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Evolution of Mammalian Dental Structures

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The Origin of Mammals and the Evolution of the Temporomandibular Joint

The temporomandibular joint is a unique feature of the Mammalia – no other vertebrates have it. While this was long thought to be absolutely true, two advanced mammal-like reptiles have recently been reported, *Diarthrognathus* (Crompton 1958) and *Probainognathus* (Romer 1970), which have contact between the two bones, squamosal and dentary, which form the jaw joint in mammals; whether this contact can be considered as a definite articulation is a moot point. In all other tetrapods the articulation is between two other bones, the quadrate in the skull and the articular in the lower jaw. These still exist in mammals but are not part of the jaw articulation at all; they have passed into the middle ear and form the incus and the malleus, two bones of the chain of three in the middle ear (the other is the stapes) which transmit sound from the drum to the fenestra vestibuli and so to the inner ear.

How has this change come about? To understand this we must delve into the history of the group from which the mammals evolved, the synapsids or mammal-like reptiles. This great group has a long history; some of the earliest reptiles known back in the Upper Carboniferous (about 280 million years ago) belonged to it. The synapsids continued until the Middle Jurassic (about 160 million years ago), by which time the true mammals, which appear in the Upper Triassic (about 190 million years ago), had long existed.

For most of the existence of these mammal-like reptiles (from their first appearance until the end of the Lower Trias, about 200 million years ago) they filled much the same place in the world as their descendants, the mammals, do today. They were the dominant group of land animals and particularly of large land animals.

Due to the vagaries of the geological record our knowledge of the early mammal-like reptiles (Upper Carboniferous and Lower Permian) comes almost entirely from the Red Beds of northern Texas and Oklahoma, and our knowledge of the later one (Middle Permian to Upper Trias) from South Africa and the Soviet Union. The early American forms are grouped as the Pelycosauria, comprising carnivorous, piscivorous and herbivorous forms. The herbivores are of interest as they were the first group of vertebrates to exploit plant life directly as food. This is not possible in the sea where the plants are microscopic and long food chains inevitable; but on land where plants are large it is not only possible but more efficient to use them directly as food. The first land vertebrates, the Amphibia, did not do this; plant material, with the protoplasmic contents of the cells shut up in cellulose boxes, needs the development of a dental battery which the Amphibia never achieved. The specialization of the teeth and masticatory apparatus is such in herbivorous forms that their capacity for further evolution is limited, so that major evolutionary changes are always initiated by carnivorous or insectivorous forms.

In the Pelycosauria the lower jaw is of an essentially reptilian form. The tooth-bearing bone or dentary has a strictly limited extension distal to the tooth row; the other bones of the jaw are well developed and comprise the posterior third of the jaw. The quadrate – the skull bone which forms, with the articular in the lower jaw, the jaw hinge – is a large bone with a considerable dorsoventral extension. The jaw joint is well below the level of the occipital condyle and there is no secondary palate, the internal nares being at the front of the buccal cavity. This last means that the food was not retained in the mouth to enable chewing to take place, as in mammals, but was swallowed fairly promptly after entering the buccal cavity. This would be true even of the herbivorous forms, where the large numbers of relatively small teeth in the dental battery would smash up the food during its backward passage along the jaw, but there would be no long-term retention of food within the jaw for true chewing to take place. The herbivorous Pelycosauria would be, in fact, like the herbivorous lizards (e.g. *Iguana*) of the present day.

In the carnivorous Pelycosauria, with which we are more directly concerned since they include the ancestors of all the later mammal-like reptiles and so of the mammals, the teeth are all of a simple blade-like form. They have distal and mesial cutting edges, often serrated like a bread saw. This demonstrates that the sharpening of the teeth by direct tooth-to-tooth contact (Every & Kühne 1971), which is so important in therian mammals, did not take place in these mammal-like reptiles.

In the carnivorous pelycosaurs, for example the well-known *Dimetrodon*, the function of the dentition was to seize and kill the prey and then to cut off large lumps which would immediately be swallowed whole. Although the teeth are all similar in shape they are different in size. Towards the anterior end of the maxilla is a pair of teeth which are the largest in the jaw. These are replaced alternately, so that, while the norm is to have a pair of functional teeth in each maxilla during replacement only one of the pair may be functional. These large teeth were concerned with the seizing and killing of the prey and may be called the canines. The teeth mesial to them on the maxilla and the premaxilla are the incisors, the teeth distal to them the cheek teeth (we cannot use the term 'molars' and 'premolars' as these terms in mammals are defined in terms of tooth replacement). Thus the functional differentiation of the teeth into incisors, canines and cheek-teeth had already taken place in the mammalian ancestors as early as the Lower Permian, although the differentiation of the teeth was really only a size difference, not a differentiation of morphological patterns.

By the Upper Permian the pelycosaurs had been replaced by a number of groups of more advanced mammal-like reptiles, which included both carnivorous and herbivorous forms. As always, if we are seeking the ancestors of higher groups, only the carnivores need concern us. There are two carnivorous groups in the Upper Permian, the Therocephalia and the Gorgonopsia. Both these are more advanced than the pelycosaurs in possessing at least an incipient secondary palate and in showing a great reduction in the depth of that part of the skull which lies below the foramen magnum, so that the quadrate is greatly reduced in length. In all except the most primitive members of the Therocephalia there is only one canine in the upper jaw, and only one or two teeth are borne on the maxilla medial to it. This change in the number of the upper canines from two to one is produced by a change in the timing of the tooth replacement.

In a pelycosaur such as *Dimetrodon* the pair of canine alveoli normally each bear a functional tooth. Only during replacement, which seems to have been a relatively rapid process, is there only one functional upper cannine. This is the condition in MCZ 1347, shown by Romer & Price (1940). The Gorgonopsia and Therocephalia have relatively much larger canines than the Pelycosauria, so that replacement took much longer. By the time the replacement canine was fully erupted the functional canine was worn out and ready to be shed. Thus only one of the pair of adjacent alveoli bears a functional canine at any time.

These teeth are shed in a rather remarkable way. The crown is cut off along the gum-line and the root is retained in the alveolus and reabsorbed. This is a common method in mammal-like reptiles and is found in some early mammals (Mills 1971). However, if we examine a number of specimens of gorgonopsids and therocephalians we shall find in many, perhaps in most, that tooth replacement has ceased in the upper canines (Kermack 1956). In these cases the functional canine is always in the more mesial of the pair of alveoli, the distal alveolus being filled with a plug of spongy bone. Thus the replacement of the upper canines in the Gorgonopsia and Therocephalia was not only limited but also determinate, in the sense that the final, permanent tooth was always borne by the anterior alveolus. It is hard to see how this could have been achieved except by the replacement taking place a fixed number of times. This is a mammalian characteristic; in placental mammals all the teeth except the molars are replaced once, and only once. In these mammal-like reptiles the number of times the upper canine was replaced was similarly limited and fixed; the fact that replacement takes place once in mammals and more than once in the Gorgonopsia and Therocephalia does not obscure the essential similarity of the process in both.

Another change, also significant for the future, has taken place in the lower jaw. Although the other bones of the lower jaw are still large and well-developed the dentary has grown back over them dorsally to form a rudimentary coronoid process. To this would have attached the temporalis muscle, which has become large and important in these mammal-like reptiles, as is shown by the greatly expanded temporal fossa. A powerful temporalis muscle is characteristic of mammals, particularly carnivorous ones.

In the Lower Trias the Gorgonopsia and the Therocephalia were replaced as the dominant carnivorous mammal-like reptiles by two other groups, the Cynodontia and the Bauriomorpha. The latter are the descendants of one line of the Therocephalia. The cynodonts first appear in the Upper Permian but their exact relationship to the more primitive groups is uncertain.

The cynodonts and bauriomorphs of the Lower Trias are more mammal-like in several ways than are the gorgonopsids and therocephalians of the Upper Permian. In both there is a secondary palate – better developed in the cynodonts, where it involves the palatine, than in the bauriomorphs – and the postcanine teeth are no longer simple and blade-like. In the bauriomorphs the teeth are still single-cusped, with a large flat occlusal surface, but in the cynodonts multi-cusped teeth have appeared. The replacement of the upper canines, at any rate in the cynodonts (it is unknown in the bauriomorphs), is similar to that in the Gorgonopsia and Therocephalia. The lower jaw in the bauriomorphs shows little advance over that in the earlier forms, but in the cynodonts the dentary has greatly enlarged and now extends to the posterior end of the mandible. Although the jaw joint is still between the articular in the lower jaw and the quadrate in the skull the reptilian jaw-bones have undergone considerable reduction in size and lie, at the posterior end, in a groove in the dentary. This reduction in size of the accessory (reptilian) jawbones was, I think, to increase the strength of the jaw joint as a whole. It must be remembered that the articular surfaces themselves are not much, if at all, reduced in size from the condition in earlier forms, and that the condyle in the quadrate fits the corresponding surface on the articular bone closely.

Although the quadrate is a small bone it fits into the squamosal by a double tenon structure and the two bones, in life, would have been bound immovably together by ligaments. Similarly the other bones in the lower jaw, although reduced in size, would have been so firmly attached to the dentary as to be quite immovable in life. Thus the whole lower jaw in the Cynodontia would have been a much more rigid and stronger structure than in earlier forms. This is what we might expect having regard to the more sophisticated role in the postcanines played in the mastication of the food, and the greater development of the masticatory muscles. This has not always been appreciated by workers in this field, some of whom have assumed that the reduction in the size of the auxiliary bones necessarily meant a weaker jaw joint. The contrary, I think, was true.

During the Trias the mammal-like reptiles declined and by the Upper Trias they had been replaced as the dominant group of land animals by the dinosaurs. But by the Upper Triassic one or more of the groups of mammal-like reptiles had crossed the boundary between reptile and mammal, so that we know two groups of mammals in the Upper Trias.

One group, exemplified by *Kuehneotherium*, is the ancestor of almost all living animals; the other, exemplified by *Morganucodon*, has as possible living descendants only the monotremes – the duck-billed platypus and echidna of the Australian region. *Morganucodon* is much the better known of the two and will be discussed first.

The postcanine teeth in *Morganucodon* differ from those in mammal-like reptiles and resemble the teeth of mammals in being elongated along the line of the jaw with two clearly separated roots. The teeth functioned as a shearing mechanism. Now, while the cheek teeth in mammal-like reptiles may have complex and broadened crowns, the teeth do not become elongated in the mesiodistal direction and remain single-rooted (the highly specialized, herbivorous tritylodonts are an exception which is not relevant here). The carnivorous mammal-like reptiles did not in fact shear up their prey as do modern carnivorous and insectivorous mammals or as did *Morganucodon* and *Kuehneotherium.* In such a shearing bite the food being cut forms a wedge which tends to force the teeth apart. This is prevented by the action of the masticatory muscles holding the teeth in active occlusion. Thus only the cheek teeth on one side of the jaw can be effective at any one time, and each side has alternate periods of activity and rest. This process may be seen readily by watching a cat eat.

But the shearing bite also applies a twisting motion to the whole jaw, tending to dislocate the articulation. This is why the glenoid in modern carnivores extends well laterally and has a backwardly-directed process at its lateral end. This last is a thrust-bearing process, to resist the forces trying to dislocate the condyle by rotating it in the horizontal plane. The shrew has a double condyle on the dentary for similar reasons.

Relative to the size of the animal the accessory jaw bones are as large in *Morganucodon* as in one of the later, carnivorous cynodonts such as *Cynognathus*, and like the cynodont the mammal has a strong joint between articular and quadrate. This reptilian joint, however, was directly in the line of the tooth row and was not able to resist the twisting movement at the hinge produced by the shearing action of the teeth. To resist this a second articulation was formed by a condyle on the end of the dentary working in the glenoid facet on the squamosal. The effect of this was to extend the articulation well lateral to the tooth row, thus enabling it to resist the forces at the hinge tending to dislocate the jaw. The primary reason for the evolution of the temporomandibular joint must have been to enable the jaw-articulation to resist the forces produced by the shearing dentition.

We know a great deal about *Morganucodon*, including all the bones of the lower jaw, but of *Kuehneotherium* much less. Of the bones of the lower jaw we know only fragmentary dentaries, from which, however, we can reconstruct the whole of this bone. We can be sure from the size and nature of the groove in the dentary to house the accessory jaw bones that *Kuehneotherium*, like *Morganucodon*, had a well developed and powerful reptilian jaw articulation. Also like *Morganucodon* and for exactly the same reason, *Kuehneotherium* had a squamosal-dentary hinge lateral to the quadrate-articular joint.

It is worth mentioning here the two mammal-like reptiles noted at the beginning of the paper, *Diarthrognathus* and *Probainognathus*. These have a squamosal-dentary contact which could have had the same function as the temporomandibular joint in the earliest mammals, that of resisting the lateral thrust produced by shearing. This is, I think, a case of parallel evolution: I should be rather surprised if either *Diarthrognathus* or *Probainognathus* had anything to do with the evolution of the mammals. Whether *Kuehneotherium* and *Morganucodon* go back to a common ancestor which already had the temporomandibular joint we simply do not know. We would need to know the skull, and in particular the braincase, of *Kuehneotherium* to begin to answer that question. At the moment I suspect they do not, for two reasons: the basic differences in the mode of function of their teeth (Mills 1971), and the great difference between the braincase of the descendants of *Kuehneotherium* (the Theria) and that of any of the Atheria (Triconodonta, Multituberculata and Monotremata – the sub-class to which *Morganucodon* belongs).

Once the temporomandibular joint had been established it could soon take over the whole of the jaw articulation, thereby releasing the quadrate-articular joint to pass into the middle ear. The quadrate and the articular were almost certainly concerned with hearing in the immediate reptilian ancestors of the mammals.

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Evolution of Mastication

Reptiles cannot chew. In general, they use their teeth only to seize their prey, and if this cannot be swallowed whole, it is torn apart by a number of animals, or by a single animal 'worrying' it. The group of reptiles which later gave rise to mammals – the 'mammal-like reptiles' – diverged at an early stage from the main reptilian stem, and by the Permian, some 250 million years ago, were widespread and might reasonably be regarded as the 'Lords of Creation'. By the middle of the Triassic (Fig 1) they were all but extinct, their place having been taken by the dinosaurs, which remained the dominant group until the latest Cretaceous. The mammal-like reptiles did not, however, quite disappear. Small members of the group survived, perhaps in areas where there was insufficient food for the large dinosaurs, or by eating items of food too trivial for their notice. In this group of tiny mammal-like reptiles a number of changes took place, all probably associated with the acquisition of the ability to maintain a body temperature above that of their surroundings. This increased their activity and their ability to avoid their enemies, but it carried the penalty that it vastly increased the food requirement (Parrington 1967). The

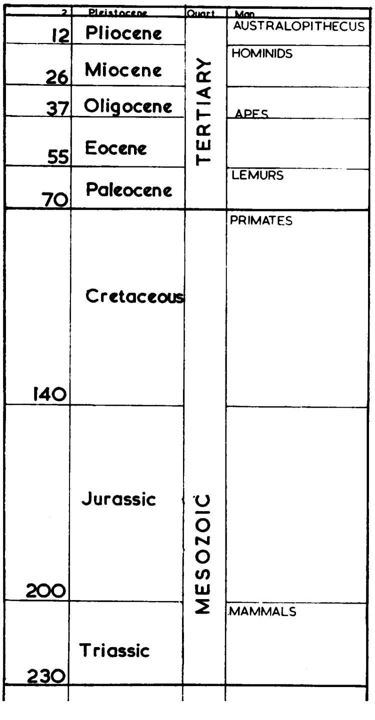

Fig 1 *Geological time scale in millions of years for the period under consideration*