

THE MAMMALIAN DENTITION, A 'TANGLED' VIEW

by

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ABSTRACT

Detailed knowledge of the mammalian dentition has increased enormously during the past few decades, yet the general view of the dentition has changed very little. Synthetic work connecting knowledge from different areas is possible and holds great promise, even if the synthesis is tangled and incomplete. The natural milieu for such a synthesis is the evolutionary framework. Important components of the tangle, as it appears at present, are identified and briefly discussed, mainly from a functional and palaeontological point of view. Such components are size in relation to function and growth, the dynamics of the masticatory machinery during chewing, and especially its changes during ageing and during evolutionary history, enamel structure in relation to wear and stress, and problems of growth, homology and phylogeny. Recognition of evolutionary constraints is possible and useful.

KEY WORDS: Mammalian Teeth, Dentition, Odontogenesis, Mastication, Dental Evolution, Dental Function, Dental Wear, Enamel Structure, Homology, Constraints.

INTRODUCTION

These are exciting times for those of us whose interests in some way include the dentitions of vertebrates. The focus of research has been very much on mammals, which will be my main topic, but many recent results have much wider implications. A historical analysis of the subject is lacking, but the development during recent decades is to some extent reflected in the proceedings of the International Symposia on Dental Morphology so far published (ANONUMOUS, 1967; DAHLBERG, 1971; BUTLER & JOYSEY, 1978; KURTÉN, 1982; RUSSELL, *et al.* 1988). GANS *et al.* (1978) provide an overview of the history and structure of research into mastication, while the early development of enamel structure research was reviewed by BOYDE & JONES (1988).

In particular, the recent great advances in developmental biology have unveiled glorious perspectives for the understanding of odontogenesis. Increasingly sophisticated analyses of chewing dynamics, mandibular mechanics and food comminution have also provided a new and more realistic potential basis for a quantitative understanding of the design of the masticatory apparatus as a whole. The study of

dental wear has emerged as a major focus of interest. At a general level, the ecological and reproductive correlates of dental wear are now well understood in some cases (SKOGLAND, 1988). The experimental study of relationships between food and tooth wear is also well under way, and the first experimental studies of the effects of enamel microstructure on wear have recently appeared (TEAFORD, 1988). Other aspects of enamel microstructure, both developmental and mechanical, are also much better understood than a decade ago (BOYDE, 1989).

Despite a steady influx of new data, however, the general picture has been slow in changing. In this perspective some old books are at least as exhilarating as, and much more terrifying than, any recent paper can reasonably hope to be. Richard Owen's '*Odontography*' from 1845, for example, always leaves me with the uncanny feeling that a century and a half has passed with little to show for it, and that we are largely engaged in reinventing the wheel. Or take Aristotle. The following extract from Book III of his '*Parts of Animals*' is typical. Aristotle is introducing the subject of Teeth:

"In the lower animals teeth have one common function, namely, mastication; but they have additional functions in different groups of animals. In some they are present to serve as weapons, offensive and defensive, for there are animals which have them both for offence and defence (e.g. the wild carnivora); others (including many animals both wild and domesticated) have them for purposes of assistance.

Human teeth too are admirably adapted for the common purpose that all teeth subserve: the front ones are sharp, to bite up the food; the molars are broad and flat, to grind it small; and on the border between the two are the dog-teeth whose nature is intermediate between the two: and just as a mean shares the nature of both its extremes, so the dog-teeth are broad on one part and sharp in another. Thus the provision is similar to that of the other animals, except those whose teeth are all sharp; but in man even these sharp teeth, in respect of character and number, are adapted chiefly for the purposes of speech, since the front teeth contribute a great deal to the formation of the sounds." (*De partibus animalium*, p. 661b)

One of the best (and most cited) recent introductions to teeth and chewing that I know is a semi-popular paper by CROMPTON & HIEMÄE (1969). The authors introduce the subject as follows, before going on to discuss relationships between chewing muscles and wear facets:

"The mammalian dentition has other functions besides chewing food; it, or parts of it, are used for food-gathering, as weapons of offence or defense, for grooming fur and for social activities. Not all these varied functions are performed by all the teeth, and a characteristic of the mammals is that they have evolved a differentiated tooth row with four types of teeth, each specialized for particular activities. The anterior teeth, incisors and canines, are used predominantly for food-gathering, as weapons of offence and defense and for

grooming. In carnivores, the canines are used as weapons in the bringing down of the prey. Food is actually cut, ground or crushed by the cheek teeth, the premolars and molars, and it is these teeth that are specialized and adapted to various kinds of diet." (CROMPTON & HIEEMÄE 1969:23)

It is not immediately obvious that two millenia and a great deal of hard work lie between the two quotations. Neither text is addressed to specialists, of course, and the similarity may not mean much. Teeth are also rather definitely teeth, and their range of possible functions is accordingly limited. But I cannot free myself of the feeling that there is a message here, especially as I am not aware of anything significantly different from the two eventful decades since 1969. It really does seem remarkable that we still approach the mammalian dentition just as Aristotle did, even though many answers available today belong to questions he would never have been able to formulate for sheer lack of knowledge.

Part of the problem (if there is a problem) is, perhaps, that dental research is rather poorly focussed as a subject, and that its practitioners have such disparate aims and backgrounds. Very schematically, the two main roots of research into mammalian dentitions reside in the domains of dentistry on one hand and palaeontology on the other, both disciplines here defined in the widest sense. For a dentist the central issue is obviously to prevent or repair dental damage. For the palaeontologist the object is to establish genealogies and reconstruct extinct animals, especially their dietary habits and thereby much of their ecology.

This plurality is also a strength, however, and there are many examples of remarkably fruitful collaboration between scientists of such different origins. One key feature is that such collaboration tends to bring together causal knowledge (from dentistry) with comparative and correlative knowledge (from palaeontology). More generally, it produces the kind of tangled web of cross-connected knowledge in which synthetic insights may grow. It is the chief aim of this paper to advocate this 'tangled' approach as a means of taking advantage of the detailed information now potentially available in specialised sub-disciplines.

Looking at the mammalian dentition from an abstract and general perspective, this tangled web includes at least the initiation of odontogenesis, the morphogenesis of teeth and its control, including differentiation. Further components are histology, the eruption of teeth and the control of their position during dental wear, the processes of wear and their relationship to the structure of the dental tissues and the mechanical properties of food, as well as all aspects of mastication, including food comminution and swallowing. The diversity of dental

form and its relationship to foods and digestion are important, as are other kinds of dental function, and, especially, the evolutionary history of all this.

I have made little effort here to present a balanced review. Basically, this is a provocative paper, and I have tried to avoid repetition of points that are well understood, as well as discussion of areas of which I have little first-hand experience. I will discuss the general background first, and then focus on some helpful interrelations and conspicuously blank, and thus potentially promising, areas for future research.

AN EVOLUTIONARY PERSPECTIVE

The idea of evolution as the unifying theme of biology and related subjects has been expressed many times. A locus classicus is DOBZHANSKY (1970:5f): "At any rate, in biology nothing makes sense except in the light of evolution". Another slightly famous phrasing comes from a book review by VAN VALEN (1973:488): "A plausible argument could be made that evolution is the control of development by ecology". The latter, very Darwinian formulation is especially apt in the present context.

Sadly, many developmental biologists either ignore evolution altogether or relate ontogeny to what one recent author called "the sequence of extant vertebrate organisms", or similar vague and misleading constructions. What we need is something more like a view of specific developmental processes and specific selection pressures acting on them. It is simply not true that we do not know enough yet. What is known can be put into this perspective, however incomplete.

Conversely, students of functional morphology have often ignored developmental biology, or been very naive about it. Indeed, much functional morphology has completely ignored evolution, perhaps because the subject was first developed by such outspokenly anti-evolutionary masterminds as Aristotle and Cuvier (RUDWICK, 1972; MAYR, 1982). I refer particularly to Cuvier's emphasis on functional relationships to reconstruct extinct animals known only from fragments, embodied in his principle of the 'correlation of parts' (CUVIER, 1915; RUDWICK, 1972; BUFFETAUT, 1987). Digest, for example, the following wonderful passage from Cuvier's 'Essay on the Theory of the Earth'. The subject is the teeth and masticatory machinery of ungulates:

"Their food being entirely herbaceous, requires teeth with flat surfaces, on purpose to bruise the seeds and plants on which they feed. For this purpose also, these surfaces require to be unequal, and are consequently composed of alternate

perpendicular layers of hard enamel and softer bone. Teeth of this structure necessarily require horizontal motions, to enable them to triturate or grind down the herbaceous food; and, accordingly, the condyles of the jaw could not be formed into such confined joints as in the carnivorous animals, but must have a flattened form, correspondent to sockets in the temporal bones, which also are more or less flat for their reception. The hollows likewise of the temporal bones, having smaller muscles to contain, are narrower, and not so deep, &c. All these circumstances are deducible from each other, according to their greater or less generality, and in such manner that some are essentially and exclusively appropriated to hoofed quadrupeds, while other circumstances, though equally necessary to that description of animals, are not exclusively so, but may be found in animals of other descriptions, where other conditions permit or require their existence," (CUVIER 1815:96f)

Observe especially how the brilliant exposition falters towards the end, in a weak attempt to account for awkward exceptions evidently known to its author. Optimal design by The Great Engineer cannot really hope to account for the myriad peculiarities which result from simple twists of fate. A genealogical view is much superior in this respect, especially when combined with a powerful causal mechanism, as by Darwin.

If one is to understand the implications of a fossil one needs to know its functional and morphological correlates. This is the nuts and bolts of palaeontology, and as true now as ever. But functional entities are only part of the picture, no matter whether they are seen as Cuvierian perfect and unchangable machines or as evolving systems of conflicting requirements and compromise. Equally important are the various kinds of limiting factors involved, most importantly historical and ontogenetic constraints (ALBERCH *et al.*, 1979; GOULD & LEWONTIN, 1979; GOULD, 1989). Both phylogenetic and ontogenetic constraints operate through the genetic information, and their recognition requires a theory of genealogical evolution with a continuity of changing information.

Actual recognition of constraints has been rare (Darwin was very much an exception). Gould and Lewontin had high hopes for explicit recognition of constraints as a means of putting "organisms, with all their recalcitrant, yet intelligible, complexity, back into evolutionary theory." (GOULD & LEWONTIN, 1979:597). Preliminary attempts to put mammalian cheek teeth into such an organismic context were made by FORTELIUS (1985) and JANIS & FORTELIUS (1988), but these have only scratched the surface of the problem. Individual cases of constraints on mammalian dental evolution have been discussed by DIETRICH (1950); KOENIGSWALD (1982), WEBB & HULBERT (1986), WERDELIN (1987b) AND JANIS (in press a) among others. Hopefully, more will follow.

SIZE IS NOT SO IMPORTANT, IN SOME WAYS

Size, and allometric size relationships are among the most general and important factors in biology. Still, as a result of the debate and research initiated by PILBEAM & GOULD (1974) and GOULD (1975), we can now be reasonably certain that tooth size in mammals generally and in major subgroups is isometric to body size (FORTELIUS, 1985, 1988, and references cited in these). This can probably be generalized to the statement that the whole masticatory system is more or less isometric to body size, that is, that the relative size of the mouth and its machinery are independent of the absolute size of the animal.

The concept of 'optimum mouthful' (LUCAS & LUKE, 1984) is helpful. Chewing works best for a certain food volume, which is probably a constant fraction of the mouth volume for any type of oral morphology and food. Thus the volume of each batch of food passed on from the mouth into the digestive system should also, in principle, be isometric to the mouth volume. This is supported by a simulation model of digestion kinetics (Illius & Gordon, pers. comm. 1989), which indicates that food intake should be isometric to body size when food availability is unlimited. In other words, the static capacity of the entire digestive system is, volume for volume, roughly isometric to body size (DEMMENT & VAN SOEST, 1985).

The crux of the matter is, of course, that energy requirements are not isometric to body size, but negatively allometric (KLEIBER, 1947, 1961; discussion in PETERS, 1983 and SCHMIDT-NIELSEN, 1984). That is, relative energy requirements decrease with increasing size. This is compensated for by a correspondingly decreasing chewing rate, so that the isometrically scaled chewing apparatus produces comminuted food in proportion to the allometrically scaled metabolism (FORTELIUS, 1985). Physiological rates are an important aspect of all functional systems, but have been neglected to an incredible degree by morphologically oriented students.

To a certain extent this means that absolute size can be ignored as a factor in the design of the mouth and its parts. It also explains why dental morphological categories seem to be more or less independent of absolute size. Dental wear is interesting in this context, for it seems to be largely isometric to tooth size, that is, the increment tissue lost per chew seems to be proportional to the size of the tooth. Why this is so is not entirely clear, but the fact has interesting implications for understanding the process of wear (FORTELIUS, 1987).

Absolute size does affect the system through the effect of 'grain' (LEVINS, 1968). For example, both hard particles included in the food (dust, phytoliths etc.) and the structural elements of the tooth (apatite

crystals, enamel prisms, protein molecules etc.) have limited size ranges unrelated to the absolute size of the animal or its parts. The impact of a phytolith on a vole's tooth ought, in principle, to cause the same amount of absolute damage as the impact of the same phytolith on an elephant's tooth, and consequently a much greater amount of relative damage (JANIS & FORTELIUS, 1988). This may be offset to some extent by modifications in the organization of structural elements. For example, Hunter-Schreger bands are almost certainly an adaptation to prevent crack propagation (KOENIGSWALD & PFRETZSCHNER, 1987). They do not appear in teeth below a certain size, and evolved in parallel in several lineages as mammalian body size increased during the early Tertiary (KOENIGSWALD *et al.*, 1987). Whether small or large forms are favoured by such grain effects is unclear. Probably both are, in different ways, and neither enough to be important, except as a background to understanding the compensatory evolutionary changes.

EXCEPTIONS ARE THE RULE

The mouse-to-elephant perspective considered above is an abstraction, useful mainly as a baseline for comparisons, a 'criterion of subtraction' (GOULD, 1975). Real animals very seldom conform precisely to such general relationships. Even when correlation coefficients are high, they often reflect a great size range rather than a tight fit to some descriptive function. Mean deviation in mammalian organ scaling, for example, is about 20-30%, and maximum deviation is much more (PROTHERO, 1984, 1986). The observed scaling patterns are thus loose descriptions rather than powerful constraints. The giraffe's neck and the human brain are real biological phenomena.

Lower taxonomic levels tend to have different relationships than the general 'mouse-to-elephant' ones described above, frequently with (size) groups transposed to bring about the higher level overall relationship (KURTÉN, 1953; MEUNIER, 1959; GOULD, 1971). There has been some more or less futile discussion as to which of the relationships is more 'real'. A more fruitful approach would be to try to identify the causes, for example by work similar to that of RISKA & ATCHLEY (1985) or PAGEL & HARVEY (1989) on the ontogenetic and ecological correlates of brain size. It is especially difficult to apply overall relationships to interpret differences between closely related forms, as attempted for australopithecines by PILBEAM & GOULD (1974). There is some hope that morphological rather than taxonomic grouping would be possible for teeth, in some cases at least (FORTELIUS, *in press*). If this is borne out it may clarify the issue considerably, especially for extinct forms.

Context is everything, even when tangled. An example is the relationship between the teeth and the digestive system, especially in the case of foregut versus hindgut fermenting herbivores. The former have the option of ruminating, and at least the true ruminants and camels do this. The teeth of ruminating forms are designed to deal with partly digested food, and their dentitions are smaller and more simple than those of hindgut fermenters of corresponding size and dietary category, which have to chew their food unprepared (JANIS, 1988). Digestive strategy is a major determinant of dental morphology and much confusion may arise if it is ignored. These relationships are also an interesting example of fruitful synthesis. The connections between food selection, dental morphology and digestive strategy that have been uncovered by ecologists (BELL, 1971; JARMAN, 1974) and palaeontologists (JANIS, 1976) have turned out to be very illuminating not only for the evolutionary history of the groups involved (GUTHRIE, 1984; JANIS, 1982; JANIS & EHERHARDT, 1988), but for the ecology, behaviour and physiology of recent species as well (BELL, 1982; DEMMENT & VAN SOEST, 1985; KINGDON, 1979, 1982; OWEN-SMITH, 1985, 1988; VAN SOEST, 1982).

A DYNAMIC VIEW OF THE MACHINERY

The masticatory apparatus is dynamic at three levels: during chewing, during ageing, and during evolution. All rare essential, and depend on each other. How the mandible moves during chewing is quite well understood in a variety of animals (reviews by GANS *et al.*, 1978; HIEMÄE, 1978), although the direction and magnitude of muscular forces is still not known in detail (DE GUELDRE & DE VREE, 1988; HYLANDER, 1984, 1985, 1986; ORON & CROMPTON, 1985; WEIJS & DANTUMA, 1981; WEIJS *et al.*, 1987, in press). The occlusal stress developed at individual facets still appears to be largely a matter of conjecture.

One example of interaction between morphological interpretation and experimental work is worth mentioning in this context. This concerns the interpretation of the historically new type of wear, phase II wear, developed after maximum incuspidation of the molars, seen in the quadritubercular molars of herbivorous mammals. In accordance with traditional opinion, KAY & HIEMÄE (1974) interpreted this in primates as indicative of grinding action on tough vegetation. JANIS (1979) questioned this functional interpretation on the basis of hyracoid wear patterns, as the species with the least developed phase II wear facets had the most fibrous diet. Later electromyographic work on a variety of mammals showed that peak muscle stress was indeed

(FORTELIUS, 1985; BOYDE & FORTELIUS, 1986). A similar case of convergent evolution is seen in the enamel of enlarged incisors (KOENIGSWALD, 1988).

Hypsodont teeth demonstrate another dynamic aspect of the machinery: the compensatory eruption that continues throughout life, and is responsible for keeping the toothrow closed and the teeth in their correct positions. How this happens is not at all well understood. However, the experiments of MARKS & CAHILL (1984) clearly demonstrate that the initial eruption of the tooth is a different process, which does not involve the tooth itself or its periodontal ligament as an active participant. In marked contrast, the later changes are almost certainly brought about by ligament traction (BHASKAR, 1980). Relatively little attention has so far been given to the often rather marked changes in the masticatory machinery from young to old individuals. The unique studies of WEIJS *et al.* (1987, in press) on chewing in young rabbits are very illuminating in this regard.

What happens to the teeth during one chew and what happens to them during one life are central factors in dental functional evolution. Along with the cumulative factor of historical constraint, this channels the evolution of dentitions into one or another of major alternatives. For example, a bilophodont dentition is functionally incompatible with hypsodonty, because a bilophodont occlusal morphology cannot be maintained during wear (FORTELIUS, 1985). A switch between bilophodonty and bunodonty, on the other hand, is evidently more easily accomplished, as both systems use low crowned teeth and a basically similar musculature and jaw design (HERRING, 1985). Examples of groups with both bilophodont and bunodont species in their history are pigs, peccaries, hippos, euelephantoid proboscideans, catarrhine primates and manatees. Further examples of such functional-historical channelling are given in FORTELIUS (1985) and JANIS & FORTELIUS (1988).

GROWTH AND FORM, HOMOLOGY AND HISTORY

If the study of the early development of teeth is in an active and exciting phase (HAMMARSTRÖM & THESLEFF, 1987; SLAVKIN, 1988), late morphogenesis has attracted much less attention (BUTLER, 1956; 1982), which is frustrating from the functional and evolutionary perspective. It is difficult to see the implications of very early processes on the evolution of the finished product, when the crucial intervening stages are missing. The often repeated worry that 'every little bump' on a tooth cannot be functionally relevant is not without foundation, and would perhaps be best approached in relation to how such little

bumps arise during development. The problems of late odontogenesis are also interesting from a phylogenetic perspective, as this is where most of the diversity is realised and homology manifested.

Homology, as the central concept of comparative anatomy, has been a complex and controversial issue since it was first introduced by OWEN (1843), but the recent years have seen some constructive developments. VAN VALEN (1982:305) redefined homology as "correspondence caused by a continuity of information", and ROTH (1984, 1988) has taken the idea further, mainly for developmental aspects. There is no need here to enter into details, but a few points may be noted.

Historical and repetitive homology are basically one and the same phenomenon, united by the continuity of developmental information, and distinctions between the two remain fuzzy to a certain extent (VAN VALEN, 1982). On one hand, all the teeth in a dentition are obviously homologous as teeth, and phylogenetic differentiation of the dentition can be seen as a historical process that copies and edits a basic 'tooth-making program'. On the other hand, serially homologous elements, such as teeth or cusps, may be historically non-homologous. Cusps are, indeed, known to have evolved from different parts of the crown, for example the hypocone of P³ and P⁴ in the oldest known horse genus, *Hyracotherium* (GRANGER, 1908; VAN VALEN, 1982). This does not necessarily mean that the hypocone of the nearly identical P³ and P⁴ of modern horses are not made in the same way, they probably are. It only means that developmental information has been shifted about. In a serial (and probably developmental) sense there is continuity of information, and thus homology. In a strictly historical sense there is no homology, only similarity (VAN VALEN, 1983).

ROTH (1988) has emphasized that Van Valen's homology concept resolves the old controversy about different developmental origins of historically homologous parts, such as vertebrate limbs (see DE BEER, 1971). Existing developmental programs may be 'pirated' by other programs, but this does not destroy the continuity of information, so historical homology is preserved. Similarly, the question of which tooth germ, in terms of position and order of initiation, gives rise to which tooth in the finished dentition, is less than critical for determining historical homology. This eliminates the need for the problematic decoupling of homology from dental form proposed by WESTERGAARD (1983). Developmental and historical homology are equally real, but relate to partly different questions.

Morphological similarity may be evidence of homology, or may be due to convergent or parallel evolution, in which case it is called homoplasy (see OSBORN, 1902 and SÖDERSTRÖM, 1925 for two

interesting windows on the unduly neglected older literature on homoplasy). A less commonly appreciated phenomenon is the morphological suppression and subsequent return of 'lost' elements (KURTÉN, 1953, 1963; WERDELIN 1987a), caused by switchback evolution (VAN VALEN, 1979). For phylogenetic reconstruction, such 'reversals of Dollo's law' are potentially a major problem, and the known history of morphological expression, although rarely known in detail, remains the only ultimately reliable criterion. Developmental understanding may nevertheless be of great help, as shown, for example, for the evolution of hominoid enamel by MARTIN (1983, 1985).

NO PROSPECT OF AN END

Are human incisors organs of speech, as Aristotle thought? Certainly speech is difficult without them, but they equally certainly did not evolve for this purpose. Instead, they were 'co-opted' into service for this new role, an example of exaptation as opposed to adaptation (GOULD & VRBA, 1982). The same appears to hold true for many other functional aspects of the dentition (FORTELIUS, 1985). Indeed, vertebrate teeth themselves seem to have evolved from dermal scales, and so have nothing to do with the mouth originally (ROMER, 1966). Chewing and occlusion are late phenomena, superimposed on a machinery which itself only came together gradually, as jaws evolved and the musculature operating them became differentiated (CROMPTON & PARKER, 1978). That the masticatory machinery of a mammal, and, indeed, the mammal itself, can still be described quite well in Cuvierian terms as a perfect functional whole, is impressive evidence for the power of natural selection. It is only in the evolutionary perspective that the constraints on optimality are revealed, however. And it is only in the tangled context of loosely connected knowledge that a general and satisfactory understanding of specific results can emerge, perhaps.

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