

# Tools and Teeth: Some Speculations Regarding Canine Reduction<sup>1</sup>

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*Starting with a critique of current beliefs that maxillary canine reduction in hominids was causally related to tool-use and tool-making, the article suggests that reduction took place because selection favored a different pattern of social behavior. Sexual dimorphism and aggressive intragroup behavior tend to be related in terrestrial primates. A shift in hormonal interactions is suggested, such that selection for diminution of aggressiveness resulted in a diminution of sexual dimorphism. Tool-making is seen as one of a number of cognitive reorganizations, not as a causal factor in canine reduction.*

THIS paper will critically examine the present orthodox view that the loss of large maxillary canines in early hominids was directly related to tool-using and tool-making, and will suggest instead that the reduction of these structures was primarily a consequence of selection for social behavioral attributes. Briefly, I submit that during early hominid evolution, natural selection favored glandular (hormonal) interactions such that: (1) selection favored social behavioral adaptations, including a reduction in intragroup aggression; (2) these same selection pressures resulted in a diminution of sexual dimorphism.

Tool-making is then viewed as a logical outcome of two basic features of hominoid behavior. First, tool-making is a logical extension of a propensity common in higher primates and other mammals to use instruments in their environment. Secondly, tool-making, the imposition of arbitrary form on the environment, is an outcome of a major "psychobiological structuralization" (Hallowell 1956, 1960, 1961; see also Tappen 1965:438) that conferred selective advantage in a number of ways, tool-making being but one example of this reorganization of life-ways in the early hominids. Thus, while tool-making is here viewed as an important aspect of early hominid evolution, this essay presents the argument that tool-making was *not* a primary causative factor of canine reduction, and that tool-making per se has been overemphasized as a critical adaptation in early hominid evolution.

The orthodox (meaning "wide consensus") view that stone tools replaced the offensive and defensive functions of the canines in early hominids has been put forward by Washburn

(Washburn and Avis 1958; Washburn 1959, 1960; Washburn and Howell 1960). This view, based on Darwin's suggestion, has been accepted by numerous students of human evolution (DeVore 1964, Hockett and Ascher 1964, Brace and Montagu 1965, to mention but a few). While this suggestion appears innocent of confusion, it is of interest to note the following quotations, so that the matter is correctly set forth. Washburn notes:

The tools of Sterkfontein and Olduvai represent not the beginnings of tool use, but a choice of material and knowledge in manufacture which, as is shown by the small canines of the man-apes that deposited them there, derived from a long history of tool use [1960:72].

Washburn and Howell state:

Darwin postulated that the reduction in the size of the canines . . . was the consequence of employing stones and clubs for fighting. . . . This interpretation may be correct, and it now appears reasonable that forms ancestral to Australopithecines were probably the earliest to employ and even, to some extent, to manufacture stone and other implements. Since the canine teeth were already small and of the human type, the substitution of the use of implements for canines in fighting (and defense in general) must have taken place still earlier [1960:46].

Further on, they say:

The evidence would favor the conclusion that those selection pressures which maintained large canine teeth seem to have changed long before those which favored large molar teeth. One interpretation of this situation is that implements were first and primarily employed for protection, hence as weapons, and only to a lesser extent in the food quest [1960:48].

Finally, DeVore has noted:

Although the Australopithecines are the earliest known hominids, the fact that their canine teeth were reduced to human proportions indicates that tool use was a habit of long standing; that is, tools had long replaced canine teeth as weapons of hunting and defense [1964:35].

Although these authors scarcely have any such intentions, it should be appreciated that until the reduction of the canines is explained causally, the structure of their arguments is uncomfortably similar to a Lamarckian approach. As far as the above analyses have been carried, the orthodox explanation implicitly suggests one of two possibilities: (1) that tool-using and tool-making *resulted* in reduced canines, or (2) that there is some basic functional opposition or contradiction in having large canines and making stone tools. It is legitimate to ask *why* a hominid or hominoid should lose its large canines (presumably effective in defense and offense) because it is using and/or making stone tools. If a hominid or hominoid precursor is using and making stone tools because it lost its large canines, *how and why* did it lose the canines in the first place? Since the formulations given by Washburn and others have never answered these two questions, the explanation linking canines and tools is incomplete and probably overly simplistic.

Brace (1963) and Brace and Montagu (1965) are the only authors I have encountered who have offered an explanation for the reduction of canines in genetic terms, avoiding in their argument any tinge of reduction through use. The following quote from Brace and Montagu succinctly states their basic framework:

In *Australopithecus*, the canines are large, but they do not project as significant defensive weapons, and one can infer that the ancestors of the australopithecines had been using tools as defensive weapons for a long enough time so that the accumulation of random mutations could result in the reduction of canines toward the level of the incisors. If this is the case for *Australopithecus*, obviously the later *Paranthropus* had been the beneficiary of such a process for a longer period of time, and this, coupled with the indications of clearly shaped tools, should have allowed still more random mutations to accumulate affecting the front teeth. Because of the reduced importance in maintaining such relatively large teeth as had formerly been valuable, the accumulating random mutations could be expected to produce smaller front teeth—especially canines—and of course this

is exactly what the anatomical evidence shows [1965:277].

It is not necessary to enter into a full discussion here regarding the theoretical difficulties of Brace's "probable mutation effect." Prout (1964) and I myself (Holloway 1966) have taken issue with this hypothesis elsewhere. "Random" mutations cannot accumulate without some kind of selection process operating. While the hypothesis does try to explain *how* reduction occurred, the second question of *why* remains, as does also the fact that human canines are spatulate and not pointed. If long pointed canines are advantageous in a hostile environment, why shouldn't an animal adapting to a new ecological niche keep them while also making stone tools? What is the disadvantage of long canines in terms of tool-making?

One constant association is contained in each of the above quotations: canines and tools as effective in defense against predators. In spite of Brace's and Washburn's contentions that small Oldowan tools would be as effective in terms of offense and defense, it seems questionable that an entire morphological pattern would be lost without some gain of a more important kind. In fact, both Livingstone (1964:150) and Clark (1964:155) have questioned the effectiveness of Oldowan tools as defensive weapons, suggesting instead their value in the consumption of food and possibly in the food quest.

More recently, Pilbeam and Simons (1965:242-244) have suggested that large canines and incisors were useful to apes in stripping vegetable foods (but see Washburn and Avis 1958:425, quoted below). The reduction of these teeth in *Ramapithecus* is interpreted by Pilbeam and Simons as evidence that this Pliocene fossil was an *ad hoc* tool-user and prepared its food with tools. They also suggest that large canines were associated with "defensive display behavior": "If tool use (and possible changes in male display behavior as well) had removed the selective advantage of large canines, canine reduction inevitably would have taken place" (1965:244). This inevitability is apparently based on Mills's (1963) suggestion that with shortening of the face (through erect posture) the canines would be in the plane of the maxillary incisors, rather than passing behind the upper incisors. Natural selection would thus have acted to reduce

the crowns of the canines. Brace and Montagu's and Pilbeam and Simons' analyses clearly advance the issue further than Washburn's views, and introduce some more meaningful factors to explain reduction. However, I find them unclear as to why the face must necessarily shorten through erect posture, and fail to see how the above explanations can answer the question of the reduction of maxillary canines, i.e., why any selective advantage should necessarily be lost.<sup>2</sup>

I suggest that one possible key to this problem rests in Pilbeam and Simons' statement regarding the canines as useful in defensive displays. As they have noted, and as Washburn and Avis (1958:431) have shown with canine measurements, sexual dimorphism is generally highest in terrestrial primates, particularly the gorilla, baboon, and macaque groups. Robinson's (1956) study on the dentition of the australopithecines has shown clearly that sexual dimorphism was greatly reduced in this terrestrial primate. Washburn and Avis state on this point:

Large canines in the male cannot be related to diet as the males and females eat the same things and the males do not provide food. They are probably related to dominance in, and protection of, the group, both of which functions were gradually replaced in early human societies by *tools* [1958: 425; their italics].

As noted before, this statement does not suggest the mechanisms of loss, and one wonders why the senior author never pursued further the question of sexual dimorphism, dominance, and protection of the group in the earlier quoted materials. Subsequent writings by Washburn and DeVore (1961a, 1961b), DeVore (1963), and DeVore and Washburn (1963) have stressed canines as functioning as a major defense against predators, although Clark (1964) and Livingstone (1964) have questioned the importance of predators. Maxillary canines are one example of extragenital secondary sexual characters, which, like genital sexual characters, depend upon gonadal hormones for their full normal development.<sup>3</sup> It is difficult to escape the conclusion from Hall's (1965) succinct summary of primate studies and the papers in DeVore's (1965) volume that terrestrial primates not only have heightened sexual dimorphism, but also show maximal development of aggressive and agonistic behavioral responses within the group. Crook and Gartlan (1966:1201) have discussed pri-

mate studies in ecological perspective and have stated that size and aggressiveness probably did *not* originate as a response to predators. Instead, these authors regard dominance and cohesion as the sexual selection mechanisms, although they apparently accept weapon possession as a substitution for high degrees of sexual dimorphism in body and canine size (1966:1202).

If this interpretation regarding sexual selection is correct for terrestrial primates, it suggests that intragroup behavioral adaptation has been of major importance and that predator pressure is not as important a factor as is claimed by Washburn (1960), Washburn and Howell (1960), DeVore and Washburn (1963), DeVore (1964), and Hockett and Ascher (1964). (2)

It seems clear that a major aspect of the "human revolution" has been a shift in intragroup behavior of the kind discussed by Etkin (1954, 1963), which is based more on cooperation than aggressiveness and dominance interactions. The questions raised earlier regarding the how and why of canine reduction and the positive gains accruing from it might be answered as follows: a shift in endocrine functioning took place so that natural selection for reduced secondary sexual characteristics (such as the canines) meant a concomitant selection for reduced aggressiveness within the group.

In other words, natural selection favored an intragroup organization based on social cooperation, a higher threshold to intragroup aggression, and a reduction of dominance displays. The neural concomitants of these behavioral processes were also related to a shift in endocrine (gonadal and growth) functioning. The positive gain and the loss of these structures are thus accounted for quite economically. Behavior was selected positively, and those structures resulted that were compatible with such behavioral changes. quite than more important

Admittedly, this hypothesis is very speculative, and, as with the other interpretations, no direct evidence can be gathered to prove it. Indirect evidence is available, however. In terrestrial and arboreal primates heightened sexual dimorphism and high degrees of aggressiveness correlate. The administration of testosterone can change dominance interactions in chimpanzees (Clark and Birch 1946), but apparently cannot in highly dimorphic species such as the macaque (Mirsky 1955). Other indirect evidence includes the following:

(1) the human female is sexually receptive on a full-time basis—which implies endocrine changes in the past that must have had far-reaching implications for intragroup behavior; (2) the relative brain size of the australopithecines is increased (Tobias 1963)—which clearly involves some change in relative growth rates that must have included some endocrine reorganization, although probably not of a gonadal nature; (3) a switch to a carnivorous diet was taken up by australopithecine times—which suggests different social adaptations, possible cooperative hunting, and a switch in metabolic requirements, again possibly involving some glandular rearrangement.

The significance of stone tools is not diminished in this framework. They become implicated, both for preparing food and for preparing weapons for greater efficiency in the food quest. The only shift here is toward putting stone tools in a proper relationship with adaptation and natural selection, and not regarding them as causal elements in canine reduction. This view of tools fits well with Hallowell's (1956, 1960, 1961) analysis of hominid "psychobiological structuralization" and is in basic agreement with his contention that stone tool-making is one of several cognitive changes wrought by the total psychobiological structuralization (see also Tappen 1965:438). With a major change in life-ways during the early Pleistocene (e.g., the "human revolution" of Hockett and Ascher 1964), it seems reasonable that more behavioral changes would have occurred than simply tool-making per se. I am firmly convinced that Hallowell and Tappen are correct in asserting that tool-making did not precede other cognitive changes, but was one outcome of such changes.

Although this treatment of the tool-canine teeth question is speculative, I believe that the problems associated with orthodox explanations have been made clearer. I am hoping that my hypothesis will stimulate dialogue and a search among extant primate groups for more indirect evidence relating behavior and structure, endocrines, and ecology.

#### NOTES

<sup>1</sup> This paper is a greatly contracted version of an unpublished manuscript, "Sexual dimorphism and early hominid evolution," in which the basis for the speculations offered here are more fully documented.

<sup>2</sup> Essentially, the shortening of the face through erect posture is explained by correlating face-shortening with forward placement of the orbits and increased binocular vision. While this de-

scriptive account may have validity for long phylogenetic sequences, it is difficult to see its application to the problems suggested in this paper. The great apes are not that different, surely, than man in terms of binocular vision, to explain totally the great reduction of the jaws, the spatulate shape of the canine, and other morphological characteristics of the dentition and supporting structures. If taken as a mechanical-causal explanation, it suggests that females are more binocular than males, are more upright, and have shorter faces with more forwardly placed orbits, and that these differences follow the distribution of sexual dimorphism in the canines in terrestrial and arboreal primates.

<sup>3</sup> Hormonal interaction is meant in a very broad sense. I do not mean to imply that the chemical structure of gonadal hormones has necessarily changed in primate evolution, or that genetic control of receptor tissues sensitive to hormones can be ignored, but rather am referring to interaction between tissue specificity, sensitivity to the hormonal milieu, and the genetic and epigenetic basis for all endocrine functioning. In this paper I am mainly concerned with androgenic hormones. Clear differences exist for other hormones in primates, particularly for "Growth Hormone" or somatotrophin. I do not provide a full review of the endocrinological literature. Strain differences in temperament are well known for many animals, and domestication has effects on glandular processes associated both with temperament variables and with body build. For a review of these problems, the reader is referred to Hafez (1962) and chapters 4, 19, 20, 21, and 22 in Young (1961).

There are, so far as I am aware, no studies showing that canine size depends directly on androgenic hormones. On the other hand, other secondary sexual characteristics *do* depend on their interactions. In this paper I am assuming that large canines are one manifestation of sexual dimorphism. Since the morphological characters that differ between the sexes depend somehow (in the broad sense defined above) upon hormonal mechanisms for their normal development, I am also assuming that some hormonal involvement in maxillary canine development takes place and that these mechanisms are specific to different species. I am further assuming that there are behavioral concomitants based on these interactions, and that these behavioral attributes have been the major focus for natural selection.

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