ARTICLES

Energy Economy in the Evolution of Menstruation

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Compared with other aspects of mammalian reproductive physiology, we know surprisingly little about menstruation. Medical research has illuminated many of the proximate mechanisms that bring menstruation about, but has left us in the dark as to why menstruation evolved. Evolutionary anthropology provides the expertise in primatology and evolutionary biology needed to shift the emphasis in this field from How to Why.

To understand the evolution of menstruation we need to address two distinct phenomena, (1) the cyclicity of the uterine lining and (2) vaginal bleeding. The uterine lining is called the endometrium. During each cycle the endometrium proliferates, developing a high secretory capacity and an elaborate microvasculature. If implantation and pregnancy do not occur the extra tissue is reabsorbed or shed with the menses.[1,2] The cyclical growth and retreat of the endometrium is universal in mammals.[3,4] The second phenomenon, the external loss of blood and other tissue through the vagina, is largely restricted to Old World primates and shrews.[1,3-5] The word menstruation customarily refers only to species with external bleeding. In this article I will present recent evidence[5] suggesting that the function of endometrial cyclicity is energy economy and that external bleeding is a side effect that arises when there is too much blood for efficient reabsorption.

ENDOMETRIAL CYCLICITY: ENERGY ECONOMY

The most important clue to the function of endometrial cycles is that they are coupled to ovarian cycles. This close coordination is accomplished via the action of the ovarian steroid hormones.[1,2] In all mammalian species, the endometrium is able to sustain implantation by the embryo during only a fraction of the cycle; this fraction coincides with the time when an embryo might actually be available to implant (Fig. 1). In humans, the window of opportunity for implantation is about 3 days long.[2] Selection to extend that time should be nonexistent because in the absence of an embryo implantation cannot occur.[5] Given that the endometrium is temporally restricted in its utility, is it more costly to sustain this tissue when it is not needed or to regenerate it in each cycle?

An economist suggested that the endometrium is like a house, and that it's cheaper to leave the house standing than to tear it down and rebuild it every month. However, the endometrium is not made out of dead wood or brick; it is a biological tissue that converts metabolic fuels into useable energy through the processes of glycolysis and respiration.[6,7] To keep the endometrium going, continuous metabolic support is required. The rate of oxidative metabolism can be determined from oxygen uptake. Price, Duncan, and Levin[8] inserted an oxygen electrode into endometrial strips and measured oxygen uptake at various phases of the menstrual cycle. Their data show that endometrial oxygen consumption increases nearly sevenfold per mg protein/hr over the course of the menstrual cycle until ovulation or implantation. In the regressed state that follows menstruation, oxygen consumption is minimal.

Glossary

Correlated evolution—The phylogenetic association between change in one character and the state of another character.

Endometrial cycle—The recurring cycle of change in the endometrium. It is characterized by growth, maintenance, and collapse.

Endometrium—The mucous membrane that lines the uterus.

Implantation—Embedding of the embryo in the endometrium.

Menstruation—The periodic discharge through the vagina of blood, secretions, and miscellaneous tissue debris from the endometrium.

Menstrual cycle—The ovarian cycle of a menstruating mammal. Day one of the cycle is the first day of menstrual bleeding.

Metabolic rate—The amount of energy liberated or expended in a given unit of time. Basal metabolic rate is the metabolic rate required to maintain vital functions, and is measured by the rate of oxygen uptake by a fasting, resting subject at room temperature.

Metabolism—The aggregate of all chemical processes that take place in living organisms.

Microvasculature—Network of small blood vessels.

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Key words: menstrual cycle; endometrium; metabolism; metabolic rate

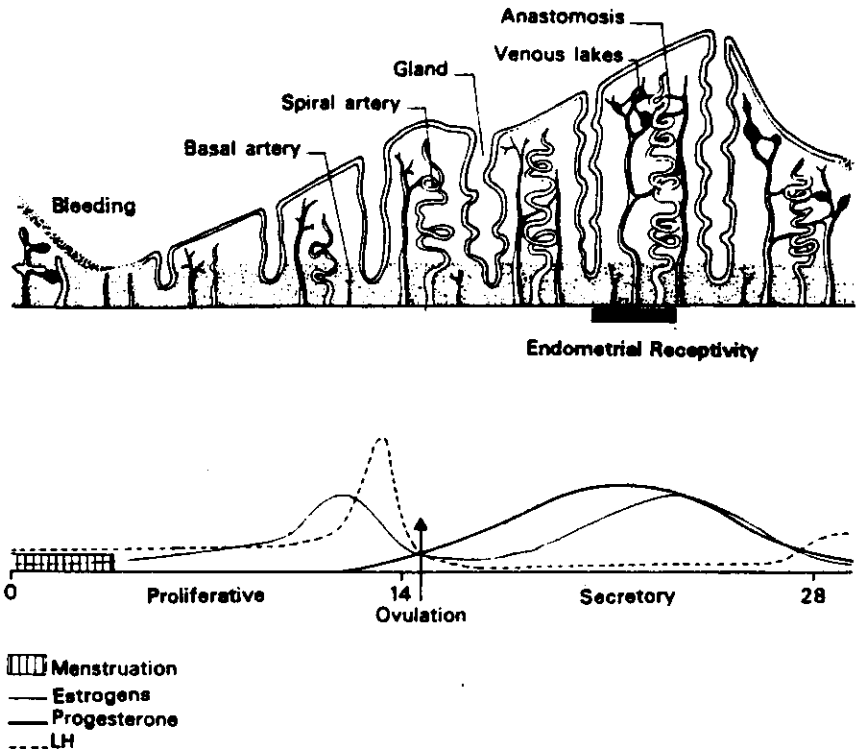

Figure 1. Changes in the uterine endometrium over the menstrual cycle (top) and associated steroid hormone changes (bottom). The brief period when implantation is possible is indicated by the black bar. From Johnson and Everitt[1] as modified by Strassmann.[5]

Thus, the endometrium consumes the most energy while it is standing by for use and the least energy after it has been torn down, with a gradient in between while it is being built. It is therefore energetically cheaper to regenerate the endometrium each cycle than to provide continuous metabolic support that will not enhance implantation.[5] Unlike the economist's house, a temporary structure is cheaper.

The high cost of maintaining the endometrium in the implantation-ready state is the result of several factors, including: (1) the glandular secretion of glycoproteins, sugars, and amino acids, and (2) the presence of a greater tissue mass with a well-developed microvasculature and abundant blood flow.[1,2,9] If the endometrium had evolved to stay perennially primed for implantation, the greatest waste of energy would occur during amenorrhea, when ovulation is absent for long periods. Both amenorrhea in menstruating primates and anestrus (cessation of cycling) in other mammals are caused by a shortage of metabolic fuels resulting from poor nutrition, stress, or lactation.[10–12] Instead of maintaining the endometrium when ovulation is absent and metabolic fuels are already scarce, the amenorrheic endometrium remains in its regressed, energy-sparing state.[5] Upon the resumption of ovarian cycling, the endometrium builds up again because the embryo cannot implant in denuded tissue.

The ovarian steroids, estradiol and progesterone, have receptors in the endometrium, the brain, and the mammaries, and coordinate the activity of all tissues involved in reproduction.[2] The cyclical action of the ovarian steroids on these target tissues results in a whole-body cyclicity of metabolic rate (energy expenditure per unit of time). In women, metabolic rate is at least 7% lower, on average, during the follicular (preovulatory) phase than it is during the luteal (postovulatory) phase of the menstrual cycle.[13–16] The food intake of women, measured in kilojoules per day, is about 11% to 35% greater during the luteal phase.[17–19] Similar increases in food consumption have been observed in rats and nonhuman primates.[20,21] The energy saving of the follicular phase in women translates into about 50 megajoules (MJ) over four cycles, the energy equivalent of about 6 days' worth of food.[5] By helping women to maintain fat deposits, this economy of energy has beneficial implications for both fecundity and survival. If a woman forgoes the cost of the luteal phase for 12 months during amenorrhea, she saves an estimated 130 MJ, or her food supply for half a month.[5] The coupling of reproductive cycling to metabolic cycling is unlikely to be fortuitous. The cyclicity of the ovarian steroids modulates metabolism in the endometrium, brain (hypothalamic pituitary unit), and other tissues, economizing on the energy costs of reproduction.

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A common mistake is to focus only on the cost of menstrual bleeding[22] and ignore the cost of the luteal phase of the menstrual cycle and maintenance of the endometrium. However, the protein lost during menstruation is less than half a percent of the required protein intake over one cycle; this is minor relative to fecal protein loss.[5,23,24] Women who have unusually heavy menses may lose enough iron to become anemic, but only if they are cycling repeatedly. Over human evolutionary history, and in contemporary populations that do not practice contraception, menstruation is a rare event (see Fig. 2).[25,26] It is unlikely that infrequent menses would have led to anemia in hunter-gatherers who con-

Figure 2. Menstruating Dogon woman tending a hearth outside a menstrual hut. By monitoring women's visits to menstrual huts on each of 736 consecutive days, it was possible to demonstrate that, in the absence of contraception, menstruation is a rare event. Dogon women aged 20 through 34 years spent most of the time pregnant or in amenorrhea, and therefore had a median of only two menses each over the 2-year study period. (Photograph by B. I. Strassmann.)

sumed meat on a regular basis. Finally, in the vast majority of mammals endometrial regression does not involve external bleeding[3,4] and therefore cannot be viewed as a nutritional expense.[5]

OTHER EXAMPLES OF ENERGY ECONOMY

The energy-sparing reductions in tissue mass and metabolic rate that occur during menstrual cycling have many parallels elsewhere in the mammalian body and even in other vertebrates. For example, nursing women gain roughly half a kilo of breast tissue that regresses with the cessation of lactation.[27] Severe food restriction, such as occurs during anorexia nervosa, results in a 19% to 39% reduction in basal metabolic rate.[28] Hibernating mammals often undergo metabolic suppression that includes atrophy of the gut and gonads.[29,30] Mere absence of food in rats and other species results in reductions in intestinal mucosal mass.[30,31] The Burmese python (*Python molurus*), in particular, saves considerable energy by not maintaining a functional gut during the long periods between meals when it has nothing to digest.[32] In seasonal breeders such as birds, the gonads commonly regress in both sexes during the nonbreeding season.[3] Yolk synthesis begins only a few days before ovulation and ceases in the nonbreeding season.[33] Thus, endometrial regression is one example of a widespread tendency for tissues to spare energy by regressing when they are not needed (for recent review see Piersma and Lindstrom[49]).

Thus, endometrial regression is one example of a widespread tendency for tissues to spare energy by regressing when they are not needed.

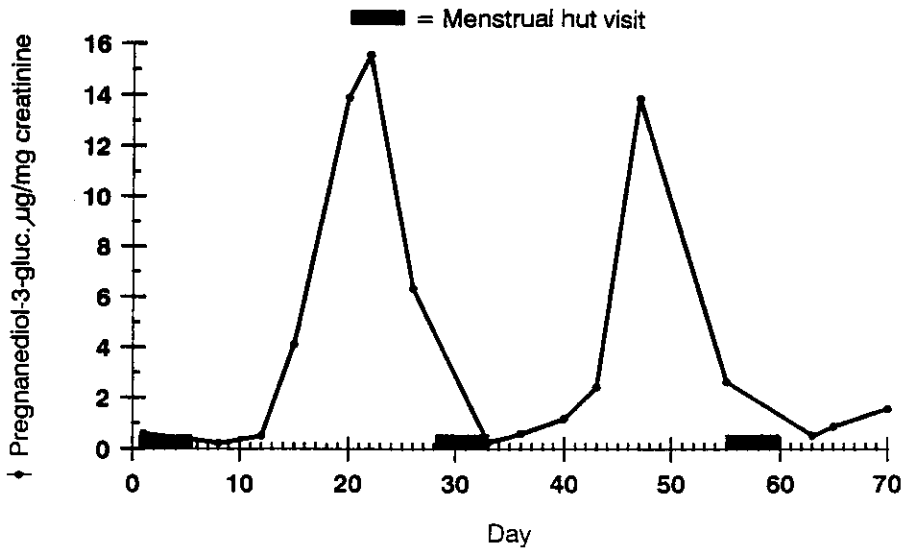
The evolutionary origins of endometrial regression may predate the appearance of mammals. The uterine endometrium in mammals is similar and, perhaps, homologous to the epithelium of the oviducts in reptiles.[5,34] Both are secretory linings that transfer nutrients from mother to embryo. The epithelium of reptilian oviducts grows in the breeding season, when it is most biochemically active, and regresses in the nonbreeding season.[35] Just like the mammalian endometrium, the secretory activity of reptilian oviducts is restricted to the time when a fertilized egg or embryo is likely to be present.

VAGINAL BLEEDING: A SIDE EFFECT

The function of the endometrial arterioles is to supply blood to the endometrium, the tissue that supports implantation. In the event of pregnancy, the endometrial arterioles channel maternal blood to the pla-

Box 1. Is Menstruation a Defense Against Pathogens?

In 1993, Margie Profet[22] published the provocative new hypothesis that menstruation evolved to cleanse the uterus of sperm-borne pathogens. She reasoned that if menstruation evolved to protect the uterus and oviducts from colonization by pathogens carried by sperm, then (1) contraceptives that suppress the menses may promote uterine infection and (2) curtailing uterine bleeding may undermine the body's natural defenses.[22] The popular media treated Profet's hypothesis as a triumph of Darwinian medicine, but three analyses concluded that it is not supported by the evidence.[5,24,42] Here I briefly discuss the data bearing on three of the main predictions.



The hormonal profile of a Dogon woman and the timing of her visits to a menstrual hut. Notice that she went to the hut after pregnanediol withdrawal when she was, in fact, menstruating. Like the other women in the sample (N = 70), she obeyed the Dogon taboos by staying away from the menstrual huts when she was not menstruating. During 12.5% of menses, women in the study village skipped a visit to the menstrual huts, but even after correction for these missed visits, menstruation remained a rare event.

Prediction 1. If the function of menstruation is to defend against pathogens, uterine pathogens should be more prevalent before than after menses.[5,22] A review of data on fluctuations in the microbes of the female reproductive system did not support this prediction.[5] On the contrary, several studies reported that menstruation exacerbates infection.[43] A likely reason for that finding is that blood contains iron, amino acids, proteins, and sugars, and therefore is an excellent culture medium for bacteria.[44] For that reason, serum is the most widely used nutrient in cell culture media.[5] Menstrual blood also breaches the cervical mucus, making it easier for pathogens to ascend to the upper reproductive tract.[44] Finally, if the lining of the uterus bleeds to defend against pathogens, then it is unique in this regard. No other mammalian tissue fights pathogens by bleeding.[5] For example, when the eye contracts conjunctivitis, the capillaries dilate and, as a result of the increased blood flow, immune agents pervade the area. However, only these agents leave the vessels; the red blood cells remain inside.[5]

Prediction 2. Profet argues that menstruation tracks pathogen burden.[22] In preindustrial societies, however, sexual activity often occurs during long stretches when menstruation is absent: pregnancy, lactational amenorrhea, and the postmenopausal years.[5,24,42] Another problem is that in the absence of contraception, menstruation is a rare event among fecund women of reproductive age.[25] For example, due to pregnancy and postpartum amenorrhea Dogon women aged 20 through 34 years had a median of only two menses each over a two-year period.[26] These data are not subject to reporting bias because they are based on women's visits to menstrual huts and are corroborated by hormonal data (see Fig.).[45] Assuming that menstruation was also a rare event in ancestral populations, it is doubtful that it evolved as a defense against pathogens.

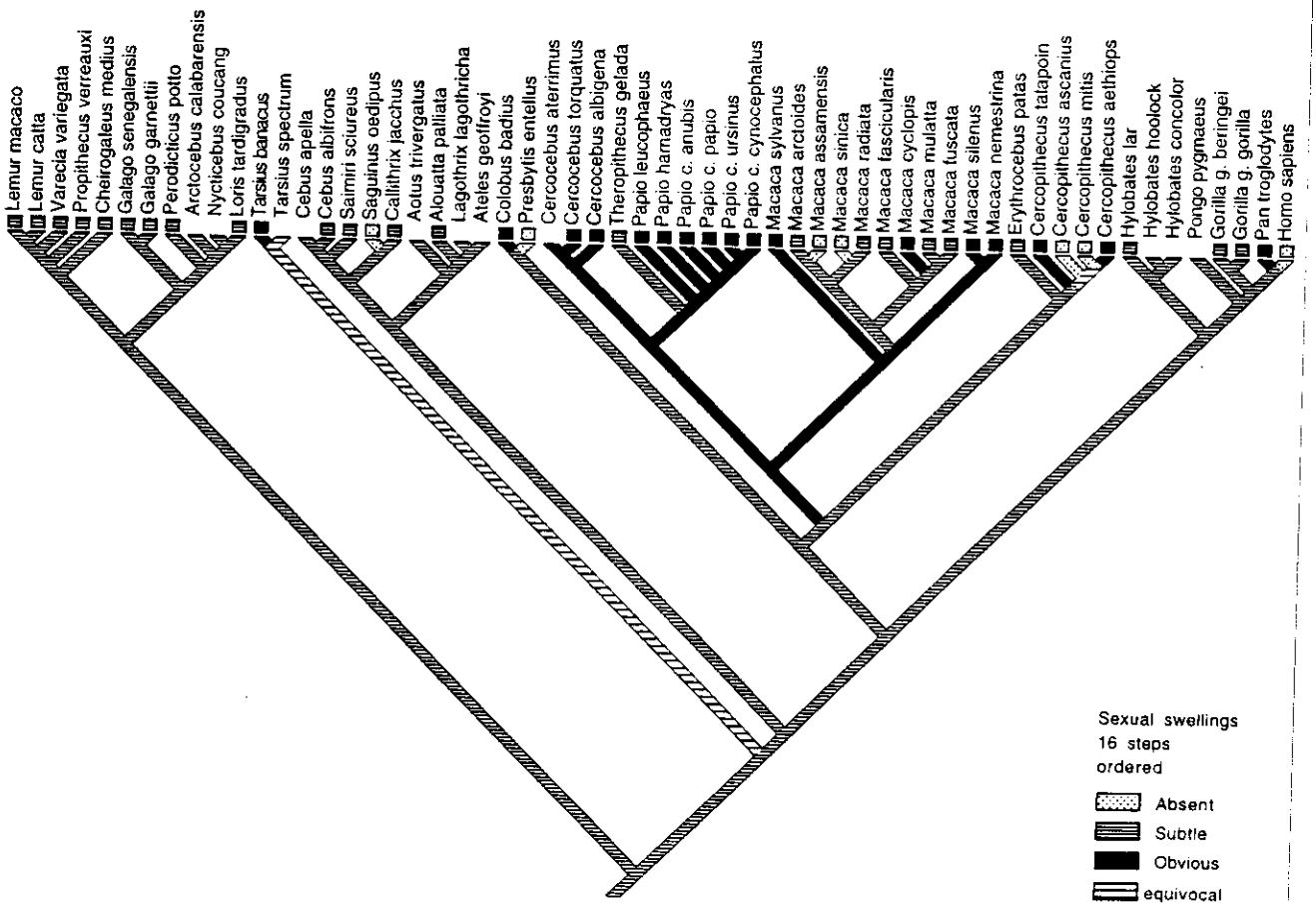
Prediction 3. In primate species that have promiscuous breeding systems, Profet[22] expects menstruation to be more copious. Her argument is that if females mate often, and with lots of different males, then there are more opportunities for contagion via sperm-borne infections, and that this exerts selection pressure for heavier flow. A quantitative analysis that controlled for the confounding influence of phylogeny failed to support this prediction.[5] Overt menstruation, defined as menstrual bleeding that is externally obvious, was gained four times in the presence of low promiscuity. In the presence of high promiscuity, it was gained two times and lost two times.[5] Thus, the evolution of copious menstruation in primates was not correlated with the evolution of female promiscuity.

In summary, a large body of evidence contradicts the pathogen-defense hypothesis, suggesting that it is rash to use this hypothesis as the springboard for medical recommendations. Nonetheless, a constructive outcome of Profet's hypothesis has been to focus attention on a central enigma of primate reproductive physiology.

Box 2. Did Menstruation Evolve as a Signal of Fertility?

Females in most preindustrial societies were subject to strict taboos during their menses.[26,46] Among the Dogon of Mali, these taboos are a male tactic for eliciting honest signals of female reproductive status.[26,45] When a woman visits a menstrual hut, all members of her husband's patrilineage learn that she is neither pregnant nor in amenorrhea, and that she will soon be ready to conceive. Information about the timing of conception is used in paternity assessments.[26,45] Although knowledge of menstruation can be exploited for information about fecundity, did menstruation evolve for this purpose?

If copious menstruation evolved as a signal of fecundity, then menstruation should be restricted to humans because no other primate species has concealed ovulation. If females convey the proximity of ovulation to the males of their species through odor or swellings, then menstruation does not add further information.[5] Four genera of primates (*Macaca, Cercopithecus, Papio,* and *Pan*), however, have both overt menstruation and obvious sexual swellings (Fig.1). Moreover, a phylogenetic analysis suggests that the absence of sexual swellings was not a predisposing factor for the evolution of menstruation.[5] The co-occurrence of menstruation and sexual swellings refutes the hypothesis that menstruation evolved as a reproductive signal.



The degree of sexual swellings (absent, subtle, obvious) mapped onto the same primate phylogeny shown in Figure 3. Four genera of primates (*Macaca, Cercopithecus, Papio,* and *Pan*) have both overt menstruation and obvious sexual swellings. Data on sexual swellings in extant taxa are from Hrdy and Whitten.[48] Figure is from Strassmann.[5]

centa.[9] In humans, there is one artery for each placental chamber.[36] In the absence of implantation, the retreat of the endometrium results in injury to the microvasculature.[37] If the blood is fully reabsorbed without external bleeding, then, to use terminology introduced by Margie Profet (see Box 1),[22] menstruation is "absent" or "covert." If blood is externally detectable, then menstruation is "slight." If blood is externally obvious, then menstruation is "overt." Variation in the degree of bleeding in primates shows a striking phylogenetic distribution (Figs. 3 and

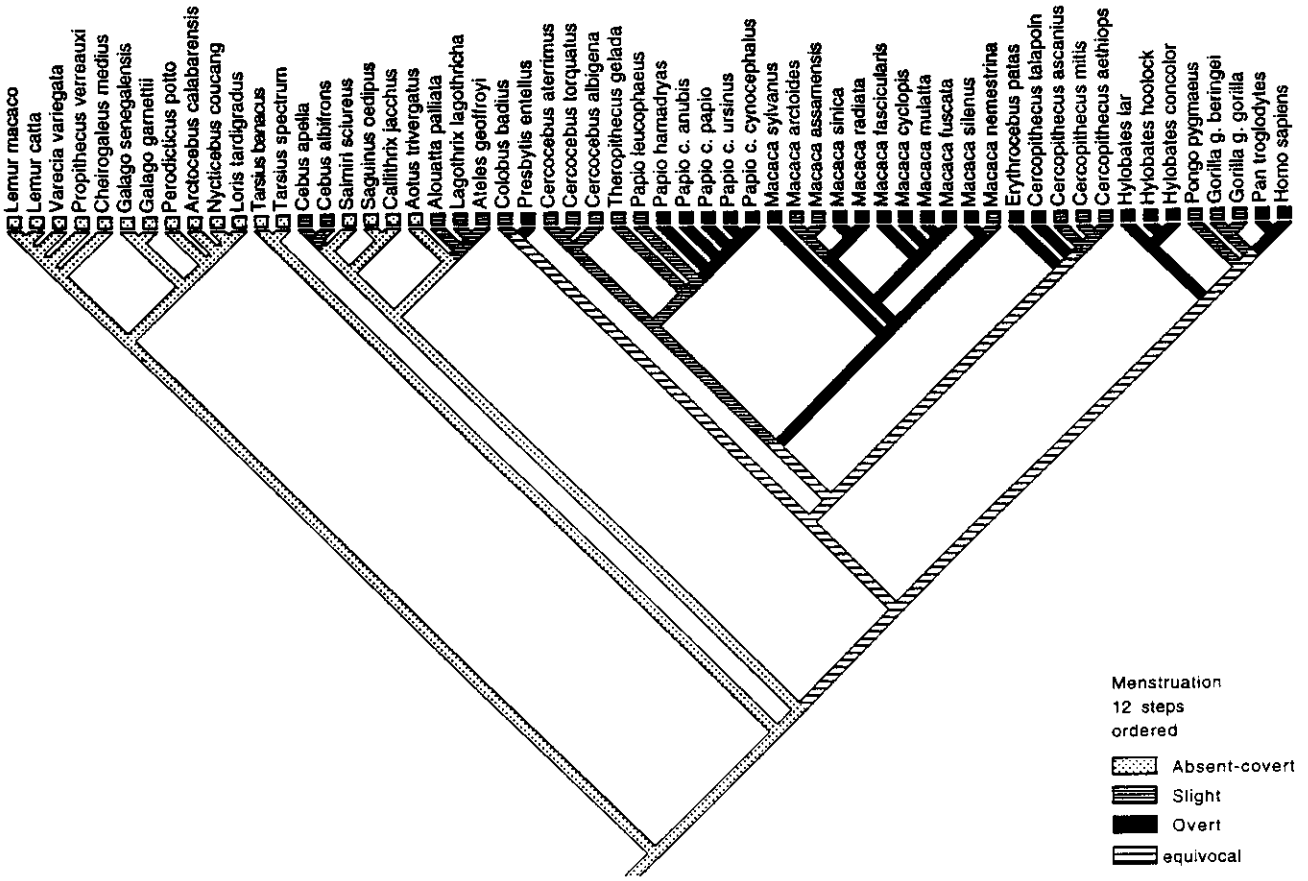


Figure 3. Phylogeny of the primates showing the distribution of menstrual copiousness (absent or covert, slight, and overt) among extant taxa and the inferred ancestral states in each lineage. This phylogeny requires 12 evolutionary steps to account for the present distribution of menstrual copiousness. Suprageneric relationships are based primarily on Fleagle[47]; see Strassmann[5] for a discussion of subgeneric relationships. Data on menstruation in extant taxa are from Hrdy and Whitten[48] and Profet.[22] Figure is from Strassmann[5].

4). Catarrhines (Old World monkeys, apes, and humans) have slight or overt menstruation; platyrrhines (New World monkeys) have slight or covert menstruation; and prosimians have covert or absent menstruation.[5]

Variation in the degree of bleeding in primates can be attributed to anatomical differences among species. From histological studies, Kaiser[38,39] concluded that catarrhines have spiral arterioles and conspicuous bleeding, whereas platyrrhines have relatively straight arterioles and microscopic bleeding. Differences in the design of the arterioles no doubt relate to their major function: nourishing the endometrium and, ultimately, the fetus itself. Because the arterioles service the fetus through the placenta, differences in the structure of the placenta may also be reflected in the degree of bleeding.[40] Endometrial thickness and depth of shedding seem to contribute to the degree of menstrual bleeding: catarrhines tend to have thick endometria and profuse bleeding, whereas platyrrhines tend to have thin endometria and scant shedding.[39] Body mass or litter mass might be good proxy variables for uterine volume, a variable for which few data are available, but which might also predict the degree of bleeding. After controlling for phylogeny, however, there is no evidence for correlated evolution between the degree of menstrual bleeding and either body mass or litter mass alone.[5] Nonetheless, phylogenetic analysis does suggest that in catarrhines the evolution of "overt" menstruation is correlated with the evolution of higher ratios of litter mass to body mass.[5] A high ratio of litter mass to body mass may permit less complete reabsorption of blood from the endometrial microvasculature or may simply make blood loss more observable.

Humans are the only species in which data are available on intraspecific variation in bleeding. Women who have given birth to more children tend to have larger, more vascular uteri and heavier periods.[41] Differences in uterine size and blood flow may also explain the heavier bleeding of taller women and women whose previous children had high birth weights.[41] These correlations are consistent with the view that menstrual bleeding is a functionless by-product of endometrial regression.

Despite an increasingly detailed understanding of the physiology of menstruation, we are only just beginning to examine this phenomenon from an evolutionary perspective. In recent years two hypotheses to explain why menstruation evolved have been put forth that can be tested using comparative information from anthropology, primatol-

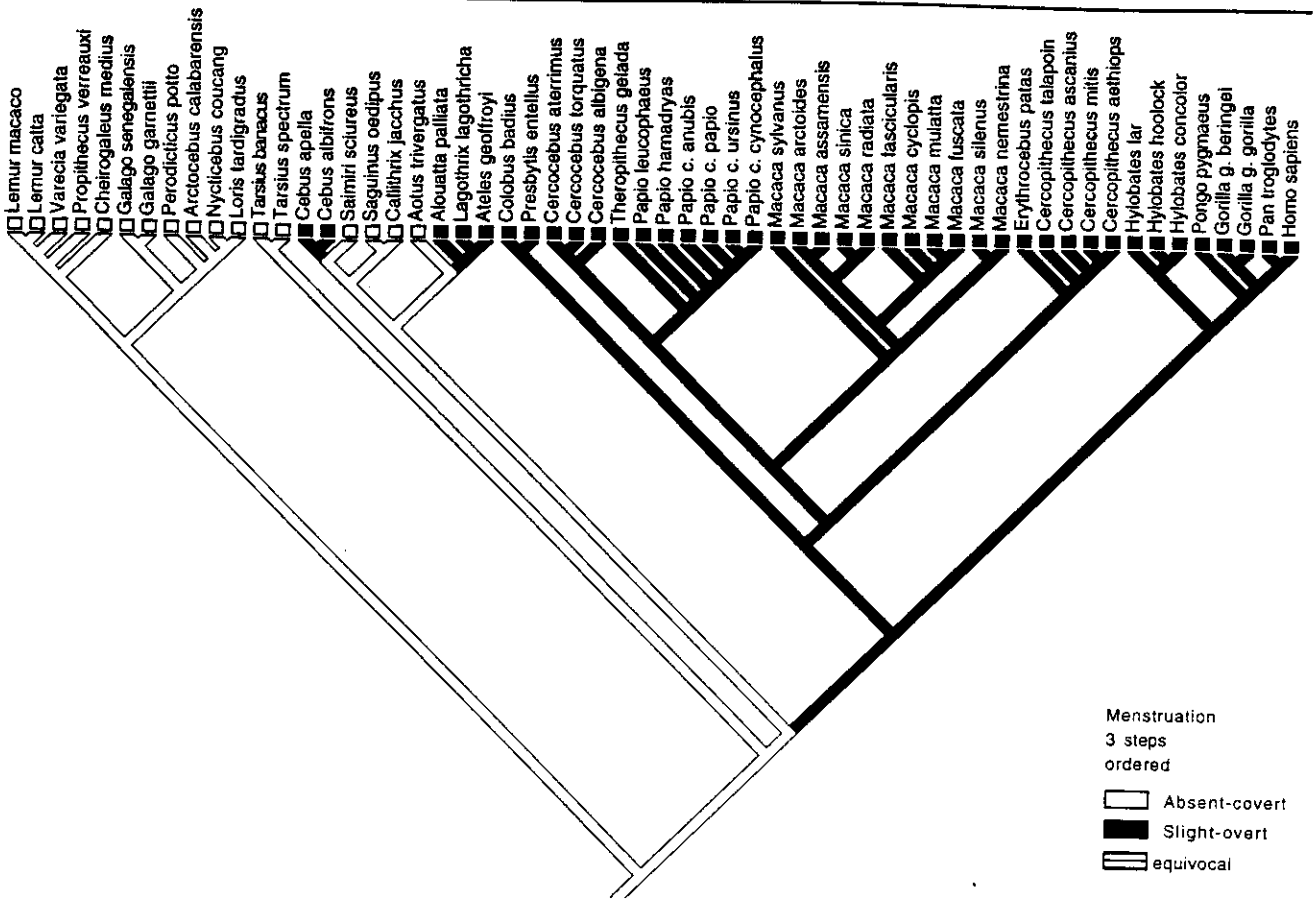


Figure 4. Same as Figure 3 except the character menstrual copiousness was dichotomized as absent or covert versus slight or overt.

ogy, and evolutionary biology. (Boxes 1 and 2.)

The hypotheses that menstruation evolved as a defense against pathogens or as a signal of fertility are incompatible with the available data. An alternative hypothesis is that endometrial cyclicity saves energy, while vaginal bleeding is a mere side effect. This hypothesis points to the need for further studies of the metabolic effects of estrogen and progesterone on all of their target tissues. Such studies will help clarify the mechanisms that bring about the increase in metabolic rate during the luteal phase and allow us to identify the relative contributions of various tissues. To gain a better understanding of why some primate species bleed more heavily than others, further data are needed on endometrial vascularity and thickness, depth of shedding, placentation, and the ratios of uterine volume to body mass in a variety of primate species. Ultimately, to gain a more complete understanding of endometrial cycles and menstruation, it will be helpful to examine the origin and periodicity of ovarian cycling.

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