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The human canine: Its evolution and adaptive significance

Pascal PICQ
Collège de France

ABSTRACT

The canine is a tooth with special characteristics and adaptive significance that varies considerably between mammalian lines and the primates. No matter what the line, canine teeth are never involved in mastication and do not interfere with masticatory dynamics. Mastication, which is one of the most complex functions that monkeys and apes display, appears well before the large canines in both phylogeny and ontogeny. In apes, their size and shape have nothing to do with diet, but are linked to sexual selection. The human line of hominids possesses smaller canines that have become incisiform and have lost their sexual and social function. They are now used exclusively to tear apart meat and other types of solid foods. The development of a wide, short buccal surface that increased medial-lateral movement during the masticatory cycle, may explain this particular development in recent hominids including humans. From an evolutionary point of view this means that the human canine has been subjected to stresses imposed by the biomechanical environment of the masticatory apparatus. In other words, the human canine, as well as those of the other anthropoids, does not guide mastication but has acquired a morphology and position restricted by masticatory functions. In evolutionary terms, it is therefore referred to as an "exaptation"; it has acquired, not a function, but a passive characteristic which makes it a marker for rehabilitation – on condition that its eruption is related to normal masticatory functions in individual histories, but it never serves as a mediator of mastication.

KEYWORDS

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Address for correspondence:
P. PICQ
Collège de France,
3, rue d'Ulm,
75005 Paris.
picq.anthrope@wanadoo.fr

1 - INTRODUCTION

In 2009 we celebrated the bicentenary of the birth of Charles Darwin and the one hundred and fiftieth anniversary of the publication of: *On the Origin of Species*. But even after this long passage of time, the theory of evolution is still poorly understood, especially when we consider the popular conception that mankind is a special case because of the lingering persuasive power of obsolete premises that attempt to detach humanity from the mammalian lineage, claiming that our species, with its genius and its cultural and technical innovations, has gained freedom from evolutionary constraints. However, this is not the case and what we call co-evolution or interaction between our biological evolution and our techno-cultural evolution is in constant operation, particularly with respect to masticatory functions, mastication and canine teeth.

Although evolutionary theory permeates all the life sciences, including medicine, outmoded, non-scientific beliefs about mankind's position in nature and its intimate participation in hominid evolution, still persist. It is not just the creationists, defending a narrow, unreasoning literalism, not based on a coherent exegesis (see Picq P., *Lucie et l'Obscurantisme*. Odile Jacob, 2007), who refuse to understand and argue against evolution. Many representatives of health disciplines, who claim to base their proposals on scientific procedures but are actually using concepts derived from theology and, especially certain schools of philosophy to take an astonishing stand opposing evolution. Paleoanthropology is not spared, with its ideas of hominisation (see Picq P., *Les Mondes darwiniens*. Syllepse, 2009) of finalised morphogenesis, internal forces guided by the divinely-inspired sphenoid, the sacred basicranial flexion, the apocalypse according to the third molar and the fairy neoteny. Oh poor epistemology!

All science is based on observation, comparison, experimentation (when possible), modelling and, above all, on the possibility of refuting the dominant paradigms, not on the basis of arguments which consist of refuting observed facts or revelation by experimentation in the name of dogmatic ideas, but properly by taking these facts into account, as new paradigms are developed. As Claude Lévi-Strauss has reminded us, studies devoted to examination of humans, as well as sciences or those whose scope encompasses humans, cannot claim scientific status if they limit their range of study to humanity exclusively. If they ignore the species most closely related to us, whether in the modern world or the past, they will produce blunders as ludicrous as those of Bouvard and Pécuchet and this applies not only to paleoanthropology but to dental science as well. The adaptive significance and evolution of the canine and its functions is, as an English investigator has remarked, "a case in point".

In this article, we shall begin with a short review of canine anatomy and comparative ethology and we shall observe that the canine has diverse types of adaptive significance, as seen in the mammalian line, with regard to natural and/or sexual

selection. We shall then see what the situation is for primates and monkeys. Next, we shall engage the main themes of the evolution of the canine in the human line over the past 7 million years. Finally, we shall address certain problems by canine teeth in dentistry today. This taste of evolutionary science may not risk tearing the flesh of Platonian idealists but could certainly tweak the sensitive souls of these devotees of an intelligent design dictated by the great heavenly occlusal architect.

2 - A GENERAL OVERVIEW OF THE COMPARATIVE ANATOMY AND THE FUNCTIONING OF MAMMALIAN CANINES

A trend in the evolution of the dentition of mammals – which is not a law but an empirical *a posteriori* observation – since they parted from their "reptilian ancestors" includes a reduction in the number of dentitions to just two, the deciduous teeth and the adult dentition, a reduction in the number of teeth, and the differentiation of types of teeth, which is called heterodontia. These varied types of teeth in humans and primates are the incisors, the canine-first premolar complex, and the molars. We shall see that, even in primates, these fields may or may not embrace neighbouring teeth. From the point of view of evolutionary and adaptive genetics, the canine is distinguished by its propensity to be more developed and prominent than the other teeth – though not always, and to form complicated functional complexes, in response to natural as well as to behavioural and sexual selection factors.

The most commonly accepted notion today links a developed canine with carnivory, as in the canidae family. But this is wrong, because the order of carnivores is not defined by the presence of well-developed canines but by its carnassial teeth, formed by the first upper molar and the last lower premolar (P4-M1). Because, contrary to what you may read or hear, the canines are not used to tear flesh, but to perforate, pierce and kill prey as you can easily see if you look at the morphology, size and shape of the canines in modern carnivores that are blunted and oval or round in cross-section. This hardly makes them well suited for cutting flesh and even less for breaking bones! Carnivores are the mammals which masticate the least, if at all. They shear meat with their carnassial teeth and swallow it whole, the stomach taking care of the rest. As for the ability to break marrow bones, only hyenas, bears and wolverines can manage this, but to do it they use conical premolars, not canines. Therefore, in carnivores, the canines are only weapons and do not contribute to mastication, which, in any case, is not a function that these animals employ. Developed canines are found in several species of herbivores and omnivores. The most surprising case is that of young musk deer. The males have fine, very prominent canines which are certainly not useful in catching and masticating tree leaves. Both sexes have horns, but only males have highly prominent canine teeth. It is a secondary sexual characteristic which has developed within a context of sexual competition. The display in individuals of one sex of

characteristics of size and shape as well as secondary bony and/or skeletal appendages, as well as in their coats, that the other sex does not have, is called *sexual dimorphism* (see Picq P., *Le Sexe, l'Homme et l'Evolution*. Odile Jacob, 2007). Sexual dimorphism is especially marked when individuals of one sex attempt to possess, forcibly, a harem of members of the opposite sex. The *intrasexual* competition that arises in this struggle, which aims to exclude members of the same sex also searching partners, favours powerful individuals, armed with dissuasive weapons, usually antlers, horns and/or canine teeth. The well-developed canines in musk deer clearly then have nothing to do with their folivorous diet. We should note in passing, that these prominent canine teeth do not interfere with the medial-lateral components of the masticatory cycle. *(The temporomandibular joint in carnivores has a pintle-hinge type anatomy which only allows movement in the sagittal plane; so it is not the canine that restricts the medial-lateral component of a form of mastication restricted to vertical shearing)*. Sexual dimorphism of canines is found in horses, being well developed in males and usually absent in females; but mares sometimes have small canines. These are vestigial characteristics, gradually disappearing.

Males in the group suida, such as wild boar and wart hogs, develop large, curved canines. In old individuals, the tip of the canine may grow so exuberantly that it pierces the animal's snout. These omnivorous species search for the underground parts of plants which they dig out with their powerful muzzles. But they do not routinely use their canines, which represent secondary sexual characteristics, to obtain food – even if they do occasionally catch small animals with them. Males in the suida group utilize their canines primarily in intrasexual competition to threaten rivals and as weapons against them. Since the suida are omnivorous, their mastication is a complex function adapted to the breakdown of different types of food. And, of course, the large size of their canines does not interfere in masticatory kinematics in any way.

The most extreme case of sexual dimorphism is found in sea elephants, where the males display the most flagrant macho characteristics as they corral and control dozens of females for their exclusive sexual pleasure. Their body mass is several times greater than that of the females and their canines, which are enormous, are used only to impress rivals, as they cannot readily be employed in combat. But their enormous bulk can appear redoubtable when a huge male sea elephant bursts out of the water.

This brief overview of the size and function of canines reveals an adaptive relationship with respect to natural and sexual selection. In carnivores they are used like daggers and the difference in size between males and females is simply correlated to body size. (It was the same for the impressive sabre-tooth tigers at the end of the prehistoric period). The function and adaptation of canines is therefore simply a factor of natural selection: to kill prey. Animals never use canines to tear flesh before eating it. This role is played by the carnassial teeth. The canines are even less adapted for breaking up marrow

bones, a manoeuvre that would require an impossibly extreme opening of the jaws and a lengthening of muscle fibres that would leave feeble covering of the sarcomeres, thus reducing the action of the muscles of mastication, even of the powerful temporal. Prominent canines cannot be blamed for the absence of kinematic mastication in this species because it is the morphology of the temporomandibular joint that prevents this process from taking place.

Prominent canines are found in several mammalian lines, in herbivores (graminae), folivores (shrub leaves) and omnivores. They may be fine, long and fragile as in musk deer, or powerful as in suidae. These canines are not used for obtaining or eating food. Their development is a response to sexual selection factors, particularly in species where the males set up harems and have to fight off other males (intrasexual competition). Their fragility, as in musk deer, or complex shapes, as in suidae, indicate that these are secondary sexual characteristics used to menace other males in intrasexual competition, but may also serve to attract females in intersexual competition. Finally, these species have strong masticatory functions and it is clear that these large canines do not interfere with chewing cycles. If you want to validate this contention, all you have to do is visit a zoo and watch them eat. You'll wonder how these animals could have survived to adulthood and reproduce successfully if they were unable to protect themselves against enemies. The answer to this false enigma is in ontogenesis: their large canine teeth emerge into the arch later than the rest of the dentition because of sexual and hormonal factors, at a time when masticatory kinematics has already been well established in a process that began when the first adult teeth erupted. During their growth period, the large canine teeth are subjected to the pressures of orthodontic forces which guide their development. Individuals for whom this procedure malfunctions will perish in the struggle for survival and thus be prevented from passing on their maladaptive characteristics to future generations. Darwin taught us how this works one hundred and fifty years ago.

3 - THE ADAPTIVE SIGNIFICANCE OF THE CANINE IN SIMIANS

Human beings and other hominids, even the males, have small canine teeth. This is one of the chief characteristics that allows us to place the Toumai (*Sahelanthropus tchadensis*) as an ancestor of our emerging line while many scientists rule out a rival contender group, the *Orrorin*, because of their larger ape-like canine teeth. The first Australopithecines, who lived between 4 and 3 million years ago, maintained slight sexual dimorphism of the canines, those of the male being only slightly larger than those of the female. We can see that in the human line a trend has developed for bodily differences between the sexes to remain marked while sexual dimorphism of the canines has almost disappeared.

This detachment has been noted in more recent Hominids like the

Paranthropes, descendents of Lucy, and the first humans, *Homo habilis, Homo rudolfensis* and *Homo ergaster*. It is a development that is especially remarkable because, on the one hand, our relatives the Paranthropes evolved by accentuating their sexual dimorphism, while our *Homo* genus has diminished it (see Picq P., *Au Commencement était l'Homme*. Odile Jacob, 2003). Therefore, for the past 2 million years, the human canine has not played a role in sexual selection.

Neither is there any correlation with diet. Although paranthropes developed an increasingly impressive masticatory apparatus, with a small incisor-canine arch and very large, strong premolars and molars, the reverse trend is true of *Homo*, in whom the incisor-canine arch is expanding as the premolars and molars tend to regress. Paranthropes and humans are both omnivores, but our relatives can chew huge quantities of tough plant material, especially roots, while most humans include a considerable amount of meat in their diets, although we still subsist primarily on fruits and vegetables. It is incorrect to claim that the human canine is linked to the consumption of meat, because all hominids, as well as modern chimpanzees, eat meat regularly. Thanks to increasingly incisor-like morphology and its powerful root, the human canine tooth tears flesh very effectively. But, as we have seen, neither carnivores nor apes ever employ their canines for alimentary purposes. And it is also true that no adaption of the human canine to tear flesh was necessary, because our earliest cave man ancestors could do this with their razor-sharp stone tools. We can consider this to be secondary "pseudo-adaptation"; in other words, the human canine has not become incisiform in order to eat meat, but has found a secondary application in doing it.

We do not yet know why canines became small and incisiform in hominids at the end of the tertiary era. The only coherent explanation is that canines changed in the framework of the evolution of the face and dental arches. With short, wide dental arches and the gap between the two temporomandibular joints at the base of the skull, the medial-lateral components of the masticatory cycles had to be more accentuated (see Picq P., *op. cit.* CNRS, 2003). One consequence is possible interference between masticatory kinematics and prominent canines. Natural selection factors take empirical priority over sexual selection factors – viability vs. reproductive success –; our immediate ancestors experienced an evolutionary modification in the size of the canines and the age at which they erupt (known as *allochrony*). All monkeys and large apes have large canines that erupt after the third molars have appeared in the arch. But in paranthropes and *Homo*, the canines erupt at the same time the second molars do. This modification in ondontogenesis confirms the antagonistic interactions which may result from large canines emerging before masticatory dynamics are in place. This clearly demonstrates that canines must adapt to the masticatory environment. Either they appear later and grow under the effect of orthodontic forces so that they interfere closely with masticatory function, or it becomes a problem, in which case they grow smaller and more incisiform. But under no circumstances do the canines guide mastication!

4 - CONCLUSION: THE CANINES IN MODERN MAN AND DENTAL PRACTICE

So how can we explain that the canine can sometimes play a major role in dental practice? Approaching a common subject by confronting related scientific disciplinary fields, does not mean that one discipline prevails over the other. I have reviewed – briefly – what we know of the evolution and adaptation of the canine in mammals in general, apes with greater accuracy and hominids in particular. No matter how fervently dental occlusal theorists claim that their notions are based on observation and experimentation in a context of modern evolutionary theory, they do not stand up under rational scrutiny. Instead we find that occluso-Platonists rely on a kind of religious hominisation and intelligent design, a belief totally incompatible with evolutionary anthropology. In science, it is not acceptable to assert, as they do, that Man is a separate species, especially when they insist on ignoring the other species as they propound their pitiful argument that is based on theological-philosophical certainties saturated with metaphysics. On the other hand, practitioners have empirical practices and knowledge validated by their clinical experience. Paleoanthropologists cannot contest techniques that give satisfactory results. Even so, experience is not enough to validate the notion of canine protected occlusion in mastication. From a phylogenetic and ontogenetic point of view, masticatory functions developed well in advance of the appearance of large canines. So how can we interpret this relationship between the canine and the rehabilitation of occlusal functions? I have suggested an answer: since the canine is subjected to a masticatory context, its eruption is influenced by the orthodontic forces linked to mastication. Consequently, its position and orientation in the dental arch result from a previous situation which imposed these stresses. Another consequence is that through its position and the orientation of its crown and facets, characteristics resulting from dynamic balances conditioned by this functional environment, the canine was, in any case, a functional marker, but is not the cause of this function but its consequence. This is the perspective in which the human canine can be extremely interesting in rehabilitating occlusal and masticatory function, not because it is the matrix, but because it is the result. To persevere in this belief we risk making the canine responsible for masticatory malfunction, which clearly does not mean that the canine is responsible for masticatory function.