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How to get excited about teeth

INTRODUCTION

Animals are destructive by nature. They do not build as plants do, by taking simple molecules and making themselves from them. Instead, animals operate by taking complex ready-made structures and breaking them down in their guts. Vertebrates are distinctive in that they are prone to attacking the largest structures. They are, and probably always were, very active organisms, with consequent big energy expenditures, and they evolved teeth and jaws early on to increase the rate of acquisition of these food items. Mammals descended from this line of biological warriors, but they evolved mechanical comminution (chewing) of food particles to precede the chemical comminution in their guts with so as to increase the rate of energy flow. They needed to turn an energy stream into a river so as to fund their all-weather activity cycle, attaining the latter at the immense cost of maintaining an internal body temperature well above their surroundings. We (making the assumption that the reader is human) are super-mammals, having extended this characteristic mechanical and chemical destruction beyond the realm of our bodies to our environment. Probably none of their devastating nature gives animals a good reputation among plants, which have developed an enormous array of defences to try to stop being eaten, and were any readers to be organisms other than human, then they would surely vouch for the exceptionally poor reputation that we currently have with every other species.

It is my set task in this book to try to dissect out facets of this general picture, to make them glint in the light and then claim that these features explain it all. Of course, this is a ridiculous remit, so I will go for a smaller assignment and just try to make something glint. That something is the mammalian dentition, set in the mammalian mouth. As with everything else in biology though, even an apparently manageable and limited undertaking can start to become awesome once you get into it. There is a lot to explain about just about anything and to be credible that explanation needs to start with the basics. Most scientists seem to have found the same thing in any field of investigation and it is as though they jump ship when they realize it, becoming honorary fellows of the plant kingdom, because explanations have to be built.

THE ORIGINS OF TEETH

Vertebrates have over 500 million years of ancestry, dental tissues being present in the very first forms. Until recently, it was thought that these tissues developed not in the mouth, because the first vertebrates were jawless and fed on very small organisms, but on the surface of the body as exoskeletal protection – 'dermal armour' as it is called (Smith & Sansom, 2000). The inclusion of dermal armour as 'teeth' definitely takes the very respectable ancestry of these organs back to the Silurian period (Janvier, 1996), and possibly to late Cambrian times, over 500 million years ago (Young *et al.*, 1996).[1] This view has teeth as the last remnants in a mammal of a vertebrate exoskeleton (an external rigid coat that not only provides support but also contributes protection as a form of armour). A mineralized exoskeleton (mineralized tissue being that which contains crystals of an inorganic compound – in vertebrates, always a compound containing calcium and phosphorus called hydroxyapatite) seems to have preceded the evolution of the bony endoskeleton that vertebrates now have. While an exoskeleton has great advantages in a small animal (that is why insects possess them), providing optimal stiffening and direct protection, a large animal would have to develop an extremely thick exoskeleton in order for it not to buckle (Currey, 1967). Such heavy, and probably very insensitive, animals would clearly be at a competitive disadvantage to those with endoskeletons, which is presumably why the exoskeleton of vertebrates has been lost.

Enamel, the outermost tooth tissue (that which may contact a reader's fingernails in some circumstances), is unusual in that it is formed from the outermost layer of the body, the epidermis, in a process involving a very distinct set of proteins. Indirect evidence from molecular analysis has recently been interpreted as suggesting that some of these proteins might even have evolved back even in pre-Cambrian times (Delgado *et al.*, 2001). Dentine is the foundation of modern vertebrate teeth and derived from underlying connective tissue. It may have evolved alongside a bone-like tissue at a later date (Janvier, 1996; Smith & Coates, 2000), but the issue of what evolved first will probably only be resolved by examination of the genes that make these proteins (Kawasaki & Weiss, 2003). There is no need to provide a fixed viewpoint on this debate here: the science itself will evolve rapidly.

Whether 'teeth' evolved first on the surface of the body or actually in the mouth, it seems probable that they evolved in jawless forms. These early forms were very likely to be active feeders that sought large prey items. We know that conodonts (vertebrates off our direct line of descent and that lived over 440 million years ago) had muscle tissue somewhat like that of modern vertebrates (Gabbott *et al.*, 1995), which indicates that they were highly active organisms. They also had teeth set in a jawless mouth that show evidence of microscopic wear, indicating they were used in food acquisition (Purnell, 1995). Microwear, as this microscopic wear is called, is a clear indicator of the manner in which teeth are used and is strongly linked to diet, as shown in Chapter 6. The first jawed vertebrates were the placoderms. Curiously, the earliest members of this group did not have teeth. Later ones did, but may have evolved their teeth independently (Smith & Johanson, 2003).

Most vertebrates have teeth just for ingestion, the term given to the process by which food is taken into the mouth. The real breakdown of food is chemical. Although all animals are distinguished by the chemical breakdown that takes place within their guts, the most distinctive feature of a mammal is the mechanical breakdown that takes place in its mouth prior to this chemical activity. Although we tend to think of teeth as a chewing instrument, it is only mammals that really chew.[2] The earliest mammals added chewing (or mastication) to ingestion. Rather than just break food down chemically with their gut, they also comminuted food with their teeth. Why?

It is generally agreed that the need for mastication is related to the rate of energy requirement by mammals. Among vertebrates, only birds and mammals have exact control over their body temperatures. Other vertebrates have restricted activity cycles and limited ecological niches. Adaptation to cooler climes requires the development of a locomotor stamina that cold-blooded reptiles do not possess. The elevation of body temperature to a standard that is usually well above the ambient is very costly and demands a large increase in basal metabolic rate (which is the rate of energy consumption required to keep the body functioning). There are two basic methods by which such energy demands could be met in mammals. One involves simply ingesting much more food and letting a very large gut extract more nutrients per unit of time. This, however, works against mobility because the mammal would have a heavy weight of inert material in its gut that would simply slow it down. The alternative solution, to which mammals have resorted, is to reduce food particle size mechanically prior to chemical reduction in the gut. This adds new surface area on which enzymes in the gut can act more quickly, so increasing the rate of chemical breakdown (digestion). It is mastication, veiled by the lips and concealed by the cheeks, that provides this key advantage to mammals.

Birds are the other surviving group of vertebrates to possess high metabolic rates and it will not have escaped the attention of observant readers that they do not chew. It is unclear why this is and it should not be assumed that mammals are somehow superior: early birds appear to have had (simple) teeth but lost them. Weight was probably an important consideration for longevity of flight. Beaks are much lighter than teeth, but have disadvantages in being much more limited in their ability to break down foods and more importantly, are relatively insensitive compared to a dentition. The sensitivity of teeth is provided by receptors housed both inside them and in their sockets, which offer fine-scale detection of forces and also modulate salivary secretions. Both features signify a key asset of a complex mammalian mouth – the ability to discriminate foods by texture and taste at the front end of the gut so as to assess food quality prior to decisions about swallowing. Non-mammalian vertebrates have much less ability to do this because they generally only perforate large food particles and cannot make any detailed assessment of their contents.

Thus, birds may lack the ability to make many of the fine judgements that mammals can achieve with the plethora of sensory receptors in and around their mouths. Instead, they probably have to rely more on regurgitation or vomiting if they make errors during feeding. These reverse movements of the gut are part of the normal behaviour patterns of many birds when feeding their young. They are also seen in owls when they expel bones and fur through the mouth and in fruit-eating hornbills that regurgitate large seeds of the nutmeg family (Kemp, 1995).[3] The reliance of a mammal on oral sensitivity is made doubly clear by the rudimentary development of the sensory capabilities of the rest of the gut. In stark contrast to the mouth, the abdominal organs send very unclear messages to the brain about problems with their contents. It is extremely difficult, for example, to get a clear idea about where visceral pain is coming from and it often gets 'referred' to the skin. There is no reason to suppose that these human sensory dilemmas differ from the situation in other mammals. Clearly, all the major feeding decisions in a mammal are being made 'up front'. This provides them with a dietary diversity that would make it difficult to interpret signals from the gut very precisely anyway. For example, a monkey might feed on several food items within a 2-hour period. How could an individual animal with a diet of that breadth connect subsequent abdominal pain or diarrhoea to any one of these particular foods? It is thus possible to argue that a limitation on sensory discrimination within the mouth forces birds to adopt a more stereotyped diet than terrestrial mammals. They (and other non-mammalian vertebrates) probably use longer-distance cues to recognize food sources than mammals do. There is clearly a linkage here to the general diurnal (daytime) niche of birds versus the usual nocturnal niche of mammals. Lacking the visual ability to forage at distance due to nocturnal activity, early mammals probably had to develop shorter-range cues that included the ability to sense food texture very accurately in the mouth. This theme is developed further in Chapter 7 in relation to food selection in primates including humans.

Considerations like the above show the enormous timeframe over which teeth have evolved. Their beginning was a very long time ago. Given the wonders of modern dentistry and medicine, we sometimes forget the evolutionary basis for much of what goes on in the mouth. What is the connection between such problematic, easily infected, structures as our teeth with a noble lineage of 500 million years? The answer lies in our very recent history.

ARE TEETH JUST HANGERS ON?

Excepting humans, there is circumstantial evidence that mammals whose dental function is sufficiently impaired die and that the lifespan of the dentition could be the operative factor limiting the lifespan of many mammals (Chapter 6). In contrast, humans have in the last 10 000 years tried to control their food supply. No longer content with merely understanding where plants grew and when their parts were potentially edible or not, nor with simply tracking animals, our ancestors started to domesticate both plants and animals to produce reliable proximate food sources. And that is when problems started. Most of the dental decay (dental caries) and periodontal (gum) disease that we see started with the high consumption of cultivated (seed) grain products just less than 10 000 years ago. The nutritional content of these food items comes from contained starches that are usually bound in seeds into relatively insoluble, and thus indigestible, granules of micrometre size. Allied to cooking, a procedure recently supposed to define humanity better than tool use (Wrangham *et al.*, 1999), the starch is solubilized and its mechanical properties radically altered, such that it breaks up into very small particles (probably fragmented granules), which do not get cleared from the mouth very easily. An enzyme in the saliva starts to break the starch down into sugars and bacteria living in the mouth then convert those sugars into acid. Unfortunately, once acidity drops to below a certain level, tooth tissues start to dissolve and decay sets in. The major problem with the modern (Western) diet is not with these starches, but with sucrose. This forms an exceptionally adhesive layer to the teeth, more so than other common sugars. It may be thought that this effect should have some natural defence, but sucrose is not a common sugar in plants. It is the transport medium for energy but is rarely concentrated, being rapidly converted to other sugars within plant cells – e.g. for building up the cell wall. Many fruits do not contain sucrose and, indeed, a large group of fruit-eating birds lacks the enzyme sucrase needed to break this sugar down, developing diarrhoea if they consume it (Martinez del Rio, 1990). Our mammalian ancestors could process sucrose, but the effects of high concentrations of this sugar on the teeth in recent human evolution have been profound.

So teeth are not intrinsically dirty structures in an unclean cavity. Far from being unclean, the mouth of mammals is a very efficient self-cleaning, self-clearing, system for natural diets. It has to be because food is certainly not sterile and many microorganisms find the mouth an acceptable environment in which to survive, if not thrive. The epithelial lining of the body provides protection, of course, but only so long as there is no break in it. The teeth, however, provide that break. Besides the risk of infection around their roots, the vulnerability of tooth material itself is great. The greatest danger facing dental tissues is acid. Any drop in the oral pH below about 5.5 (which is really only very mildly acidic) and tooth tissues start to dissolve. What prevents this? The major factor is oral fluid. Saliva jets out into the mouth from four major orifices, and many smaller ones, providing a mildly alkaline bicarbonate spray to prevent dissolution (Edgar & O'Mullane, 1996). For further detail, see Chapter 3.

I believe that that the presence of teeth in every major vertebrate lineage except birds makes it obvious that there was very high selective pressure for the development of sturdy teeth in strong jaws. This pressure is also responsible for the diversity of tooth form in mammals in relation to diet. The strongest evidence for this comes from the frequency of convergent (independent) evolution of dental features in mammals. The most striking of these is the suggestion that the basal form of the mammalian cheek tooth, the tribosphenic molar (the evolution of which can be flicked between pages 1 and 159), may have evolved twice, quite independently, about 200–150 million years ago (Luo *et al.*, 2001).[4] More recently, a prominent feature of upper molars called the hypocone, not present in the tribosphenic form, has arisen independently (convergently) in many mammalian lineages (Hunter & Jernvall, 1995). In fact, the adaptability of hard tissues like the teeth has recently been termed too great to rely on for characters by which to judge the evolutionary separation of mammalian groups: some aspects of soft-tissue arrangements may be more conservative (Gibbs *et al.*, 2000). This is a complete reversal of the predominant view just 20 or so years ago. This pliability of the teeth is despite these structures being the complex product of the action of more than 200 genes (Jernvall & Thesleff, 2000), and the fact that a dental tissue like enamel (Chapter 2) possesses a sophistication far beyond that which can be produced artificially.

BASIC FUNCTIONAL CONSIDERATIONS

The teeth are set as close as possible to the sense organs (the ears, eyes, nose and tongue) so that they can aimed accurately, and set close to their central processing unit (brain) so that signals can be sent to and fro with minimal delay.[5] All this apparatus is housed in a light appendage (the head), set on an agile muscular stalk (the neck). The following is an attempt to sketch the arrangement of the functions of the mammalian head and neck and the compartments that they occupy (Fig. 1.1), emphasizing just how distinct mammals are from their reptiliomorph ancestors and other vertebrates.

Chewing and swallowing

The major function of the head is to ingest (take in) food. Much of the anterior (front) part of the head contains the jaws and teeth that ingest food particles. Mammals chew (masticate) food whereas virtually all other vertebrates do not. The evolution of mastication has required many evolutionary modifications to the head from the reptilian state. Moving the jaws so as to break food particles requires large muscles. These masticatory muscles, the temporalis, masseter and pterygoids (Chapter 2), have differentiated in mammals so as to bite food without sending this force pointlessly through their jaw joint. This keeps head weight down because the food should absorb a considerable amount of the energy imparted by muscular work, the optimum being to channel all this work eventually into its fracture.

In most vertebrates, ingestion is followed immediately by swallowing, with a very sensitive muscular bag, the tongue, organized to direct food particles backwards to the next part of the gut. In mammals, the tongue

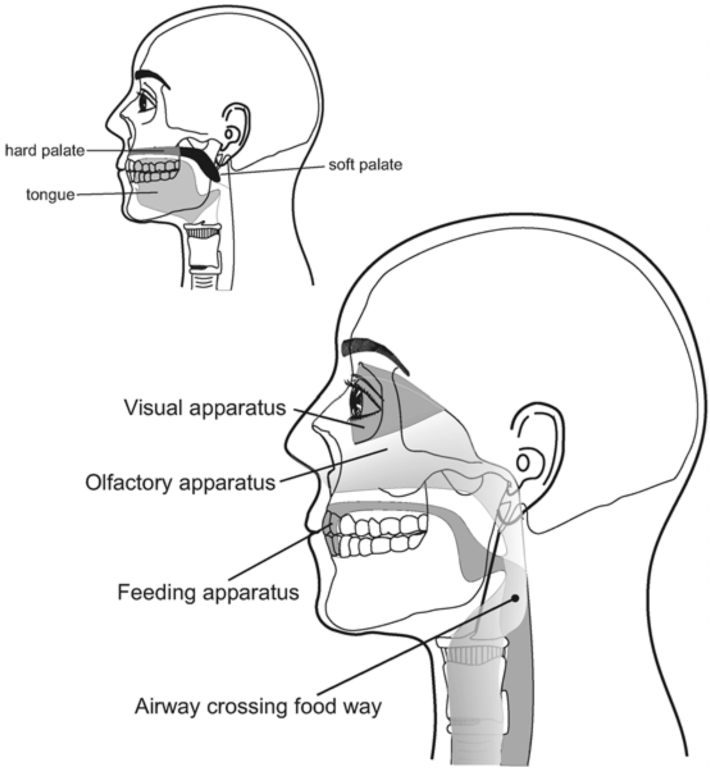

Fig. 1.1 The main diagram shows functional compartments of the anterior part of the head and neck in the human. The diagram above left shows how small the oral cavity really is, being the unshaded space lying between the tongue and hard palate. The rigid hard palate extends backwards into the pharynx as the soft palate, which is a mobile flap.

has developed a capacity to throw food sideways onto the teeth for chewing as well as backwards for swallowing. Assessment of whether to swallow or to chew further requires the tongue to have a surface positioned directly above it against which it can manipulate the food. The palate, another mammalian innovation, acts as this template.

Throwing food sideways requires a wall on the other side of the dentition to prevent food from escaping. Muscular cheeks provide this. When food particles have been chewed sufficiently, they tend to aggregate into a sticky mass called a bolus. The tongue can then propel this bolus backwards for swallowing. The tongue, palate and pharynx (the muscular tube directly behind the mouth), all act together during swallowing. The pharynx is uniquely mammalian possessing a musculature that appears to have no equivalent in other vertebrates (Smith, 1992).

Sensing food

The senses are mounted largely as paired organs on the head and are generally separated widely so as to allow the location of food to be fixed. The ears sit on the sides of the head while the eyes sit in the orbits just above the jaws. Both are admirably equipped to localize food direction. However, the nostrils (not the eyes) are too close together. Thus, the nose probably has little directional ability to recognize smells, which have to be determined by the animal following the concentration gradient of a particular chemical until it reaches the source (or the source reaches it). Airflow is needed for smell, so this sense is built into the air intake for the lungs. The nostrils lead to large nasal cavities lying above the mouth and separated from it by the hard palate. However, smell is not just important for leading mammals to food. When food is being chewed, the soft palate does not seal off the foodway from the airway completely. It is probable that food vapours pass from the mouth back around the soft palate, and up into the nasal cavity (Fig. 1.1). In the part of the pharynx behind the mouth, the so-called oropharynx, the airway and foodway are a single structure to allow this. Lower down, the airway and foodway separate with the larynx and trachea lying in front of the oesophagus.

The last sense is that of taste, which is largely embedded in the surface of the tongue.[6] Potentially, anything in solution in the mouth can be tasted, but it appears that many vital substances are not, key among these being proteins, calcium and phosphate ions. Recent developments in taste research make pronouncements uncertain though, and I postpone more consideration until Chapter 3. Taste and salivation combine as detection mechanisms.

Much of the head is dedicated to housing and protecting the central processing unit of this sensory information, the brain. This needs to be set close to the jaws because timing losses due to the speed of nervous impulses are then minimized.

Communication

The crossing of the foodway and airway not only allows the ability to smell food in the mouth, but also the possibility of vocalizing through it. Most mammals make noises. These noises can seem rather limited to us because these animals seem to communicate better by smell and body language (perceived by sight). Wilson (1975) sets communication via sound on the highest grade. In order to speak, humans use the larynx to break up expired air into bursts by opening and closing the airway. Our larynx lies very low so that these bursts of air pass through the oral apparatus, with the tongue moving against the palate and teeth, not to chew, but to produce speech. The consequence is a potential for choking. However, unless it can be demonstrated that this need to communicate has influenced the design of the oral cavity, this is all really beyond the scope of this book. There are other candidates for evolutionary modification to the chewing apparatus than sound. Higher primates (monkeys and apes, including ourselves) can make faces, adding these expressions to behavioural gestures and vocalizations. These movements are mostly a function of our facial muscles. However, some of these have important actions during food ingestion and chewing, so there is the potential for conflict and compromise of function here too.

THE BASIC MODEL

This book considers the function of teeth in relation to the ingestion, chewing and swallowing of food. It attempts to elucidate the principles that underlie the evolution of tooth shape and size and those mechanisms by which the dentition can be maintained. To do this, I need to understand the properties of foods that drive evolutionary change. The following model has its antecedents in food science, most particularly in a paper by Szczesniak (1963), but it differs slightly in emphasizing a food surface versus non-surface dichotomy and by viewing the action of the teeth as to change the boundary between the two by the process of fracture.

When a mammal chews food, it usually breaks particles into fragments, producing new surface area by cracking. This extra area increases the rate at which digestive enzymes in the gut act. This is the only general explanation advanced for the evolution of mastication in mammals (though more specific explanations will be offered in Chapter 3). I assume in this book that the rate of food breakdown is optimized to an animal's needs and, therefore, that features of its anatomy and physiology can be interpreted in this light.

The effectiveness of the forces that are produced when teeth contact food depends on the characteristics of the food surface that they act on. The form and extent of the external food surface is referred to as the *external physical attributes* of the food. These characteristics include food particle size and shape, the total volume of particles in the mouth and attributes