3. The Jurassic Mammals and the Origin of the Mammalian Molar Teeth.

By

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(With 10 text-figures.)

Introduction.

Since 1938 I have, in various connections, made closer acquaintance with the Mesozoic mammals in the literature of the subject, and have speculated on the question of their bearing on the evolution of the Mammalian molar teeth. Gradually I formed an opinion of my own on this subject. It was only after I had plotted my essay in outline that I read BUTLER's publications which culminate in his »new theory of the evolution of mammalian molar teeth» (1941). BUTLER claims to have solved the so-called »premolar paradox», and his theory is undoubtedly one possible way of so doing. I did not set out with the same purpose, but the conclusions reached by me evidently provide a somewhat different solution. I shall put down my points of view without constant references to BUTLER's theory, as I was not influenced in respect of any point by his reasoning; instead, a comparison between our results will be given in a summary.

Further, I have often omitted to refer to the literature when mentioning well-known facts and suggestions as to their interpretation. These can after 60 »years of trituberculy» be considered as *commune bonum*, and the specialists at least must know where to find their origin.

Regarding *Bienotherium* and *Tritylodon*, it can hardly have escaped an observant reader of YOUNG's paper (1940) that these genera must be definitely removed from the mammalian class. Therefore, when I now enter on the subject I do not do so in the hope of working out anything particularly new and remarkable, but because it is essential for other parts of my paper to take up a position in reference to this question, and because no literature has reached me to which I could refer.

I had better to point out that I have not seen any of the Jurassic Mammals and that my discussion of these forms is based entirely upon the splendid monographs (together with preliminary papers and later additions) published by SIMPSON. For thus having made the priceless and difficult material accessible to palaeontologists all over the world, science is for ever indebted to this author.

Which were the first mammals?

The oldest remains supposed to belong to mammals (*Tritylodon* and others) are from the Rhaetic; according to SIMPSON (1935, p. 178) »it seems improbable that the origin of the class was much antecedent».

But was *Tritylodon* really a mammal? Like two other early mammal-like forms, *Dromotherium* and *Microconodon,* it has oscillated to and fro over the line of demarcation between the mammals and their reptilian ancestors. The two genera from the American Trias were dispatched to the reptilian side by SIMPSON (1926 b), thus widening the range of the *Cynodontia* to comprise also Northern America. The same author considers *Tritylodon* as a mammal, but other authors, particularly SEELEY, held an opposite view. A review of the vicissitudes that *Tritylodon* has gone through since it was first described by OWEN in 1884 is found in SIMPSON's »Catalogue» (1928, pp. 17 *et seq.*). Only SEELEY is mentioned as an opponent to the interpretation of *Tritylodon* as a mammal, but not OSBORN who, at least temporarily, shared the same opinion. In his »Evolution of Mammalian Molar Teeth» (1907), OSBORN deals with *Tritylodon* in Chapter VI under the subhead »Reptilian Ancestors of Mammals in the Trias»: »The teeth of the Theriodonts» (!) »exhibit four types as follows...» (p 92). »The fourth type is the *multituberculate*, seen in the genus *Tritylodon* ...» (p. 93). In a note the editor, Dr. W. K. GREGORY, remarks that »Broom has recently shown that *Tritylodon* is more probably a mammal». Though GREGORY edited what was evidently OSBORN's view on the subject in 1907, he does not mention in his »Orders of Mammals» (see p. 166) that OSBORN ever believed that *Tritylodon* was a reptile. OSBORN evidently changed his opinion, but I am under the impression that this was somewhat reluctantly in the face of such an authority as BROOM (*cf.* SIMPSON, *op. cit.* p. 18: »In 1910 he was content to call *Tritylodon* simply a multituberculate *incertae sedis.*» See OSBORN 1910, p. 518).

Wherever *Tritylodon* may belong, it has proved a most inconvenient encumbrance to the Mammalian class. As a mammal it was merely a curiosity (»the oldest mammal»), but as it was coupled with the *Allotheria* it gave to this group the appearance of being older than any other, and thus rendered it impossible to refer the *Allotheria* to their proper place in the system. Another mischief wrought by *Tritylodon* is that its reputation as the oldest known mammal lent strong support to the so-called »polybuny theory» which still has adherents and has even found its way into text books used in high schools in Sweden.

Tritylodon has no importance whatever as an ancestor of any group of mammals, either living or extinct. It is a large, unwieldy and highly specialized type that marks the end of a special phylum. It has been made a mammal by grace of the rather generous minimum definition of this class: »mandible a single bone; dental series differentiated into incisors, canines, premolars and molars; all post-canine teeth, and sometimes also the canine, bifanged» (SIMPSON 1925 *b*, p. 560). Of these, only the first and the last are said to be exclusively mammalian (*op. cit.*, p. 562). Some arguing has been needed to retain *Tritylodon* as a mammal, and one cannot get away from the impression that in one passage SIMPSON argues in a circle to ward off the suspicion that *Tritylodon* is a reptile after all. He states, regarding the prefrontal distinguished by SEELEY and PETRONIEVICS, but supposed by BROOM to be the superior portion of a large lachrymal: »The latter appears, on the whole, to be the case, and in any event, without denying the possibility, we must demand better evidence before accepting the presence in *Tritylodon* of a bone otherwise not represented in the Class to which it belongs» (1928, p. 14).

SIMPSON refers *Tritylodon* (together with *Stereognathus* etc.) to a separate suborder of the *Multituberculata,* but his view on its position changes remarkably during the decade covered by his publications (the last of his papers dealing with *Tritylodon* that is available to me was published in 1937). In 1928 SIMPSON states (p. 20): »1. It is a mammal. 2. It is probably, but by no means surely, a member of the Order Multituberculata. 3. Within this Order it is so peculiar, so clearly cut off from almost all of the other forms that it must be placed in a distinct Suborder, as defined above.» In 1935 he writes (p. 158): »The most satisfactory view at present seems to be to consider it as an early side branch (suborder) of the Multituberculata, rather distinctly and indeed somewhat doubtfully related to the more typical members of that Order.» Finally, in 1937 (p. 758): »There seems to be no good evidence that *Tritylodon* and its allies, the Tritylodontoidea, really belong to the Multituberculata, and they are placed there only hypothetically and because there is no more natural position for them in the established system and inadequate basis for erecting a new major division for them.» In this last passage SIMPSON in reality removes *Tritylodontoidea* from the *Multituberculata,* and one may ask why he did not go the whole way and let them form an isolated group of unknown affinities. It is certainly a device of very dubious worth to attach such utterly aberrant forms to otherwise well-defined groups in order to make the system look simpler than it really is. In due course new fossils will turn up and give us clues for the conclusive classification.

This is exactly what has happened recently with the *Tritylodontoidea.* In a preliminary note (1940), YOUNG describes a new genus *Bienotherium* that is undoubtedly closely related to *Tritylodon*, although many of its

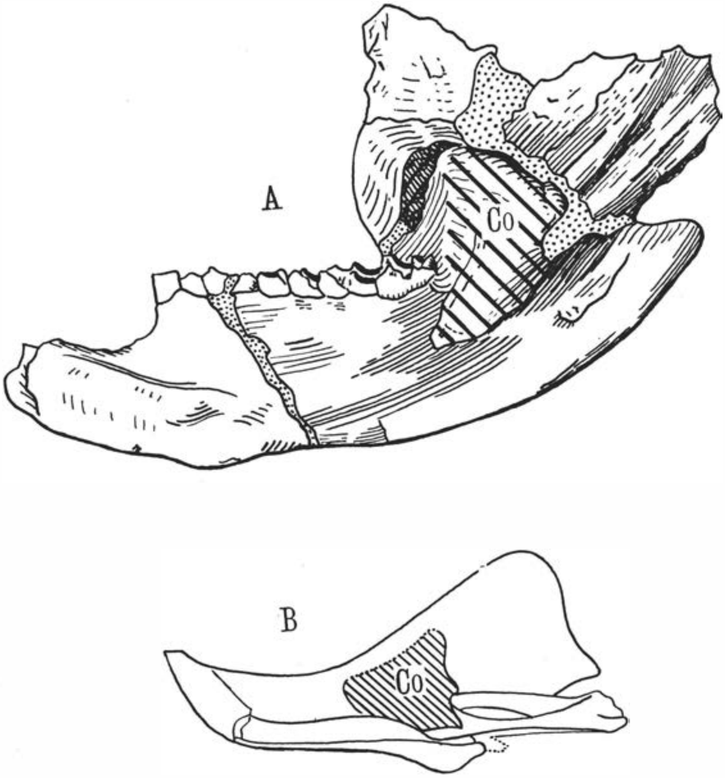

Fig. 1. A. *Bienotherium yunnanense* Young. Lower jaw. After YOUNG 1940. B. *Cynognathus craterodontus*. Lower jaw. After GOODRICH 1930. — Co = coronoid (hatched).

characters show that it must belong to a separate genus. YOUNG referred it to the suborder *Tritylodontoidea* of the order *Multituberculata*, following SIMPSON 1928. In a list of fossil Chinese mammals published by TEILHARD in 1942 we find the same classification. A more detailed description of *Bienotherium* is evidently going to be published, but from what has been set out by YOUNG, one thing seems to be quite evident: *Bienotherium* is not a mammal, and the same must then be true of *Tritylodon*. The internal view of the lower jaw (*op. cit.* Figs. 5 and 6) is described by YOUNG thus (p. 101): »In inner aspect, the lower jaw is characterized by the ridge like swollen starting below the posterior part of the teeth row up to the condyle of which the posterior portion is very sharp and narrow. Behind the last postcanine tooth, a peculiar protuberance of boss, triangular in outline, is developed, perhaps for the reinforcement of the muscle attachment.» It is striking how well YOUNG's drawings (and the passage quoted) agree with what is seen in certain advanced cynodont reptiles (Figs. 1 A and B). The triangular piece of bone is undoubtedly the reptilian coronoid. The ridge-like elevation might be some of the rod-like bones found in this region in the cynodont jaw, or part of a relief on the inner side of the dentary

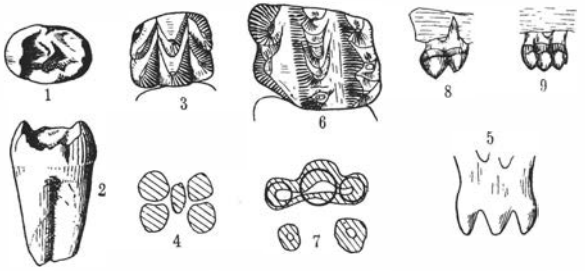

Fig. 2. *1* and *2*. *Diademodon brachytiara*. After SEELEY from OSBORN 1907. *3—5*. *Stereognathus oolithicus*. Molar. Crown view, roots, and front view. After SIMPSON 1928. × 3. *6* and *7*. *Tritylodon longaevus*. Molar. Crown view and roots. After SIMPSON 1928. The rings indicate that the anterior root is divided farther from the crown (*cf.* SIMPSON 1928, p. 17). × 2. *8* and *9*. *Bolodon*. Last and 4th cheek teeth. Lateral view. After OSBORN 1907. × 4.

developed to hold such bones extending backwards to the lower jaw articulation. This evidence of the reptilian nature of *Bienotherium* drawn from the lower jaw is supported by the general habitus of the skull which, though it lacks the postorbital bar, is strongly reminiscent of the cynodonts (e. g. GOODRICH 1930, Figs. 342, 343, 396).

The cheek teeth of *Tritylodon* have more than one root (Fig. 2: *6* and *7*), and the same is undoubtedly true of *Bienotherium*. It is true that this is a mammalian character, but it alone can surely not raise these forms to the rank of mammals. We need only turn over the pages in ZITTEL-EASTMAN's »Text-book of Paleontology» to find how, among the *Synapsida* (*Therapsida*), the various suborders can have different characters in common with the mammals and retain correspondingly different reptilian features. Thus even some of the more advanced *Cynodontia* have the finger formula 2 3 4 5 3, whereas in forms with a single occipital condyle and a vestigial secondary palate we meet with the formula 2 3 3 3 3. We should therefore not be surprised to find that the teeth of some of these groups have more than one root, as in the mammals. It may also be remarked that it is not enough to count the roots, it is also a question of what the roots look like (*cf.* BUTLER 1941, p. 425). *Tritylodon* has a transverse anterior row of three roots and a posterior row of only two. A comparison with *Stereognathus* (Fig. 2: *3—5*) suggests that the short and broad teeth with fewer transverse cusp rows might be the more primitive condition. An earlier stage might have had a single such row, — and possibly also a single transverse row of roots, an arrangement that probably differed considerably from the primitive condition in the *Multituberculata* (in the Jurassic forms the large posterior upper »premolars» have two roots one behind the other and so have also the molars — Fig. 2: *8* and *9*). *Diademodon*, which has broad crowns and a broad root that tends to divide into a buccal and a lingual branch (Fig. 2: *1* and *2*), shows that teeth of the postulated type might have existed among the *Theromorpha*.

The tritylodonts must evidently be considered as a rodent-like specialization of the *Cynodontia*, though their incisor apparatus was not fit for real gnawing.

Since yet a further point of the minimum definition seems to be unreliable it becomes very difficult to find a satisfactory definition distinguishing the mammals from the mammal-like reptiles. As a matter of fact, it is not so very important how and where the limit is to be drawn, as the very interesting problem of the transition from »reptile» to »mammal» is independent of this definition. The systematically important limit does not fall there but between the Sauropsids and the Theropsids (*cf.* GOODRICH 1916, and VON HOFSTEN 1941).

Multituberculata.

Since it has now been settled — as I believe it has — that the *Tritylodontoidea* are reptiles, they can, of course, not be referred to the *Multituberculata*. Some authorities might, however, maintain that they belong to the very group of *Theromorpha* from which the *Multituberculata* derived their origin, thus trying to keep the forms with multituberculate teeth together as a phyletically connected unit. Not even this seems to be possible. The disposition of the roots — especially if we are right in assuming that the transverse arrangement in the *Tritylodontoidea* is derivable from a primitive condition with only one transverse row of roots, or a single broad root subdivided as in *Diademodon* — constitutes one serious obstacle. Further, I am inclined to lay great stress upon the development of the angle of the jaw. It is remarkably constant within the subclasses of the Mammalia and, in each of these, it is probably an inheritance from the reptilian ancestors. In the drawings of the lower jaws of Cynodonts, we notice that in some of them the dentary has a distinct angle (called by BROOM the processus angularis), in others not. As the reptilian angular gradually diminished, the muscles attached to it were transplanted on the dentary. The type of angle that was preformed in the reptilian ancestors was one that the animals probably had to retain after the complete loss of the angular (as an element of the lower jaw), because the angular region of the lower jaw was inserted in a mechanical system with an important function as attachment for masticatory muscles and could not develop or withdraw processes at its convenience. The lower jaw of the tritylodonts (*Bienotherium*) possesses an angular process, that of the *Multituberculata* does not, and this difference contributes to widen the chasm between the two groups. There are evidently cynodont jaws in which the reptilian bones managed to withdraw without leaving a notch, e. g. *Dromatherium*, and from such forms the Mesozoic *Triconodonta*, *Multituberculata*, and *Symmetrodonta* might have developed. This question was discussed by SIMPSON in 1928 (p. 69).

Thus, we can disregard *Tritylodon* as an ancestor of any of the known mammalian orders; and since the presence of more than one root in the molars is evidently not an exclusively mammalian character, we can disregard all the small peculiar teeth from the Rhaeto-Lias in England and Germany as well (*cf.* SIMPSON, *op. cit.*, p. 54). An interesting consequence of the classification proposed above is that a cynodont reptile, *Stereognathus*, survived in England until the Middle Jurassic.

After the exclusion of the tritylodonts, the *Multituberculata* form a remarkably pure and uniform group, although comprising a great variety of interesting phyla. But a more important fact is that the group is no longer the oldest one among the mammals, its first representatives occurring in beds of Upper Jurassic age (Purbeck and Morrison). Representatives of two other groups, the *Triconodonta* and the *Pantotheria*, are known from the Middle Jurassic, several millions of years earlier. Thus it might be possible to regard the evolution and relationships of the Mesozoic Mammals from another point of view than the one met with in SIMPSON's papers.

SIMPSON distinguishes four well-defined orders among the earliest mammals, and as these lived not very long after the age of the theromorph reptiles, his supposition that they had (at least partly) developed separately from different reptiles might prove correct. But three of his orders have a character in common to which he returns over and over again, stressing its importance, viz. the absence of an angular process in the lower jaw. At first glance, one feels inclined to consider the *Triconodonta*, the *Symmetrodonta*, and the *Multituberculata*, which all belong to the first radiation of mammals (SIMPSON 1928, p. 200), as forming one Class inside which the three orders were differentiated in a similar way as the placental orders of mammals. We have true carnivores (*Triconodonta*), insectivores (*Symmetrodonta*), and herbivores or omnivores (*Multituberculata*). The types are not so manifold as among the placentals, possibly because we know only part of what was really present; the more probable assumption is, however, that the triconodont molar was a less suitable starting-point for the development of other types of molars than the tritubercular molar, the possibilities of which seem to be almost unlimited.

SIMPSON admits that »triconodonts might be remotely related to the multituberculates» (1937, p. 761). Now, since it is evident that the multituberculates appear much later than the triconodonts, the possibility of a closer relationship must be seriously considered.

The multituberculates are a highly specialized group, rodent-like from their first appearance; and some of them later became true equivalents of rodents. Thus, in *Taeniolabis,* the tips of the incisors join from both sides so that a real gnawing apparatus was formed as a substitute for the peculiar shearing device persistently present in the *Plagiaulacoidea*. In the latter, the dentition behind the incisors is so altered that the limit between

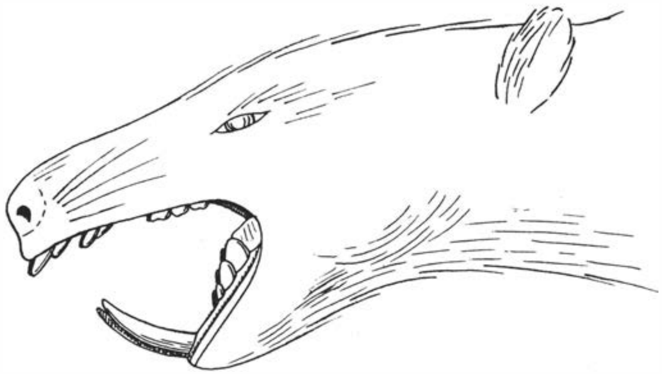

Fig. 3. *Ctenacodon.* Reconstruction of head. Modified after Simpson 1926 *a.*

premolars and molars is obscured; widely differing opinions about the tooth formula are therefore found in the literature. As conceived by Simpson, and earlier by Marsh, it comprises in the upper jaw 5 premolars and 2 molars. As the triconodonts have a number of premolars not exceeding 4, the multituberculates would therefore not be derivable from any known triconodont. But Osborn and Broom wrote the formula differently: Osborn P^3 M^4, Broom P^4 M^3. Simpson admits the possibility of the first of these interpretations, but against Broom he argues that »the fourth and fifth upper cheek teeth are almost identical in structure, in function, and in degree of wear in the known specimens» and that it therefore »is logically impossible to refer them to different dental series». Against this, it can be answered that as long as we do not know anything about the succession (in such a highly specialized dentition it might be suppressed or occur so early in life that it left no trace in the dentition of the adult — another parallel with the rodents —; *cf.* Simpson 1937 *b*, p. 86), almost any tooth formula is logically possible. There may have been factors other than the original limit between premolars and molars which determined what shape the teeth were going to assume.

A shearing mechanism was acquired to meet new needs in connection with the food. So far back as the teeth were clear of the corner of the mouth and could be of use for cutting pieces out of fruits or roots too large to be taken into the mouth they developed into shearing edges (Fig. 3). Further back, inside the jaw muscles, the teeth became tuberculate. For a parallel we need only go to the *Carnivora,* in which the mechanically best situated teeth developed into carnassials, irrespective of what category they originally belonged to.

The triconodonts had shearing molars and could furnish material for teeth with the same function in their descendants. Regarding the tubercular teeth in the multituberculates we might assume (and certainly with as much right as this has been done within other groups) that the extra rows of

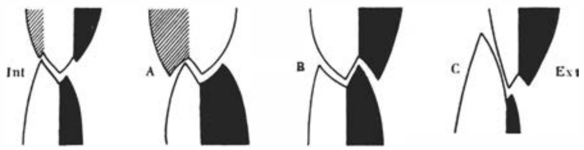

Fig. 4. Diagrammatical cross-sections showing the evolution of multituberculate molars (A—C) from the triconodont molar (to the left). A. Posterior tuberculate molars; B. Anterior tuberculate molars; C. Posterior shearing teeth. Internal cingulum hatched, main cusp white, external cingulum black.

cusps developed from cingula, and such are present in both the upper and lower teeth of the triconodonts. Here, however, we meet with greater difficulties than regarding the tooth formula:

1) The last and the second last upper cheek teeth alternate in a peculiar way, and it must be assumed that in the last one the internal cingulum in the triconodont molar developed into a row of cusps, whereas in the second last tooth this happened to the external cingulum.

2) The lower molars of the triconodonts bite inside the upper ones, and they have only an internal cingulum. To obtain the occlusion of the multituberculate »molars», one must assume that the lower teeth shifted to outside the upper ones, a possibility that is not worth considering. We encounter the same difficulties in the anterior part of the dentition. The last lower shearing tooth in *Ctenacodon, Plagiaulax* and *Psalodon* (but evidently not in later forms, at least not in *Meniscoëssus*, *Ptilodus* and several others; *cf.* SIMPSON 1929, p. 18) has a row of small external — five or more — cingulum cusps at the middle and posterior parts of the base (the size of the last shearing tooth and the presence of these accessory cusps might indicate that the tooth is really a molar; the number of the small cusps is perhaps not quite insignificant).

We are forced to the conclusion that the multituberculates cannot be derived from any known triconodont, but that they might take their origin from unknown forms with a dentition of the triconodont type, but with an outer cingulum.[1]

This is suggested by:

1. the alternation of the two last upper teeth, which is more easily explained if we assume a development of new cusps from different cingula in triconodont teeth than if we try to derive the multituberculates from reptilian ancestors like *Diademodon*, since this would imply a shifting of the most posterior tooth inwards in relation to its opponent in the lower jaw, leaving all the other teeth in their original position;

2. the addition of a third row of cusps from cingula in later multituberculates;

3. the fact that in the Jurassic forms the last upper molar has only

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[1] Among the *Symmetrodonta* which must be closely related to the *Triconodonta* (see below), an external cingulum is present in *Spalacotherium* (SIMPSON 1928, p. 101).

two cusps in the outer row. The same number of cusps is present in the last upper molar of most triconodonts (not in M^4 of *Triconodon mordax*; this tooth is, however, also strongly reduced; SIMPSON 1928, p. 83);

4. the shearing apparatus, which is most easily explained as an inheritance from ancestors with a shearing dentition (see above).

The presumed presence of an outer cingulum in the lower teeth of the ancestral forms does at least account for all the features in the early multituberculate dentition from which the dentition in all later forms is derivable. See the diagrams Fig. 4.

Symmetrodonta.

The derivation of the *Multituberculata* from triconodont ancestors implies the introduction of hypothetic forms (though by no means so hypothetic that they are unlikely to have occurred) and might therefore be regarded as doubtful. The close relationship between the *Symmetrodonta* and the *Triconodonta* is more evident in spite of the triangular molars in the former group.

The lower jaw is very similar in the two orders (as observed by SIMPSON), especially if we compare *Spalacotherium* with the earliest *Triconodonta*. SIMPSON lays stress on the different shape of the coronoid process and different position of the condyle in relation to the tooth row. The latter character is variable in the triconodonts (SIMPSON 1928, Fig. 19): in *Phascolotherium* the condyle lies above the level of the tooth row, in *Trioracodon* distinctly below. In none of the triconodonts does the condyle face so distinctly upwards as in *Spalacotherium,* but *Tinodon,* on the contrary, shows no difference from the triconodonts in this respect. The molars of *Spalacotherium* suggest other food habits than those of the triconodonts, and the suspension of the lower jaw has changed accordingly (*cf.* the jaws of the modern insectivores and carnivores; see also below).

The premolars in *Spalacotherium* and *Trioracodon* are of exactly the same type: recurved main cusp, higher in P_4 than in M_1, only a posterior accessory cusp. In *Tinodon* the premolars are of the primitive *Amphitherium* type.

I am aware that SIMPSON considers the structure of the jaw as »largely a negative character» (1928, p. 176), and that the premolars »conform in general type to those already seen in triconodonts and to be seen again among the pantotheres».[1] »This form clearly was a fundamental one — indeed it is closely approached in a number of cynodonts and no doubt even preceded the mammalian organization» (1928, p. 100). I must confess that I am far more impressed by these obvious similarities between tricono-

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[1] In the *Pantotheria* the premolars are not of the same type as in the triconodonts. The posterior cusp is a small heel, i. e. a derivate from the cingulum.

donts and symmetrodonts than by the triangular molars in the latter, which have, as their sole feature in common with those of the pantotheres, that they are triangular; otherwise they are fundamentally different. To make clear the structural relationship between the molars of triconodonts and symmetrodonts, I must first compare the latter with those of the pantotheres, and this, in its turn, cannot be done without first giving a review of the evolution of the pantothere molars.

Molar evolution in the *Pantotheria*.

In 1936 (pp. 22—23), SIMPSON enumerates the stages passed through by the pantotherian dentition: alternation, shear, and opposition. The question presents itself: which was the first to appear, shear or opposition?

Of the different opinions expressed on the first steps in the evolution away from the simple reptilian cone, that of GIDLEY (1906) seems mechanically the most satisfactory. In his deduction he starts from a primitive triconodont type, but what the original type of tooth looked like must at present remain a field open for hypotheses, — it may have had the three cusps assumed by GIDLEY, but it seems very improbable that the ancestral forms to which this tooth belonged was a triconodont in the taxonomic sense of this term. It must be noted that GIDLEY tried to build up his theory from the same starting-point as COPE and OSBORN, and therefore had to start from a tricusped tooth. I prefer to choose a simple cone, as GREGORY has done when building up his wedge theory (1910, p. 185 *et seq.*).

These simple original teeth may have been true cones or they may have had an oval or subtriangular base. They were of similar type in the upper and lower jaw, the upper ones biting outside the inner ones. As GIDLEY did with his triconodont first stage, we shall let this disposition enter the more complicated dentition unaltered: the primitive cone in the upper jaw that was inherited from the reptilian ancestors — I shall call it the *eocone*[1] — did not change its position so that it finally bit inside the corresponding cone in the lower jaw, but, instead, cingula grew out linguad into the interspaces between the lower molars, crossing over cingula growing backwards from the base of these teeth. The same space was shared by the

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[1] For this short and handy term, which replaces a somewhat clumsier one proposed by myself I am indebted to Professor G. SÄVE-SÖDERBERGH.

A term designating the original cone without regard to where it has its place in the specialized mammalian molar is most urgently needed. This is the reason why I have protested energetically against the present use of the term protocone (1942, p. 37), though I am well aware of the confusion that would result from an attempt to give it back its original meaning.

The original cone in the lower molar may be called the *eoconid*.

upper and lower cingula; thus opposition was the first step towards a functional complication of the molars. That cingula expand to fill out gaps in the tooth-row is a common phenomenon; the best-known example is the development of the true hypocone. In this way the foundation was laid from the very beginning for broad upper and elongate lower molars, a condition that is changed only in highly specialized forms.

Quite naturally, the two cingula adapted themselves to each other as the elements in a dentition always do (occlusion does not only imply that upper and lower teeth are in contact, but that they are so for some special purpose). Thus the upper cingulum produced a cusp that grew up to a considerable height, whereas the lower cingulum remained low and received the tip of the upper cusp in a basin (originally a notch or a groove between a posterior cusp and the eoconid; *cf.* SIMPSON 1928, p. 117).

The upper cingulum cusp was of course not conical, but formed a crescentic swelling on the ridge bordering the wedge-like cingulum shelf (just as the hypocone originates on a ridge that fades out in both directions from it). When this cingulum squeezed itself in between two lower molars, its sides came in contact with the posterior side of the main cone of the tooth in front and with the anterior side of the tooth behind; in this way shearing was initiated and gradually perfected by the development of crests on the main lower cusps. On these crests the metaconid and paraconid were formed. A dentition with quite new mechanical relations between upper and lower teeth came into existence. The eocone, which belonged to a dentition adapted for seizing and holding prey, but not for chewing, either by crushing or by cutting, lost some of its importance in this new system, as it stood in the centre of the tooth away from the sides that formed the cutting edges and without any element in the lower tooth row to bite against. Evolution tried to correct this anomaly in different ways.[1]

1. The simplest way was to get rid of the eocone entirely. This was realized in *Miccylotyrans* by stages represented (structurally if not phylogenetically) by *Melanodon*, *Malthacolestes*, and ? *Herpetairus* (Fig. 5). GREGORY reversed this order (1934, p. 250, Fig. 45), but I do not believe that a cusp could grow up from the bottom of a basin and reach such a considerable size as in *Melanodon* to serve a purpose which, since the dentition became tribosphenic, was only of secondary importance. Only the premolars, which were not rebuilt according to a new mechanical plan but retained their original function as grasping and holding weapons, still have the eocone — in fact, the only cusp of any importance in these teeth.

GREGORY'S contention is, of course, that the cusp (according to him

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[1] A series of holding cusps is often developed from the external cingulum in the upper molars, *viz.* the styli, and therefore it is of course not excluded that the eocone was retained in several cases with this function.

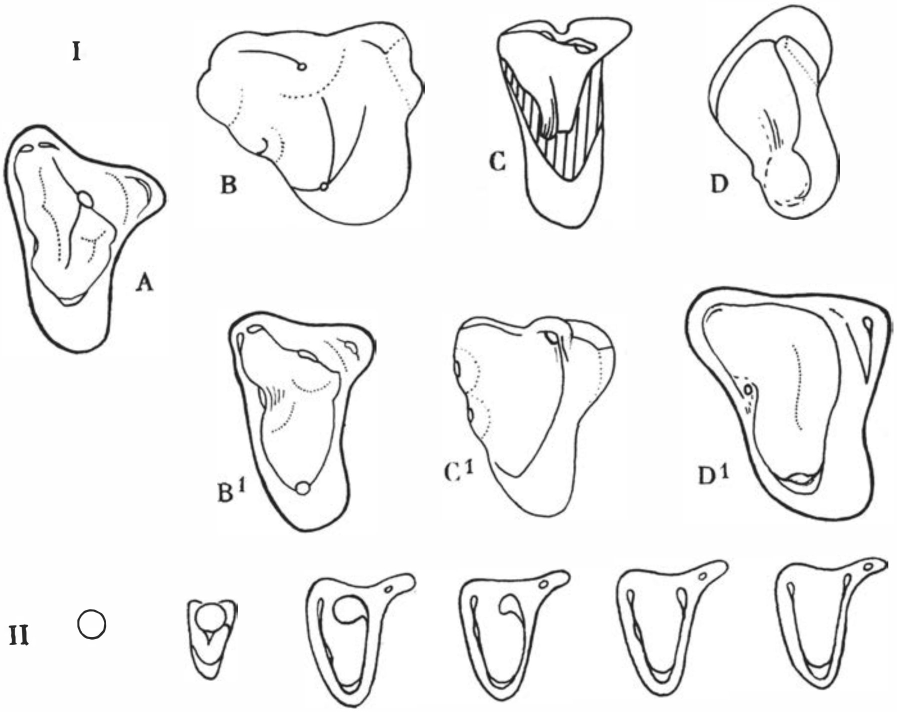

Fig. 5. I. Pantotherian right upper molars. A *Melanodon* M^3. × 13. B *Malthacolestes* M^2. × 22. C *Miccylotyrans* M^5 (reversed). × 25. D *Pelicopsis* last molar. × 25. B^1 *Herpetairus* M^4. × 14. C^1 *Euthlastus* second last molar. × 25. D^1 *Pelicopsis* second last molar, × 25. All after SIMPSON 1929.
II. Diagram showing the transformation of the eocone according to »2» (see the text).

the amphicone) developed from the external cingulum, but apart from the general appearance of the *Melanodon* molar, which gives the impression of being a main conical cusp surrounded by cingula of varying sizes, there is the presence of a cingulum externally to the conical cusp to be considered (*cf. Docodon*); further, the presence in *Miccylotyrans* of the transverse crest, which in *Melanodon*, *Docodon*, and *Malthacolestes* connects the outer and the inner main cusp, is more easily intelligible if we assume that an outer cusp existed in the ancestral forms; the other alternative: first the ridge and then the cusp, seems less plausible, as the bottom of a basin between two elevated ridges is not the place where ridges (just as little as cusps) usually originate.

The eocone was also reduced in the molars of *Kurtodon* (SIMPSON 1928, p. 141) and evidently also in *Amblotherium nanum* (»on M^5 there is a rudiment of a transverse median crest in the basin, running from the internal cusp to the minute centro-external one, and a faint suggestion of such a rounded ridge is also seen on M^4» !; SIMPSON 1928, p. 137), whereas the molars of *Amblotherium pusillum* are of the *Herpetairus* type (see below).

In other forms the eocone entered the new mechanical system and became an indispensable part of it.

2. It was connected by a ridge with the anterior cingulum ridge (anterior arm of the internal cusp; *Melanodon*, Fig. 5 A) and then, so to speak, dragged forwards till it finally came to form the antero-external corner of the tooth (but for the hook-like cingulum cusp; Fig. 5 II). This process may have initiated with *Herpetairus* (Fig. 5 B^1) and is evidently accomplished in *Pelicopsis* (Fig. 5 D, D^1) and *Euthlastus* (Fig. 5 C^1). *Malthacolastes*, on the other hand, lacks the connection between the eocone and the anterior border of the tooth (Fig. 5 B) and might have been losing its eocone (see above). In practice, this method also led to the final loss of the eocone and it may not be sharply distinguishable from 1.

3. The most important type is the one leading to the higher mammals. In this the eocone (under the name of the amphicone) split and gave off one element forwards and one backwards (paracone and metacone).

4. *Docodon* has solved the problem in its own way. The eocone was retained and much enlarged; the main lower cusp (eoconid = protoconid) was equally enlarged and established contact with the eocones and internal cingulum cusps (»protocones») of two adjacent upper molars when the tooth rows were occluded (*cf.* SIMPSON 1929, p. 85).

5. Regarding the zalambdodont insectivores, it would seem possible to interpret their molars in the same way as those of *Miccylotyrans* and *Kurtodon*, thus considering the eocone to be lost. GIDLEY has, however, given a different interpretation that seems to be based on good evidence.[1] The pantotherian molar cannot be explained in the same way, as there is no more complicated stage known that proceeded it. *Centetes* is, however, remarkably like *Pelicopsis* (the antero-internal and postero-internal cingula are missing in the Jurassic form).[2]

If the arrangement observable in the known upper tooth rows of Jurassic mammals can at all be used as evidence of cusp homologies between molars and premolars, the main cusp of the last premolar (and undoubtedly of all antemolars) is homologous with the outer cusp (considered by me to be the eocone) in the molars.

In *Docodon* (Fig. 6 A), the main cusp in P^4 forms a three-sided pyramid of the same shape as the eocone in M^1; postero-externally, there lies in P^4 and M^1 a small cusp of exactly the same appearance in both teeth, and, antero-externally, another cuspule that is more prominent and more

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[1] A process similar to the one assumed by GIDLEY (and his predecessors; *cf.* also BUTLER 1937) for the *Zalambdodonta* undoubtedly produced the *Uintatherium* upper molar.

[2] GREGORY mentions an »internal cingulum indicated in Professor Osborn's figures of the upper molars of *Dryolestes*» that »may represent the beginning of the protocone» (1916, p. 248). No such cingulum was described by SIMPSON.

intimately connected with the main cusp in P^4 than in M^1, but undoubtedly the same structure in both cases. Finally, P^4 has a small internal cusp that is undoubtedly homologous with the much larger internal cusp in the molar.

In *Melanodon* (Fig. 6 B) there is no internal cusp in P^4. The external cingulum has a middle cusp that is not present in the molars; this must, however, be an accessory cusp, as, undoubtedly, the inflated conical main cusp, with its two ridges, is homologous with the similarly shaped outer cusp in M^1 and M^2.

In *Kurtodon* P^4 is also inflated, and not at all like the crescent-shaped inner cusp of the molars. The homologon of the premolar cusp was lost in the molars (see above). The P^4 of *Amblotherium nanum* is described by SIMPSON (1928, p. 136) as »nearly conical but slightly compressed transversely». To judge from SIMPSON's drawings (1928), the main cusps of the premolars are not on a line with the internal cusp of the premolars in any of the two species.

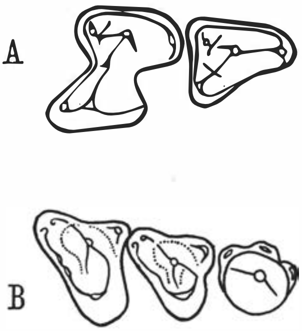


Fig. 6. A *Docodon* P^4 and M^1. B *Melanodon* P^4—M^2. After SIMPSON 1929.

In later mammals in which the eocone (amphicone) has split into para- and metacone the tip of the premolars is undoubtedly homologous with this pair of cones, as has been suggested by several authors. It is interesting to notice how in the zalambdodont insectivores the tip of the premolars is on a line with the tip of the large V-shaped cone, even if this reaches the lingual side of the tooth (in contradistinction to the *Pantotheria*, which in this respect remind one more of *Ictops*; OSBORN 1907, p. 118 and 120).

An interesting theory in which heels developed from more direct derivates from the main reptilian cone play an important role was put forth by FRECHKOP (1933 *a*). In his attempts to find a »homodynamie renversée» between upper and lower molars, this author arrives at the conclusion that a heel originally grew out forwards in the upper molars into a position »qui doit être considérée comme *la position répondant exactement aux relations existant dans les molaires inférieures*». The »crossing-over» exemplified by *Chrysochloris* (*op. cit.* Fig. 1) is supposed to be »pas ... très primitive» (*op. cit.* p. 4). FRECHKOP may be right, but to me it seems as if this author were first of all anxious to find morphological analogies between upper and lower teeth and as if, in reality, he treated mechanical relations as being of secondary importance (*cf.* BUTLER 1941, p. 446). It is true that many rodents and other specialized mammals have upper and lower molars with reversed patterns, but in them the movements of the jaws influence the respective teeth in opposite directions; under such circumstances, the reversed arrangement of cusps and ridges is apparently the one that is mechanically most favourable. Another question is how the modelling of the teeth is accomplished — whether by the aid of »organizers», or by some other known or unknown agency. As stated above, it is not necessary to involve the triconodonts in the dental evolution of the pantotheres and higher mammals, especially as the lower jaws of the respective groups indicate that they probably diverged before they became mammals. According to FRECHKOP's theory, however, the development of the important upper heel was postponed to a still later stage than the one represented by the primitive triconodont molar.

Let us now turn to the *Symmetrodonta*. According to SIMPSON, their upper molars differ from those in the pantotheres in the following respects (1928, p. 177): »4. In the symmetrodonts the lesser cusps of the upper molars are along the anterior and posterior borders, and there are no cusps along the external border, whereas in pantotheres there may be a large centro-external cusp and the chief cusps (except for the internal one) are always on the outer border. Pantothere upper molars are also generally more transverse.» The symmetrodont molars are also more symmetrical, although the symmetry is not absolute. To fully understand the difference, one has to go back to the much depreciated cusp-rotation theory. SIMPSON, GREGORY, and other authors have insistently tried to refute it but, at the same time, they have allowed a substitute theory to flourish that involves an even cruder form of cusp displacement, though it passes under a new name. According to the original theory, small cusps on the anterior and posterior slopes of a laterally compressed main cusp moved outwards in the upper jaw and inwards in the lower jaw so that the cusps came to mark the corners of a triangle (OSBORN 1907, p. 7). This seems to me a small matter compared with the »inward growth», according to which the fixed point of the earlier theory starts moving, leaving the smaller cusps behind. GREGORY has anticipated this criticism (1934, p. 248) and suggests that the paracone plus metacone (= amphicone) »might have arisen *in situ* ... on the outer slope of the protocone». This cannot, however, be true of the symmetrodonts where, in the presumably more primitive *Eurylambda*, the incipient cuspules are wider apart than in the more advanced *Peralestes*. (I will return to this question below.) In these forms the eocone is the internal cusp, and always the most prominent one. There is an external cingulum described by SIMPSON thus (1928, p. 106): »The median part of the crown is basined, with its external border elevated into a sharp cuspidate ridge, but this is not so high as the anterior and posterior margins, nor are its cusps so prominent. The largest of these is antero-external, directly external to the median anterior cusp just described. At the median emargination the external rim is lowest and on the posterior lobe it rises again and becomes obscurely cusp-like.» The premolar (only the last one is known) has »a single high cusp, somewhat compressed laterally» and »a sharp continuous external cingulum running obliquely across the base of the outer surface, being nearer the alveoli posteriorly than anteriorly». Apart from the lack of accessory cusps on the slopes of the eocone, the premolar is, in all its parts, so closely reminiscent of the molars than its main cusp must without the slightest doubt be homologous with the main, *i. e.* the internal, cusps in the molars.

The upper molars of symmetrodonts and pantotheres evidently show differences of such a fundamental nature that the triangle met with in both rather concurs in emphasizing the gap existing between the two types than to bring them closer together, as this relatively complicated form has been reached possibly from a quite similar starting-point but by entirely different paths.

It was recognized by SIMPSON that the *Symmetrodonta* resemble the *Triconodonta* in a number of characters. In his tabular comparison (1925 *b*, p. 560) this author enumerates 9 such characters (1—7, 10 and 12); to these must be added no. 15 (SIMPSON had not seen any material of *Spalacotherium* when this paper was published). Nos. 8, 9, 11 and 13 are not absolute differences, as the variation within the two groups overlaps, or can be explained as being due to different food habits. Regarding no. 14, see below. No. 16 can be subdivided:

Triconodonta.	*Symmetrodonta.*
a. Lower molars with three main cusps	a. as in the triconodonts;
b. arranged in a nearly or quite straight line.	b. cusps standing at the corners of a triangle.
c. The middle cusp primitively the highest,	c. As in the early triconodonts,
d. later all three subequal.	d. never subequal.
e. Internal cingulum present, may form strong anterior or posterior cingulum cusps;	e. As in the triconodonts;
f. no external cingulum.	f. an external cingulum sometimes present.

Regarding no. 17, we must first set down that the symmetrodont upper molar is, of course, not derivable from the highly specialized ones in the Purbeck triconodonts, but probably from those in *Amphilestes*, which were certainly provided with a high eocone and small anterior and posterior cusps. Thus we get:

Triconodonta.	*Symmetrodonta.*
a. Upper molars with flat outer wall.	a. On the external side a basin extending inwards.
b. Three (in unworn condition probably conical) cusps in antero-posterior line.	b. Cusp convex buccally, flat lingually.
c. Outer and inner cingula that	c. No internal cingula,
d. may form anterior, posterior, or internal cusps.	d. the external cingulum may form anterior and posterior cusps.

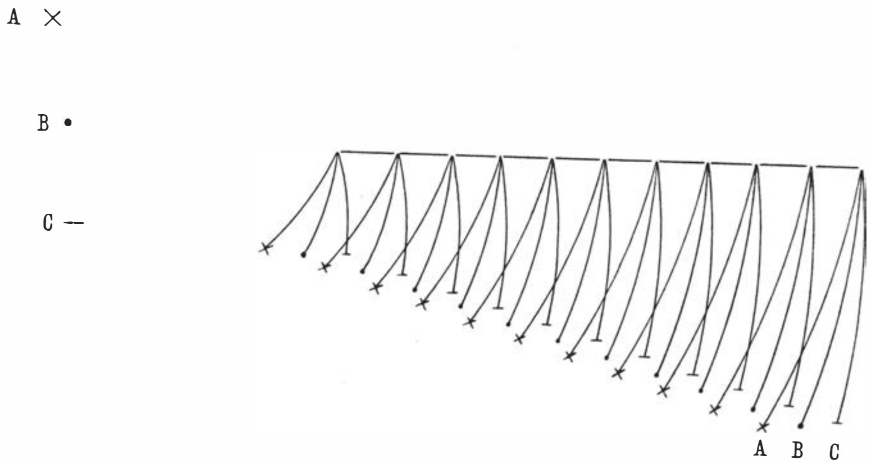
The function of the molars in *Amphilestes* was undoubtedly piercing and cutting, i. e. the same as in the symmetrodonts.

A comparison between the triconodonts on the one hand and *Spalacotherium* and *Tinodon* on the other shows that when they agree in some character this is not merely in a general way. Whereas *Amphitherium* and *Amphilestes* have quite different lower premolars: unsymmetrical eocone and large posterior heel (reminiscent of the heel in the molars) in the former, strictly symmetrical in the latter, *Tinodon* has the *Amphilestes* premolars practically unaltered, and the premolars of *Spalacotherium* resemble those in *Trioracodon* in every detail. Apart from the triangular disposition of the cusps, the *Spalacotherium* lower molars are identical with those in *Amphitherium*; the two types even have the small middle internal cingulum cusp in common.

The molars of *Spalacotherium* are not strictly symmetrical, but as the teeth in this genus are interlocking, we may expect to find a slight curvature of the cusps corresponding to an arc of a circle with its centre at the condyle. Perfectly straight teeth would perhaps even lock the jaws if the upper ones fitted perfectly between the lower ones. The asymmetry is thus a necessary consequence of this kind of specialization and has no bearing whatever on the affinities of the group. The same is true of the position of the condyle above the level of the tooth-row, an arrangement that helps to press the oblique shearing edges in the upper and lower molars closer together, as can be experimentally shown with the aid of a small model of a jaw (Fig. 7).

There is such a striking resemblance, not only in several primary characters but also, so to speak, in finishing off the details that it definitely brings the *Symmetrodonta* closer to the *Triconodonta* than to the *Pantotheria*; and since it is evident that the triangular molars have no bearing on the problem, the question is: how did the primitive triconodont molar develop into the one met with in *Spalacotherium*, *Tinodon*, etc.?

Over and over again SIMPSON states that there is no evidence of cusp rotation. To prove that it has taken place one must, of course, have series



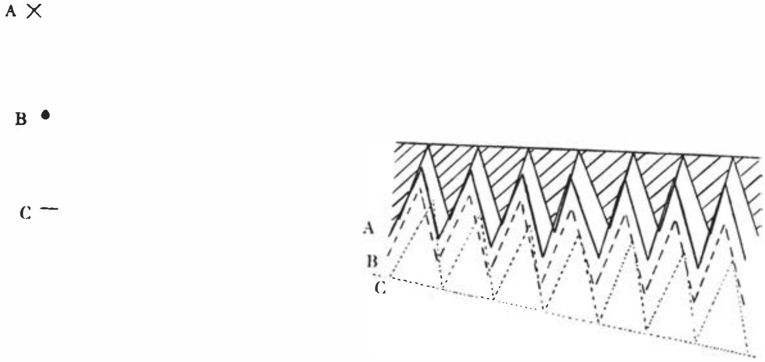


Fig. 7. The upper diagram shows the arches described by the tips of the molars at different position of the condyle in relation to the tooth row.
The lower diagram shows how, immediately after the mouth was opened, the upper and lower teeth lose contact with each other if the condyle lies on a level with the toothrow (C). Such an arrangement evidently does not favour the shearing function of interlocking teeth. If the condyle is raised (A and B), the posterior side of the lower triangles will be pressed against the anterior side of the upper triangles, since a backwards directed component will be added to the orthal movement. The molars are represented as cones or pyramides; in reality the sides of the teeth are more nearly perpendicular.

where it can be followed step by step, and such series we do not really possess, though we have scattered indications.

First: what is meant by »cusp rotation» and what happenings are connected with this phenomenon?

The series: triconodont upper molar — *Eurylambda* — *Peralestes* seems to show that we must not expect the smaller cusps to wander, *sponte sua,* to a position antero-externally or postero-externally to the eocone; there is, as far as I can find, no mechanical reason why they should, and on this point I am willing to declare SIMPSON to be in the right. But there is a mechanical relation between adjacent teeth that could possibly cause a rotation of the smaller cusps outwards or inwards in the upper or lower jaw respectively.

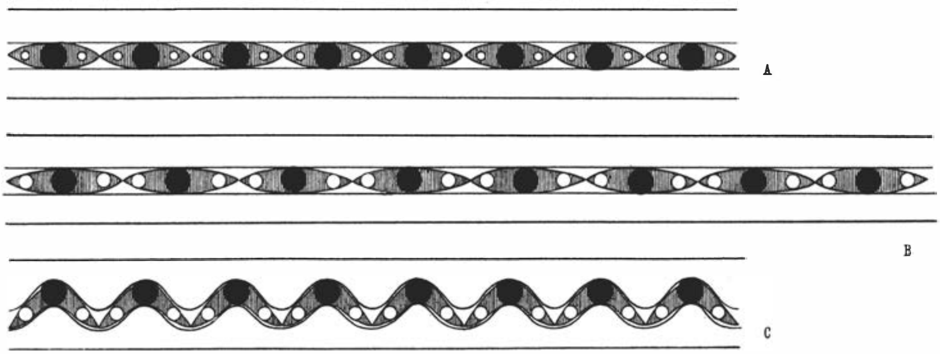


Fig. 8. Diagrams illustrating the evolution of the molars of specialized triconodonts (B) and symmetrodonts (C) from a primitive triconodont stage (A).

We may assume as an example that in an early form there were eight molars, laterally compressed, and with quite small anterior and posterior cusps (Fig. 8 A). As is evident from the triconodont evolution, these small cusps increased in size and finally became as large as the central cusp. This was followed by an increase in size of the whole molar and the enlarged molars called for more space (Fig. 8 B). But a limit was set by the length of the jaws, and only so many teeth could be retained as the jaws could accomodate. No known triconodont has as many as the eight molars chosen as a possible number in the immediate common ancestors of symmetrodonts and triconodonts, but the series: *Amphilestes* — *Phascolotherium* — *Triconodon* — *Trioracodon* illustrates that the principle postulated above is not altogether hypothetical. *Phascolotherium* is especially worthy of notice. It has 5 molars like *Amphilestes*, but they are larger than in this genus, except M_5, which is reduced and undoubtedly on the road to disappearance [it is not shown by any specimen, but SIMPSON remarks (1928, p. 74) that »in both 112 and M 7595 M_4 is exactly the size of the last tooth of the Oxford specimen, while M_5 is much smaller»; also M_4 is a comparatively small tooth (*op. cit.* Fig. 23); in *Amphilestes*, on the contrary, it is the size of M_3]. In *Triconodon* which has 4 molars M_1 is quite small; *Trioracodon*, which has developed all its molars to approximately the same size, has only 3 of them, M_4 and M_5 being lost.

Other forms also enlarged their molars by extension in an antero-posterior direction; they did not, however, practise molar elimination, but obstinately retained a more complete tooth formula. This resulted in a crowding of the molars. There was no space for the enlarged elements in front of and behind the main cusp; therefore they were forced to the sides, and the result was that the teeth became triangular (Fig. 8 C). The more the teeth increased, the more they were compressed, and thus the base of the triangle was gradually shortened and the space between the rotating wings filled up.

To further illustrate the effect of this folding, it may be mentioned that measurements on SIMPSON's figures show that if the *Spalacotherium* molars were all straightened out, this would carry the posterior end of the last molar unto the middle of the ascending ramus.

In the *Triconodonta* the angle formed by the cusps is 180°, in *Spalacotherium* it is less than 90°. An intermediate stage is represented by *Amphidon* and *Eurylambda* with an obtuse angle (approximately 135°). It puzzled me, long before I seriously started to think of the matter how *Amphidon* could be considered by the authors as ancestral to the later symmetrodonts (*cf.* SIMPSON 1925 *a*, p. 469 *et seq.*: »On the other hand, *Amphidon* approaches in many respects the ancestral type which would be postulated on the theory that the accessory cusps arose in place, instead of migrating or rotating»). If there existed a process by which an angle of 135° could be compressed to less than 90°, each of the small cusps thus describing an arc of more than 22.5°, why could not the same process have been active between 180° and 135°? And if we keep strictly to »the theory that the accessory cusps arose in place», *Amphidon* and *Eurylambda* should, to push the matter to extremes, form an order of their own!

It seems from SIMPSON's figure of *Spalacotherium* (1928, p. 68; see also 1925 *a*, Figs. 1 and 3) as if the first and last molars were more open inwards than the middle ones, with intergrades between the extremes. The mode of development outlined above is in accordance with this, as there must have been less resistance to the expansion of the molars at the ends of the series. In the *Pantotheria* the molars differ only in size, but are otherwise true copies of each other (there are exceptions of another kind, e. g. the M_1 of *Peramus*).

It may be objected that *Tinodon* has only 4 molars and thus, though a symmetrodont, has reduced the number of its molars. As the suggestions made above are speculations based on what little we otherwise know about the *Symmetrodonta*, I may as well add my point of view on *Tinodon*. I firmly believe that the symmetrodonts developed from primitive triconodonts, no matter how this came about. When the type was once established, it underwent similar modifications as within the other orders; thus in the *Pantotheria* the number of molars varies between 8 and possibly only 3. In *Tinodon* the premolars are enlarged and occupy much space; further, the coronoid process is enormous. Thus there are two good reasons for the molars to be reduced in number. Whether molars were really lost since the symmetrodont stage was reached cannot, of course, be ascertained, but the small M_4 at least suggests that this tooth is also on the road to disappearance.

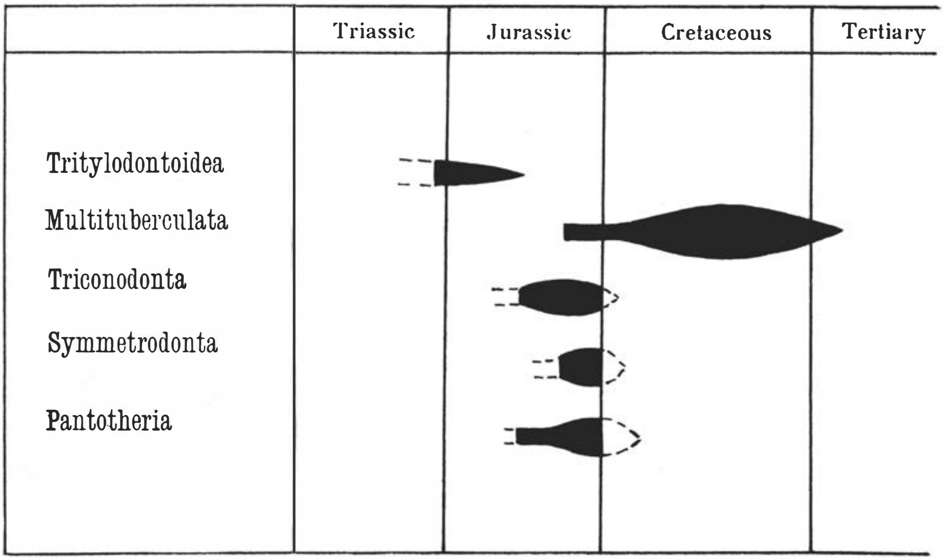


Fig. 9. Diagram of the geological distribution of Jurassic mammals and the *Tritylodontoidea*. Modified after SIMPSON.

Summary.

1. *Tritylodon* is a reptile and it is not ancestral to the multituberculate mammals.

2. This postpones the appearance of the first mammals till shortly before the Stonesfield stage (it was earlier assumed that they appeared shortly before the deposition of the Stormberg beds).

3. The earliest mammals known to us, and probably the earliest ones to appear, are representatives of the *Triconodonta* and the *Pantotheria*. The highly specialized *Multituberculata* and the *Symmetrodonta* are unknown before the Purbeck. Thus the chronology raises no objection to a derivation of the *Multituberculata* and *Symmetrodonta* from primitive triconodonts.

4. An attempt to derive the multituberculates from triconodonts is made, but it is found that this must be done from still unknown forms with an external cingulum on the lower molars. The presence of such a cingulum in *Spalacotherium* and its absence in *Tinodon* shows that cingula are not quite fixed as ordinal characters; therefore, an irregularity within the *Triconodonta* can be reasonably postulated.

5. The shearing apparatus in the multituberculates is not necessarily furnished by the premolars only, but may also comprise the anterior molars, its development being determined by the relation of the teeth to the point of maximum efficiency of the jaw muscles (*cf.* the modern carnivores). The reconstruction of SIMPSON's (1926) was redrawn so as to allow the shearing

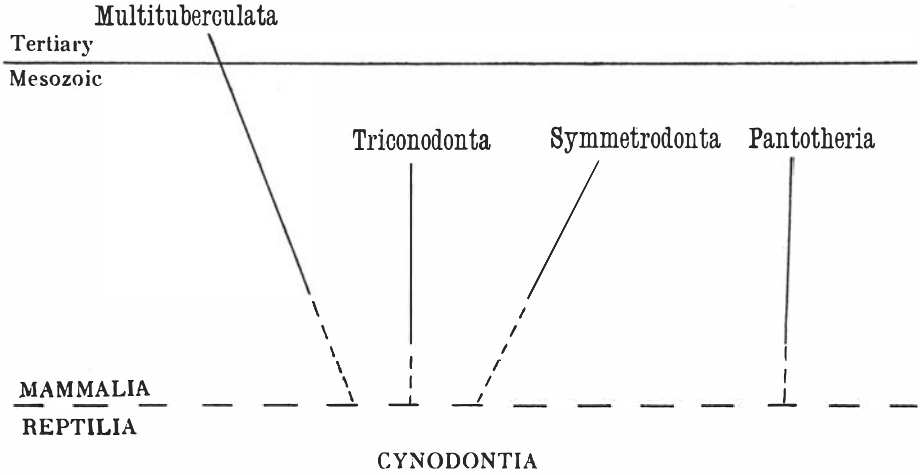


Fig. 10. Relationship of the groups of Jurassic mammals.

apparatus to be used also on objects too large to be taken into the mouth cavity.

6. The symmetrodonts are with certainty derivable from the same ancestral group as the triconodonts; their ancestors may even have been true triconodonts.

7. There is nothing in the symmetrodonts that suggests a specially close relationship to the *Panthotheria*, although their molars are triangular, since the triangles in the two groups are of quite different origin and consist of cusps with quite different homologies; in fact, in extreme cases, e. g. *Pantolestes* and *Kurtodon*, they have not a single element in common.

8. In the *Pantotheria* the primitive reptilian cone for which the term eocone is proposed (meaning precisely this original cusp without regard to where it is presumed to have its place in the complicated mammalian upper molar) can either disappear or be assimilated with the new tooth pattern in different ways. The interlocking of the teeth is due to cingula growing inwards from the base of the primitive upper molars (which were presumably simple cones; see below).

9. In the symmetrodonts, the interlocking is brought about by means of a zigzag folding of a primitive triconodont tooth row.

10. The relationships and stratigraphical occurrence of the Jurassic mammals is shown by the diagrams Figs. 9 and 10.

Butler's theory.

Butler starts out from a pretriconodont type of tooth, consisting of a laterally compressed main cusp and small cingulum cuspules, and follows Gidley in letting the protocone develop from an internal cingulum shelf.

Against BUTLER, as well as against the present writer, it can be objected that cynodonts usually have triconodont teeth.

The paracone is considered the homologue of the main reptilian cusp, the metacone arising on its posterior slope. Between this conception and the idea of the origin of the two cusps from an amphicone there is only a difference of degree.

Our conception of the dryolestid upper molars is different: according to BUTLER it is zalambdodont in type, though not ancestral to the true *Zalambdodonta*. The docodontoid type of molar (»docontoid condition») is supposed to be of greater importance for the further evolution, though the peculiarly specialized *Docodon* itself is, of course, not considered as the ancestor of any later forms.

BUTLER gives an analysis of the symmetrodont molars and applies the prevailing terminology to the cusps. He denies the presence of a metaconid in the lower molars[1] and calls the cusp usually considered as such a »posterior accessory cusp». The small cingulum cusp behind it is, however, considered to be the hypoconulid. This may all be correct but, as the problem presents itself to me, it is of little importance what the cusps are called, as the triconodonts and symmetrodonts probably represent lines of which the evolution of the pantotheres is entirely independent.

The multituberculates are excluded from the discussion with reference to SIMPSON (p. 434; SIMPSON denies, it is true, that the multituberculates are ancestral to marsupials or placentals, but he is less negative regarding a possible relationship between triconodonts and multituberculates).

BUTLER deals to a great extent with the evolution of zalambdodonts, dilambdodonts and trituberculates. I am more concerned with the interrelations of the mesozoic groups of Mammals and therefore the scope of my present paper need not in general conflict with BUTLER's work. Unfortunately I have not seen BUTLER's paper on the Jurassic mammals (Proc. Zool. Soc. Ser. B, CIX, p. 329, London 1939) and therefore my knowledge of how he arrived at his conclusions on these forms is incomplete.

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[1] To be accurate the posterior cusp in the triconodont molar is the metaconid, as the term no doubt originally referred to that cusp (OSBORN 1907, p. 40 *et seq.*; *cf.* p. 31), but again it might be considered convenient to let the original meaning yield to the prevailing use of the term.

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