

HOMINID BIPEDALITY AND SEXUAL-SELECTION THEORY

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ABSTRACT: Penile display is an entailment of consistent upright posture and locomotion. Hominid bipedality is thus distinguished by a genitalic exposure gender-opposite to that of quadrupedal primates. This paper presents an explanation of the relationship between bipedality and penile display in the preeminently morphological terms of Darwin's original exposition of sexual selection theory and of Eberhard's recent application of that theory in his analysis of male genitalia as tactile stimulators. The explanation takes into account four critical factors: the bipedal incentive; the inverse relationship between nonhominid vulva and hominid penis; the biological significance of pleasure; the large human penis as evolutionary product.

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. . . male structures that are specialized to contact females in sexual contexts have an extraordinary propensity to evolve rapidly and divergently. . . . The ability [of females] to discriminate among males using mechanical or stimulatory genitalic cues could . . . spread genetically through the females of a population. Once such female discrimination was established, selection would favor any male that was better able to meet the females' criteria (by squeezing her harder, touching her over a wider area, rubbing her more often, and so on) even though his genitalia were no better at delivering sperm than those of other males. My hypothesis, sexual selection by female choice, proposes that male genitalia function as "internal courtship" devices. . . .

William G. Eberhard

Introduction

Eberhard's (1985) evidence for sexual selection through female choice of male genitalia accords closely with Darwin's (1871) original and preeminent concern with morphological aspects of sexual selection. Given the ambient Victorian culture of his time, it is not surprising that Darwin himself did not remark openly and directly upon male primate genitalia. His cryptic and oblique references to "naked parts . . . oddly situated," to "a part confined to the male sex," or to "large surfaces at the posterior end of the body," (pp. 313, 291, 376, respectively) all belie his usual descriptive precision and clarity. Eberhard's thesis that male genitalia function as "'internal courtship' devices," (p. 14) i.e., as tactile stimulators, that they evolve through female choice, and that this sexual selection by females occurs in runaway fashion, reinvigorates a Darwinian focus on evolutionary sexual morphology at the same time that it gives new meanings to comparative anatomy through its recognition of differential spatio-tactile/kinetic (and tactile/kinesthetic) genitalic potentialities. Eberhard's practical and theoretical separation of the act of copulation from the processes of insemination and fertilization constitutes a critical methodological step. The more usual lumping of the three phenomena leads less to a consideration of morphological characters and their possible display value than to a concern with economic, political, and social factors, (e.g., Trivers, 1972; Borgia, 1979) with the result that analyses and explanations of the sexual characters themselves--for example, the evolution of an atypically large penis like that of the human primate (e.g., Wickler, 1969; Morris, 1967; Short, 1979, 1980; Crook, 1972; Eberhard, 1985)--are

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by-passed.

The purpose of this paper is to show first that bipedality and penile display are inextricably linked. Second, it is to show in elaboration of Eberhard's thesis (a) how a large penis--the most conspicuous feature of hominid reproductive anatomy (Short, 1980)--and bipedalism--the most conspicuous hominid behavioral character by Darwin's (1871) original account--might originally have been linked through sexual selection and (b) how their evolutionary bond was cemented by pleasure, the hominids' finding "sweet" (Barash, 1982) the activities in which they engaged. The thesis is not that hominid bipedality originated exclusively in sexual selection, but that given its incontestable link to penile display, sexual selection was a prime and critical factor in the move to consistent bipedality. Several major concepts attach to the undertaking and will be considered in turn: 1) the bipedal incentive; 2) the inverse relationship of nonhominid vulva to hominid penis; 3) the biological significance of tactile pleasure; and 4) the large human penis as evolutionary product.

The Bipedal Incentive

A posturally significant and behaviorally critical aspect of hominid bipedality has been overlooked in assessments of its evolutionary impact. Hominid bipedality eventuated in a radically different primate bodily appearance: male sexual characters relatively hidden in quadrupedal primates are visibly exposed in bipedal ones. Conversely, female sexual characters normally visible in quadrupedal primates are relatively hidden in bipedal ones. The radical reversal in visible male/female sexual morphology clearly has substantial implications; penile display needs to be examined within the purview of Darwin's original sexual selection theory. Loss of estrous--physiological and behavioral--can be explained in the light of continuous and direct male genital exposure. So explained, typical primate estrous cycling was replaced not by year-round female receptivity--as is so commonly claimed (e.g., Wolpoff, 1980; Symons, 1979; Hrdy, 1981; Lancaster, 1975; Morris, 1967; Lovejoy, 1981; Pilbeam, 1972)--but by year-round penile display.

Set within a motivational perspective, the inverse visual/morphological relationship between quadrupedal and bipedal female genitalia and quadrupedal and bipedal male genitalia shows that a bipedal incentive would not attach to female primate sexual behavior as it would to male primate sexual behavior. Indeed, as a feature already engendered in many primate displays--sexual as well as nonsexual (e.g., Sugiyama, 1969; van Lawick-Goodall, 1968, 1972; Schaller, 1963; Hamburg, 1971; Nishida, 1970)--bipedality appears to be practiced more often by males than females. The comparatively substantial incentive for males to maintain a consistently erect posture follows from the fact that in its entailment of penile display (in particular the display of an erect penis), erect posture attracts female attention and potential response in the same way that a quadrupedal female's presenting posture attracts male attention and potential response. The entailment perfectly exemplifies the kind of matrix structural relationship described by Gould and Lewontin (1979) in their article, "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme": consistent bipedality imposes as specific and rigorous a Bauplane vis a vis visible male hominid genitalic features as the fan-vaulted ceiling of St. Mark's Cathedral vis a vis its structural design features. Granted that displays count for nothing short of the animal to whom the display is directed (Rowell, 1972;), a display is nonetheless a two-term relationship: the incentive is as important a constituent of the display as the response, particularly so where it is a question of how a behavior on the order of bipedality might have been reinforced and come ultimately to be consistently established.

A male hominid's incentive toward bipedality is empirically evident in both the heightened force of his sexual display--in both erect posture and erect penis

apparent size is substantially increased, for example, and the two erections are vectorially linked with respect to upward movement--and in his correlative new power of ambulatory sexual display. Bipedality for primate females holds the possibility of neither of these sexual optimizations; in terms of display, it minimizes rather than optimizes advertisement of her sexual powers.

A male primate's incentive toward consistent bipedality is in effect qualitatively greater than that of a female. Consistent bipedality is not simply a question of more but of (among other values) sexual enhancement. The thesis that it arose in conjunction with male behavior and had fundamental and far-reaching significance with respect to sexual display and selection, accords with the assessment of Stern and Susman (1983) that terrestrial bipedality was more common among male than among female earliest known hominids. Their assessment is based upon an inferred sexual dimorphism, fossil evidence indicating that males were larger than females. If the postulated dimorphism proves correct as more fossil evidence is accumulated, then there is further reason for maintaining that the initial bipedal incentive was on the side of the male rather than of the female: the shorter stature of the female would make even more sexually disadvantageous the assumption of a bipedal posture for display. The directional facing of female genitalic swellings would no longer coincide with the male's line of vision. In contrast, initial bipedal posture in the male would not only optimize his greater size, but would position his genitalia in the (shorter) female's line of vision--in a way precisely similar to that in which a female chimpanzee's genitalia (by a relative lack of sexual dimorphism) is on a line with the male's line of vision. The thesis that bipedality arose in conjunction with male behavior is also supported by research which shows that male primates are more prone toward exploratory behavior than females (e.g., Reynolds, 1972), that males are more mobile (e.g., Trivers, 1972), physically active, and engage in contact play and threat behavior more often than females (e.g., Burton, 1972; Harlow, 1962).

The bipedal incentive warrants further clarification within the context of primate bipedality generally. Primates are bipedal in a variety of circumstances (Pilbeam, 1972; van Lawick-Goodall, 1968, 1976; Schultz, 1950). What, then, from a common primate heritage standpoint explains the bipedal incentive? What is the critical difference between a 55% terrestrial bipedality in australopithecines and a 10% terrestrial bipedality in their ancestor (Pilbeam 1986)?

Since tools, once associated with the beginnings of bipedality (e.g., Washburn, 1960), are no longer associated with earliest hominids (Johanson and Edey, 1981) (though this is not to say that ready-made or non-fossilized tools could not have been used by earliest hominids for scavenging [see Binford, 1981, 1983; Shipman, 1986], or for nut-cracking and extractive foraging generally [see Parker and Gibson, 1979])), tool-making/tool-carrying cannot be postulated as the major incentive toward consistent bipedality. The idea that the earliest hominids were nonetheless motivated toward consistent bipedality primarily in order to carry things, and to carry them regularly, i.e., more often and habitually than their ancestors or co-speciating confreres, nevertheless prevails. For example, recent explanatory models of the origin of bipedality center on food-carrying behavior, specifically provisioning (Lovejoy, 1981) and nuptial feeding (Parker, ms), males in each case supplying the females. An odd irony is evident in that the latter model, although rooted in sexual selection theory, makes scant reference to sexual morphology while postulating material resources and benefits as the pivotal factor, while the former model, although rooted in natural selection theory, postulates "the unique sexual and reproductive behavior of man" (p. 341) as the pivotal factors at the same time making scarcely any more reference to sexual morphology. In neither account is the exposed hominid body considered except to remark (Lovejoy, p. 346) that strong selection pressure would be exerted on anatomical characters reinforcing pair-bonding, "the conspicuous penis of human males" being among these; and (Parker, p. 22) that "bipedal carrying and presentation of nuptial

gifts would have been favored by females because it would allow them to accurately assess the size of the male and the size of the gift; it would also allow them to assess the size and tumescence of the male's genitals." Both accounts illustrate the generally pervasive failure of transport explanatory models of bipedality to take into account the spatio-kinetic bodily transformations entailed by upright posture and the sexual significance of those transformations.

In contrast to transport models of bipedality generally, a basically corporeal model takes into account the fact that bipedality did more than free the hands for carrying; it freed the whole body in the sense of exposing it, and in so doing changed male and female genitalic valencies. Acknowledgment of the radical shift in genitalic valencies leads directly to a consideration of the relationship of nonhominid primate vulva and hominid primate penis, a relationship ultimately critical to an understanding of analogies and disanalogies between hominid and nonhominid primates.

The Inverse Relationship of Nonhominid Vulva to Hominid Penis

A human primate's "distinctive and oversized penis," as Eberhard (1985, p. 79) describes the male organ, is the sexual inverse of a nonhuman primate's distinctive and oversized vulva. With hominid bipedality, the vulva loses its public status; in its stead the penis becomes a public sexual object. Its swellings--size and shape differentials, degree of tautness--directional orientation, and upward movement become natural foci of attention and potential response. Bipedal females indeed no longer have a sexual organ, an object on visual par with a penis, a fact which perhaps explains why exhibitionism is regarded a sexual deviation possible only to males (Stoller, 1976; Green, 1980; Short, 1979). While it might be deemed curious that both the stark visibility of male genitalia and the comparative invisibility of female genitalia in the shift from quadrupedal to bipedal posture have not been acknowledged, it is even more curious that recent research attention to sexual concealment (of ovulation in hominid females: see Hrdy, 1981, for a general summary and discussion) has not raised the correlative question of what is sexually visible in hominids. Clearly the public object about which sexual behavior centered necessarily shifted from pudenda to penis with upright posture. Loss of estrous--understood with respect to its visual manifestations--is in consequence explainable on morphological grounds; it no longer served any sexual function since a male could no longer immediately see and inspect female swellings and changes in coloration. Presenting behavior was in turn no longer advantageous and its physiological correlates became modified, i.e., hominid menstrual cycles became established. Male display replaced female presenting.

It is important to call attention to the underlying rationale for the difference in sexual nomenclature. Relatively speaking, the habitually bipedal male does nothing in order to display his penis. He does not present it to a female; it is already there--a public object, plainly visible. The difference between male hominid display and female nonhominid presenting is in other words a difference between natural and modified socio-sexual bodily orientation. Its import is sizeable. The frontality of the penis, its anterior positioning in bipedal posture/locomotion, makes it a cynosure on three counts: it is always facing whatever or whomever the male addresses; it is perpetually oriented in the direction of the male's forward movement; it is on the socially as well as kinetically and sensorily strongest surface of the body. Not only this but correlated primate anatomical changes maximize its conspicuousness: hip-joint flexion typical of nonhominid ape anatomies contrasts markedly with the relative flushness of frontal abdominal/thigh surfaces of hominids. In effect, the hominid hip joint brings the frontality of the hominid penis to even greater visual prominence. In short, anatomical changes correlated with bipedality (Robinson, 1972) correlate with optimal penile display.

The contrasting posterior orientation of presenting involves a re-positioning of the body relative to normal direction of movement and social address such that the vaginal area is "exposed" (see Beach, 1976, p. 302). Moreover a presenting posture is a vulnerable one in that the animal faces away from and thus cannot concurrently assess, the immediate reaction of the animal to whom it is presenting. As Hall and De Vore (1972, p. 174) point out, "presenting . . . is often accompanied by nervous, even fearful behavior on the part of the presenting animal." The frontality of bipedal penile display is clearly of stronger positional advantage than posterior presenting in sexual invitational behavior.

The nonhominid primate vulva is nonetheless a public object on par with a hominid phallus; it is readily and immediately visible; its dynamic changes in appearance make it a ready object of attention and potential response; it is readily accessible to tactile and olfactory exploration. Of interest in this regard is Hanby's (1976) data on tactile-manual genitalic exchanges among adult male and female chimpanzees. Female tactile contact of male genitalia ranks far below male tactile contact of female genitalia--and in fact below female tactile contact of female genitalia. (The exact percentages are: female/male 25%; male/female 67%; female/female 70%; male/male 52%.) The visual and tactile accessibility of female genitalia by males in contrast to male genitalia by females provides an empirical explanation of the low female/male contact. The high incidence of male/male contact can be explained on similar spatio-corporeal grounds, i.e., a male's visual/tactual experience of his own body (see for example van Lawick-Goodall's, 1968, p. 273, description of a juvenile chimpanzee's thrusting movements as it stood quadrupedally: "[he looked] back between his arms and legs as his scrotum bounced against his penis; this always occurred when he was frustrated.") While present-day humans might react quite differently to concealed genitalia of the opposite sex, it is reasonable to conclude that what is not tactilely or visually accessible in a nonhuman primate's corporeal world--what is not a readily available public sexual object so far as other animal bodies are concerned--is not a corporeal object commonly sought out for sexual touching. Further documentation of this fact is had in van Lawick-Goodall's (1968) description of a mother's fondling of her infant son's readily accessible genitals: where quadrupedal primate females do have immediate access to male genitalia, they are more likely to touch them.

The Biological Significance of Pleasure

Tactility is a source of pleasure. Eberhard's evidence showing that male genitalia function as tactile stimulators, and his related thesis that "selection for tactile stimulation [is] the most likely selective factor explaining the human males' distinctive and oversized genitalia" (1985, p. 79) are both of seminal import. To begin with, they provide an empirical backbone to otherwise speculative reflections, for example, to Short's (1980, p. 14) surmise that "Perhaps the large size of the erect penis is related to the act of intercourse," and his ensuing estimation (p. 16) that the human penis developed "to entice the opposite sex" and "to enhance enjoyment of the copulatory act."

They furthermore call into question analytical accounts in both classic and recent ethological studies. Wickler's (1969) original and influential (e.g., Crook 1972: see below) descriptions of the use of the primate penis for display center on intrasexual competition, not on intersexual attraction. Apart from a passing reference to Hewes's (1957) cross-cultural data on human sitting postures--in which males, if unclothed would be clearly displaying their genitals, while women, if unclothed, would clearly be hiding theirs--there is not the slightest intimation that penes could or do function in intersexual display, much less as tactile stimulators.

Subsequent research utilizing Wickler's ethological studies goes no further in

relating "human males' distinctive and oversized genitalia" either to intersexual display or to tactile stimulation; in spite of inquiries into its "adaptational value," the size of the human penis remains an unexplained mystery. Crook (1972, p. 251), for example, while raising the question of the purpose of "the large (among primates) phallus," briefly discusses its possible significance only in a Wicklerian perspective: as an intraspecific symbol of power and dominance. There is in fact a peculiar silence about the uncommonly large phallus in his discussion of both visual and contact signals as human sexual releasers. While visual signals emanating from women and arousing men are relatively detailed (e.g., "high heels enhancing the provocative body movements of the walking female, breast deportment--the 'sweater girl' . . . voice quality and tone . . . areolar tumescence, body flush, eye glitter . . ."), visual signals emanating from men and arousing women are minimal ("athletic deportment and movement, buttocks, eye glitter and pupillary distention") and noticeably unrelated to male genitalia. This is puzzling since, as some of the enumerated female visual signals clearly indicate, Crook's model subjects are naked as well as clothed. In effect, penile tumescence would be as much a releaser--if not more a releaser, since it is noticeable at a greater distance--as female areolar tumescence, which Crook mentions. Furthermore, while "genital sensation" is among those female contact signals Crook lists as arousing to men (others include "epidermal touch quality, breast tumescence, lip-feel, . . . and body scent"), no such specific genital reference is listed for women. In fact no itemization of contact signals arousing to women is given at all. The result is that while tactile stimulation ("genital sensation") of the penis by the labia and vaginal walls is implicitly acknowledged, tactile stimulation of the clitoral-labial-vaginal complex (see Sherfey 1972; Masters and Johnson, 1961, 1962) by the penis is not. The same peculiar omission is found in the original Hite reports (1976, 1981) on female and male sexuality, with males being questioned explicitly about "the pleasure of the vagina on the penis," but females not being explicitly questioned equivalently about the pleasure of the penis in the vagina. While a reticence to put the penis on the measuring line, not of reproductive competence but of arousal, pleasure-giving competence, has perhaps been fed by the notion that "female animals are mere egg repositories waiting for something to happen" (Kevles, 1986, pp. 288-289), fixation on orgasm, on whether females have orgasms, and on where anatomically they come from, often appears to blot out straightforward acknowledgment and investigation of the penis as a tactile stimulator.

Though anchored predominantly in studies of insect male genitalia and mating behaviors, Eberhard's analyses and references are directly relevant to primate sexual anatomy and behavior precisely insofar as insects, unlike birds--Darwin's predominant model--mate through internal fertilization. His detailed data on genitalic tactility and focus on genitalic tactile pleasure strongly support the growing body of observations on the primacy of primate tactility and evolutionary significance of tactile pleasure. (See, for example, Lancaster, 1972, on the importance of tactile satisfaction to mothering; Hamburg, 1967, on the centrality of pleasure to survival; Bramblett, 1976, van Lawick-Goodall, 1968, 1972, Harlow, 1958, Harlow and Zimmerman, 1958, on the positive sensual experience of grooming; Montagu, 1971, on the general evolutionary significance of tactility and the specific importance of tactility in mother/child relationships; Harlow, 1965, on the seminal importance of 'contact comfort' to healthy socio-sexual development in primates; Lorenz, 1972, on the importance of sensual pleasure in appetitive, stimulus-releasing behavior; Beach, 1976, p. 299, on the unlearned "positive effect" or 1973, p. 361, on the "mutual physical gratification" of human intercourse; Jolly, 1985, on the role of pleasure in the evolution of female sexual response [orgasm].)

What Eberhard's theory explains is in a fundamental sense the obvious: like the genitalia of other males in the animal kingdom who procreate by internal fertilization, the "distinctive and oversized human males' genitalia" has species-

specific tactile powers. The obvious appears indisputable--and is in fact corroborated both indirectly by fossil evidence showing an increase in cortical area for tactility in hominids, and directly by laboratory evidence graphically depicting cortical representation of tactility, body part by body part, including genitalia. What is less obvious, but what as Darwin (1871, p. 100) first attempted to show, is that females choose certain males over others and that "it is to a large extent the external attractions of the male" over "vigor, courage, and other mental qualities" which determine her choice. Put in evolutionary hominid perspective, and in a re-focused conceptualization of competence (Lancaster, 1985, see below), tactile stimulatory competence was assessed by early female hominids through penile display and determined their choice of copulatory mate. Pleasure--the promise of pleasure and the experience of pleasure--was thus a key variable in hominid female choice, and in consequence, in hominid reproductive effort and success.

A number of points attach to this relationship between somatic pleasure (or the anticipation of same) and sexual selection in the literal sense of choosing a copulatory partner. First, choice by definition is exercised in the context of possible alternative selections; it is the end result of perceptual experiences and judgments. Hominid female choice must thus be considered a behavioral response to a behavioral signal, i.e., an answer to penile displays. At the same time, penile signalling behaviors are themselves the end result of perceptual experiences and judgments. When females are partially or fully bipedal (their incentive to bipedality is treated below) such that genitonic swellings and changes in coloration are either no longer present or no longer immediately apparent, then a male's field of mate possibilities is open: virtually any female may be chosen as the object of his display attentions. In effect, the female to whom he actually addresses his display is a choice among possible females. In such circumstances, intrasexual competition is similarly a female as well as male phenomenon. The twin questions are, on what specific grounds would proto-early hominid females have competed, and on what specific grounds would proto-early hominid males have competed?; and alternatively, what was the exact nature of the criterion of male choice and of female choice?

Male choice and intrasexual female competition will be considered first. Both were a matter of sexual behavior by females in response to penile display. Bipedality, specifically the female incentive toward bipedality, provides the context for identifying that behavior.

Savage-Rumbaugh and Wilkerson (1978) state that ventro-ventral mating is preferred over dorso-ventral mating by female pygmy chimpanzees when the females are in less than their maximally tumescent state. They suggest in consequence that "increased positional flexibility" is linked with an increased disposition toward copulation at times other than at the height of the estrous cycle. It is reasonable on these and other (to be identified) grounds of "flexibility" to assume that the most likely proto-early hominid female behavior signalling an increased disposition toward copulation and promising greater pleasure through ventro-ventral copulation was a bipedal, face-on response and approach to an erect penis-displaying male. Not only was the female showing herself a ready and willing source of pleasure, but her bipedal approach suggested a relatively greater sexual pleasure through more variable, novel, and arousing bodily contact. (See West-Eberhard, 1983, and Eberhard, 1985 on the value of sexual novelty; see also below.) The point warrants detailed analysis in order to show clearly how consistent bipedality, ventro-ventral mating, tactile pleasure, and sexual novelty are related.

Ventro-ventral mating offers "increased positional flexibility" not only with respect to dorso-ventral mating, as Savage-Rumbaugh and Wilkerson point out. The spatio-intercorporeal orientation itself makes a variety of coupling positions possible and an equal variety of tactile contacts possible in the way of particular body-on-body, or body-to-body, touchings including facial touchings. (For circa

2,000 year old examples, see the Hindu classic, The Kama Sutra of Vatsyayana.) The orientation is furthermore kinetically as well as positionally enhancing of tactile pleasure. Significant in this respect is the fact that thrusting is an essentially forward movement, not a backward one. A bipedal female, one approaching and mating with a male ventro-ventrally, is capable of thrusting movements during copulation as a quadrupedally-presenting female--for the sake of relevant comparison, a chimpanzee--is not. True thrusting movements on the part of a quadrupedally-presenting female chimpanzee during typical dorso-ventral copulation would disengage her genitals from those of the male. Yet thrusting is a well-documented female as well as male primate movement pattern: male and female chimpanzee infants thrust, and female chimpanzees engage in thrusting behavior when they mount a conspecific just as males do (e.g., Hanby, 1976; Hanby et al., 1971).

Successful dorso-ventral chimpanzee copulation precludes female thrusting movements on the grounds of directional incompatibility; successful ventro-ventral chimpanzee copulation precludes them on the grounds of structural incompatibilities. The incompatibilities center on loss of contact in the withdrawal phase of the movement--the exact inverse of the phase at risk in dorso-ventral copulation. Female chimpanzee thrusting during successful ventro-ventral copulation is contravened 1) by natural anatomical hip-joint flexion (male and female), 2) by a posterior or less than fully anterior vagina, and 3) by the average length of the male chimpanzee's penis. Hominid female thrusting during successful ventro-ventral copulation is facilitated either directly or indirectly on all three counts by consistent bipedality; namely, by 1) anatomical restructuring of the hip-joint toward extension such that abdominal/thigh bodily surfaces are virtually flush, 2) a more fully anterior positioning of the vagina, and 3) a longer average penis length (see below for a further discussion of this factor). Consistent bipedality thus enhanced proto-early hominid female movement possibilities during copulation by reinforcing the practice of ventro-ventral copulation. Such kinetic flexibility as thrusting during copulation is clearly in the service of tactile pleasure--for male and female alike. With the advent of hominids kinetic flexibility during copulation was no longer the unique prerogative of male primates generally, only quadrupedal male primates. Were present-day evidence called for to suggest vestiges of this fact, belly dancers and female strippers are obvious (if differentially-sanctioned) showcases of female enhancement of male tactile pleasure through kinetic flexibility. (See also the eminent American art critic, Berenson, 1962, on the essentially tactile-kinetic values of visual aesthetic form.)

Along with other aspects of optimal contact resonance already identified, greater movement flexibility of the female made ventro-ventral mating qualitatively superior to dorso-ventral mating. In addition to a bipedal approach toward the male, these qualitative aspects constituted tactile desiderata underlying male choice. Proto/early hominid males copulated less or not at all with those females who responded to their display quadrupedally, i.e., by presenting; they chose less to copulate with females with posteriorly-aligned vaginas than with those with more anteriorly-aligned ones; they chose less to copulate with females with naturally flexed hip joints than those with extended ones. Choice females were those who approached males frontally, whose genitalia were more frontally accessible, and who, in copulating, were positionally and kinetically stimulating to the male. Those females were at reproductive advantage. Those females were also most likely to be consistently bipedal.

Corollary to these tactile desiderata, those males with "larger" (see next section) penes promised greater tactile stimulatory competence. As with male choice, female choice hinged also on the promise of more variable, novel, and arousing bodily contact, contact which would not be compromised by greater female kinetic flexibility through consistent bipedality. Males competed on the grounds of penile display--size and shape, tautness, directional orientation, and upward

movement--and of penile prominence and full-body contact through natural hip-joint extension. As Eberhard (1985, p. 71) points out, "Once . . . female discrimination was established, selection would favor any male that was better able to meet the females' criteria (by squeezing her harder, touching her over a wider area, rubbing her more often, and so on) even though his genitalia were no better at delivering sperm than those of other males." It is pertinent to spell out "the females' criteria" in specific detail.

Beach (1973, p. 360) points out that the possibility of female orgasm at any time through clitoral stimulation "tends to reinforce and increase the frequency with which she [the human female] desires and accepts intercourse." He also suggests a concrete link between clitoral stimulation and ventro-ventral (as opposed to dorso-ventral) mating. The point is not one of establishing whether proto/early hominid females had orgasms--a question in any case best left to prehistoric clairvoyants--but that female genitalic tactile pleasure is significantly enhanced by penile stimulation of the clitoral-labial-vaginal complex (Sherfey, 1972; Masters and Johnson, 1961, 1962). Genito-genital rubbing by female pygmy chimpanzees, and Hanby's data cited earlier, are important considerations in this regard.

Genito-genital rubbing (by which clitoral stimulation is effected) is a sexual behavior widely and regularly practiced by female pygmy chimpanzees (Kuroda, 1980). It begins in infancy (Thompson-Handler et al., 1984). Savage-Rumbaugh and Wilkerson (1978) report in fact that clitoral intromission is occasionally achieved, and that in such cases, thrusting behavior preempts rubbing behavior. In addition, Kuroda (1980) reports that genito-genital rubbing appears to last longer than male/female copulation, a fact which would confirm the role of tactile pleasure in choice of sexual positioning.

Hanby's (1976) data showing female/female (Pan troglodytes) tactile-manual genitalic contact higher than any other partnering contact also strongly supports the notion that female chimpanzee tactile pleasure is centered on clitoral-labial stimulation and in effect, that it is both facilitated and enhanced by ventro-ventral copulation. In light of both genito-genital and tactile-manual intrasexual practices--and of the fact that both chimpanzee species are represented--it is reasonable to assume that proto/early hominid females also found pleasure in clitoral stimulation. Again, the point is not whether these intrasexual female tactile contacts led to orgasm, but that given the anatomical focus of genitalic pleasure in nonhuman female primates, ventro-ventral copulation significantly enhanced sexual pleasure in female as well as male proto/early hominids. In such enhanced male/female copulatory circumstances, genito-genital rubbing and hand-to-genital contact, i.e., female/female sexual behavior, would become more and more a secondary mode of sexual pleasure for females.

The above analysis of the role of tactile pleasure in male and female choice and its relationship to bipedality focuses solely on 'the corporeal facts of the matter'. The facts describe a situation of fundamental sexual parity:

- 1) Tactile stimulation, an entailment of internal fertilization, was necessarily experienced by both male and female proto/early hominids in copulating.
- 2) Tactile stimulation is a source (or potential source) of pleasure.
- 3) Both males and females chose partners who offered them maximal tactile stimulation, and both competed intrasexually on the grounds of tactile stimulatory competence.

The corporeal facts document Darwin's (1871, p. 276) brief suggestion of the possibility of "a double process of selection, . . . the males having selected the more attractive females and the latter the more attractive males." When attractiveness is transposed from the visual to the tactile, that is, when the criterion of sexual selection shifts from what Darwin regularly calls a taste for

beauty to a taste for optimal contact resonance, male/female hominid morphological and behavioral sexual differences are explained at their most fundamental level. The same point follows from the observation that Darwin's theory of sexual selection involves only female choice and male/male competition because it rests mainly on avian anatomy and behavior. When anatomical structures and behavioral practices peculiar to internal fertilization are taken into account--as in Eberhard's research--it is clear that contact resonance is potential for both sexes.

The Large Human Penis as Evolutionary Product

When bipedality and its entailment of a permanently exposed penis are reckoned with literally in reconstructions of the hominid past, the fundamental and far-reaching significance of penile display becomes obvious. Permanently-enlarged breasts, hypothesized to have evolved as an advertisement of "lactational competence" and to be in consequence a prime factor in male choice (Lancaster, 1985), can also be tied to an enhanced exposure of the body through bipedality. As lactational advertisements, however, permanently enlarged breasts are a reproductive, not sexual signal. They were furthermore not a visual datum immediately entailed by the move to consistent bipedality: as Lancaster's theory itself proposes, permanently enlarged breasts evolved in their purported role as signals. That the penes of the Great Apes are not permanently exposed but are extruded when erected (see Short, 1979, on the relative visibility of Great Ape penes)--and that in this sense the permanently exposed hominid penis may also have evolved--does not contravene immediate bipedal entailment of penile display but on the contrary supports it. Hominid penile erection and flaccidity are equivalent to nonhominid penile visibility and invisibility. In both cases, the erect penis (together with its respective flaccidity or invisibility) is a visual datum--a sexual signal--immediately entailed by bipedality.

In Eberhard's (1985, p. 175) interpretation, "male structures that are not modified in some way to consistently hold or contact females do not evolve rapidly and divergently, while those that are modified for this function show clear signs of rapid and divergent evolution." In this evolutionary context, three inter-related analogies and disanalogies can be identified which flesh out further the evolutionary significance of an atypically large primate penis:

- (1) analogies and disanalogies in ventro-ventral coital positioning behaviors between female pygmy chimpanzees and hominids
- (2) analogies in morphological and behavioral paedomorphisms between pygmy chimpanzees and hominids
- (3) disanalogies in external female genitalia, particularly labia, between nonhominid and hominid primates

(1) For penes to be maximally effective tactile stimulators, inter-genital tactile fit is critical. In ventro-ventral copulation, coital positioning by female pygmy chimpanzees requires leaning back, lying down and wrapping the legs around the male's waist (Thompson-Handler et al., 1984)--presumably to tilt the pelvis upward--or sliding under the male (Patterson, 1979). Quite apart from a more anterior positioning of the vagina, tactile fit in these instances is the result of behavior, specifically female behavior. A longer penis would mean the less mechanically accommodating the female's behavior need be (see Leonardo da Vinci's drawing reproduced in Short, 1979); in positive terms, the more pleasure-accommodating. Genitalic variation in the direction of greater penile length thus had short- and long-range consequences. It immediately facilitated sexual signalling; a longer penis was more visibly prominent in bipedal penile display than a shorter one. It furthermore immediately facilitated frontal coital positioning and maintenance of that position without risk of loss of contact. Long-range value is evident with respect to the latter facilitation, viz., the

female was no longer of necessity statically positioned; mechanical accommodation was no longer a female behavioral constraint but a built-in of male genitalic anatomy. In effect, a longer penis freed the female posturally and kinetically. Mutually stimulating pelvic movements (thrusting) and embracing postures were ultimately facilitated; not only genital areas were in contact but entire frontal surfaces were; arms and hands were furthermore free to develop a repertoire of touching gestures and movements. The overall result was that tactile stimulation potentially radiated throughout the whole body. Thus while increased penile length functioned immediately as a stronger, more arousing sexual signal and one promising uninterrupted en face copulation, it ultimately functioned to enhance tactile pleasure generally by opening up female postural and kinetic possibilities.

(2) The fact that there is greater variability in male than in female secondary sex characters (Darwin, 1871) lends credence to Eberhard's theory (see also Fisher, 1958) that rapid and divergent evolution of male genitalia can set the tempo and mode of speciation such that female characters catch up quickly with changes in male genitalic anatomy. Greater natural variability in male than in female secondary sexual characters supports the further hypothesis that the anterior positioning of female hominid genitals, while definitively linked to consistent bipedality and ventro-ventral coital positioning, was not rooted basically in female intrasexual genetic variability, but in a paedomorphic morphology similar to that in adult female pygmy chimpanzees: it was less the result of selection acting on a distributional extreme than of selection for the retention of a juvenile genitalic character: ventral orientation of the vaginal canal (Gould 1977). Reinforcing just such a paedomorphic female hominid genitalic morphology was a behavioral paedomorphism common to present-day male and female pygmy chimpanzees: ventro-ventral mating. While not classified outright as paedomorphic, ventro-ventral mating in pygmy chimpanzees is more typical of juveniles than adults and is consistently interpreted as paedomorphic (e.g. Kuroda, 1980; Thompson-Handler et al., 1984).

Viewed comparatively in terms of inter-primate analogies and disanalogies, the evolution of human sexuality begins with an explanation of the move toward greater visibility of the primate penis, and its sizeable increase in girth and length--the chimpanzee penis is "pencil-thin" or "filiform" (Halliday, 1980; de Waal, 1982; Short, 1979, 1980), and averages 8 cm as opposed to an average 13 cm human penis. The explanation shows how, at the same time that the larger hominid penis liberated females kinetically and posturally, it both reinforced ventro-ventral copulation and optimized the reproductive success of females with morphologically paedomorphic genitalia. Such an analysis provides empirical, i.e., corporeal, grounds for Short's (1979, p. 149) general statement that "Undoubtedly, increased penile length has made a wide variety of copulatory positions not only possible, but enjoyable, and may have increased female satisfaction from intercourse by increasing the probability of female orgasm." Orgasms aside, tactile pleasure is a quite sufficient reason for early hominid females to have chosen males with longer--and possibly thicker--penes as copulatory partners.

(3) The sexual paedomorphisms discussed above are relevant to disanalogies in external genitalia, specifically in labia majora, between adult nonhuman and human primates. Labia majora are an infant-to-juvenile trait which disappears in adult female nonhuman primates (Osman Hill, 1972). Though a variable trait in human females, their general retention is considered paedomorphic (Gould, 1977). No explanation has been proposed for this hominid hold-over. An eminently simple one can be given in terms of differentially visible male/female primate sexual morphologies, and in turn radically different primate sexual-signalling behaviors.

Sexually immature nonhuman female primates have no need of a visible vaginal orifice since pudendal swellings and changes in coloration are not yet hormonally triggered. In other words, the sexual signalling value of her vulva is not yet central to the social relations of the female. From this perspective, the labia

majora serve as a protective covering that deflects purely sexual interests. Support for this view is found in the fact that "In [nonhuman primate] females, there is a clear positive relationship between the onset of regular menstrual cycles and the appearance of mounting, reception of mounts by males, presenting to males, and certain vocalizations and gestures" (Hanby, 1976, p. 45). In effect, only with maturity does the vulva become an abiding focus of sexual attention; only then do the labia majora disappear.

Where genitalic visibility is not of signal priority, there is no functional reason for the disappearance of the labia majora. That they are generally retained in female hominids is a function of the nonvisibility of female hominid genitalia: what is not in view is not seen; what is not seen does not serve as a visual signal. While an analogy can be drawn between nonhuman (Pan paniscus) and human adult females with respect to a paedomorphic orientation of the vaginal canal, a disanalogy exists with respect to the overall visual appearance of the vulva: "At no age does the chimpanzee (Pan) present a vulva resembling the human pudenda, i.e., a slit-like rima guarded by swollen labia majora, with the labia minora and other parts all hidden within" (Osman Hill, 1958, p. 698; italics added). The evolution of hominid female genitalia is, from this perspective, an evolutionary move toward greater invisibility, beginning with bipedality and morphologically ending with the closing over of the vaginal orifice by the labia majora.

In sum, the primate Bauplane imposed by consistent bipedality mandates a reappraisal of hominid sexuality. Homo exhibere was an undeniable ancestor of present-day humans. An understanding of how this hominid affected the course of hominid evolution necessarily rests on an examination of corporeal matters of fact: animate form and a concomitant species-specific tactile-kinesthetic/kinetic body.

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