 1950s and 1990s, an estimate that is probably attributed, at least in part, to changes in the reporting of this diagnosis, and in short-term changes of economic development and nutritional status (such as postwar recovery). In this case, women developed in a period of poor nourishment, resulting in smaller body size, whereas when they became pregnant, their fetuses developed in an environment without nutritional deprivation, which fostered fetal growth. Such environmental mismatch between maternal and fetal development adds to the increased frequency of cephalopelvic disproportion in countries recovering from famine or experiencing rapid socioeconomic development[94].

The evolutionary pressures that had increased the frequency of cephalopelvic disproportion are now reduced by increasing access to neonatal care and treatment of pelvic floor

disorders, promoting survival of neonates, and a higher rate of preterm neonates with a lower birthweight and women with a weak pelvic floor. This, in turn, reduces selection towards larger fetuses and narrower pelves. Fetal size is further constrained by maternal factors other than birth canal size, such as metabolic capacity[95], that are not removed by caesarean delivery, and will set limits on an evolutionary increase in cephalopelvic disproportion.

What are the benefits for obstetrics and gynecology of understanding the evolutionary history of human traits and the selective pressures that have shaped them?

Evolutionary explanations for frequent obstetrical challenges (obstructed or prolonged labor, etc.) can facilitate research on medical disorders, including developing models for their prediction and strategies for prevention[96–99]. For example, the idea that distinct pelvic disorders can result from a pelvis that is either too broad for some functions or too narrow for others can refine research questions and help to predict and interpret research outcomes. Contingency on pelvic architecture may also explain some of the variation associated with mutations affecting connective tissue and associated pelvic floor disorders. Furthermore, evolutionary understanding can guide targeted interventions for women who need support for carrying, or who are particularly prone to injury at childbirth.

Finally, the insight that the male pelvis is likely subject to selective pressures for lower width raises questions about which functions mediate this selection. We discussed erectile function in this article, but other reasons may exist. Studying the male pelvis and its relationship with other disorders or traits is a promising area of investigation for understanding the conundrum of human childbirth and pelvic architecture.

Specific evolutionary models, such as the cliff edge model, allow for predictions of how regular medical treatment may affect ongoing evolutionary dynamics[93]. The evidence presented herein shows that medical interventions can sometimes lead to evolutionary changes that can take place in several generations, rather than across millennia. Importantly, the reduction of natural selection by medical treatment does not necessarily reduce evolutionary change; indeed, the disruption of evolutionary equilibriums can even induce new biological trends. Clearly, the goal of evolutionary reasoning is neither to criticize medical interventions, nor to impose naturalistic ideals on modern society, but to understand the transition of complex biosocial interactions and to inform public health and research policies.

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Glossary

Altriciality (secondary)
Characterizes species in which the offspring are born at an early developmental stage; the newborns thus are relatively immobile and helpless with a need for intensive parental care. Typical altricial species are rodents, such as mouse. and rat, or bears; their fetuses depend on the mother for many functions, e.g. food, protection, warmth. At the opposite end are precoccial neonates, which are highly developed and functional at birth, such as antelopes. Human neonates develop long and are, compared with mammals in general, precoccial, as are other primates. However, when compared to other primate species, human neonates are underdeveloped and more dependent, hence the term "secondary altricial".

Australopithecus
An early genus of the human lineage, from which the genus *Homo* arose. According to the fossil record, the genus originated in Africa and covered a period from 4 to 2 myr ago. Most species belonging to this genus were considerably smaller (1–1.5m height, ca. 35% of the cranial volume of modern human), bipedal, and strongly sexually dimorphic. Some of the best-known species are A. afarensis (to which the famous Lucy skeleton belongs), *A. africanus, A. sediba* and *A. anamensis.*

Bipedalism
A form of terrestrial locomotion by means of two rear limbs or legs. In the human lineage, it evolved 7–5 myr ago. The wide time range is due to the difficulty to draw a line between various degrees of evolving bipedalism and due to scarce conclusive fossils.

Cephalopelvic index (also fetopelvic index)
A broadly applied measure of the match between maternal and fetal dimensions [100–104]. In humans it is usually estimated by the ratio between the biparietal diameter of the fetal head at term and the smallest pelvic diameter (either anteroposterior diameter of the inlet or bispinal diameter of the midpelvis). In comparative biology, the cephalopelvic index refers to neonatal head breadth, divided through the transverse diameter of the maternal pelvic inlet.

Divergent evolution
Refers to the relatively strong accumulation of phenotypic differences between closely related populations, mostly due to differing selection pressure, leading to phenotypic divergence.

Encephalization

An evolutionary increase in relative brain size and complexity. Increase of relative brain size in the genus Homo involved prenatal as well as postnatal growth acceleration of the brain, relative to closest primate relatives[105].

Genetic correlation between sexes

Because most of the genes expressed in one sex are also expressed in the other sex, selection on a trait in one sex will also lead to a correlated evolutionary response in the other sex. The magnitude of genetic correlation can be estimated by quantitative genetic methods[106].

Heritability

The fraction of observed phenotypic variation in a population that can be attributed to genetic variation within this population. Heritability measures the degree to which trait values are inherited and thus also the degree to which a trait responds to natural selection. E.g., a heritability of 0.5 indicates that half of the observed variation among the studied individuals is due to genetic variation, whereas the other half is due largely to environmental differences. It also implies only half of the effect of natural selection within a generation is inherited to the next generation.

Homo

The genus of modern humans, the *Homo sapiens*. The genus originated about 2 myr ago, and most of its species are characterized by taller stature, greater cranial capacity, and less size dimorphism than *Australopithecus*. Species of this genus include, among others, *H. habilis, H. erectus, H. neandertalensis, and H. naledi. H. sapiens* originated in this genus about 300,000 years ago.

Last common ancestor

A concept used by evolutionary biologists when inferring how traits have evolved during the species' evolution. For example, when multiple closely related species possess a certain trait, it is more likely that they all inherited it from their common ancestor than the alternative scenario that all evolved the same trait independently.

Obstetrical conjugate

The distance between the closest bony points of the sacral promontory and the pubic bone next to the symphysis (approximately 10–12 cm). It represents the shortest pelvic diameter through which the fetal head must pass during birth.

Obstetrical dilemma

A concept originally proposed by the anthropologist Sherwood L. Washburn (1960) to explain the tight human feto-pelvic fit. It suggests that human pelvic form results from a compromise between the ability to walk upright and the ability to give birth to large neonates.

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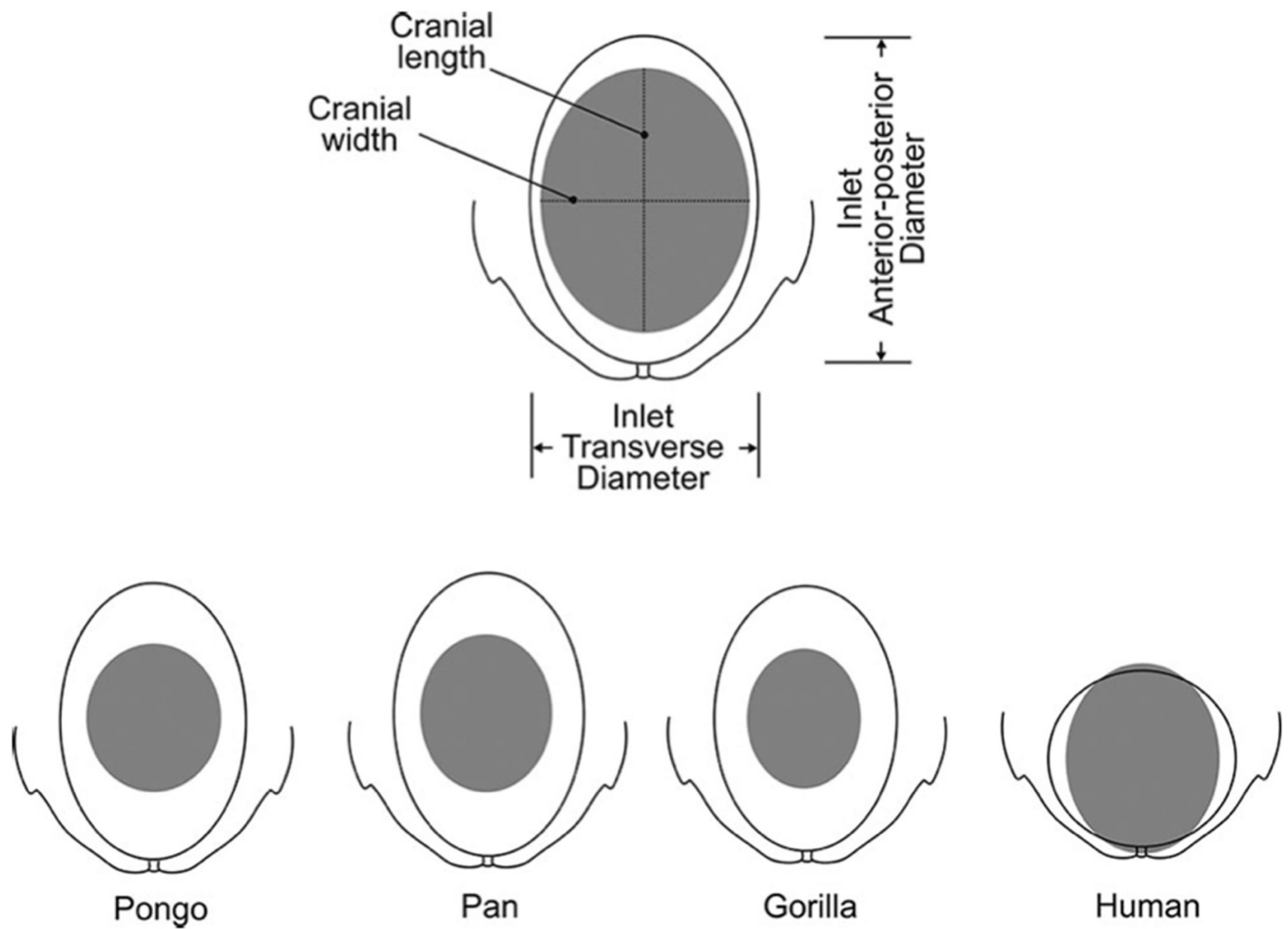
Figure 1.
Comparison of cephalopelvic proportions at the level of the pelvic inlet across closely related primates: Orangutan (*Pongo*), Chimpanzee (*Pan*), Gorilla (*Gorilla*) and modern humans (*Homo sapiens*). Humans show a very close fit between the pelvic inlet and the fetal cranium. Figure from Wittman & Wall[107].
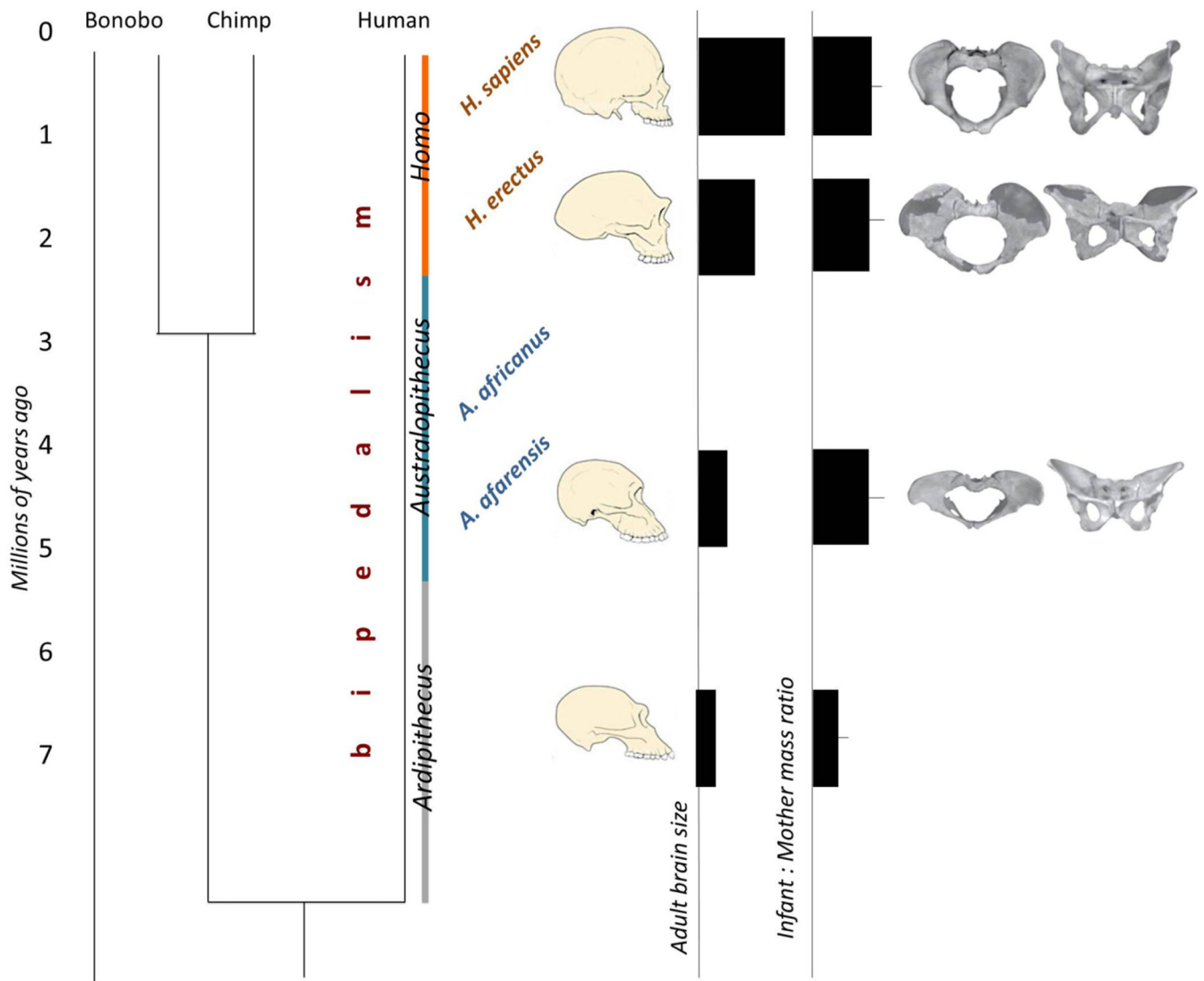
Figure 2. Timeline of human evolution, along with obstetrically relevant traits.

The phylogenetic tree (left) shows the split between the humans and the closest living relatives of the genus *Pan* (Bonobo and Chimpanzee). Bipedalism arose early in the human lineage and is common to the three genera, *Ardipithecus*, *Australopithecus*, and *Homo*, of which relatively good fossil remains have been studied. Overall body size, adult brain size, and also the neonatal body mass increased in the human lineage (middle panel). Relative size and shape of the skull reflect the encephalization in genus *Homo* throughout the last 2 myr. The pelvic birth canal increased in the human lineage and shifted to a gynecoid shape. Figure combined from Pontzer[25,108] and Gruss & Schmitt[25,108].
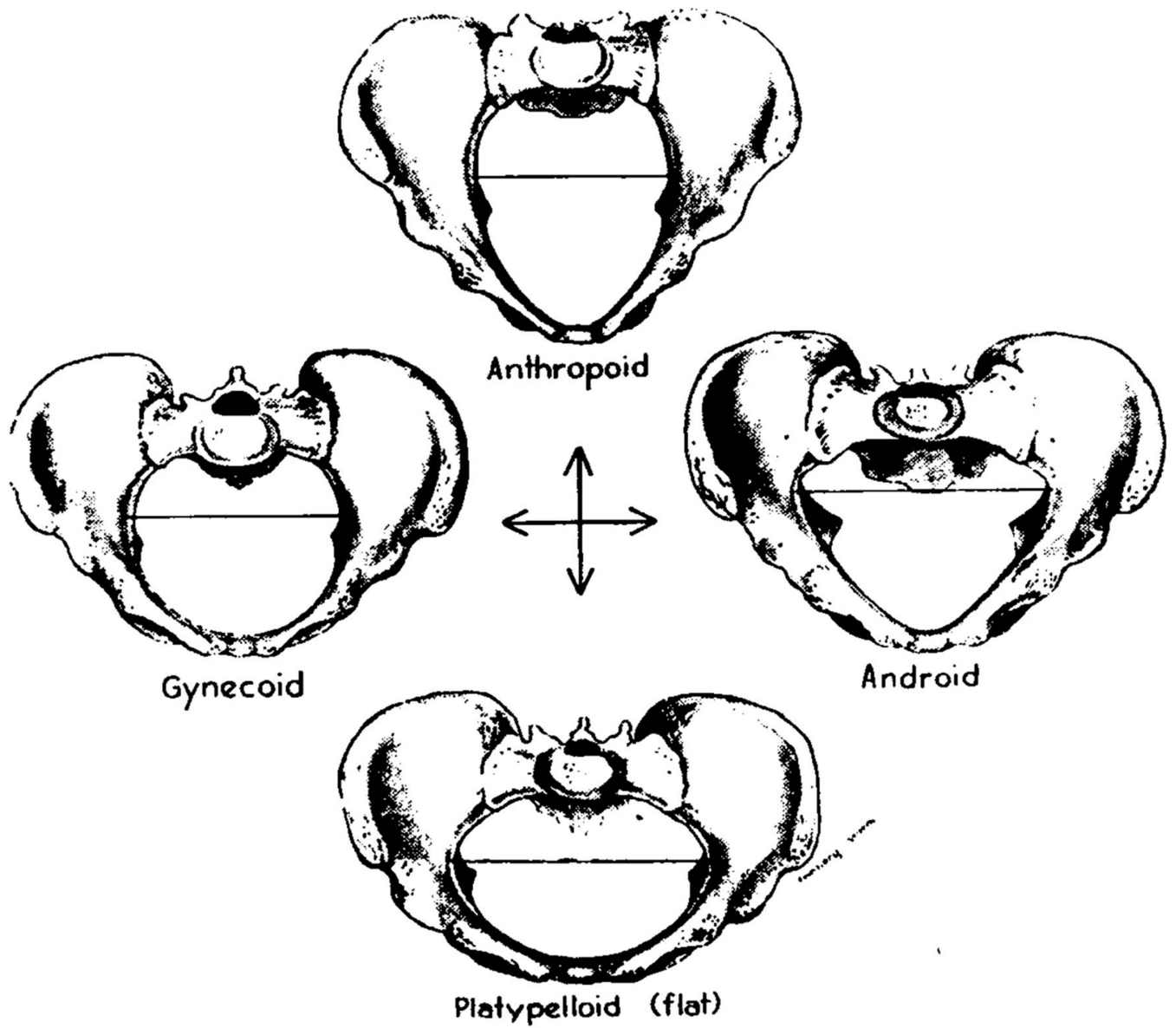
Figure 3.
The classic pelvic types with respect to the shape of pelvic canal[109]. The predominant type is gynecoid. Figure from Caldwell-Moloy[26].
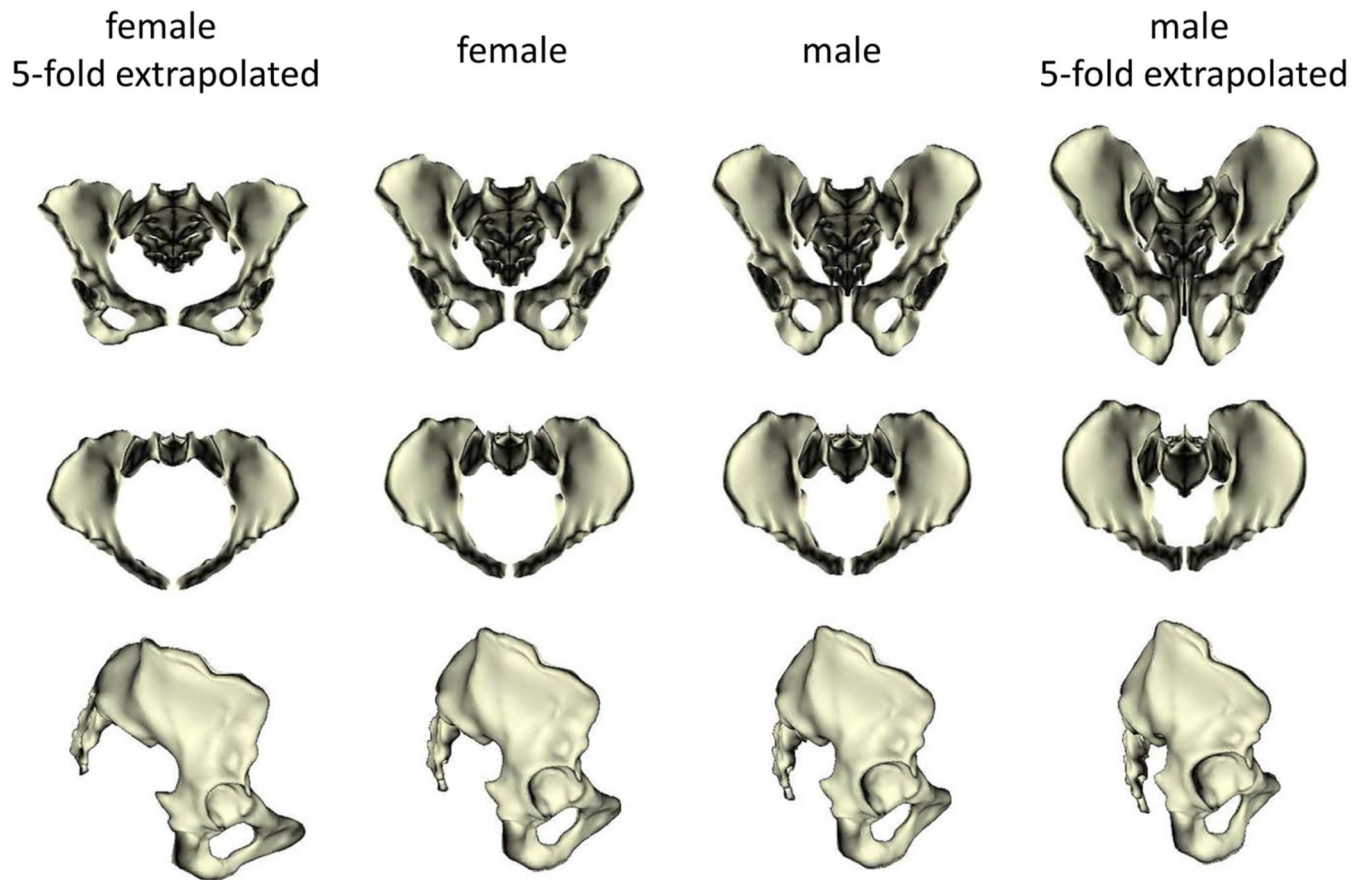
Figure 4. Pelvic sexual dimorphism.
Average male and female pelves (the two middle columns) in anterior, superior and lateral views, along with five-fold linear extrapolations of the sex differences in pelvic shape (leftmost and rightmost columns). In females the pelvic canal is more spacious, the illiac blades are shorter and reach further laterally, the subpubic angle is broader, and the sacral bone is shorter and more outward projecting than in males. Figure from Fischer & Mitteroecker[32].
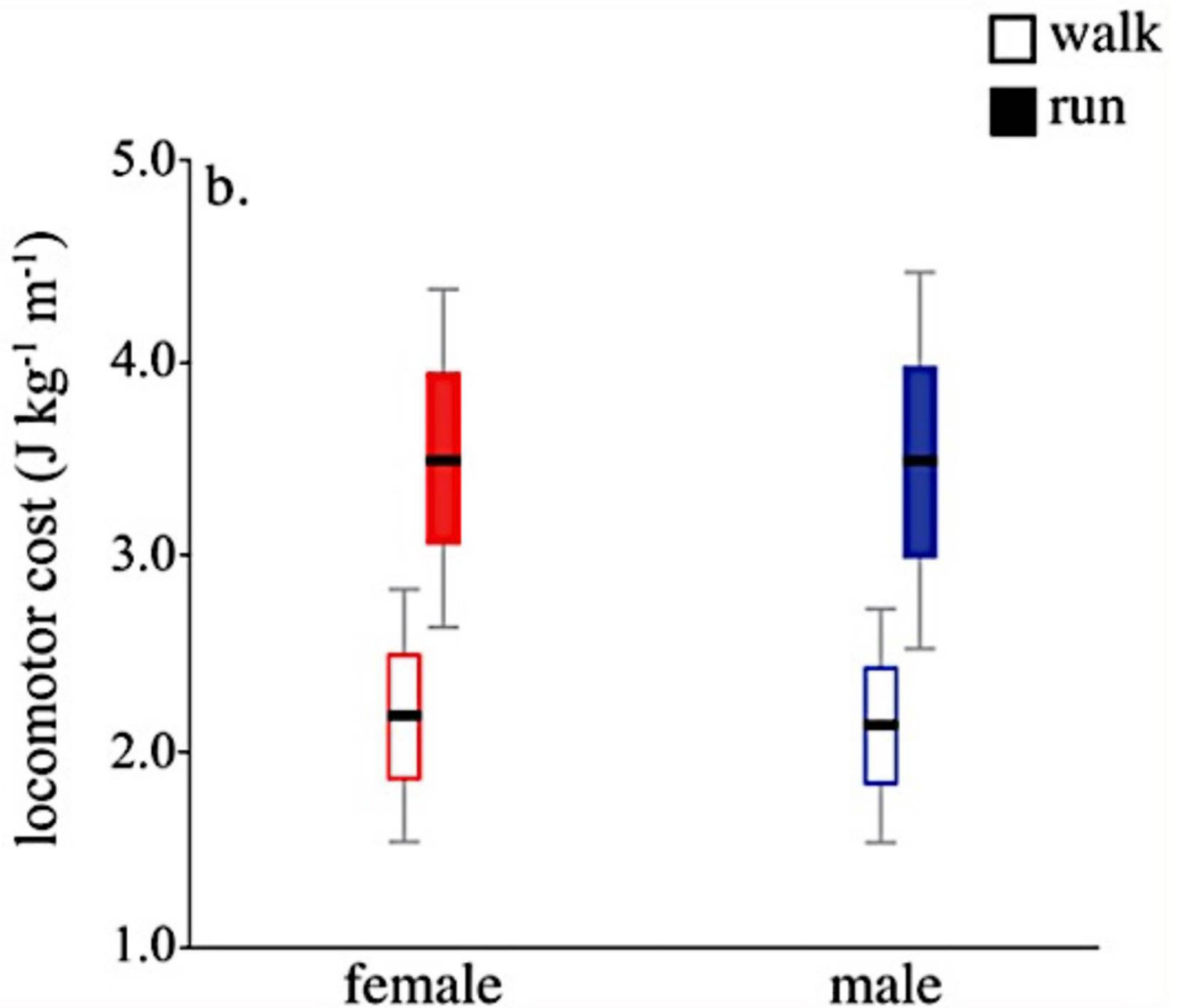
Figure 5.
The results of Warrener and colleagues[34], who tested Washburn's hypothesis that pelvis width negatively affects gait efficiency. Mass-specific locomotor costs (net volume of oxygen consumed during exercise) during walking and running on a treadmill was measured for 8 males and 7 females. Results showed no significant difference between the sexes despite wider hips in women than in men. These results suggest that bipedal gait is not be the source of selection for a narrow pelvis. Figure from Warrener & colleagues[34].
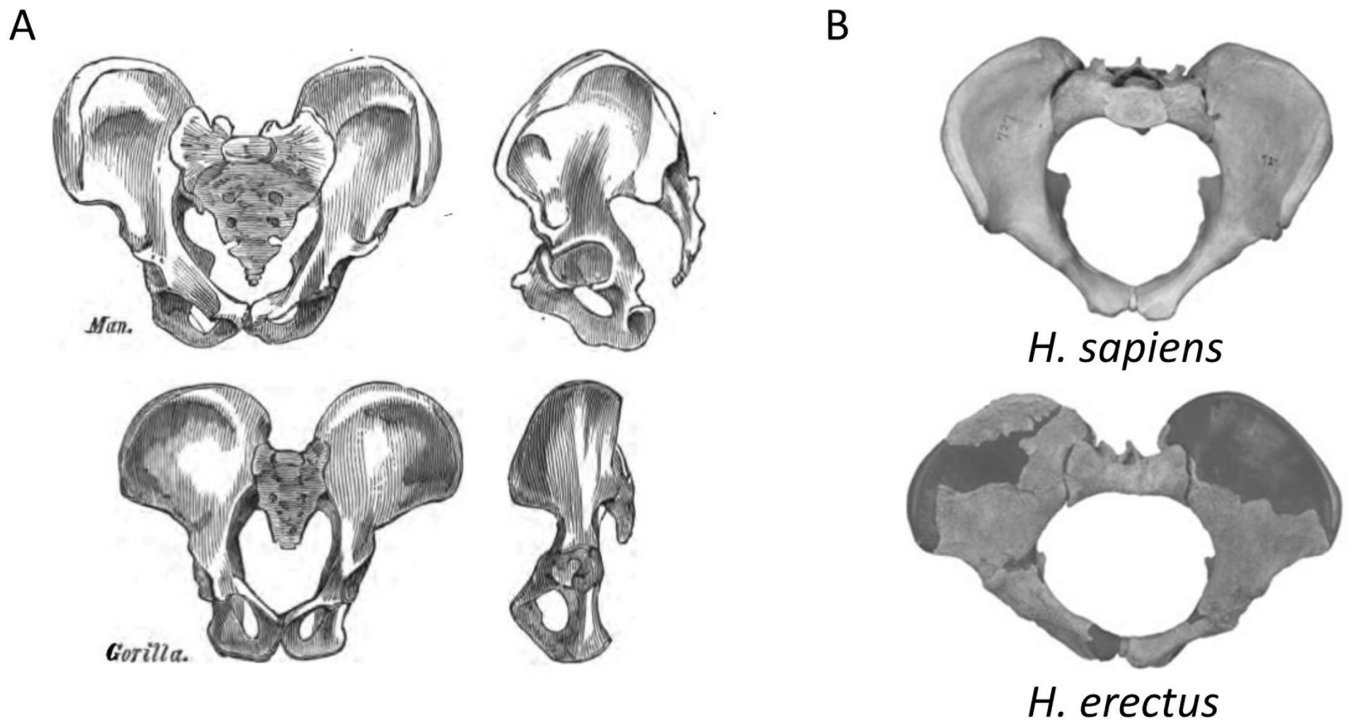
Figure 6. Evolution of pelvic floor support.
A: In the transition from quadruped to biped, the weight of the inner organs came to lie on the pelvic floor. The comparison of pelves between quadruped gorilla and bipedal human shows an increase in the size of pelvic floor-supporting structures: the ischial spines and the sacrum. B: The comparison between *H. erectus* and modern human pelvis shows a further enlargement of the ischial spines, concomitantly with an increase in mass and cranial size of the fetus. Figures from Huxley[110] (A); and Gruss & Schmitt[25] (B).
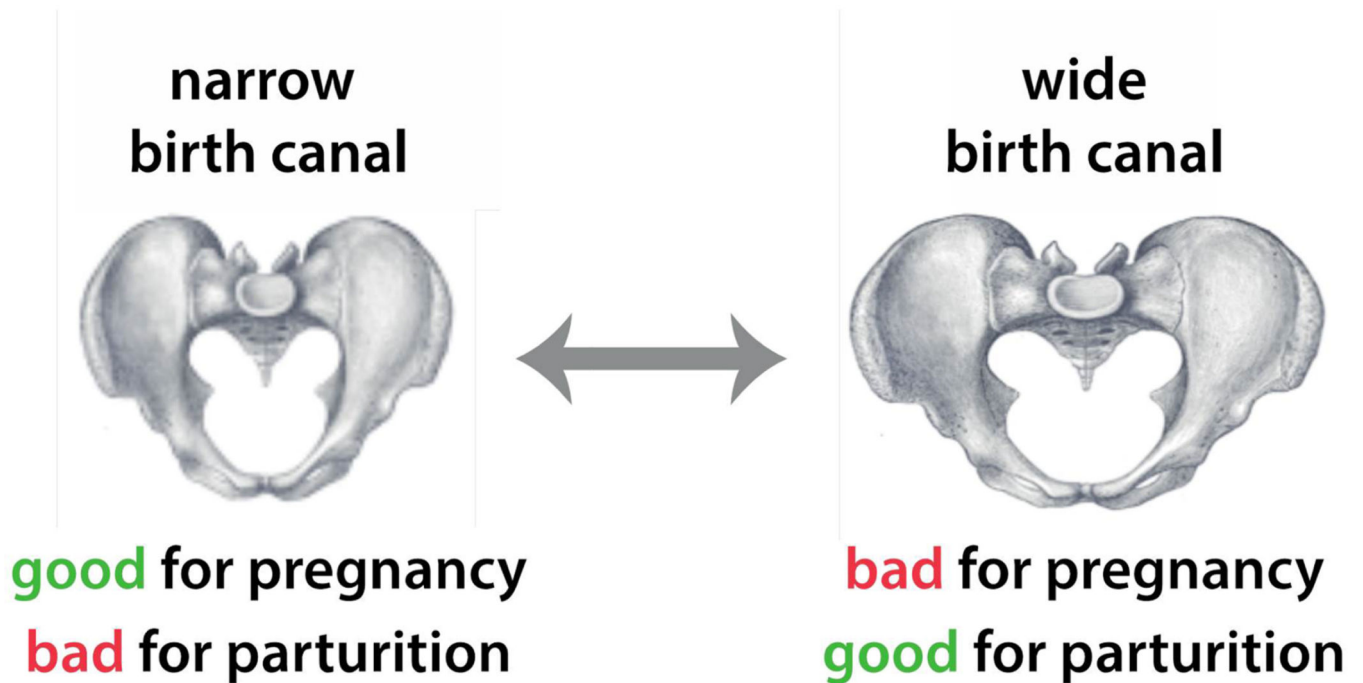
Emerging obstetrical trade-off

Figure 7. The model of obstetric selection trade-off.
According to this model, advantages and disadvantages of a broad pelvis do not pertain to different functions, such as pregnancy and walking. Rather, they both pertain to pregnancy: while a broad pelvis is advantageous for childbirth, it is disadvantageous for supporting the large fetus. We propose that this disadvantage is limiting the broadening of the pelvis.

Bulbospongiosus
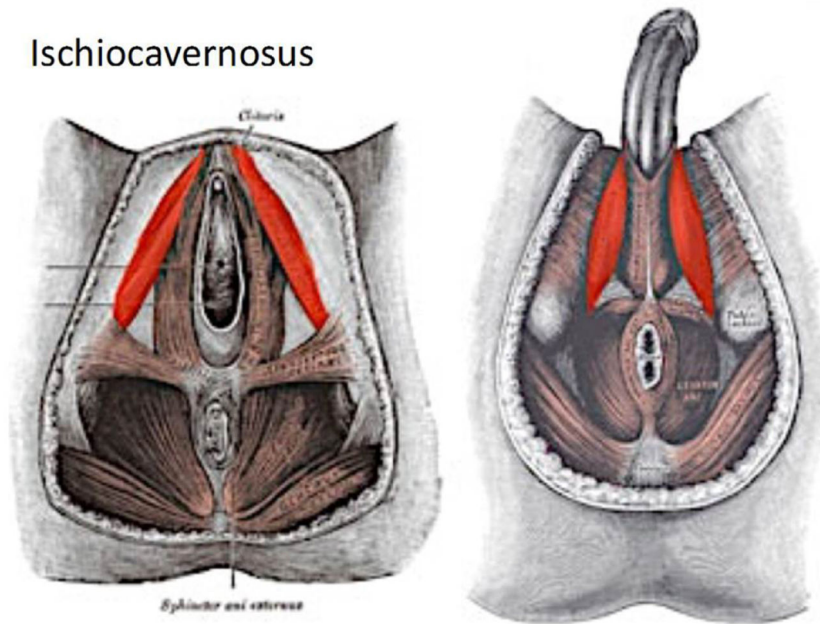## (bulbocavernosus)
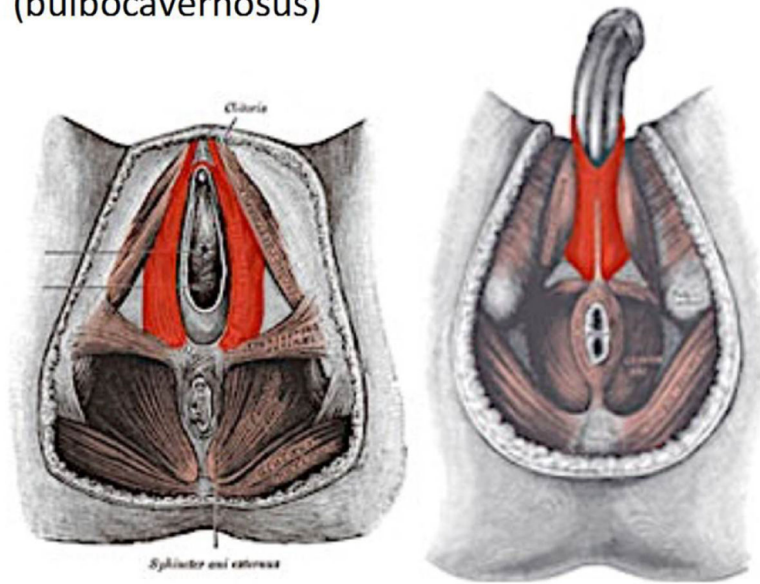
Ischiocavernosus

Figure 8. Comparison of the male and female pelvic floors.
The two muscles shown in red, bulbospongiosus and ischiocavernosus, are involved in the female pelvic floor and also crucial in maintaining the erection in males. Figures from https://www.qrsthai.com/erectile-dysfunction/.
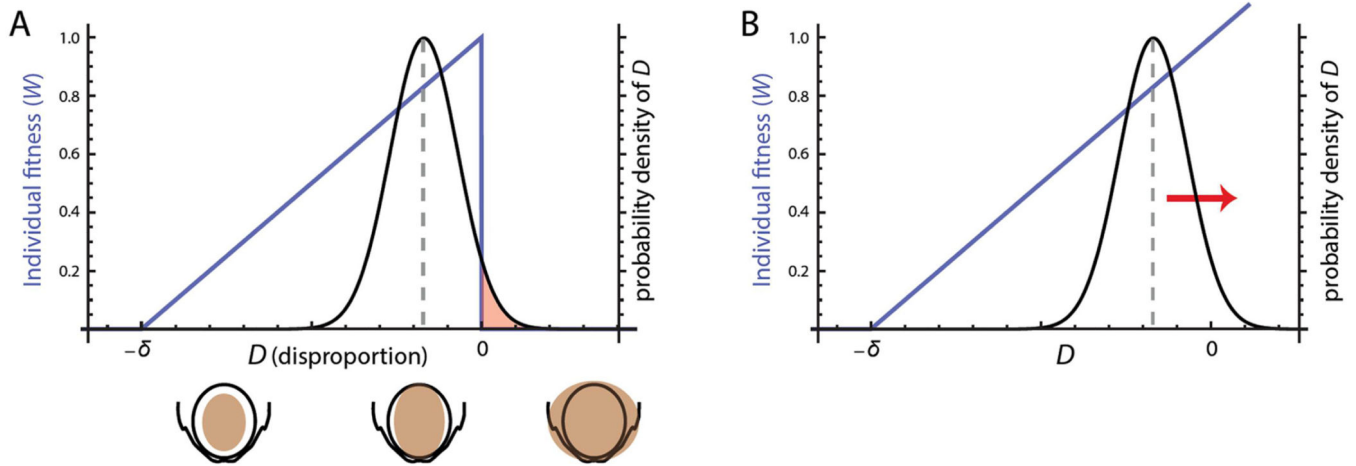
Figure 9. Cliff-edge model.

(A) The x-axis represents the variable D (*disproportion*), which captures the difference between cranial size and pelvic size. This value is negative when the fetal cranium is smaller than the pelvic canal ($D<0$) and positive when fetal size exceeds the size of the pelvic canal, leading to cephalopelvic disproportion (CPD). The y-axis on the left represents individual fitness. As long as birth canal can encompass the fetus (D<0), individual fitness (blue curve) increases linearly with D (both a larger fetus and a narrower pelvis lead to higher fitness). For $D>0$, fitness is zero because of CPD. The black curve represents the probability density function (pdf) of D, that is, the distribution of pregnancies across different values of D. Evolution by natural selection maximizes the *average* fitness in a population, which leads to an evolutionary "optimum" that entails an average value of D (grey dashed line) smaller than the individual optimum (i.e., on the left side of the cliff edge) and a fraction of individuals with CPD (the red area beyond the cliff edge, at $D>0$). This evolutionary stable state trades off the high fitness for the pregnancies with $D<0$ (large fetuses that still fit through the birth canal) against the fraction of pregnancies with CPD. Figure modified from Mitteroecker & coleagues[77].

(B) Caesarean delivery removes the cliff at the fitness threshold at $D=0$, thus leading to a further evolutionary increase of D and the resulting CPD rate. Note that only cesarean sections performed due to actual disproportion have this effect. Figure modified from Mitteroecker & coleagues[77].