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“Loss of Estrus” and Concealed Ovulation in Human Evolution: A Reevaluation.

Joshua S. Wagener

April 19th, 2006

For Stephen (Esteban) J. Lopez de Gallegos, my loving
grandfather, for never giving up a fight and having the
determination to reach your goals up until your last breath.

“Loss of Estrus” and Concealed Ovulation in Human Evolution: A Reevaluation.

Joshua S. Wagener

Accounts of human evolution tend to highlight a number of significant characteristics as critical in defining humanity including bipedalism (Jolly 1970, Lovejoy 1981, Wheeler 1984), enlarged brains (Falk 1990, Foley 1996), hairlessness (Morris 1963, Schwartz and Rosenblum 1980), and language (Pinker and Bloom 1990, Dunbar 1996). Less frequently, scholars have focused on the unique aspects of human sexuality. In this paper, I seek to demonstrate that sexual swellings are not the norm among allo-primates and that the prevailing absence of estrus among female humans is better viewed as a derived trait which is no more unique than that of any other primate. As such, I would argue, current theories of the “loss” of human estrus should be reevaluated.

Concealed Ovulation vs. Loss of Estrus

Before launching into a discussion of theories about the development of concealed ovulation and loss of estrus in humans it is first necessary to explain what these two conditions are as well as how they differ. Indeed, it appears that there has been some confusion over estrus and ovulation in various theories.

Although related it is important to emphasize that ovulation and estrus are distinct biological events. Ovulation occurs when an egg is released from an ovary (Marieb 2004). There is some variance in the ovarian cycle (the cyclic series of events associated

with the maturation of an egg) both across species and within species. The human ovarian cycle on average repeats at an interval of 28 days with ovulation generally occurring around mid-cycle in humans (Marieb 2004).

Estrus, on the other hand, implies a behavioral change in which a female is attractive to males, proceptive (seeking out male attention), and receptive to advances (Small 1995). Among most species of animals, females are not continually receptive to sex. Rather there are certain time periods in the cycle in which the female of a given species is interested in sex. The period of sexual interest – commonly referred to as a heat period - usually occurs around the time of ovulation and perhaps arose as a means of increasing the probability of impregnation and therein reducing the risk of wasting the energy put into ovulation (Small 1995). In some species the hormonal changes associated with a period of estrus trigger biological signals which alert others that an individual is in estrus - such as patches of special skin around the vulva and anus which become a noticeable pink or burgundy color as they swell up known as estrus swellings (Small 1993, Hrdy 1981) or the release of pheromones which are detected by others through olfaction (Stoddart 1990). The estrus swellings of Chimpanzees, for instance have a volume of about 1400 cc – comparable to that of a modern human brain (Ehrlich 2000). Prosimians, however, have no true sexual skin which can swell in estrus. Instead prosimians communicate estrus status through smells – the female will rub urine on branches and males will often inspect females' genitalia for the smells which signal estrus (Small 1995).

Humans do not exhibit the suite of behavioral changes known as estrus. Research indicates there is no particular time when female humans are more apt to seek out sex

from males nor is there any time during the cycle when females have been shown to be more receptive to male advances (Small 1995). It seems that sexual arousal in humans has been “disassociated from hormonal control of ovulation and conception (Thiessen 1997). Indeed female humans are often considered “continually receptive” as they may be willing to have sex at any given point during the ovarian cycle. Additionally females are continually considered attractive. Since female humans have no circumscribed time period in which they are attractive, receptive, and proceptive they are not considered by biologists to have a clearly defined period of estrus. In evolutionary perspective, writers often refer to this lack of estrus as a “loss” of estrus, implying that human ancestors at one time had a clearly defined estrus period (Morris 1963, Bolin and Whelehan 1999). For example, J.H. Clark in his *The Loss of Estrus Behavior in Humans: A Physiological Explanation* states that, “A momentous event in the evolution of humans was the loss of this behavioral estrus” (Clark 1992). Similarly, Mina Davis Caulfield makes a similar statement in her *Sexuality In Human Evolution: What Is “Natural” in Sex?* that “our own ancestors similarly experienced such estrous periods and that at some point in evolutionary history some kind of selective pressures operated to extinguish the physiological base for them (Caulfield 1985).

However, the absence of a clear estrus period is seen as well in other primates, albeit to a lesser degree. Overall only 20 out of 200 primate species exhibit forms of estrus signaling – swellings, pheromones, or behavioral gyrations (Small 1993). The degree to which an estrus period clearly signals ovulation in the ovarian cycle varies widely within the primate order (Small 1995). For example, gorillas have an estrus period

of only one day while bonobos continually exhibit estrus swellings and behavior (Small 1993)

In addition to the absence of estrus, humans have often been said to have concealed ovulation, suggesting that the biological act of ovulation is not marked by sexual swellings or any other cues which might signal to others that a female is ovulating. Often the notions of concealed ovulation and loss of estrus have been interchanged in the naming of this phenomenon. For instance Birgitta Sillen-Tullberg and Anders P. Moller use the terms concealed ovulation, loss of ovulatory signs, and loss of estrus interchangeably (1993). However, loss of estrus should only be applied to behavioral changes and therefore is not an equivalent term for concealed ovulation. Instead loss of estrus swellings should be used as an alternative naming of concealed ovulation. Concealment of ovulation in humans is not due to a lack of estrus (behavioral changes) but is rather do to a lack of the physiological changes associated with an estrus period. Care needs to be taken so as not to confuse the terminology utilized in loss of estrus and concealed ovulation.

A Discussion of Theories

Having discussed what concealed ovulation and loss of estrus are it is now appropriate to turn to a discussion to how these states arose in humans. A number of theories have been proposed over the years. Many of the theories involving the evolution of the sexual biology of humans place an emphasis on the type of mating system under which a lack of estrus swellings would have evolved. Although it cannot be ignored that the type of mating system in which a species lives has some effect on the sexual behavior

and the physiology of a species, the amount to which mating system corresponds with the presence or lack of estrus swellings varies (Sillen-Tullberg and Moller 1993). Though no monogamous groups have sexual swellings, a lack of sexual swellings is not exclusive to monogamous groups. Indeed “Although the preponderance of sexual swellings is found in multimale taxa, ovulatory signs are absent in many taxa with this mating system” (Sillen-Tullberg and Moller 1993). In primates, “estrus swellings have been lost 0-1 time under monogamy, 3-7 times under a unimale system, and 3-6 times under a multimale system” (Sillen-Tullberg and Moller 1993). Since, the majority of cases wherein a lack of estrus swellings evolved did not occur under monogamy, and did occur a similar number of times under unimale systems and multimales systems, the mating system cannot be said to be the determining factor in the development or loss of estrus swellings. Thus, I shall not put a large amount of emphasis on mating systems in my study.

The “hunting hypothesis” proposed by Desmond Morris was based on the “need for a pair-bond to ensure the survival of especially helpless human young” (Morris 1963, Hrdy 1981). Morris and other supporters of the hunting hypothesis view the loss of estrus as well as the development of continuous receptivity to be uniquely human adaptations which are present in order to strengthen the human pair-bond as well as the group relations (Morris 1963, Hrdy 1981). It is assumed in this theory that the sexual traits of humans evolved under group living conditions in which a female in estrus would have been disruptive. If an irresistible female was present in a group males may not be willing to go out on hunting excursions which would limit the amount of meat available to the group as a whole (Hrdy 1981). Under such conditions it is reasoned that estrus displays would have been suppressed to prevent disruptions to the group. A female exhibiting

estrus displays would be disastrous for pair-bonds in that the male partner would not be able to leave the group to hunt or another male would have the potential to mate with the female (Morris 1963). In order to keep the male interested in commitment females increased their sexual receptivity to males.

Katharine Noonan and Richard Alexander suggest that ovulation in humans became concealed in order to draw males into a monogamous relationship with females. If females had ovulatory periods which males could easily detect it would only be necessary for the male to be around during ovulatory periods in order to impregnate a female. When the female was not ovulating he would be free to go off and spend time with other females, “secure in the knowledge that the wife he left behind was unreceptive, if not already fertilized” (Diamond 1992). With no estrus display the only way that a male would be able to ensure he had the chance to impregnate a female during her fertile ovulatory period would be to remain in close contact with her for an extended period of time (Diamond 1992). Concealed ovulation “enabled females to force desirable males into consort relationships long enough to reduce their likelihood of success in seeking other matings, and simultaneously raised the male’s confidence of paternity by failing to inform other, potentially competing males of the timing of ovulation” (Hrdy 1981). In Noonan and Alexander’s scenario both males and females benefit – females gain assistance in caring for their offspring and males gain security in knowing that the offspring are his own.

Zoologist Nancy Burley proposes an explanation for concealed ovulation which relies on the intellectual capability which is unique to humans. In Burley’s model emphasis is shifted from males not being able to detect ovulation to the fact that females

are not able to detect ovulation (Burley 1979). Early humans would have realized the connection between sex and childbirth – a painful and dangerous event for humans since newborns are large in comparison to the birth canal through which they must pass (Burley 1979, Diamond 1992). Therefore, females would have intentionally avoided the pains and potential complications of childbirth through the only means of contraception available – abstinence (Burley 1979, Hrdy 1981). Females who were able to detect their ovulation could avoid sex during periods of fertility and limit the pains of childbirth leading to fewer offspring than females who could not detect and therefore could not prevent their pregnancy. With each generation there would have been fewer females who were able to detect their ovulation until concealed ovulation became the norm among female humans (Burley 1979). In Burley's theory it is human intelligence which allowed for the manipulation of fertility in order to prevent pregnancy which eventually led to the condition of concealed ovulation and no estrus signals in humans.

A new approach has been taken by Sarah Blaffer Hrdy which does not utilize monogamy as a means for explaining concealed ovulation and lack of estrus swellings. Hrdy utilizes the idea that the likelihood of survival of a female's offspring is greatly affected by the males in a multimale group – which is likely to be the group composition within which humans evolved (Hrdy 1981). Under the condition of living in a multimale group, it is Hrdy's opinion that a female who attracts and copulates with a number of partners increases the likelihood that her offspring will survive. Males are not likely to harm their own offspring. In mating with multiple males a female can effectively confuse paternity and reduce potential harm to her offspring from males because, "If he has mated with a female, it is unlikely that he could rule out completely the possibility that he

fathered subsequent offspring” (Hrdy 1981). However this deception could not occur if there were clear signs of ovulation on the female’s behalf since the male would be able to rule out his paternity if he did not mate with the female around ovulation. In response, concealed ovulation in women evolved “in order to manipulate men by confusing the issue of paternity” (Diamond 1992). If there is no physical signal of ovulation which can be detected by males, a female is able to effectively choose a male as the ideal father of her offspring by copulating with them around ovulation while still convincing other males that they could potentially be the father by copulating with them in non-ovulation periods. By doing so a female would benefit by obtaining the genetic stock which she wanted for her offspring while at the same time preventing aggressive acts towards her children from other males. Under such circumstances Hrdy believes concealed ovulation evolved (Hrdy 1981).

Another hypothesis suggests that bipedalism led to a loss of estrus swellings and concealed ovulation. As bipedalism developed in the ancestor of *Homo*, a number of skeletal and muscular changes occurred. One such change was the tilting forward of the pelvis which moved the female genital area into a position between the legs which was not easily viewable (Bolin and Whelehan 1999, Fischman 1994). Since the swellings were no longer visible they became useless as a signal of fertility (Tanner 1981, Taylor 1996, Pawlowski 1999). Additionally a bipedal female with an estrus swelling would have experienced difficulties walking around. Therefore estrus swellings became a maladaptive trait and those females with smaller swellings or no swellings would have been more reproductively fit and therefore would have had more offspring (Gallup 1982, Fischman 1994, Pawlowski 1999).

Along with bipedalism reducing the size of estrus swellings in humans, some suggest that breasts in humans became enlarged as a replacement of estrus swellings. The appearance of permanently enlarged breasts at puberty is a feature unique to humans (Mealey 2000). It is suggested that when the estrus swellings of the ano-genital area became hidden by the legs due to bipedalism interest shifted to the breasts visible on the ventral surface of the human body because they mimicked “the ancient genital display of hemispherical buttocks” (Morris 1967). With sexual interest placed on breasts, females with larger fat deposits in their breast (and therefore larger breasts) experienced a reproductive advantage. However, instead of breasts signaling ovulation – as ano-genital swellings had – large, swollen breasts signal that a female is of age for reproduction or potential for ovulation (Small 1995, Jolly 1999).

It has also been suggested that ovulation in humans is not actually all that concealed – especially among humans living in “more natural conditions” (Pawlowski 1999). Supporters of this hypothesis claim that some women can actually tell when they are ovulating. It may be the case that females emit certain pheromones around ovulation which signal to others that the female is fertile but that these pheromones are often not noticed due to interference from clothing, perfumes, and personal hygiene products (Small 1995). Human anatomy and physiology suggest that olfaction is important to humans. Though the mucosa of the human nose have fewer receptor cells than those of other mammals, the quantity of olfactory substances produced by humans is almost the largest of all the primates (Stoddart 1990, Pawlowski 1999). Additionally, as evidenced from the “number, size, and production of the sebaceous and apocrine glands, humans are the smelliest hominoids (Pawlowski 1999).

If ovulation in humans is detectable, a hunter-gatherer society which has less emphasis on hygiene and lives under more “natural” conditions should provide the ideal opportunity for the detection of ovulating females (Marlowe 2004). In an attempt to test this suggestion Frank W. Marlowe conducted a study among the Hadza of Tanzania – a hunter-gatherer society – to see if men and women could detect ovulation by reasoning that if ovulation is detectable by males the frequency of copulations should increase around ovulation (Marlowe 2004). However, Marlowe concludes that there is “no evidence that ovulation is any less concealed among people living under natural conditions than it is in our hygiene-conscious culture” (Marlowe 2004). Marlowe further goes on to state that “because the Hadza smell so strongly of smoke, it is possible that it is even more difficult for them to detect ovulation” (Marlowe 2004).

All of the proposed theories for the development of concealed ovulation and loss of estrus in human evolution set out with the understanding that concealed ovulation and loss of estrus behavior and swellings are uniquely a human trait. However other species of primates also have concealed ovulation with a lack of estrus swellings or behaviors. One such primate is vervet monkeys which “do not exhibit any reliable external visual signs of ovulation” (Andelman 1987). It is time that we attempt to move beyond the anthropocentric notion that human sexuality is a unique condition which demands vast amounts of explanation.

Reexamining the Approach

Sillen-Tullberg and Moller share the sentiment expressed by most who attempt to explain sexual swellings in their statement that “the absence of visual signs of ovulation

requires an explanation” (Sillen-Tulberg and Moller 1993). Perhaps there is an error in the approach to our subject. Why is there a need to explain a lack of sexual swellings? Sexual swellings among primates are certainly not the norm. Neither prosimians nor new world monkeys exhibit sexual swellings to signal estrus periods (Small 1995). Even in Old World Monkeys and Apes sexual swellings can not be said to be the norm with only half of the 18 genera exhibiting any form of estrus swelling (Small 1995, Sillen-Tullberg and Moller 1993).

The approach used in the past seems to be biased. There has been an assumption made that the “normal”, unmarked condition is for primates to exhibit estrus swellings and that any deviation from this norm (a lack of sexual swelling) must be explained. The bias is probably due to the fact that a majority of the primates to which the earliest studied were devoted – baboons, mangabeys, and chimpanzees – exhibit extravagant sexual swellings which were then taken to be the basal, unmarked condition (Hrdy 1981). Is a lack of estrus swellings really the marked state though? Perhaps it would be more effective to question why chimpanzees and bonobos (as the closest living relatives of humans) have such extravagant sexual swellings. As an estrus swelling requires an extra caloric output to maintain itself it is unlikely that such large swellings would have evolved without providing some advantage (Small 1995). Additionally, the size and weight of the swellings interfere in the daily activities as a chimpanzee swelling includes more than a liter of water as it swells to roughly the size of a human brain – 1400cc. (Small 1995, Ehrlich 2000). Or perhaps we should be asking why some primate species display sexual swellings while others do not? Such approaches do not make the assumption that a lack of estrus swelling is a marked state.

In order to distinguish whether the lack of estrus swellings in humans is a derived, state which would merit explanation it is helpful to establish a phylogeny of generally accepted taxa relations based upon genetic evidence. Once this phylogeny is established it is possible to map over it the lack or possession of estrus swellings. This phylogeny can then be analyzed by invoking the rules of parsimony – the principle of invoking the minimal number of evolutionary changes to infer phylogenetic relationships (Futuyma 2005) - to establish which of the conditions represents the ancestral state and which are derived states.

Let us begin by examining the phylogenetic tree for apes which is generally agreed upon (Fig. 1). The homo lineage and the chimpanzee/bonobo lineage are commonly considered to be sister taxa which split off from a common ancestor (ancestor A) about 6 million years ago. Approximately 8 million years ago the common ancestor of gorillas and the chimpanzee/bonobo lineage (Ancestor B) split into two lineages. Around 14 million years ago according to this tree there was a split that led to the lineages which would become the African apes and the Orangutan lineage (Ancestor C). The title of Ancestor D will be assigned to the common ancestor of the lesser apes (gibbons and siamangs) and the great apes (orangutans, gorillas, chimpanzees, bonobos, and humans).

Now let us map onto this phylogeny the presence or absence of estrus swellings (Fig. 2). Humans, as has already been discussed, do not exhibit estrus swellings. Chimpanzees, bonobos, and gorillas do exhibit estrus swellings (Sillen-Tullberg and Moller 1993). Orangutans do not exhibit estrus swellings while gibbons and siamangs do have estrus swellings (Sillen-Tullberg and Moller 1993). At first glance it is noticeable that our phylogeny (Fig. 2) reveals a lack of estrus swellings among apes to be a rarity.

The established phylogeny with the mapped on presence or absence of estrus swellings (Fig. 2) allows an attempt to determine the plausible state of the various common ancestors. The law of parsimony tells us that in a phylogeny with maximum parsimony a trait should undergo the least number of changes among taxa in the phylogeny as possible. Using this rule, let us now examine the plausible states for the various ancestors.

Since both chimpanzees and bonobos have estrus swellings it is most parsimonious for their common ancestor to also have had estrus swellings. Ancestor A led to the chimp lineage which does have estrus swellings and the homo lineage in which the extant species (*Homo sapiens*) does not have estrus swellings. If ancestor A did have estrus swellings then only one state change is necessary to explain the derived state of the *Homo* lineage as having no estrus swelling while no change in state of estrus swelling occurred in the *Pan* lineage (chimpanzees and bonobos). If Ancestor A did not have estrus swellings then, again, only one state change is necessary to explain the different states of the *Pan* and *Homo* lineages. In this scenario the *Pan* lineage holds estrus swellings as a derived state. Since both situations – Ancestor A having estrus swellings or not having estrus swellings – would both only need one change in character state of estrus swellings, neither situation can be said to be more parsimonious. Therefore it is not possible to conclude whether Ancestor A – the common ancestor of the *Pan* and *Homo* lineages displayed estrus swellings or not.

Ancestor B is the common ancestor of the gorilla lineage and the lineage of chimpanzees, bonobos, humans, and Ancestor A. As previously stated gorillas do exhibit estrus swellings. Since we were not able to conclude whether Ancestor A did or did not

exhibit estrus swellings we must instead use the extant members of Ancestor A's offspring lineages – the *Pan* lineage and the *Homo* lineage. So of the three extant descendents of Ancestor B, two taxa exhibit estrus swellings while one taxa does not. Since only one state change would be necessary to explain a lack of estrus swellings in the *Homo* lineage if Ancestor B had estrus swellings, while two state changes would be necessary to explain the presence of estrus swellings in the *Pan* lineage and *Gorilla* lineage if Ancestor B did not have estrus swellings. As reflected in figure 3, the most parsimonious state would be for Ancestor B to have had estrus swellings. This also means that it would be most parsimonious for Ancestor A to have had estrus swellings.

Ancestor C was the ancestor of the Orangutan (*Pongo*) lineage and the African Ape lineage (including gorillas, chimpanzees and bonobos, and humans). Orangutans have no display of estrus swellings. Ignoring the proposed states of Ancestor B and Ancestor A if Ancestor C did not have estrus swellings there would have to be 2 character state changes to account for the character states of the extant taxa. Therefore the *Gorilla* and *Pan* condition of having estrus swellings would be derived conditions. If Ancestor C did have estrus swellings there would also be two state changes needed to account for the states of the extant taxa. (This would set up no estrus swellings as derived states in orangutans and humans). So the two possible conditions for Ancestor C would be equally parsimonious. When we consider Ancestor B as having had sexual swellings (as previously stated as most parsimonious) then we are left with one lineage which had sexual swellings and one which did not. Therefore, we are not able to determine at this point whether Ancestor C had sexual swellings.

Two lineages came from Ancestor D came two lineages – that of the Great Apes and that of the Lesser Apes. Since gibbons have estrus swellings, orangutans do not, and Ancestor B does have estrus swellings (based on our previous analysis), it is most parsimonious for Ancestor D to have had sexual swellings. Indeed if Ancestor D had sexual swellings (note: Ancestor C would then also have sexual swellings) then there would only be two character state changes in the entire phylogeny from taxa with estrus swellings to those without rather than three changes from taxa without estrus swellings to those without if Ancestor D did not have estrus swellings. So Ancestor D, Ancestor C, Ancestor B, and Ancestor A must all have had estrus swellings (Fig. 4). Therefore, the lack of estrus swellings in humans (as well as orangutans) is a derived character state. Birgitta Sillen-Tullberg and Anders P. Moller came to the same conclusion in the phylogeny they constructed in their “The Relationship between Concealed Ovulation and Mating Systems in Anthropoid Primates: A Phylogenetic Analysis” (8).

In this analysis there is no issue with the assumption that lack of estrus swelling in humans is a derived state which needs to be explained. However the entire analysis may rest on a flawed assumption that only two dichotomous states exist – presence or lack of estrus swellings.

The size of estrus swellings varies greatly in those primates that do exhibit estrus swellings. For example, although the estrus swellings of chimpanzees and bonobos are large, extravagant, pink swellings which are easily noticeable from a distance, such large swellings are only found in 22 out of about 200 total primate species (Small 1993). Some primates such as gorillas and gibbons, however, exhibit changes which consist of merely a slight whiteness about the labia which is only noticeable when in close proximity

(Small 1993, Sillen-Tullberg and Moller 1993). It seems more effective to view the presence of estrus swellings as existing along a continuum with large, extravagant swellings at one end and no swellings at the other rather than as existing as two distinct character states. What occurs to our analysis of the constructed phylogeny? When viewing a characteristic which varies along a continuum it is no longer possible to speak of distinct character states. Instead of mapping character states onto the phylogeny it is helpful to map the relative swelling size onto the phylogeny so that we can still make an attempt to utilize the law of parsimony. With the relative sizes of estrus swellings mapped onto the phylogeny we can then utilize the concept of relative size change in order to create parsimony rather than the number of character state changes. The terms we will use to quantify for comparison the change in estrus swellings are large size change (moving from one end of the spectrum to the other), small size change (moving from one point in the spectrum to another point roughly half-way across the spectrum), and no change. Figure 5 shows the distribution among the great apes of the associated size of estrus swelling. Orangutans and humans have no estrus swellings, gorillas and gibbons have slight, scarcely noticeable swellings, and chimpanzees and bonobos have large estrus swellings (Small 1993, Sillen-Tullberg and Moller 1993).

The swelling size of Ancestor A (Fig. 6) is open to three possibilities – no estrus swellings, slight estrus swellings, and large estrus swellings. If we view these three estrus states as existing along a continuum and Ancestor A had no estrus swellings, then the chimpanzee lineage would have had to go a large change in size (moving from one end of the spectrum to the opposite end) in order to end up with full estrus swellings they now have. Similarly, if Ancestor A had full estrus swellings, the *Homo* lineage would have

had to go through a large size change in order to end up with no estrus swellings.

However if Ancestor A had slight estrus swellings its descendants would be poised to develop estrus swellings, lose estrus swellings, or maintain slight swellings; that is, more small size change options are available for the descending lineages. Both the chimpanzee lineage and the *Homo* lineage would have each gone through a small size change (from slight to full estrus swellings and from slight to no estrus swellings respectively). It seems more probable that both lineages would have undergone a small size change rather than one lineage undergoing a large size change while the other remains constant. If this is the case then the question should not be why did Humans lose the state of having estrus swellings, but rather why did chimpanzees and bonobos develop large estrus swellings while humans lost estrus swellings from a common ancestor who had slight estrus swellings.

Viewing the three possibilities of estrus states for Ancestor B can only serve to strengthen our conclusion that Ancestor A had slight swellings. Figure 7 shows the three potential phylogenies for the descendants of Ancestor B. If Ancestor B had no estrus swellings then the gorilla lineage would have had to go through a small size change to achieve the modern condition of having slight estrus swellings while the *Pan* lineage would have undergone a large size change to reach the modern condition of having large estrus swellings. If Ancestor B had large estrus swellings then the gorilla lineage would again have to have undergone a small size change while the *Homo* lineage would have had to undergo a large size change to achieve the modern condition of having no estrus swellings. If Ancestor B had slight estrus swellings then the gorilla lineage would have had to undergo no changes and the *Pan* lineage and the *Homo* lineage would have both

had to undergo a small size change. Since character state changes with Ancestor B having no estrus swellings or full estrus swellings were a large size change and a small size change, and with slight estrus swellings were two small size changes, it would be most parsimonious for Ancestor B to have had slight estrus swellings.

If Ancestor C had no sexual swellings then a small size change would have occurred in gorillas to obtain slight sexual swellings a large size changes would be necessary to explain the presence of large sexual swellings in the *Pan* lineage. If Ancestor C had large sexual swellings then a small size change would have had to occur in the gorilla lineage while large size changes occurred in both the orangutan and the *Homo* lineage. In a scenario where Ancestor C had slight sexual swellings one small size change would have occurred in the *Pongo* lineage, one small size change in the *Pan* lineage, and one small size change in the *Homo* lineage. I propose that it is more likely that 3 lineages would have each undergone one small size change a piece rather than one lineage undergoing a small size change while another lineage underwent a large size change. Therefore the character state of having slight sexual swellings seems most appropriate for Ancestor C.

The pattern of the most parsimonious phylogeny including an ancestral character state of slight sexual swellings continues with the possible character phylogenies with Ancestor D as the most ancestral state. In the event that Ancestor D had no sexual swellings two small size changes and one large size change would be necessary to account for the modern character states of all living ape taxa. In a scenario in which Ancestor D has large sexual swellings two small size changes and two large size changes would be necessary to account for the modern character states of all apes. It is most

parsimonious for the character state of Ancestor D to be slight sexual swellings as this would provoke a phylogeny with only three small size changes (one each in *Pongo*, *Pan*, and *Homo*) in the descendent lineages.

When sexual swellings are viewed as existing along a continuum and not as a simple dichotomy a reevaluation of the earlier conclusion of anthropologists that the presence of sexual swellings is characteristic of the ancestral state of apes can occur. If it holds that a small size change is more probable than a two large size changes within a lineage then slight sexual swellings can be seen as the ancestral character state throughout the ape phylogeny. With such a conclusion made it becomes clear that human's lack of estrus swellings should not necessarily be viewed as an extreme oddity in the world of apes which needs drastic theories for explanation. Rather it should be seen as equally necessary to explain why the human lineage ended up with no sexual swelling and chimpanzees ended up with large sexual swellings.

Conclusion

It is important to note that the presence or absence of estrus swellings in any primate must be understood as only one piece of a larger suite of sexual characteristics which interact with each other in highly intricate ways. The lack of estrus swellings in humans did not evolve on its own as a trait unaffected by any other traits. At some point in human ancestry the patch of skin surrounding the vaginal opening became less sensitive to the hormonal changes which trigger swelling in some species. During the same course of time the skin around the vaginal opening in chimpanzees became more sensitive to the hormonal changes around ovulation. In each scenario it is possible that

the change increased the reproductive fitness of individuals. However it could also be the case that the change in size of estrus swellings occurred as a byproduct of the evolution of some other trait. For example, a reduction in the size of estrus swellings could have occurred as a result of bipedalism which realigned the body in such a way that swellings were no longer useful as a visual signal of ovulation. Or perhaps some change in the hormones which drive the stages of the ovulatory cycle resulted in a loss of sensitivity of the patch of skin around the female genitalia. It is suggested that further studies be done which examine the intricate ways in which the elements of the suite of sexual traits interact within both humans and chimpanzees. Such a study would provide valuable insight into how the size of estrus swellings in both humans and chimpanzees evolved in such divergent pathways.

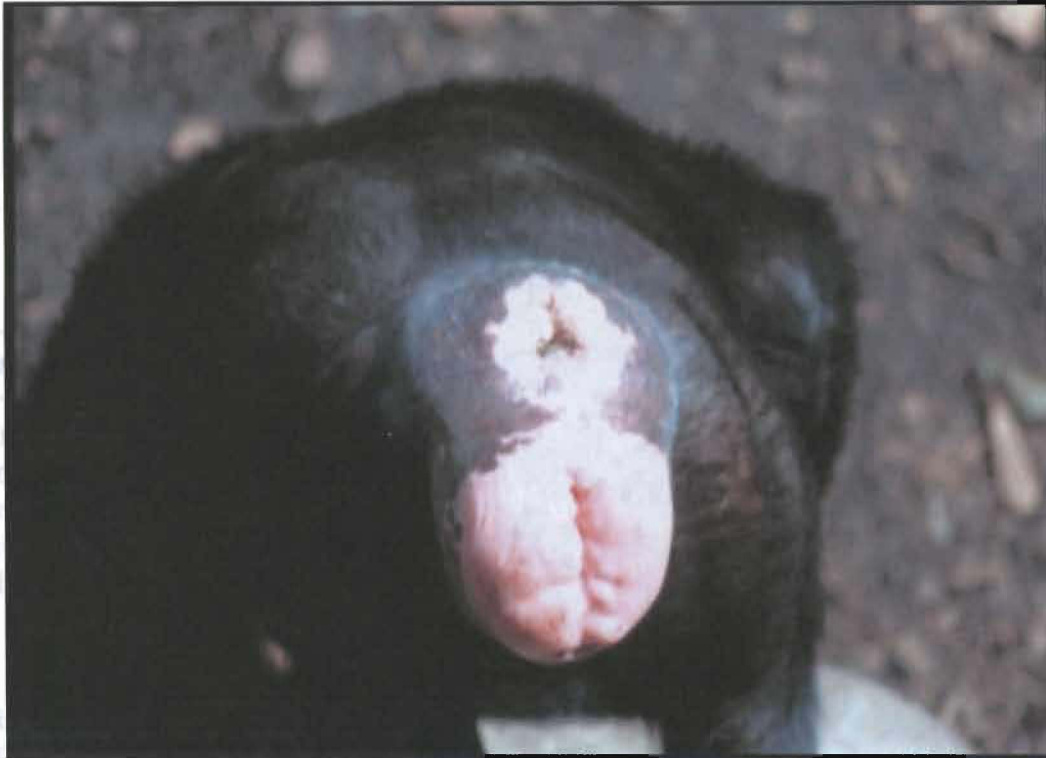


Image 1: Estrus Swelling of a Female Chimpanzee. The large, pink swelling of the skin of the labia extending back to the anus acts as a signal of ovulation.

Photos provided by Melissa Emery Thompson of Harvard University



Images 2 & 3: Easily Noticeable at a distance, the large estrus swellings of chimpanzees can be seen through the obstacles of the forest.

Photos provided by Melissa Emery Thompson of Harvard University



Image 4: Estrus Swellings are large and would have made bipedal locomotion difficult in the ancestor of *Homo* if they were present. Notice how far the swelling extends out from the body of the chimpanzee.

Photos provided by
Melissa Emery Thompson
of Harvard University

Image 5: The Quadrupedal Locomotion of Chimpanzees situates estrus swellings in a position that they are easily viewable to others and do not inhibit locomotion.

Photos provided by
Melissa Emery Thompson
of Harvard University



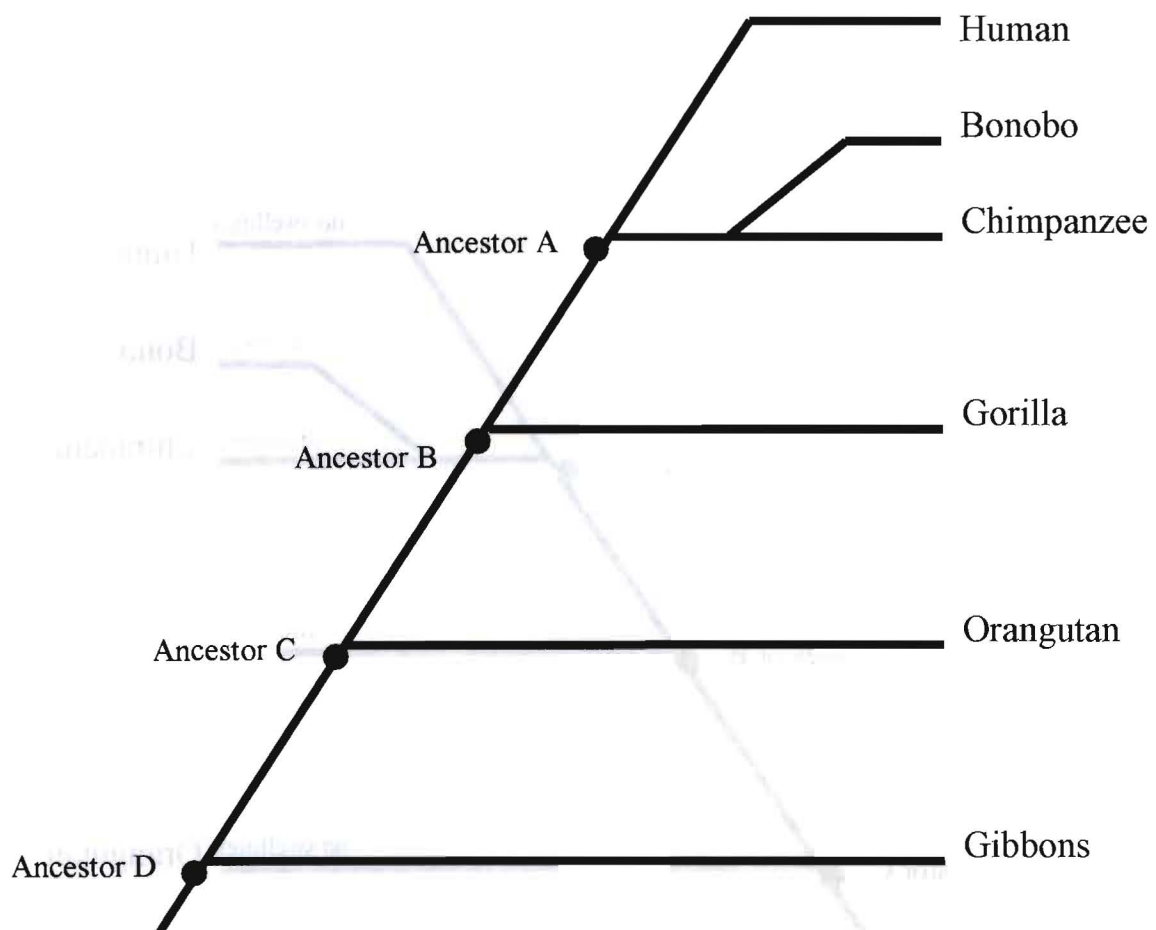


Figure 1 – The phylogeny of apes which is generally agreed upon as correct.

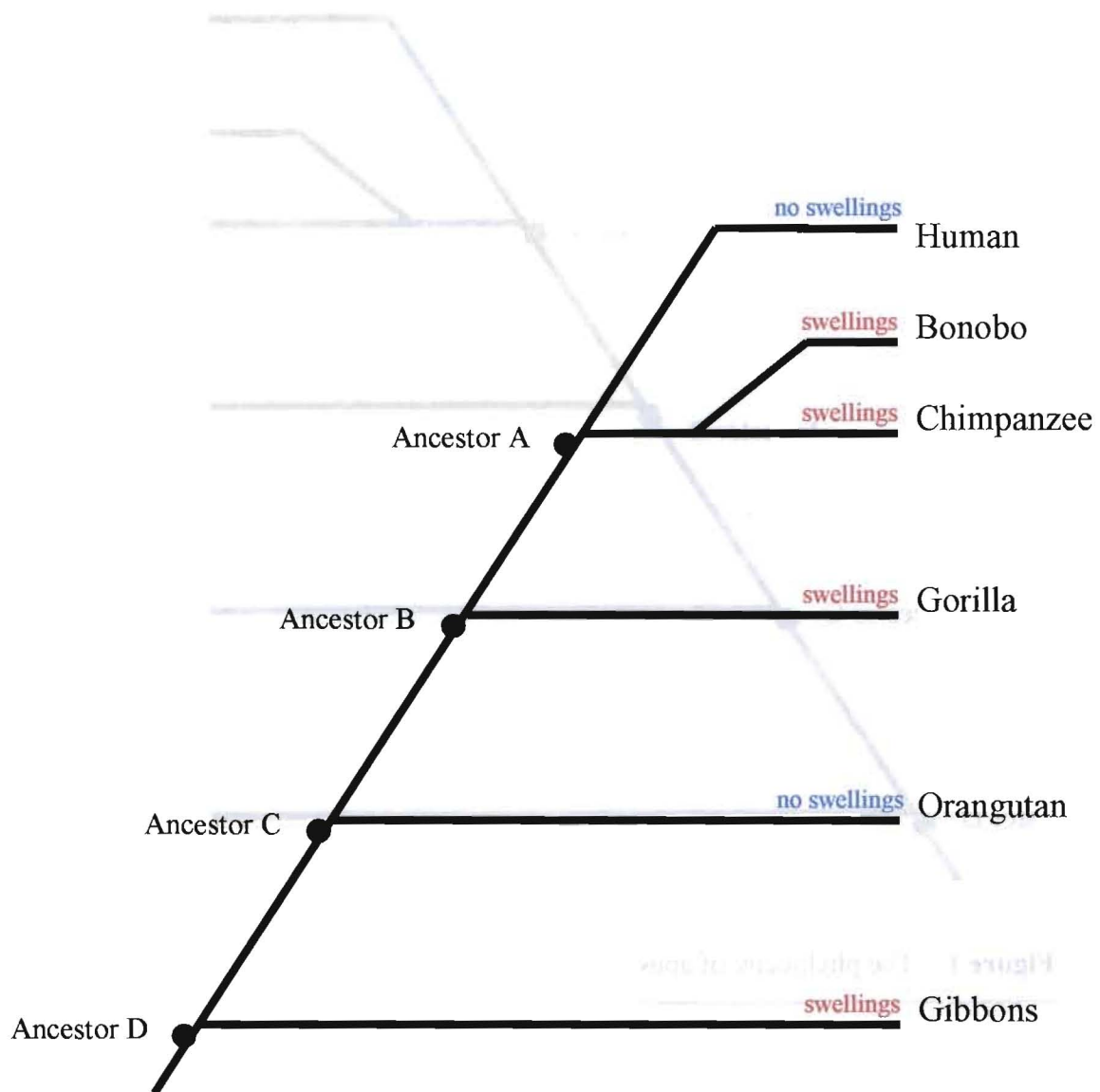


Figure 2 – Phylogeny of apes with the character state of associated sexual swellings mapped onto each species.

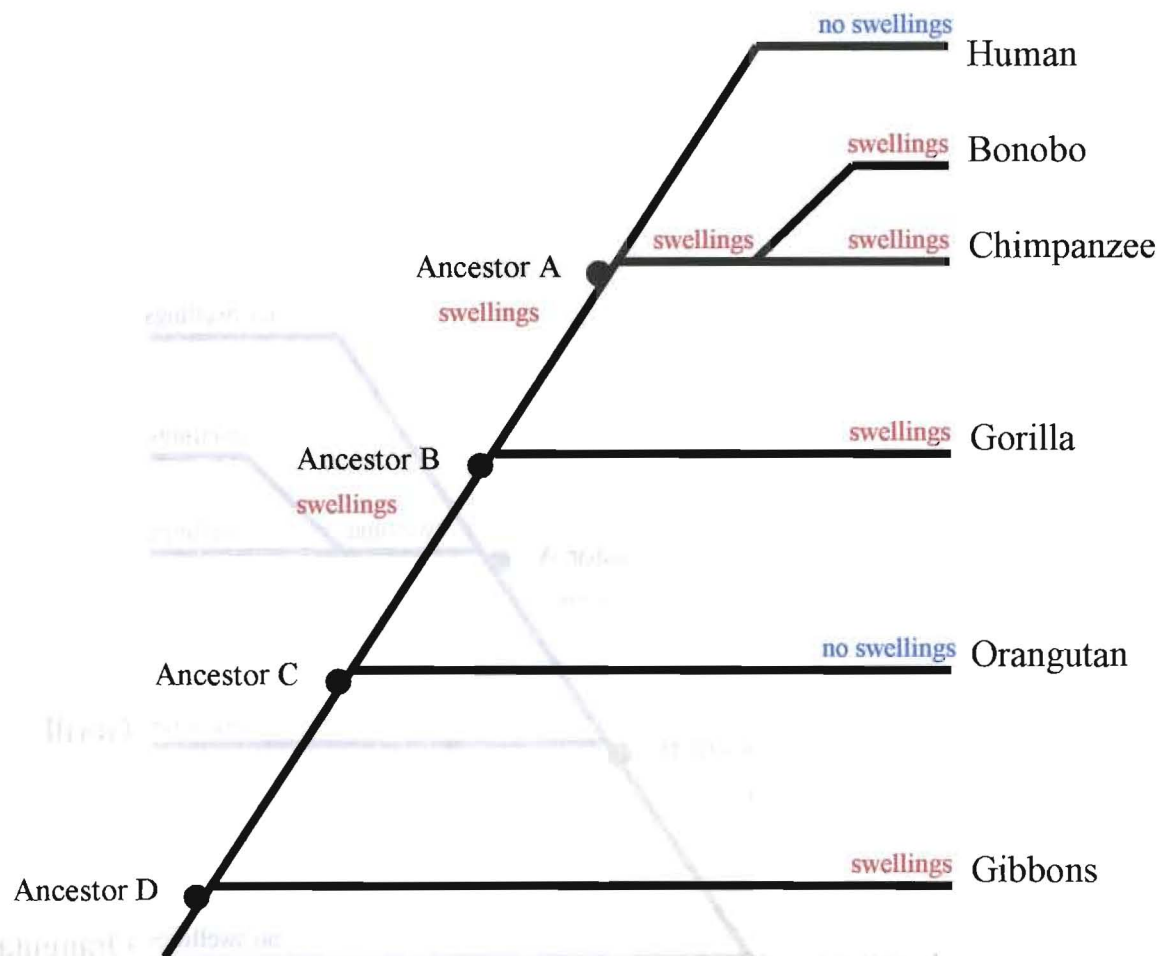


Figure 3 – Phylogeny of Apes including the inferred likely character states of ancestors A and B based on 2 potential character states.

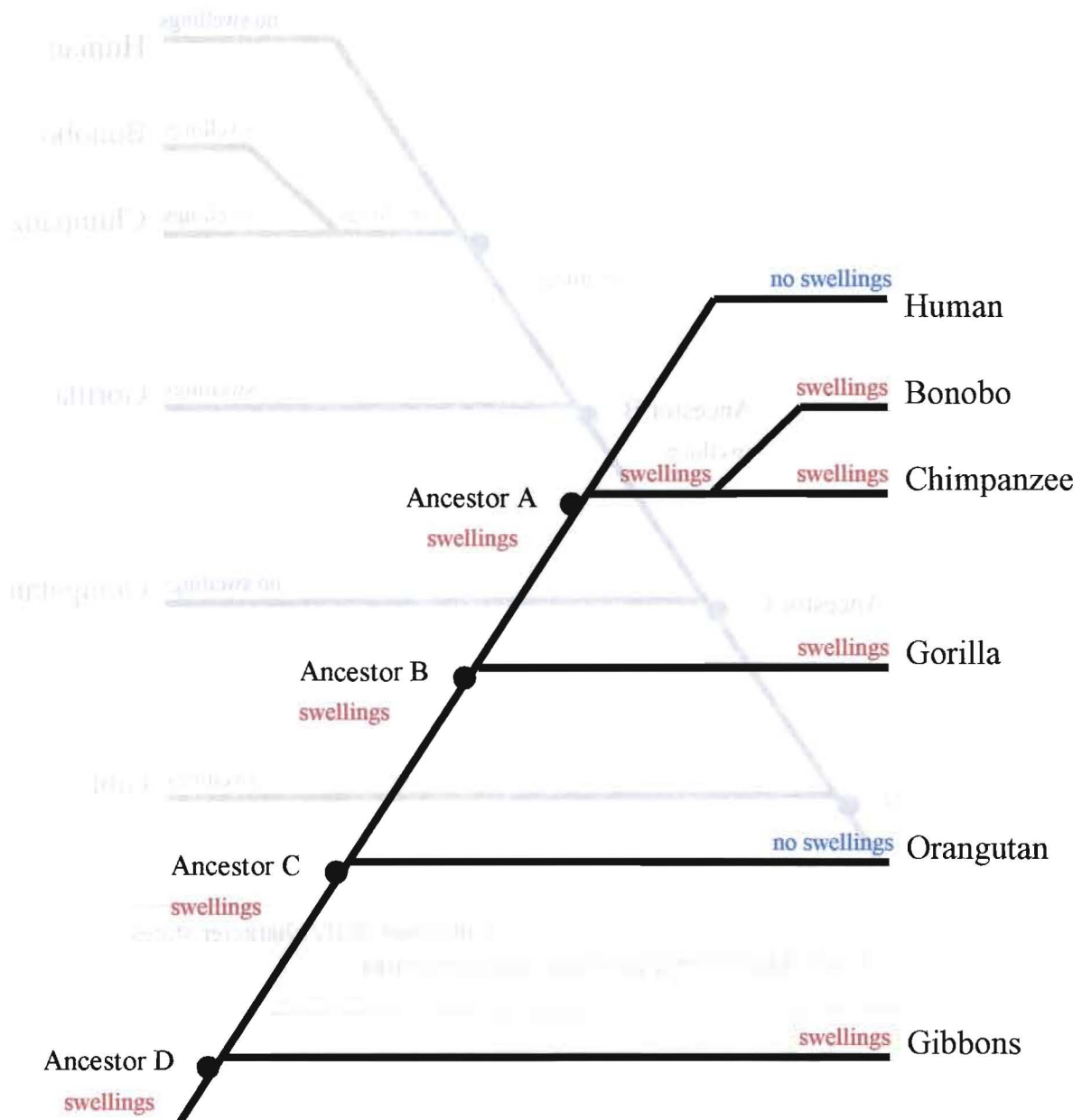


Figure 4 – Phylogeny of Apes and Ancestors based on analysis of 2 potential character states.

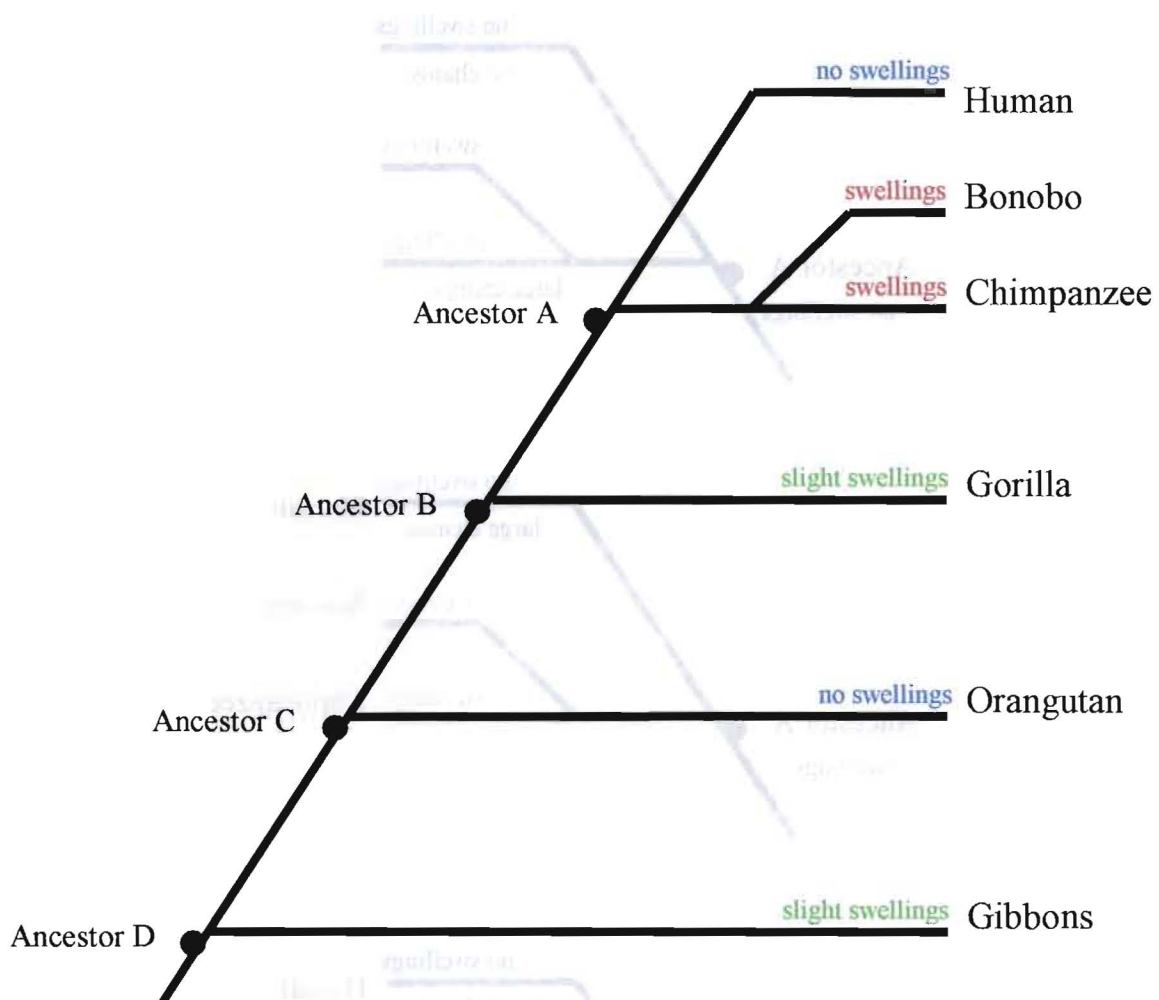


Figure 5: Phylogeny of Apes with the 3 potential character states mapped onto each extant species.

Figure 6: 3 potential phylogenies with based on the state of sexual swellings of Ancestor A. Note the number of state changes necessary to explain the modern condition of estrus swellings. The phylogeny with Ancestor A with slight swellings requires two single changes rather than one double change.

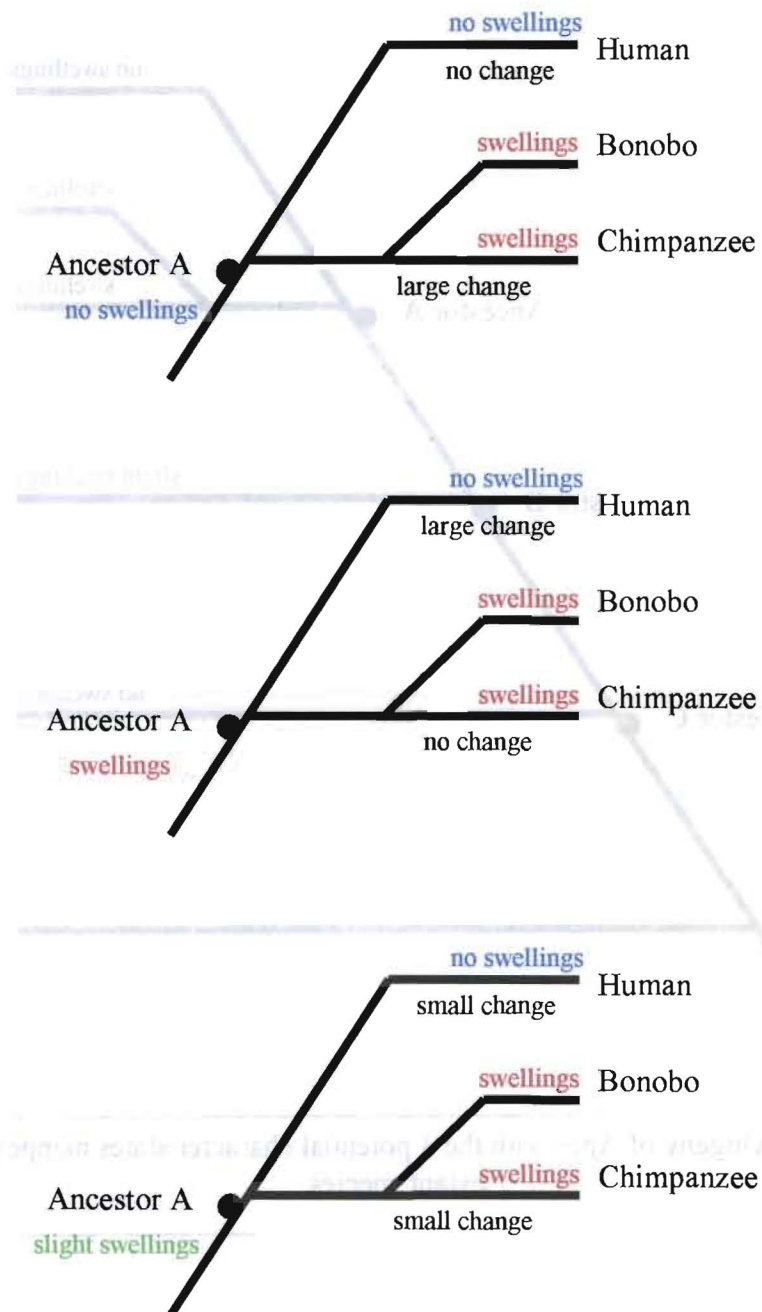
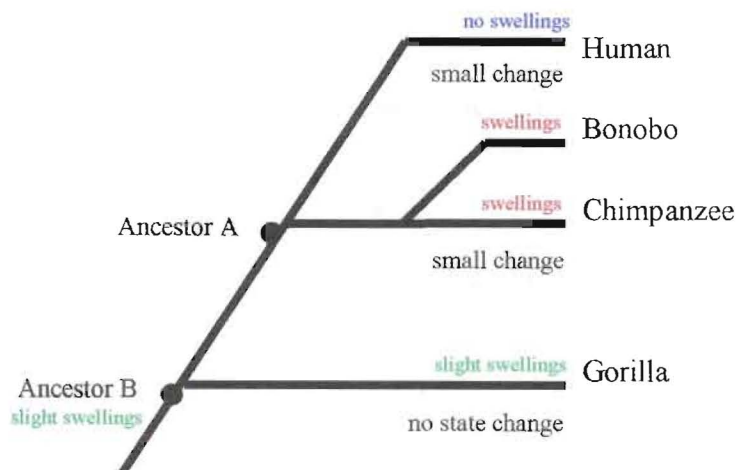
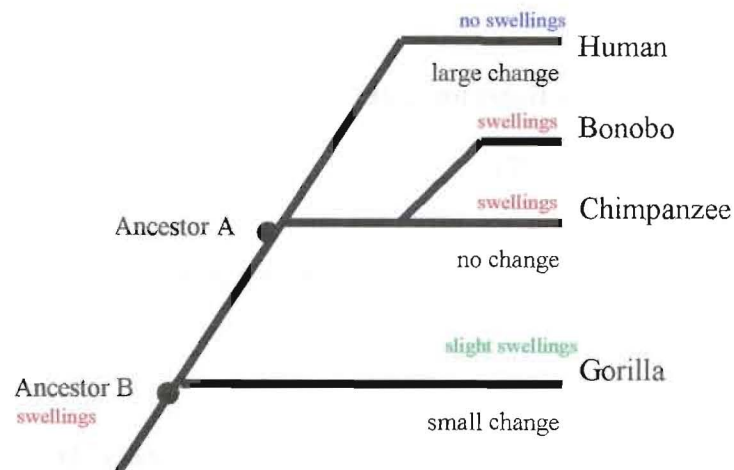
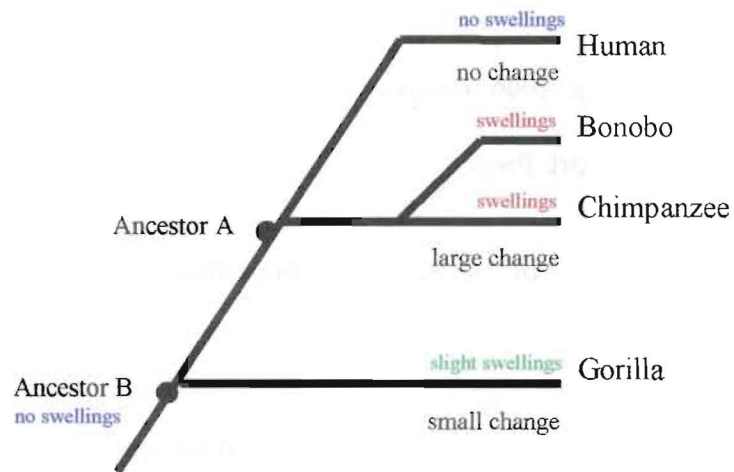


Figure 7: 3 potential phylogenies with based on the state of sexual swellings of Ancestor B. Note the number of state changes necessary to explain the modern condition of estrus swellings. The phylogeny with Ancestor B with slight swellings requires the least amount of state changes.



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