A THEORY OF THE EVOLUTION OF MAMMALIAN MOLAR TEETH.

P. M. BUTLER.

ABSTRACT. A criticism of the Tritubercular Theory of Cope and Osborn. In addition to the tritubercular upper molar tooth, two other types are distinguished in primitive Cenozoic and Cretaceous mammals—dilambdodont aud zalambdodont. Lower molar patterns are correlated with those of the upper molars. The relationship between the three types is discussed in the light of the teeth of Jurassic mammals, with the conclusion that the tritubercular molars are more advanced than the dilambdodont and zalambdodont molars. This is borne out by an analysis of their occlusal relationships.

INTRODUCTION.

THE evolution of mammalian molar teeth has been, and still is, one of the most controversial problems of vertebrate morphology. The importance of the problem lies in the fact that the teeth are the hardest organs in the body and are therefore preserved as fossils much more easily than other parts of the body. Our knowledge of the evolution of mammals depends to a very large extent upon evidence derived from teeth.

The difficulty of the problem is largely due to the evolutionary plasticity of the teeth, which not only reflect the habits of the mammal but are capable of parallel evolution to a degree that is confusing. The form of a tooth is seldom very complex, and relatively few morphological characters can be distinguished; because of this a general resemblance between teeth belonging to quite diverse types of mammal is common. Add to these difficulties the imperfection of the geological record, particularly in the Mesozoic era in which the greater part of mammalian evolution took place, and the controversial nature of the problem is very understandable.

In the last century two main rival theories of molar morphology held the field. According to one, first stated by Gervais (1854) and developed by Röse (1892a), the molar tooth has arisen by the concrescence of a number of simple teeth such as are found in reptiles and fish; each cusp of the mammalian molar was once an independent tooth. According to the other theory, of Cope (1874) and Osborn (1888), the mammalian tooth has been derived by the formation of additional cusps arising as buds from the base of a primitive cone inherited from the reptiles. The concrescence theory in its original form is now completely discredited, though other theories involving concrescence have been put forward, notably that of Bolk (1921-22). As Bolk's theory is mainly based on the human dentition and is not easily reconcilable with palaeontological data it will not be further discussed in this paper, which is concerned more especially with a criticism of the Cope-Osborn theory of Trituberculy.

A very complete review of the theory of Trituberculy has been published by Gregory (1934), and only a very brief sketch is given here. The theory consists of two distinct parts: (1) the tritubercular origin of the molar patterns of Tertiary mammals, and (2) the origin of this tritubercular pattern from the reptilian cone.

The palaeontological exploration of the American West made it clear that in many orders of mammals the most primitive upper molar pattern is a triangular, three-cusped type, with three roots. This type of molar was called tritubercular, and it was recognized in the Primates, Artiodactyla, Condylarthra, Creodonta and some Insectivora. The assumption was made, on less compelling evidence, that it is also primitive for other groups of mammals. The three main cusps were called paracone (anteroexternal), metacone (posteroexternal) and protocone (lingual) ; round the edge of the crown there is often developed a ledge or "cingulum," from which other cusps can arise, e.g. the parastyle, mesostyle and metastyle on the outer edge and the hypocone on the posterior edge. A protoconule and metaconule are often present as small cusps between the protocone and the paracone and metacone respectively. The corresponding lower molars consist of a "trigonid" of protoconid, paraconid and metaconid, and a more posterior "talonid" of hypoconid, entoconid and hypoconulid.

Criticism of this part of the theory has come mostly as a result of the study of orders which were not considered in much detail by Osborn: Insectivores and Rodents in particular. Forsyth-Major (1893), Hinton (1926) and Friant (1933), working on Rodents, supported a Multituberculate Theory, that the original Placentals had upper molars with more than three cusps, and the primitive type of upper molar pattern is a tooth with three rows of cusps, from which the tritubercular type has been derived by simplification. Forsyth-Major noticed that most Insectivores, which in other respects are the most primitive Placentals, have more than the three cusps postulated by Osborn, and that is true also for the Cretaceous mammals. He laid emphasis on the buccal cusps ("styles") which are very common in primitive mammals. Many years previously Winge (1882) had developed a theory of molar evolution which led to the hypothesis that the buccal styles are the most ancient part of the crown, and that their loss in many Primates, Ungulates and Carnivores is a secondary specialization. Gregory (1916) supported the view that the paracone was originally placed at some distance from the buccal edge of the crown, and that there was a "primary trigon" of parastyle, paracone and metastyle which was more archaic than the "secondary trigon" of paracone, protocone and metacone.

Simpson (1928c, 1936), who is one of the leading living supporters of the Cope-Osborn theory, as far as its application to Tertiary mammals is concerned, recognizes that in primitive upper molars the "external shelf" was probably fairly wide. He says that where the shelf is wide, the paracone and metacone are crescentic. The shelf usually bears small cuspules called styles, of which he holds that the individual history can be traced in the Marsupials, but in many other cases they are very variable, and he is doubtful whether they can be traced from group to group in the way that Winge supposed. The primitive lower molar, according to Simpson, has a heel of the same size as the trigonid, with a rim of three cusps; the hypoconulid is small and inconspicuous except on m_3; the paraconid is sometimes slightly more external than the metaconid. In the upper molar the internal root is larger than the buccal roots in primitive forms.

The second part of the Cope-Osborn theory postulated a series of stages by which the tritubercular upper molar has been derived from the reptilian cone. The original cone is the protocone; the paracone and metacone were added in front of and behind the protocone; then the protocone became displaced lingually, relative to the other two cusps, and the triangular crown was attained. Various Jurassic mammals were believed to represent stages in the process.

Opponents of this theory have held for the most part that the paracone, and not the protocone, is the original cusp. Gidley (1906), for instance, suggested that the protocone arose as a lingual ledge from the base of the paracone and metacone, and that there has been no rotation of cusps. This view is consistent with embryological evidence (Röse 1892b, Taeker 1892, Woodward 1896) that the paracone is the first cusp to appear, the protocone being budded off from its base. It is also consistent with the "premolar-analogy" theory (Wortman 1902, Leche 1907, Gregory 1916) that in molariform premolars the most archaic cusp corresponds to the paracone of the molar, as may be shown both by studying the process of molarization in palaeontological series and by comparing molariform premolars with the simpler premolars placed further forward in the jaw (Butler 1937).

An important modification of the theory arose from the discovery of the Mongolian Cretaceous Insectivores, *Deltatheridium* and *Zalambdalestes* (Gregory and Simpson 1926, Simpson 1928a). Of these, *Deltatheridium* was believed to have a single cusp in the place of the paracone and metacone, and it was thought that these two cusps were united to form an "amphicone." In *Zalambdalestes* they are separate, and thus the two genera were regarded as steps in the evolution of the Insectivore upper molar. In 1934 Gregory rejected the premolar-analogy theory and accepted Osborn's view of the primitive nature of the protocone; he maintained that the amphicone arose on the buccal side of the protocone and divided into two. The similarity between molars and molariform premolars is ascribed to convergence (cf. Scott 1892), and the ontogeny of the molar cusps is believed to have been secondarily modified.

There has been less disagreement about the evolution of the lower molars. The Cope-Osborn theory stated that the trigonid has arisen in a similar way to the origin of the upper molar, the protoconid being the original cusp and undergoing a process of buccal displacement relative to the paraconid and metaconid. The talonid was held to be a development of the cingulum comparable with the hypocone of the upper molar, and later in development than the trigonid.

Direct palaeontological evidence for these theories of the origin of the tritubercular tooth is scanty. The known Jurassic mammals display a wide variety of molar pattern, and reliable criteria of the homology of their cusps are few. Resemblances between the molars of different forms may be merely coincidental or due to convergent evolution, and Simpson (1928b) held that the molars of different orders of Jurassic mammals have probably been independently derived from the reptilian condition.

During the past five years I have been carrying out investigations on the dentition of mammals, and some of the conclusions reached go some way, I believe, towards solving the difficulties in the original statement of the Cope-Osborn theory. They are here discussed under two headings: the molar patterns of primitive Cenozoic mammals, and the relation of these molar patterns to those of Jurassic forms.

PRIMITIVE CENOZOIC MOLAR PATTERNS.

In research on the teeth of mammals attention has been paid principally to the cusps. There has been no general survey of the roots of mammalian teeth, and the form of the base of the crown is usually considered to be of secondary importance. This is largely due, no doubt, to the greater variety of arrangement of the cusps, as compared with the roots, and their consequently greater value in systematic studies.

The upper cheek-teeth of primitive mammals, when seen from an oral or aboral aspect, are triradiate or three-lobed structures. One lobe is lingual, one anterior or anterobuccal, and the third is posterobuccal. Each lobe is supported by one root. The three lobes or radii vary in their form, their distinctness and their relative size (Fig. 1). They may be pointed, as in *Didelphis*, or rounded, as in *Tenrec*; they may be separated by emarginations of the outline, as in *Nesoryctes*, or the outline may be triangular without any emarginations, as in *Galeopithecus*, or it may be sub-circular as in man; the three lobes may be subequal, as in p^4 of *Nesoryctes*, or the lingual lobe may be enlarged, as in *Tenrec*, or the posterobuccal lobe may be enlarged, as in the carnassial of the dog, or the posterobuccal lobe may be reduced, as in last molars generally. Another modification of the outline consists in the subdivision of the lingual lobe to form a four-lobed tooth, as in most Ungulates, and the lingual root in such cases tends to subdivide.

There is a serial modification of the outlines of the teeth within the cheek dentition. (Fig. 2.) The most anterior premolars are often oval in outline, and have only one or two roots. Further back the lingual lobe develops, and the lingual root splits off from the posterobuccal root. The lingual lobe reaches its maximum size, and may further subdivide, in the typical molars, and in the more posterior teeth the posterobuccal lobe becomes reduced. The roots follow a parallel course; their relative sizes are closely related to the relative sizes of the corresponding lobes.

According to Orban and Müller (1929), the embryonic molar tooth is first of all approximately circular in outline, but it begins to grow out along a number of radii till the final form is acquired. The originally single basal opening into the pulp cavity becomes divided accordingly, till there is a separate opening to each lobe of the base. The roots are then formed in relation to these openings, and so there is one root to each lobe. The outline and the roots are therefore the product of the basal, or aboral, portion of the enamel organ, while the cusps are formed from the oral portion.

It is not yet certain whether the formation of cusps is due entirely to unequal growth of parts of the epithelial enamel organ, or whether the pulp and odontoblast layer take part, but it is generally accepted that cusps are evaginations of parts of the oral surface of the enamel organ. This implies that a relative independence between cusps and roots is to be expected, and this is in accordance with the facts. The paracone, for instance, is situated over the anterobuccal root in human molars, but in *Tenrec* it is placed over the lingual root. Certain authors (Naef 1925, Hertz 1925) have questioned the homologies of the lingual cusp of *Tenrec* on the grounds of its relation to the roots, but their views have not been accepted, as they are opposed by the evidence of palaeontology (Schlaikjer 1933).

If the view is accepted that the primitive Tertiary molar was triangular, this is not in itself evidence for the Tritubercular Theory, which is concerned not so much with the outline of the tooth as with the arrangement of cusps on the crown. Triangular teeth do in some cases have the main cusps placed over the three roots, as in *Notharctus* and *Ictops*, but this is by no means always so. The possible positions of the paracone lie in a line parallel to the anterior edge of the crown, and extending from above the anterobuccal root to above the lingual root. It is buccal in the Leptictidae and Erinaceidae, median in *Tupaia*, *Didelphis* and the Soricoidea, and lingual in the Zalambdodonts. There is no reason to suppose that the buccal position was the most primitive, for even in the Cretaceous the Didelphidae and Deltatheridiidae had median or lingual paracones.

The metacone arises in embryology as a fold of the enamel epithelium behind the paracone. A number of types of metacone can be distinguished (Fig. 3): (1) In *Notharctus*, the dog, man, Erinaceidae, etc., the metacone is a more or less

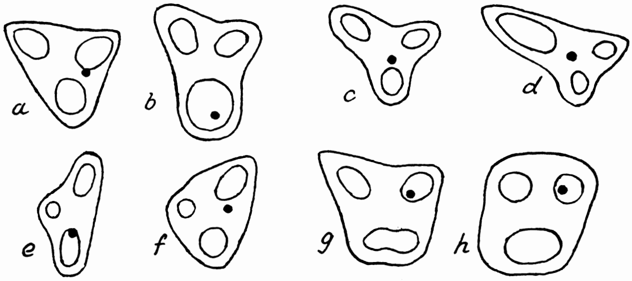

Fig. 1. Outlines and root-patterns of a number of upper cheek-teeth. The position of the paracone is marked. (a) *Didelphis*, m^1; (b) *Tenrec*, m^1; (c) *Nesoryctes*, p^4; (d) *Canis*, p^4; (e) *Potamogale*, m^3; (f) *Tupaia*, m^3; (g) *Erinaceous*, m^1; (h) *Homo*, m^1.

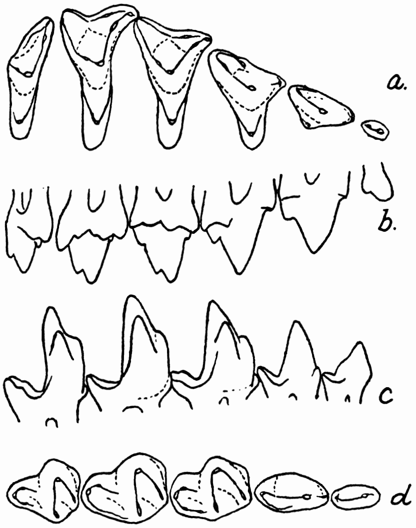

Fig. 2. Restoration of the cheek-teeth of *Palaeoryctes*. (a) Right p^2-m^3, crown view; (b) right p^2-m^3, buccal view; (c) left p$_3$-m$_3$, lingual view; (d) left p$_3$-m$_3$, crown view.

conical cusp placed near the buccal edge of the crown, over the posterobuccal root, and separated from the paracone by a deep valley. (2) In the Leptictidae the metacone is similar in position but it is less distinct from the paracone and more or less connate with it. (3) In Didelphidae and *Didelphodus* the metacone is placed at some distance from the buccal edge of the crown, and is connected with the paracone by a crest. (4) In the Soricoidea, *Tupiaia* and many bats it is similar in position to (3) but is separated from the paracone by a deep V-shaped groove. (5) In *Potamogale, Palaeoryctes* and *Oryzorictes* it is merely an elevation of the posterobuccal crest of the V-shaped paracone. (6) In most Zalambdodonts it is completely absent.

The protocone, though less variable in position (it is always placed over the lingual root) is very variable in size. In such forms as man, *Ictops* and *Erinaceus* it is large and comparable with the paracone and metacone; in the Soricoids it is reduced in size and appears as a lingual shelf; in the Zalambdodonts it is still more reduced and is often absent as in *Tenrec* and *Ericulus*.

In addition to the three main cusps recognized by Osborn, a number of other cusps are nearly always present, and there is no reason to believe that they are in all cases secondary formations. The buccal styles are well developed in forms in which the paracone is not buccal. In Zalambdodonts (Butler 1937) it is possible to distinguish (a) a parastyle at the anterior apex of the crown, (b) a large "anterior buccal cusp," immediately buccal to the paracone, (c) a number of more posterior cusps, (d) a metastyle near the posterobuccal apex. In the Didelphidae there is (a) a parastyle, (b) an anterior buccal cusp, (c) one or more posterior buccal cusps, and (d) a metastyle; in other words the arrangement is essentially similar to that of Tenrecoids. In Soricoids and in *Tupaia* similar cusps can be detected, except that the anterior buccal cusp is small or absent, and the first of the more posterior cusps is enlarged to form a "mesostyle." In the Leptictidae, Erinaceidae, etc., only the parastyle occurs as a distinct cusp, the rest of the buccal series being represented only by a ledge, and even this is absent in Macroscelididae and in man. The buccal styles do not occlude with the lower teeth, and are of doubtful value in feeding; similarities in their arrangement in different mammals may be due to more than coincidence (as Winge suggested). Simpson (1928a) denies this, but on what appear to be inadequate grounds.

Inversely correlated with the buccal styles are the protoconule and metaconule, which are almost always present on

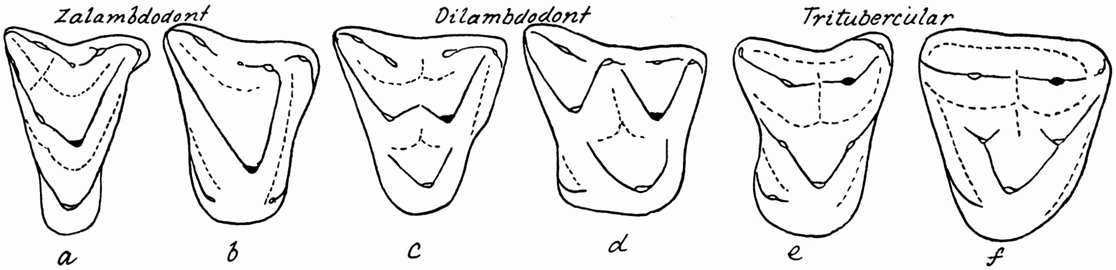

Fig. 3. Right upper molars of some primitive mammals. The paracone is marked in black. (a) *Potamogale,* (b) *Tenrec,* (c) *Didelphis,* (d) *Tupaia,* (e) *Esthonyx,* (f) *Miolaenus.*

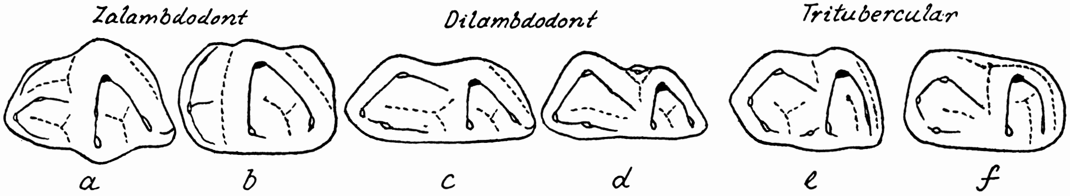

Fig. 4 Left lower molars of the same genera as in Fig. 3. The protoconid is marked in black.

teeth in which the paracone and metacone are buccal in position, but are rarer in Soricoids and Didelphids and absent in Zalambdodonts. Their development seems to be correlated with the size of the part of the crown that lies lingually to the paracone and metacone. The hypocone on the other hand is correlated with the development of the lingual root: where this root is enlarged and the tooth approaches a quadrangular outline the hypocone is well developed, as in man, most Ungulates, Erinaceidae, Soricidae and *Solenodon*; where the lingual root is less enlarged the hypocone is represented merely by a ledge ("cingulum") on the posterior side of the protocone (*Notharctus*, *Ictops*, dog) ; where the lingual root is no larger than the buccal roots the hypocone is not present at all (most Zalambdodonts, Didelphidae, Talpidae).

This description of the range of variation of the upper molar patterns of primitive mammals reveals that the parts of the tooth are not entirely independent, but show a number of correlations. It is possible to arrange the teeth into groups according to the position of the paracone, which may be (a) buccal, (b) median or (c) lingual (and of course in intermediate positions), and with each position there are correlative developments of the other cusps (Figs. 3 and 5):

	(a) paracone buccal	(b) paracone median	(c) paracone lingual
Metacone	buccal, large (except Leptictidae)	median, large	rudimentary or absent
Buccal styles	absent or rudimentary	moderate	large, especially "anterior buccal cusp"
Protocone	large	smaller	small—absent
Conules	usually distinct	often absent	absent

The size of the hypocone is correlated with the lingual root, as has already been stated, and this is not so closely correlated with the position of the paracone. The enlarged lingual root and quadrangular outline are, however, more common in teeth with buccal paracones than in the other types, and the presence of a hypocone in Zalambdodonts is rare (*Solenodon*).

It is interesting to note that the shape of the paracone varies with its position: when it is buccal it is conical, but as it recedes from the buccal edge it becomes more V-shaped.

The Leptictidae are exceptional in that their metacones, though placed near the buccal edge, are less developed than in other families with similarly placed metacones.

The lower molar teeth of primitive mammals normally have two roots, and are oval or oblong in outline (in some Soricidae, etc., the molar roots may subdivide). As in the upper molars, there is no exact correlation between the position of the cusps

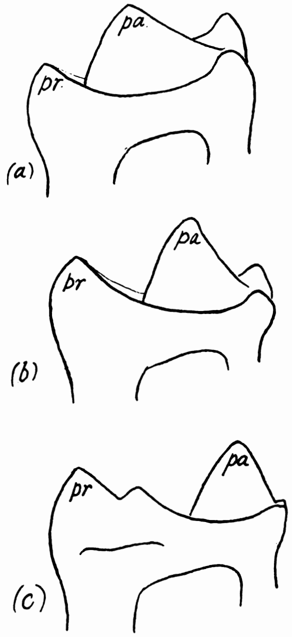

Fig. 5.

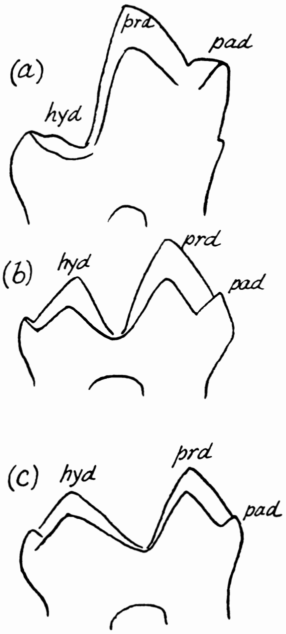

Fig. 6.

Fig. 5. Anterior view of typical upper molars: (a) zalambdodont, (b) dilambdodont, (c) tritubercular. *pa*, paracone, *pr*, protocone.

Fig. 6. Lingual view of typical lower molars; (a) zalambdodont, (d) dilambdodont, (c) tritubercular. *hyd*, hypoconid; *prd*, protoconid; *pad*, paraconid.

and that of the roots. The protoconid is placed above the anterior root in most forms, but in Zalambdodonts it is median in position, between the two roots. It is possible to correlate the patterns of the lower molars with those of the upper molars. (Figs. 4 and 6.)

The paraconid is well developed in the Zalambdodonts, where it is comparable with the metaconid in size; it is almost as large in Soricoids and Didelphids, but in forms with a buccal paracone the paraconid tends to be lost, especially in the more posterior molars (man, Erinaceidae, Leptictidae, dog, etc.). The reduction of the paraconid is not correlated with the enlargement of the hypocone of the upper molar, as Osborn supposed, but with the buccal position of the paracone. The Leptictidae, Canidae, many Hyopsodontidae, etc., have reduced paraconids while the hypocone is still in the cingulum stage of development. The completest development of the trigonid does not occur, as would be expected from the Tritubercular Theory, in forms of which the upper molars are most nearly tritubercular.

The metaconid is always well developed, and is placed lingually to the protoconid; in forms in which the paracone and metacone are relatively buccal, the protoconid and metaconid are relatively anterior.

The talonid region of the lower molar is quite variable in development: it is small in Zalambdodonts, and enlarges as the paracone of the upper molar becomes more buccal. When the talonid is small the hypoconulid appears to be the only cusp, the hypoconid and entoconid being added when the talonid is larger. The hypoconulid is lingual in position in Soricoids, Zalambdodonts and Didelphids, but is more median in forms with buccal paracones. It is the so-called "entoconulid" of Stirton (1930), as pointed out by Patterson and McGrew (1937). Supporters of the Tritubercular Theory appear to believe that the hypoconulid is a secondary cusp, but there is some evidence that it is older than the hypoconid.

Each of the three main types of upper molar is thus associated with a corresponding type of lower molar. For convenience, I proposed (1939a) to restrict the term "tritubercular" to molars in which the paracone is near the buccal edge; those, like the molars of Didelphids and Soricoids, in which the paracone is median in position, were distinguished as "dilambdodont," and the molars with lingual paracones were called "zalambdodont." These terms will be used in the remainder of this paper. It should be pointed out that the "trituberculate" molars of Osborn, and the "tribosphenic" molars of Simpson, are sometimes to be considered as tritubercular in my sense, sometimes as dilambdodont. The term "dilambdodont" was originally used by Gill (1885) to include all insectivore molars other than those of the Zalambdodonts, i.e., including my tritubercular types.

THE ORIGIN OF THE CENOZOIC MOLAR PATTERNS.

In distinguishing three types of molar pattern in primitive Cenozoic mammals I do not imply that they represent three phylogenetically distinct groups of mammals. It is not difficult to conceive of transitional forms, in fact many such forms are known. Certain groups have retained similar tooth patterns for a long time, e.g., the Tenrecoidea were represented by *Palaeoryctes* in the Palaeocene (Fig. 2), and the modern Didelphidae are not appreciably different from some of the Cretaceous forms: at some time in the past, however, there is every reason to believe that transitions occurred even between two such distinct groups as these. If *Tupaia* is related to the Primates, a transition between the dilambdodont and tritubercular conditions (witness *Ptilocercus*) is probable; if *Notoryctes* is related to the other Polyprotodonts a transition between the zalambdodont and dilambdodont conditions must be assumed. There is also no reason to suppose that such transitions took place only once. The possibilities of parallel evolution are illustrated quite clearly by the development of the hypocone, which became enlarged independently in Erinaceidae, Hyopsodontidae, Ungulates, Marsupials and Primates. The buccal or lingual movement of the paracone, and the loss of the paraconid, may quite well have taken place in a similar way more than once.

The question remains, however, is it possible to say which of the types of molar organization is generally the most archaic; for example, is there any tendency for the dilambdodont pattern to give rise to the tritubercular pattern, rather than the reverse?

This question cannot be answered by direct appeal to palaeontology, for there are no clear fossil series showing such transitions: one has to rely on the comparison of contemporary and related forms, and to decide the direction of evolution on the assumption that simple or less differentiated forms are more primitive than complex forms. On their general anatomy the Insectivores and the Polyprotodont Marsupials are universally regarded as primitive, and to these must be added the Jurassic mammals because of their great age. In early Tertiary times the Insectivores were not clearly distinct from the ancestors of other orders of mammals, for example, the Primates, Carnivores and Ungulates (Simpson 1937a), in which derivatives of the tritubercular molar pattern are almost universal. The dilambdodont and zalambdodont types of molar pattern are largely confined to the more specialized families of Insectivores and Marsupials (together with such groups as the bats, Pantolambdidae, etc.): can they be regarded as relics of a primitive condition, or are they specializations like the spines of the hedgehog and the enlarged incisors of the shrews? The palaeontology of Insectivores is not well enough known to enable this question to be answered: the living families, with the possible exception of the Tenrecidae, cannot be traced back far into the Eocene, and their relationships with fossil families are not very clear. Of Marsupials, the Didelphidae are the only adequately known group, and they throw little light on the problem.

The handful of known Cretaceous mammals contains representatives of all three types. *Zalambdalestes* and *Gypsonictops* have tritubercular molars, the Deltatheridiidae have zalambdodont molars, and the molars of the Upper Cretaceous Didelphidae are for the most part dilambdodont.

On the other hand the Jurassic mammals have a series of molar patterns widely different from those of Cretaceous and Cenozoic forms, and they might be expected to have a bearing on the problem of phylogeny. The diversity of hypotheses among those who accept this general point of view is due to the great difficulty of deciding the homologies of molar cusps in Jurassic mammals. Accepting Simpson's argument (1937b) that the Multituberculata are quite distinct from other mammals and were not ancestral to either the Marsupials or the Placentals, there remain three orders, the Triconodonta, Symmetrodonta and Pantotheria. Of these, the Pantotheria are generally considered to be nearest to the ancestors of the later mammals.

The upper molars of the Pantotheria are characterized by the possession of three roots, as in primitive Marsupials and Placentals, and of two main cusps, one buccal and the other lingual. Two interpretations of this pattern have been put forward. Gregory (1916) held that the lingual cusp was the paracone and that the molars were comparable with those of Zalambdodont Insectivores. Simpson (1929) regarded the buccal cusp as a "parametacone" or "amphicone," while the lingual cusp was considered to be the protocone; this view was adopted by Gregory in 1934. The solution of the problem depends on the possession of a satisfactory criterion of a protocone and a paracone, by which the homology of the lingual cusp could be established.

Such a criterion is, I believe, to be found in a study of the premolars and milk molars. In all mammals of which the molar patterns are understood the differentiation of the antemolars is basically similar. At the anterior end of the series the upper teeth tend to be one-rooted, and to bear a single large cusp (the paracone). Further back the root divides into two, and the tooth becomes oval in outline, while accessory cusps begin to appear. The metacone arises on the posterior ridge of the paracone, and the protocone develops from a ledge on the posterolingual border of the crown. With the subdivision of the posterior root the protocone enlarges and acquires the form characteristic of a fully molariform tooth. This sequence is found in all Cenozoic and Cretaceous mammals (Butler 1939a), and it provides a basis for the interpretation of molar patterns. The paracone may be defined as that cusp on the molar which is serially homologous with the main cusp of the canine and similar teeth, while the protocone is serially homologous with a posterolingual ledge on the less molariform teeth. It is a reasonable hypothesis that, as this type of antemolar sequence occurs universally in the later mammals, it was also found in the Jurassic mammals. Assuming this to be so, it is possible by a study of the antemolar teeth of Pantotheria to decide between the two alternative interpretations of their molar patterns.

The result of such a study (Butler 1939b) is that the Pantotheria fall into two distinct groups (Fig. 7). In the Dryolestidae the lingual cusp is the paracone, and the protocone is absent, so that the pattern is of an extreme zalambdodont type; in the Docodontidae the paracone is buccal in position, and the lingual cusp is the protocone. The large buccal cusp of the Dryolestidae appears to be homologous with one of the styles of Tenrecidae and Didelphidae, but in the Docodontidae there are no such styles, except for the parastyle, the other styles being represented by a buccal ledge. There is a metacone in both families: in the Dryolestidae it is on the posterior edge of the tooth, and in the Docodontidae it is posterobuccal in position; it is never sharply differentiated from the paracone, and resembles the metacone of the Leptictidae or of *Potamogale*.

Applying the same method to the Triconodonta and Symmetrodonta, it is found that the principal cusp of the upper molar (the middle one of the three main cusps of *Triconodon*) is the paracone, and the protocone, if present at all, is represented by a lingual ledge or cingulum.

The lower teeth of the Pantotheria also fall into two groups, the Amphitheriidae and Paurodontidae (of which the upper teeth are unknown) approaching the Dryolestidae rather than the Docodontidae. The Pantotheria as a whole differ from later mammals in the absence of a hypoconid, the protoconid having a nearly median position as in Zalambdodonts.

In the Symmetrodonta and Triconodonta there is no metaconid. The cusp which has hitherto been called the metaconid in such forms as *Spalacotherium* is probably a "posterior accessory cusp," lacking in the molars of other mammals. The metaconid arises in a posterolingual position, the posterior accessory cusp in a posterior position, relative to the protoconid.

The molar teeth of mammals may thus be arranged in three grades of evolution, as follows:

A. Upper and lower molars with similar and apparently homologous cusps, two-rooted (the upper molars of *Peralestes* are triangular and possibly three-rooted); no metaconid, but a posterior accessory cusp. Here belong the Triconodonta and the Symmetrodonta. The Triconodonta are characterized by the equality of the two molar roots and the median position of the main cusp (paracone or protoconid), while the Symmetrodonta are characterized by the enlargement of the posterior root, probably in both jaws, and by a displacement of the paracone lingually and the protoconid buccally.

B. The upper molars are three-rooted, the posterior root having divided into two; the lower molars remain two-rooted; there is a metaconid, and the posterior accessory cusp is lost on the molars, though sometimes present on the premolars. The protoconid and metaconid are connected by a transverse crest, which divides the lower molar into two parts, the trigonid and the talonid. The talonid is poorly developed, however, and has no hypoconid or entoconid. Here belong the Pantotheria, and also later mammals with zalambdodont teeth.

C. The talonid becomes better developed, and the hypoconid and entoconid are formed; the metacone becomes more distinct from the paracone. Here belong the majority of the Marsupialia and Insectivora, as well as the more advanced mammals.

As all the known Jurassic mammals come from only two or three horizons, it is clearly impossible to arrange them in a phylogenetic series. They represent divergent specializations from a primitive type. Nevertheless it is possible to regard the Pantotheria (stage B) as more advanced than the other orders (stage A), and within the Pantotheria two widely divergent groups can be distinguished: in the Dryolestoidea the paracone is in an extreme lingual position, and the talonid and posterior root of the lower molar tend to be reduced; in the Docodontoidea the paracone is buccal, the protocone is well developed, and in the lower molar the talonid is as broad as the trigonid. Neither of these groups can be regarded as ancestral to the known Cretaceous mammals. The Zalambdodonts approach the Dryolestidae in molar pattern, but except in some advanced forms like *Tenrec* and *Betifer* there is always a distinct protocone, whereas this cusp is completely absent in the Dryolestidae. On the other hand, the Docodontidae are specialized in the opposite direction, having lost the buccal styles and enlarged the protocone. A hypothetical intermediate form, in which the paracone was near the middle of the crown, and in which both protocone and buccal styles were present, would provide an ideal ancestor for *Deltatheridium* and the modern zalambdodonts (Figs. 8 and 9).

Such an ancestral zalambdodont could also give rise to the dilambdodont condition, by the development of a hypoconid and an increased separation between the paracone and metacone. In primitive dilambdodonts the paracone and metacone were probably connected directly by a crest, as in the Didelphidae and in *Didelphodus*; in such forms as the Soricoids a V-shaped groove developed between the paracone and metacone, and into this occluded the V-shaped hypoconid. The tritubercular condition could be derived from the primitive dilambdodont condition by the buccal displacement of the paracone and metacone, the further development of the protocone region, and the reduction of the paraconid.

It is also possible that in some cases the tritubercular condition could have been derived directly from a Docodontoid condition, by enlargement of the metacone and the talonid. The Leptictidae could be regarded as an early stage in this process; although they have a distinct small hypoconid, the metacone is not as well separated from the paracone as in most tritubercculates.

According to this view, the main trend of molar evolution has been from zalambdodonty through dilambdodonty to tritu-

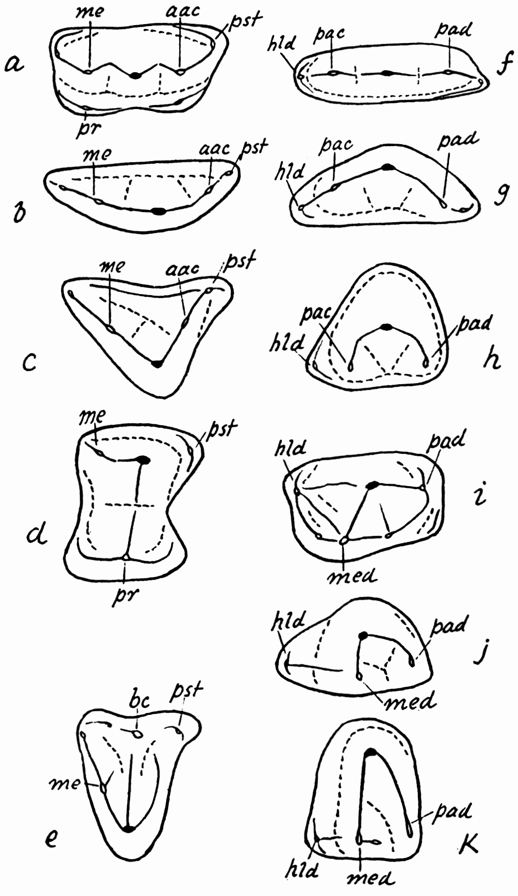

Fig. 7. Molar patterns of Jurassic mammals. (a)–(e) upper molars, (f)–(h) lower molars. The paracone and protoconid are marked in black. (a) *Priacodon* (Triconodonta), (b) *Eurylambda* (Symmetrodonta), (c) *Peralestes* (Symmetrodonta), (d) *Docodon* (Pantotheria, Docodontidae), (e) *Melanodon* (Pantotheria, Dryolestidae), (f) *Triconodon* (Triconodonta), (g) *Tinodon* (Symmetrodonta), (h) *Spalacotherium* (Symmetrodonta), (i) *Docodon* (Pantotheria, Docodontidae), (j) *Tathiodon* (Pantotheria, Paurodontidae), (k) *Laolestes* (Pantotheria, Dryolestidae). *aac*, anterior accessory cusp; *bc*, buccal cusp; *hld*, hypoconulid; *me*, metacone; *med*, metaconid; *pac*, posterior accessory cusp; *pad*, paraconid; *pr*, protocone; *pst*, parastyle.

berculy, the tritubercular tooth representing the highest stage. From the tritubercular condition have of course been derived the various types of pattern found in Primates, Ungulates and other groups, but the teeth of Didelphidae, Soricoidea, many bats and other groups of primitive mammals have not passed through a tritubercular stage. Corroboration for this view can be obtained from a study of occlusal relations.

THE EVOLUTION OF THE MOLAR FUNCTION (FIG. 10)

In primitive mammals, with the exception of the Multituberculata, the jaw movement is vertical (orthal), as in the majority of lower vertebrates. The cusps are sharp, and on the crown there are sharp, vertical crests which shear against one another in a nearly vertical plane as the jaw closes. Owing to the height of the cusps and ridges little lateral movement of the jaw is possible while the teeth are in contact, except such as is necessary to press the shearing crests closely together. The occlusal function therefore consists of two main parts: a vertical cutting or shearing function, carried out by the crests, and a crushing or pestle-and-mortar function, carried out by the tips of cusps which bite into valleys on the opposing teeth.

The dentition of mammals is so arranged that the teeth of one jaw alternate with those of the other jaw. This characteristic was also inherited from the reptiles, and the result of it is that each tooth occludes with two teeth of the opposite jaw. In the Triconodonta and Symmetrodonta this type of occlusion persists in a relatively little modified form. The principal cusps (paracone and protoconid) bite between two teeth of the opposite jaw, and their crests shear against one another as the jaw closes, the upper teeth shearing outside the lower teeth. The shearing function is predominant, and the length of the cutting edges is increased by the development of cusps on the crests of the main cusps. In the Symmetrodonta the teeth have become wedge-shaped, and the planes of shear, instead of being longitudinal, are oblique, the paracone and protoconid being V-shaped. This type of occlusion persists in the simple antemolars of other mammals in which the more posterior cheek teeth have advanced to a further stage of evolution.

The metaconid appears to be absent in Triconodonts and Symmetrodonts, but on the posterior crest of the protoconid there is a cusp that I have called the "posterior accessory cusp," probably homologous with the metacone of the upper molar. This cusp is retained on some milk molars and premolars of more advanced mammals, e.g., the Docodontidae, *Potamogale* (p_3 and pd_3), *Tenrec* (pd_3), Leptictidae, Macroscelididae, etc., but it has been lost in the molars. In *Potamogale*, however, it is possible to see it as a small cusp lying between the protoconid and the metaconid of the molars. In primitive Pantotheres the metaconid must have arisen lingually to the posterior accessory cusp, near the posterior end of the crown. Its function originally was probably that it sheared in front of the protocone of the upper molar, which also arose in a posterior position. The subdivision of the posterior root of the upper molar and the development of the lingual lobe of the crown would result in a movement of the protocone inwards and forwards, and at the same time the protocone probably enlarged from its original condition as a cingulum cusp. In the early stages of this process the protocone would overhang the anterior part of the more posterior lower tooth, and its tip would tend to bite on the inner side of the paraconid, while the tip of the paraconid would be received by the groove between the protocone and the metacone. This is so in the Docodontidae, as well as in the antemolars of various later mammals; the protocone of pd^3 of *Potamogale*, for example, occludes with the paraconid of pd_4. As the protocone enlarged further it would occlude more and more with the rudimentary talonid at the posterior end of the more anterior tooth, and the talonid would enlarge by the forward displacement of the metaconid and a reduction of the posterior accessory cusp.

The primitive shear between the paracone and protoconid is found in all Jurassic mammals, and is retained in the modern zalambdodonts. It is, however, reduced in dilambdodonts and almost lost in trituberculates. In Dryolestidae the tip of the paracone bites against the talonid, and this occurs also in modern zalambdodonts: in *Potamogale*, both paracone and protocone occlude with the talonid, biting on either side of a ridge that runs along the talonid and ends in the hypoconulid. This ridge in other forms develops into the hypoconid, which by its enlargement pushes the paracone out of the talonid basin. In dilambdodonts there is often a small ledge between the hypoconid and the protoconid; this appears to represent the outer part of the talonid, and it bites against the tip of the paracone.

The metacone of modern forms can be traced back to the

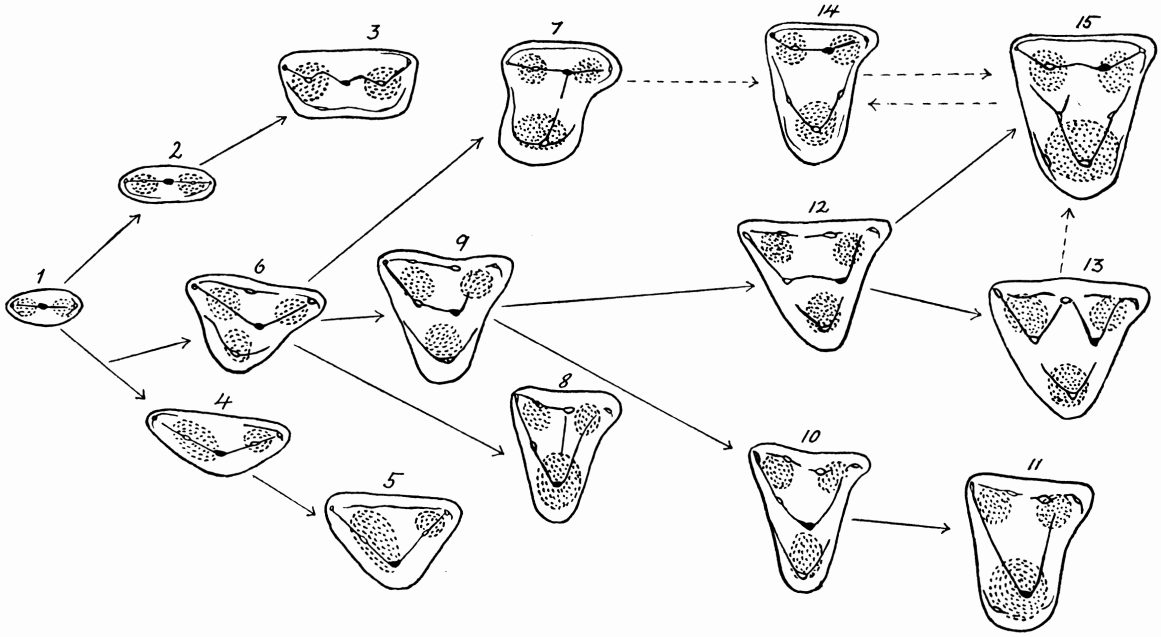

Fig. 8. Suggested evolution of the upper molar. The paracone is marked in black; the position of the roots is indicated by stippling.

Stage A: (1) hypothetical primitive condition, (2) hypothetical primitive Triconodont (Amphilestine), (3) advanced Triconodont, (4) primitive symmetrodont, e.g., *Eurylambda*; (5) advanced Symmetrodont, e.g., *Peralestes*.
Stage B: (6) hypothetical primitive Pantothere, (7) Docodontoid, (8) Dryolestoid, (9) hypothetical intermediate condition, (10) primitive zalambdodont, (11) advanced zalambdodont, e.g., *Tenrec*.
Stage C: (12) primitive dilambdodont, e.g., *Didelphis*, (13) advanced dilambdodont, e.g., Soricoid, (14) Leptictid, (15) tritubercular.

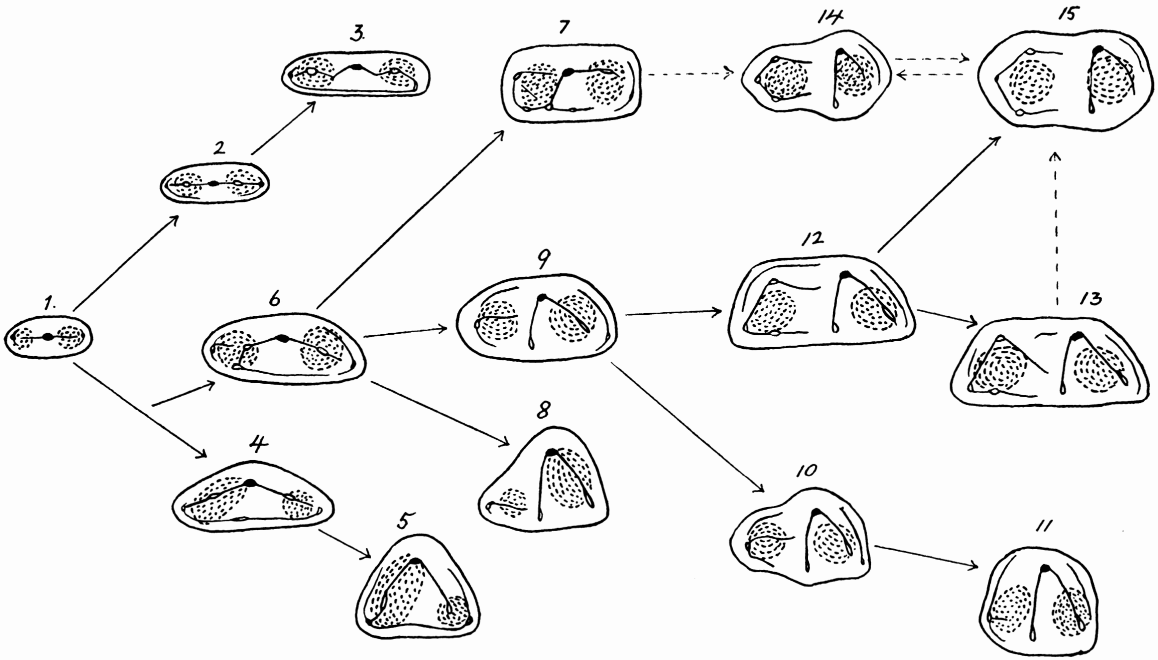

Fig. 9. Suggested evolution of the lower molar. The protoconid is marked in black; the position of the roots is indicated by stippling.

Stage A: (1) hypothetical primitive condition, (2) primitive Triconodont, e.g., *Amphilestes,* (3) advanced Triconodont, (4) primitive Symmetrodont, e.g., *Tinodon,* (5) advanced Symmetrodont, e.g., *Spalacotherium.*

Stage B: (6) hypothetical primitive Pantothere, (7) Docodontoid, (8) Dryolestoid, (9) hypothetical intermediate condition, (10) primitive zalambdodont, (11) advanced zalambdodont.

Stage C: (12) primitive dilambdodont, (13) advanced dilambdodont, (14) Leptictid, (15) tritubercular.

Triconodonta, and must be regarded as having been secondarily lost in such forms as *Tenrec* and *Solenodon.* In *Deltatheridium* the condition of wear of the teeth is such that it is not possible to state definitely that no metacone was present; if so, it probably resembled the metacone of *Palaeoryctes* or *Puercolestes.* In the most primitive forms the metacone is merely an elevation of the posterior crest of the paracone, and it takes part in the shear against the anterior crest of the protoconid (on which the paraconid develops). As the development of the hypoconid pushes the paracone forwards, away from the protoconid, the metacone becomes more distinct from the paracone and takes over the function of shearing against the protoconid-paraconid crest. The groove between the metacone and the paracone receives the hypoconid, and in many dilambdodonts this groove becomes V-shaped and its edges shear with the crests of the V-shaped hypoconid.

In the trituberculates the paracone and metacone are displaced buccally, so that they bite outside the lower teeth and largely lose their shearing function. Correlated with this is the reduction of the shearing function of the protoconid and hypoconid; the paraconid, which no longer shears with the metacone, is also reduced. At the same time the lingual part of the upper molar enlarges and becomes complex. The protocone bites into the talonid basin as usual, and on its anterior and posterior crests there develop respectively the protoconule, which takes over from the protocone its shear with the metaconid, and the metaconule, which probably primitively sheared in front of the paraconid. The hypocone bites into the trigonid basin of the more posterior lower molar. The tritubercular tooth is apparently more plastic than the other types, and its evolutionary success is probably due to the large variety of adaptational modifications into which it has radiated. By reduction of the height of the cusps a flatter crown is attained, and the orthal type of jaw motion is lost. By the union of the cusps into ridges in various ways, grinding teeth, functioning with a horizontal motion of the jaw, were evolved.

CONCLUSIONS.

The Tritubercular Theory, though true for the groups to which it was originally applied, the Ungulates, Primates and Carnivora, breaks down when applied to more primitive mammals. A study of the known Jurassic mammals appears to indicate that the zalambdodont dentitions of Tenrecoidea, Chrysochloroidea and perhaps *Notoryctes* retain the largest number of Pantotherian characters at the present day, and must be regarded as the most primitive existing dentitions. The dilambdodont teeth of opossums, many bats, Soricoids, *Tupaia* and others represent a further step forward in the evolution of the trituberculate teeth, which have probably been derived from dilambdodont teeth independently in different groups. This is fairly clear in some cases: the buccal styles are lost or reduced in some Cretaceous opossums and many modern Marsupials, in many bats, and in *Ptilocercus*, all of which belong to groups which contain many types having dilambdodont teeth. The position of the paracone and metacone far from the buccal edge is to be regarded as a primitive character: it is found in a number of Creodonts (e.g., *Deltatherium*, *Oxyaena*), some Ungulates (e.g., *Pantolambda*, Titanotheres, Chalicotheres), and possibly also in a number of rodents. The usual view, that these represent departures from a primitive condition in which the paracone and metacone were buccal is probably incorrect. This view seems to be held by Simpson, who in his description of the "tribosphenic" molar (1936) says that there was probably a wide external shelf in primitive mammals.

The theory outlined in this paper solves the "premolar paradox" of Gregory (1934). The similitude in many mammals between the posterior premolars and the molars is in Gregory's view due to convergence, as he holds that the inner cusp (protocone) of the molars is homologous with the anterior buccal cusp (paracone) of the premolars. It seems unlikely that teeth so close together as p^4 and m^1, and so similar as these teeth frequently are, should differ so fundamentally in morphology. This difficulty disappears if one accepts the view that the paracone is the original molar cusp, and that, in evolution as in ontogeny and in the premolar series, the protocone has arisen as a ledge at the base of the paracone. The Premolar Analogy Theory, that the stages through which antemolar teeth pass in their progression towards the molar pattern represent stages in the evolution of the molar pattern, is, I believe, essentially true. In the evolution of the dentition the teeth that are functionally the most important have been the most progressive, while the anterior premolars and milk molars, which are functionally the least important, have tended to retain archaic characteristics.

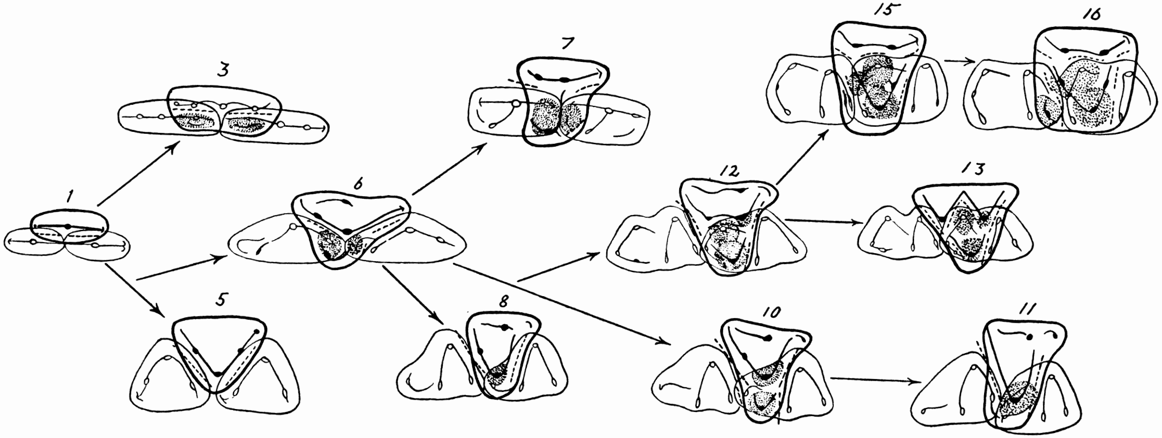

Fig. 10. Suggested evolution of occlusal relations. One upper molar and two lower molars are shown in each example. The numbers correspond to those of Figs. 8 and 9, with the addition that (16) represents an advanced tritubercular type with a hypocone (quadritubercular type). The planes of shear are marked by broken lines the crushing areas are stippled.

Owing to the great difference between upper and lower molars of existing mammals, theories of the homology of upper and lower molar cusps have been very diverse. The view of Osborn, which is expressed in the nomenclature in common use, is based upon his conception of the development of the tritubercular tooth in the Mesozoic, a conception which has had to be modified in the light of subsequent knowledge. Osborn's view is based on the similarity between the upper and lower teeth of the forms now called Triconodonts and Symmetrodonts. It is of course possible that this similarity is entirely deceptive (as I believe are the similarities noted by Frechkop (1933) between the upper and lower molars of various rodents), but the early geological age of the teeth, and their similarities to those of reptiles, suggest that Osborn was probably correct. He called the three main cusps in the upper molar, paracone, protocone, and metacone, and in the lower molar, paraconid, protoconid and metaconid. These terms have been widely applied to modern teeth, but I believe that Osborn's views of the relation between the teeth of Triconodonts and those of trituberculates are erroneous. Study of the premolars indicates that the three cusps should be called "anterior accessory cusp," paracone and metacone in the upper molar, and paraconid, protoconid and "posterior accessory cusp" in the lower molar. The so-called accessory cusps are lost in the molars of Pantotheres and later mammals, so that the homology of the paracone to the protoconid is all that remains. It seems likely that the buccal side of the upper molar corresponds to the lingual side of the lower molar (e.g., in Symmetrodonts, as the paracone moves away from the buccal edge, the protoconid moves away from the lingual edge), and the lingual metaconid may correspond to the large buccal style that occurs in Dryolestidae and probably also in other zalambdodonts and a number of dilambdodonts. The protocone probably has no homologue in the lower teeth, and the hypoconid probably has no homologue in the upper teeth.

The occlusion of teeth is a good example of the mutual adaptation of parts of the body. Evolution has proceeded in the teeth of both jaws in such a way as to improve their mode of interaction on each other. To some extent the upper and lower teeth are probably correlative in their variations, i.e., they are affected in the same way by the same genes. This probability is easy to see in cases where the upper and lower teeth are closely similar, as in Triconodonts and Symmetrodonts, and in the anterior teeth of later mammals. In other cases the similarity between the teeth of the two jaws has been masked by the development of new cusps in the teeth of one jaw only. The divergence between the teeth of the two jaws is a particular case of the general problem of morphological differentiation, and is presumably of the same character as the divergence between teeth in the same jaw, e.g., canines and molars. Natural selection has acted not upon individual teeth but upon the mammals possessing them, and the adaptive character of the dentition has all along been dependent upon the interrelations between the teeth of the two jaws, rather than upon the characteristics of teeth taken singly. This implies that any mutation in a tooth of one jaw, if it is not correlated with a similar mutation in the teeth of the other jaw, would probably cause malocclusion and would be disadvantageous, unless the change were very small. A certain amount of adjustment is of course possible by alterations in the relative position of the teeth during eruption, and by subsequent wear, but the greater part of dental evolution appears to have taken place by the accumulation of numerous small mutations rather than by a small number of large ones. The great variability of teeth is obvious to anyone who examines a series of individuals of any mammalian species, and in spite of this variability the upper and lower teeth nearly always occlude. How far this mutual adaptation is post-eruptive, and how far it is due to basic characteristics of the morphology of the dentition, it is impossible to say at present.

ACKNOWLEDGMENTS.

The work described in this paper was carried out partly in the Zoölogical Museum, Cambridge, England, under the direction of Dr. C. Forster-Cooper, and partly in the American Museum of Natural History, under Prof. W. K. Gregory. I am also indebted to Dr. G. G. Simpson for some valuable criticisms and for the loan of material, to Dr. M. R. Thorpe for permission to examine Mesozoic material in the Yale Peabody Museum, and to Dr. L. A. Hopwood of the British Museum for much kind assistance. The work in America was carried out during the tenure of a Commonwealth Fund Fellowship at Columbia University.

SUMMARY.

The upper molars of primitive mammals, with the exception of the Triconodonta and probably also of the Symmetrodonta, are triradiate structures supported by three roots. The three-rooted condition has been derived from a two-rooted condition by the subdivision of the posterior root consequent on a broadening of the posterior part of the crown. The lower molars remain two-rooted.

The most primitive cusps are the paracone in the upper molar and the protoconid in the lower molar. These cusps are serially homologous with the tips of the canines and are the first cusps to appear in ontogeny. The protocone has arisen at the base of the paracone in the posterior part of the crown.

In primitive Tertiary mammals the relative size of the other cusps is correlated with the position of the paracone on the crown, which varies considerably. Three main types can be distinguished: (a) zalambdodont, (b) dilambdodont, (c) tritubercular.

The tritubercular type, in which the lingual part of the upper molar (including the protocone) and the talonid region of the lower molar are enlarged, while the buccal styles and the paraconid are reduced, is the most advanced of the three types; the zalambdodont type, in which the protocone is small, the buccal styles are enlarged, the metacone is indistinctly differentiated from the posterior crest of the paracone, and the talonid is small without a distinct hypoconid, is the most primitive. The teeth of Pantotheria approach more closely to the zalambdodont type than to the others.

The evolution of the occlusal function is described.

The principal differences from the classical theory of Cope and Osborn are:

(a) the protocone and the metaconid were absent in the most primitive mammals (Triconodonta and Symmetrodonta);

(b) the talonid did not arise as an addition to a tooth that originally consisted of the trigonid only;

(c) the hypoconulid is the oldest talonid cusp, and the hypoconid is not present in any known Jurassic mammal;

(d) the possession of a broad region buccal to the paracone and metacone is a primitive character in Cretaceous and Cenozoic mammals;

(e) the reduction of the paraconid is not correlated with the development of the hypocone.

REFERENCES.

Bolk, L.: 1921-2, Odontological essays, *J. Anat., Lond.* LV, 138; LV, 219; LVI, 107; LVII, 55.

Butler, P. M.: 1937, Studies of the mammalian dentition. I. The teeth of *Centetes ecaudatus* and its allies. *Proc. zool. Soc., Lond.* Ser. B, 103.

——————: 1939a, Studies of the mammalian dentition. Differentiation of the post-canine dentition. *Proc. zool. Soc., Lond.* Ser. B, CIX, 1.

——————: 1939b, The teeth of the Jurassic mammals. *Proc. zool. Soc., Lond.* Ser. B, CIX, 329.

Cope, E. D: 1874, On the homologies and origin of the types of molar teeth of Mammalia educabilia. *J. Acad. nat. Sci., Phila.* VIII.

Forsyth-Major, C. J.: 1897, On some Miocene squirrels, with remarks on the dentition and classification of the Sciurinae. *Proc. zool. Soc., Lond.* 179.

Frechkop, S.: 1933, Notes sur les mammifères. XIII. Note préliminaire sur la similitude des molaires supérieures et inférieures. *Bull. Mus. Hist. nat. Belg.,* VIII, no. 6.

Friant, M.: 1933, Contribution a l'étude de la differentiation des dents jugales chez les mammifères: essai d'une theorie de la dentition. *Publ. Mus. nat. Hist. nat.,* Paris. I, 1.

Gervais, P.: 1854-5, *Histoire Naturelle des Mammifères.* Paris.

Gidley, J. W.: 1906, Evidence bearing on tooth-cusp development. *Proc. Wash. Acad. Sci.* VIII, 91.

Gill, T. N.: 1885, *Standard Natural History.* V, 134. Boston.

Gregory, W. K.: 1916, Studies in the evolution of the Primates. *Bull. Amer. Mus. nat. Hist.* XXXV, 239.

——————: 1934, A half-century of Trituberculy. The Cope-Osborn theory of dental evolution, with a revised summary of molar evolution from fish to man. *Proc. Amer. phil. Soc.* LXXIII, 169.

——————, and Simpson, G. C.: 1926, Cretaceous mammal skulls from Mongolia. *Amer. Mus. Novit.* No. 330.

Hertz, M.: 1925, Beobachtungen am primitive Säugetiergebissen. *Z. Morph. Ökol. Tiere.* IV, 570.

Hinton, M. A. C.: 1926, *Monograph of the Voles and Lemmings (Microtinae). Brit. Mus. nat. Hist.* Memoir.

Leche, W.: 1907, Zur Entwickelungsgeschichte des Zahnsystems der Säugetiere zugleich ein Beitrag zur Stammegeschichte dieser Tiergruppe. 2.Teil: Phylogenie. 2.Heft: Die Familien der Centetidae, Solenodontidae und Chrysochloridae. *Bibl. Zoologica,* XX.

Naef, A.: 1925, Notizen zur Morphologie und Stammegeschichte der Wirbeltiere. 6. Zur Stammegeschichte der Säuger-Molaren. *Biol. Zbl.* XLV, 668.

Orban, B., and Muller, E.: 1929, Die Entwicklung der Bifurcation mehrwurzeliger Zähne. *Z. ges. Anat. 1. Z. Anat. EntwGesch.* XC.

Osborn, H. F.: 1888, The evolution of mammalian molars to and from the tritubercular type. *Amer. Nat.* XXI, 1067.

Patterson, B., and McGrew, P. O.: 1937, A Soricid and two Erinaceids from the White River Oligocene. *Field Mus. Publ. Geol. Ser.* VI, 245.

Röse, C.: 1892a, Phylogenese des Säugetiergebisses. *Biol. Zbl.* XII.

——————: 1892b, Uber die entstehung und Formabänderung der menschlichen Molaren. *Anat. Anz.* VII.

Schlaikjer, E. M.: 1933, Contributions to the stratigraphy and palaeontology of Goshen Hole area, Wyoming. I. Detailed study of a new Zalambdodont Insectivore from the Middle Oligocene. *Bull. Mus. comp. Zool., Harv.* LXXVI, 1.

Scott, W. B.: 1892, Evolution of the premolar teeth in the Mammalia. *Proc. Acad. nat. Sci., Phila.* 405.

Simpson, G. G.: 1928a, Affinities of the Mongolian Cretaceous Insectivores. *Amer. Mus. Novit.* No. 330.

————: 1928b, *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum.* London.

————: 1929, American Mesozoic Mammalia. *Mem. Peabody Mus., Yale,* III, Pt. 1.

————: 1936, Studies of the earliest mammalian dentitions. *Dent. Cosmos.* LXXVIII, 791 and 940.

————: 1937a, The Fort Union of the Crazy Mountain Field, Montana, and its mammalian faunas. *Bull. U. S. nat. Mus.* No. 169.

————: 1937b, Skull structure of the Multituberculata. *Bull. Amer. Mus. nat. Hist.* LXXIII, 727.

Stirton, R. A.: 1930, A new genus of Soricidae from the Barstow Miocene of California. *Univ. Calif. Publ. Bull., Dept. Geol. Sci.* XIX, 217.

Taeker, J.: 1892, *Zur Kenntniss der Odontogenese bei Ungulaten.* Dorpat.

Winge, H: 1882, Om Pattedyrenes Tandskifte isaer mer Hensyn til Taendernes Former. *Vidensk. Medd. naturh. Foren. Kbh.,* 15.

Woodward, M. F.: 1896, Contributions to the study of mammalian dentition. Part II. On the teeth of certain Insectivora. *Proc. zool. Soc., Lond.,* 557.

Wortman, J. L.: 1902, Studies of Eocene Mammalia in the Marsh Collection, Peabody Museum, *Amer. J. Sci.* XIII, 215.

UNIVERSITY COLLEGE,
EXETER, ENGLAND.