On the Upper Triassic Mammals

F. R. Parrington

Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

[231]

ON THE UPPER TRIASSIC MAMMALS

BY F. R. PARRINGTON, F.R.S.†

University Museum of Zoology, Cambridge

CONTENTS

1. The various accounts of the Triassic mammals which have been published since 1941 are summarized.

2. It is claimed that the identification of a tooth of *Kuehneotherium* as evidence that a similar tooth of *Eozostrodon* cannot be identified is fallacious. It is held that for the most part differences in the appearances of the roots of these teeth illustrate growth stages and do not provide useful taxonomic data. *Eozostrodon problematicus* and *Morganucodon watsoni* are held to be synonyms of *Eozostrodon parvus*.

3. The dentition of *E. parvus* is described and the formula is given as

$$I\ \tfrac{4}{4}\quad C\ \tfrac{1}{1}\quad PM\ \tfrac{5}{4}\quad M\ \tfrac{4}{5}.$$

4. The loss of premolars, followed by the plugging of their sockets by bone, is described, and it is shown that in the lower jaw the process usually starts with the first and then the second premolars. Examples of irregular loss and plugging are given and evidence of the same happening taking place in the upper jaw is described.

5. A series of abnormal postcanine teeth are described. Some are of interest in the light they throw on possible relationships.

6. On the evidence of four cases of tooth replacement, and other relevant considerations, it is claimed that the mammalian diphyodont condition had been achieved in *Eozostrodon*. It is suggested that, in view of the great amount of tooth wear found in many teeth, such a reduction could only have been tolerated if the life cycle was short. This is in accordance with the very small size of the animal.

7. Some evidence on the nature of the hind limb is given.

8. Trituberculate teeth of the form *Kuehneotherium praecursoris* are described. It is shown that some are very similar to those of the symmetrodont *Spalacotherium* and support the interpretation that the form is a symmetrodont as first recognized by Kühne and later demonstrated by Crompton & Jenkins.

9. It is claimed that the view that the eozostrodonts are triconodonts and represent the basic mammalian stock from which later triconodonts, the trituberculates, the docodonts and possibly the multituberculates evolved, is well founded.

† Present address: Kaim Hill, Lochwinnoch, Renfrewshire, Scotland.

1. Introduction

In 1939, while collecting teeth of the rare and problematical little microlestids now known as *Haramiya* from Rhaetic fissure fillings in Carboniferous limestone quarries at Holwell in Somerset, Walter Kühne obtained two teeth of quite different form. These were described as triconodonts and given the names *Eozostrodon parvus* and *E. problematicus* (Parrington 1941). A little later Peyer obtained similar teeth from Rhaetic deposits at Hallau in Switzerland, and in 1947 models of two of these teeth were described in a further account of *Eozostrodon* (Parrington 1947). Kühne discussed the age of the specimens from Somerset and concluded that, in view of the finds in Switzerland, it must be regarded as Rhaetic but without regard for Upper or Lower Rhaetic (Kühne 1947).

After the war Kühne carried his explorations of limestone fissures into Wales and in 1949 he described a tooth which he had collected from Duchy Quarry in South Glamorgan. This tooth, like the tooth called *E. problematicus*, was somewhat damaged and Kühne thought that it lacked the 'tilting of the cusps in a posterior direction as shown on the two teeth of *Eozostrodon*' and gave it the name *Morganucodon watsoni*. He was quite confident that this tooth, like those from Holwell and Hallau, belonged to a triconodont mammal, and he attempted a reconstruction of the lower dentition. Having accepted the larger of the two teeth from Hallau as an upper 'molar' he placed the smaller one as a lower 'premolar'; he put *E. parvus* also as a lower 'premolar'; *E. problematicus* in the position of a posterior 'premolar' or an anterior 'molar'; and the new tooth, *Morganucodon*, as a posterior 'molar'. Only in putting *E. parvus* as a lower rather than upper tooth was he wrong. Kühne came to the conclusion that '*Eozostrodon* and its allies were certainly ancestral to the Jurassic Triconodonta and possibly all other mammals except the Monotremata'. Examination of the excellent figures of *Morganucodon*, and of the now abundant material collected from the same neighbourhood, show that the two forms *Eozostrodon* and *Morganucodon* cannot be distinguished by the tilting of their cusps as Kühne believed.

Perhaps the most important character of the new tooth was the presence on the internal cingulum of a distinctly enlarged cuspule. This cuspule has caused considerable discussion and not a little confusion and it is proposed to call it the 'Kühnecone', a name which avoids involvement in the difficult and contentious matter of cusp nomenclature (Parrington 1967). In 1949, or thereabouts, Professor P. M. Butler made the suggestion, *verbis*, that *Morganucodon* might in fact be allied to *Docodon*, a rather curious Upper Jurassic mammal which had been included by Simpson (1929) among the Pantotheria. Butler claimed that if the anterior accessory cusp of *Morganucodon* were to be lost the likeness to the docodont *Peraiocynodon* would be remarkable. Kühne accepted this view, which he promulgated in a typewritten 'Addendum' to the reprints of his account of *Morganucodon*, stating that the form was in fact a 'prepantothere'.

The discovery of a triconodont mammal in Rhaetic deposits was an event of the greatest importance to those interested in the very rare remains of Mesozoic mammals. Yet in 1950 Kühne was able to announce a further important discovery; that of a trituberculate tooth, a symmetrodont, from the same quarry that had yielded *Morganucodon*. He designated this tooth as 'Duchy 33'. The discovery of both triconodont and symmetrodont teeth in Rhaetic deposits changed the whole picture of the origin of the triangles of cusps which (as had been known since the previous century) dominate the crowns of almost all early Tertiary mammals; and the objections which had been raised to Osborn's theory of the origin of the triangles now required entirely fresh consideration. At the same time Kühne announced the discovery of

a further fifty teeth, most of which were 'triconodonts' similar to those collected by Peyer at Hallau, and announced that Butler had suggested that *Morganucodon* might be a 'predoco-dontid'. This was the first time that the possible alliance between *Morganucodon* and *Docodon* was officially published.

In 1956 D. M. Kermack, Kermack & Mussett announced the discovery in the previous year of the remains of both triconodonts and symmetrodonts in three localities in Glamorgan (including Kühne's Duchy Quarry), the triconodont being represented by thousands of specimens—an extraordinary discovery in view of the hitherto great rarity of Mesozoic mammals. In this announcement it was stated that the squamoso-dentary articulation had been found; that the triconodont had a monotreme-like extension of the periotic and so should probably be classified as a monotreme; and that it had an 'angle' (i.e. an angular process) to the dentary and so the lack of such a process in later triconodonts must be secondary.

In 1956 also, Patterson published a paper of great importance. In it he described the teeth of a true therian which lived about the middle of the Cretaceous Period and was thus the earliest known form. In addition he discussed the Rhaetic mammals and their relationships. He accepted *Eozostrodon* as a triconodont and *Morganucodon* as a docodont, but he put forward a new interpretation of the angular process in this form. Because it is situated further forward than the similar processes in such forms as pantotheres, he suggested that it was not a true angular process but a 'pseudangular' process for the attachment of depressor muscles, possibly the monotreme detrahens muscle. But there are reasons for rejecting this interpretation. First, no mammals are known which have processes of at all comparable size for the attachment of jaw-opening muscles, the forms mentioned by Patterson (*Tachyglossus*, *Solenodon*) having structures which are trivial by comparison. Secondly, there is no satisfactory functional explanation available for this interpretation, since there would be no obvious mechanical advantage obtained by the provision of such a process. On the contrary it is a common happening for adductor muscles (masseter, pterygoideus) to be provided with such an angular process for which a sound mechanical explanation is available, a suitable process allowing the maximum biting force to be achieved when the teeth are about to be clenched rather than when the jaws were agape (Parrington 1960). Moreover, a convincing mechanical explanation is available to account for the forward position of the process in very primitive mammals in that it transfers the biting force on to the teeth and off the (weakened) articulation (Crompton 1963). Furthermore, this interpretation is consistent with the other data, the retention of the double articulation in the Upper Jurassic docodonts (inferred by the presence of the large mandibular trough) requiring the retention of the forward position of the process, while evidence for the backward movement of the process elsewhere is given by *Peramus*, a pantothere now sometimes held to be ancestral to the Theria in general. Here the process is about intermediate between the anterior position and the more normal posterior position and in this Upper Jurassic form the full mammalian jaw articulation appears to have been achieved. Patterson, like Kretzoi (1946) before him, concluded that the Docodonta form a distinct order and that they and the triconodonts, multituberculates and monotremes differ fundamentally from the symmetrodonts, pantotheres and Theria in never having passed through a condition in which the molar teeth had reversed triangles of cusps.

It was in the same year that Peyer (1956) described the teeth he had collected at Hallau and showed that his collection included haramiyids, triconodonts and symmetrodonts.

The year 1958 saw two important papers published on these new mammals. K. A. Kermack & Mussett described the posterior part of the dentary in detail, calling attention to a conspicuous

trough and ridge which, they claimed, must have housed and supported the articular bone, an inference strengthened by the presence in the more anterior internal mandibular groove of pieces of bone which they regarded as remains of either the prearticular or the angular. K. A. Kermack & Mussett accepted the similarities between the lower molars and those of the docodonts; claimed that the upper molars resembled those of the triconodonts; stated that the 'similarities in the structure of the dentary in *Docodon* and *Morganucodon* count for very little in proving relationships'; yet they classified the form as a docodont, a classification they have maintained in later writings. If the form of the lower jaw is the test of a docodont then the symmetrodont *Kuehneotherium* must also be a docodont (Kermack, D. M., Kermack & Mussett 1968).

K. A. Kermack & Mussett put forward a classification of early mammals which has most undesirable consequences. A new subclass, the Eotheria, was proposed for the Docodonta but this was, in fact, described as a Grade and should, on this description and the authors' own opinions as to the jaw structures, have included the Rhaetic symmetrodont. The new subclass was subsequently abandoned (K. A. Kermack 1965) only to be revived still later (K. A. Kermack 1967c). But another, and much more troublesome, proposal was advanced. In his 1928 catalogue of Mesozoic mammals Simpson had recognized considerable similarities between his newly founded order Symmetrodonta and the Pantotheria and plainly felt that they were likely to be of common origin. But he was faced with the fact that, though the Symmetrodonta seemed to be the more primitive of the two groups, it appeared for the first time only in the Upper Jurassic, whereas the order Pantotheria was already present in the Middle Jurassic and so, except in his diagram, where he indicated this relationship, he did not group the two orders together. But later he proposed that they should be grouped together in an Infraclass Pantotheria (Simpson 1945). Kermack & Mussett objected to this use of Marsh's term Pantotheria for both the Infraclass and Order (though they themselves use the term Marsupialia for both an Infraclass and Order in the same classification), they coined the new name Eupantotheria for the pantotheres and retained the name Pantotheria for the new Infraclass which included the Symmetrodonta. This proposal has consequences which are highly undesirable. If accepted, it results in all the extensive literature about the Pantotheria (*sensu* Simpson 1928) which was published between 1928 and 1968 becoming incorrect in the use of the word, and every future reference to work carried out during these years will require to be qualified. Still worse, it becomes possible, since the symmetrodonts are included among the Pantotheria, to call the Rhaetic symmetrodont a pantothere as Kermack has since made a habit of doing. Yet, as Crompton & Jenkins (1967) have shown, Kühne was perfectly right when he identified his specimen 'Duchy 33' as a symmetrodont. Such muddling of the literature is not to be accepted. Instead of proposing a new name for the so-often discussed Pantotheria, all that was necessary was to put forward a name for the new Infraclass and all confusion would have been avoided. Even this is unnecessary since Osborn's term Trituberculata is both available and suitable because the Infraclass would, in general, contain the animals he placed in his order. This is the classification put forward by Romer (1966); it expresses the views of the relationships of these form which appear to satisfy most students of these animals; and it introduces no unnecessary complexities of nomenclature to confuse future students.

The second important paper published in 1958 was one in which Kühne described the specimens he had mentioned in his 1955 publication. Boldly he attempted to reconstruct the dentition from his isolated teeth giving this form a minimum of fourteen postcanine teeth

between the two jaws. He claimed incorrectly that the premolariform teeth shaded imperceptibly into the molariform teeth with no clear distinction between the two, a feature in which the form differed from all other Mesozoic mammals and was therefore more primitive. Like Kermack & Mussett he recognized the compound nature of the lower jaw but he claimed that his 'Morganucodon' was ancestral to both the triconodonts and the pantotheres and that the symmetrodonts were related to neither and were probably an independent line of evolution from the reptiles. In conjunction with this he identified the small lingual cusp on the lower molars, here called the Kühnecone, as the incipient metaconid.

In 1959 K. A. Kermack & Mussett published a semi-popular account of their discoveries, which included photographs of two maxillae and a dentary carrying most of the postcanine teeth, and they gave the dental formula as I $\frac{5}{5}$, C $\frac{1}{1}$, PM $\frac{2}{2/3}$, M $\frac{4}{5/4}$, stating that the total number of lower postcanine teeth was always seven. This article was important for several reasons. It long remained the only account of the dentition other than that given by Kühne of his isolated and for the most part damaged teeth; it gave a photograph of a monotreme-like shoulder girdle; and it described a dentary which resembled that of 'Morganucodon' but lacked the angular process. This latter was reasonably ascribed to the symmetrodont. But the dental formula is extensively wrong.

The next decade was remarkable for the description of four new Triassic mammals.

First the animal Sinoconodon rigneyi from China was described by Patterson & Olson (1961) as a triconodont mammal and a member of the subfamily Triconodontinae. Yet the animal lacked premolariform teeth and cingula were said to be 'essentially non-existent'. The animal appeared to be mammalian in such features as twin-rooted postcanine teeth, an alisphenoid with a foramen ovale and a fenestrated false palate, but peculiar and primitive in retaining the splenial bone. They denied that it could be a 'Morganucodont'. Crompton (1964) pointed out that the appearance of the dentary recalled those of cynodonts and suggested that the form was quite likely to prove to be a surviving cynodont. Recently Mills (in press) has suggested that it is in fact a 'Morganucodont' and allied it to Megazostrodon. Few people would today accept this animal as a member of the Upper Jurassic subfamily Triconodontinae, though the presence of a splenial can be regarded as the retention of a reptilian bone now known to have survived in various early mammals and so might not be held against this view. Patterson & Olson claimed that the form had a pseudangular process and that this was for the attachment of a depressor muscle other than the therian digastric, probably the monotreme detrahens muscle, a suggestion which received support from Simpson (1961). But there is in fact no real process on the dentary of this form, only a thickening of the angle, and Watson described such a thickening on the dentary of the cynodonts half a century ago. The cynodonts possessed a retroarticular process which can only reasonably be interpreted as providing the position of attachment of the reptilian depressor mandibulae muscle. As pointed out earlier an interpretation of the angular process as the same as that found in other primitive mammals is supported by a consideration of its functional possibilities (p. 233).

In an important paper published in 1963 K. A. Kermack described in detail the periotic bones of the triconodonts Trioracodon and Triconodon and the basisphenoid of the latter. He claimed that the periotics were essentially similar to that of Morganucodon in having an anterior lamina enclosing the mandibular branch of the trigeminal nerve and so forming a foramen pseudovale. He claimed also that it could be shown that, as in Ornithorhynchus as described by Watson (1916), the semilunar ganglion lay within the periotic flange, instead of, as in reptiles,

in the cavum epeptericum. He claimed that the small size of the foramen for the facial nerve indicated that the mammalian facial muscles had not been fully developed but gave no details. He withdrew the claim that *Morganucodon* was a monotreme, but did not point out that the condition of the periotic supported the claim that it was a triconodont.

In 1963 Rigney gave a brief account of an eozostrodont from China which, on account of its dental formula, he designated a new species of morganucodont. *M. oehleri*. The importance of this discovery lay in two things; the evidence that this form of early mammal occurred in Asia and the discovery of an uncrushed skull which will supplement the limited information available from the scraps collected from fissures.

The next discovery of a Triassic mammal to be announced was that by Crompton (1964) of the skull and lower jaws of an eozostrodont from the Red Beds of Basutoland in South Africa. Named *Erythrotherium parringtoni* in a preliminary account based largely on the lower jaw and its dentition, the animal is important, not only because like the Chinese form the skull is present and will yield valuable information, but also because it shows that the eozotrodonts ranged far into the Southern Hemisphere. Furthermore it provides some evidence of value in the problem of tooth replacement (p. 261).

In 1965 there was published a paper by K. A. Kermack, Lees & Mussett on the lower molar of a Cretaceous mammal, named *Aegialodon*, and believed to be the earliest therian to have evolved a protocone. The importance of the paper in this account lies in the description it gave of two trituberculate teeth from the Triassic-filled fissures, an upper and a lower, which appeared to be those of a symmetrodont but were regarded by them as a pantothere. The lower tooth is exceedingly like that of *Spalacotherium*, though the cusps are less acutely angled and the external cingulum is only partly formed. The upper tooth is exceedingly like the molar tooth called *Eurylambda* by Simpson, a tooth which, he felt, might be the upper molar of the symmetrodont called *Tinodon* by Marsh (Simpson 1928, 1929). No attempt was made to compare and contrast these new teeth with those of symmetrodonts, as Crompton & Jenkins (1967) have done, seeking likenesses and differences on which a balanced judgement could be made. The reasoning is difficult to follow. It appears to be that since these new teeth might have given rise equally well to those of pantotheres and symmetrodonts, they must be classed with the former because these were the main line of evolution. Zoologists classify animals according to degrees of likeness. By the same reasoning a primitive agnathan, at the base of the vertebrate stem, would become a gnathostome. In fact the new form resembles the known symmetrodonts more closely than any pantothere yet described.

In 1967 (a) K. A. Kermack discussed molar evolution in Mesozoic mammals describing one upper and one lower molar of the Triassic symmetrodont. He claimed that the cusps of both upper and lower molars formed obtuse-angled triangles, in both cases nearly right-angled triangles. The specimens figured, however, show the principal cusps arranged in lines meeting at about 125° and 115°. This is important in view of his findings, for the wide angles of the great majority of molars (very few approach 90°) conform more closely to those of the symmetrodonts than to those of pantotheres. He reported the presence of a 'tiny talonid' with a hypoconulid and claimed that 'although these Welsh Rhaetic teeth lead as easily to the symmetrodonta as to the later eupantotheres, they are best classified in the latter order'. No reason for this statement was given unless this was one to the effect that *Amphitherium* (a pantothere from the Middle Jurassic) retained 'great evolutionary potential'. He also described for the first time a 'linear lower molariform' tooth as a pantothere tooth from which sort, he claimed, the Middle

Jurassic amphilestine triconodonts could have evolved. Finally he discussed *Aegialodon*, from the Cretaceous, and its importance in mammalian history.

In 1967 (*b*) also, K. A. Kermack discussed the interrelations of early mammals. Claiming that *Diarthrognathus* was probably a late cynodont derivative quite unrelated to the other borderline forms, he divided the Mesozoic mammals into the Theria and non-Theria, the former with the mandibular nerve leaving the brain case through a true foramen ovale in the alisphenoid, the latter having the periotic with an expanded wing and a foramen pseudovale for the nerve. He claimed that these latter forms, the Docodonta (*sensu* Kermack & Mussett), Triconodonta, Multituberculata and Monotremata, were of quite separate reptilian origin from the therian mammals which comprised the Eupantotheria, the Symmetrodonta and the Eutheria. The amphilestines were regarded as of uncertain origin, belonging, possibly, to either group.

In the same year Crompton & Jenkins (1967) published a redescription of the American Upper Jurassic symmetrodonts *Tinodon* and *Eurylambda*, figuring the teeth in detail and discussing the significance of the wear facets. They showed that in *Tinodon* (*Eurylambda* is known from a single tooth) the angulation of the principal cusps of the molars ranged from a condition in which they were more or less in a straight line to one in which they were angulated to about 100°. They then compared these teeth with those of the trituberculate from Wales (designated a Welsh pantothere by K. A. Kermack, Mussett & Lees) showing the remarkable resemblances and claimed that the Welsh animal could only be regarded as a symmetrodont.

In 1967 Parrington, working on new material, discussed the relationships of these earliest mammals. Claiming that *Morganucodon* is a synonym of *Eozostrodon*, he argued that the sum of the characters of the 'premolars' and 'molars', both upper and lower, showed plainly that it was much more closely allied to the Upper Jurassic triconodontines than to the docodonts. He described the wear of the molar teeth and claimed that it gave them a shape which approximated to that of the contemporaneous symmetrodont. He claimed also that the wide-angled symmetrodont teeth resembled those of *Eozostrodon* remarkably closely and suggested that any such triconodont which tended to angulate its molar cusps might suffer less wear and that this might have a selective advantage. He suggested that the two Upper Triassic mammals were closely related and that it might still be shown that all Mesozoic mammals evolved from one triconodont-like form.

Next, in 1968, D. M. Kermack, Kermack & Mussett gave the name *Kuehneotherium praecursoris* to the Triassic symmetrodont, describing it from ten teeth and four fragments of dentaries obtained, together with five teeth of *Eozostrodon*, from a pocket in Pont Alun quarry. They claimed that one of the premolariform teeth which they identified as belonging to *Kuehneotherium* could not be distinguished from the type specimen of *Eozostrodon parvus*, which was thus not determinable, and made no mention of the existence of the tooth described as *E. problematicus*. They claimed (p. 416) not to be able to distinguish upper from lower premolars on the grounds that there is a clear distinction between premolars and molars (the explanation is not self-evident), yet later (p. 420) noted the obvious difference between what is clearly an upper premolar, which they compared with the type of *E. parvus*, and several lower premolars which they illustrate in the following figure. They attempted a reconstruction of the dentary suggesting five or six premolars and from three to as many as six molars. Finally they offered another classification of the Mesozoic trituberculates, downgrading Simpson's order Symmetrodonta to a suborder within the order Eupantotheria of Kermack & Mussett. The circle was now complete. All were 'true pantotheres' and the position existing before Simpson

distinguished the symmetrodonts as an essentially primitive stage of organization in the formation of the trituberculate molars reigned again—in a new guise.

In 1968 Crompton & Jenkins published an important paper on early mammals. They described a new eozostrodont from South Africa, *Megazostrodon rudneri*, a second form to have the skull and lower jaws, together with postcranial material; made a detailed comparison between the molars, upper and lower, of *Eozostrodon* and *Kuehneotherium* showing that they are basically the same; described and discussed the tooth wear of these molars emphasizing the improved cutting properties indicated by the wear; showed the remarkable resemblances between the postcanine teeth of the younger specimens of the cynodont *Thrinaxodon* and the molars of *Eozostrodon*; and concluded that *Thrinaxodon* and *Eozostrodon* represented stages in the evolution of the symmetrodonts, the pantotheres and the docodonts. Their views refuted those of D. M. Kermack *et al.* published the previous year.

The most recent publication on the earliest mammals is that of Hopson & Crompton (1969). This is a substantial discussion on the origin of the Mammalia entailing an account of all the published data on the Triassic forms and an analysis of the possible polyphyletic origin of the class. Taking into account both the dentitions and the brain cases, and the detailed structures as well as functions, they concluded that the eozostrodonts were derived from the cynodont family Galesauridae and themselves represent the basic mammalian stock from which all mammalian orders were probably derived.

Mills, at a meeting of the Linnean Society held in the summer of 1970, has described and discussed the dentition of the eozostrodonts. This account is now in the press. It differs substantially from the account given here.

It will be seen from the foregoing account that there are four principal matters of dispute. These are: (i) the question of the synonomy of *Eozostrodon* and *Morganucodon*, (ii) their classification as triconodont or docodont, (iii) the correct classification of the trituberculate form *Kuehneotherium*, and (iv) the possible relationships of these two earliest known mammals.

The material described in this account was obtained partly from a block of clay found by Mr Alex Baynes in Pont Alun quarry, Glamorgan, when it was about to be lost in quarry-clearing operations; but largely from clay which had been collected several years earlier in Pont Alun quarry by Mr Les Middleton, quarryman, and stored by him in the neighbouring Ewenny quarry, but subsequently abandoned and left to weather in the open. I am greatly indebted to Mr Alex Baynes for his discovery of this material, and also to Dr K. A. Joysey who carried out the necessary salvage operations and worked out the most efficient procedures whereby the bones and teeth have been extracted from the clay. It is very unfortunate that the material, left to weather so long, has become extremely fragmentary.

It is of interest to note that while haramiyid teeth occur with *Eozostrodon* in Somerset, and with both triconodont and trituberculate teeth at Hallau, no trace of them was found in Glamorgan. Because no new data have been acquired since the specimens collected by Kühne in Somerset were described (Parrington 1947), and it is still not possible to be sure whether they are early mammals or surviving theriodonts, they are not discussed in this account.

One of the most troublesome features of the teeth of *Eozostrodon*† is the great range of size,

---

† It has recently become the fashion to describe such teeth in the language used by dentists who are concerned solely with the human dentition. This gobbledegook, in which anterior becomes medial and proximal distal, makes no pretence to greater accuracy; it has no historical precedence among zoologists; and is not used internationally. Since it serves only to obfuscate straightforward description it will not be used here.

some teeth having twice the crown length of others without showing other recognizable differences (figure 2). This has introduced a number of problems since it is not certain that only one species is present. It is convenient to suppose that only one is in fact present and that it has considerable size range, until the whole of the available material has been studied. But there is a real possibility of dimorphism.

A register has been made of the better specimens which have been numbered under the following letters: D, dentary; MX, premaxilla or maxilla; PM, premolar; M, molar; MM, milk molar; SY, symmetrodont. Since, for example, over 200 fragments of dentaries have been registered, the numbers of specimens establishing certain points have been given in the text.

Wherever helpful for making comparisons mirror images of original drawings and photographs have been used.

2. *Eozostrodon parvus* Parrington

(a) Synonomy

The introduction of the name *Morganucodon watsoni* has caused considerable confusion. Thus Patterson (1956), in his discussion of the evolution of early mammals, classified *Eozostrodon* as a triconodont and *Morganucodon* as a docodont, and the two names have appeared in many important texts. Meanwhile, K. A. Kermack, who has a large collection of Rhaetic mammals from Glamorgan, has made four statements. In 1958 he claimed that '*Morganucodon* is probably only a synonym of *Eozostrodon* Parrington (1941)', and at the International Colloquium on the Evolution of Lower and Non-specialized Mammals, held in Brussels in 1961, he announced categorically that this was so, though he continued to use the name *Morganucodon* in his publications. However, at the Fourteenth Symposium on Vertebrate Palaeontology and Comparative Anatomy held in London in 1967 he stated that the tooth named *Eozostrodon parvus* could not be distinguished from similar teeth belonging to the trituberculate animal found in the same deposits, and that the tooth named *E. problematicus* was too badly preserved to be of any use. Finally he and his co-workers have discussed the former point in their account of the mammal they have called *Kuehneotherium precursoris* (D. M. Kermack *et al.* 1968). The result of all this is that the name *Morganucodon* has appeared frequently in print yet it is clear that it is a synonym of *Eozostrodon*.

When Kühne (1949) described the first tooth from Glamorgan he thought that it lacked the 'tilting' of the cusps seen in *Eozostrodon* and gave it a new name, but he recognized that it was of the same essential type and he wrote of *E. problematicus* (p. 348) '...it compares closely, as far as it is preserved, with the new tooth from Glamorgan'. Reconstructing the lower dentition Kühne (1949, Figure 2) placed one of the teeth found by Peyer in Switzerland anteriorly, *E. parvus* slightly more posteriorly, *E. problematicus* slightly more posteriorly still, and his new type near the back. It is now clear that, except in regarding *E. parvus* as a lower tooth, he was perfectly correct. Moreover, the tilting of the cusps does not distinguish the teeth of two types. The new genus was not well established.

Next, that the tooth named *E. parvus* matches accurately the last upper premolar of the animal occurring in Glamorgan is clear from the teeth illustrated in figure 1 and many others. Kermack *et al.* do not appear to dispute this though, curiously, they do not appear to be able to recognize the tooth as an upper premolar. But they claim that it cannot be distinguished from a tooth they identify as belonging to *Kuehneotherium praecursoris*. Their reasoning is curious. The tooth they illustrate was picked out of a mixture of five teeth of '*Morganucodon*' (one upper and four

lower molars) and thirteen teeth credited to *K. praecursoris*. If they can identify this tooth as a premolar of *Kuehneotherium* and not ' *Morganucodon*' how can they then claim, as they do, that such premolar teeth of *Eozostrodon* cannot be distinguished from those of *Kuehneotherium*? Their argument is entirely without logic. It will be seen (figure 1) that their tooth has a distinct
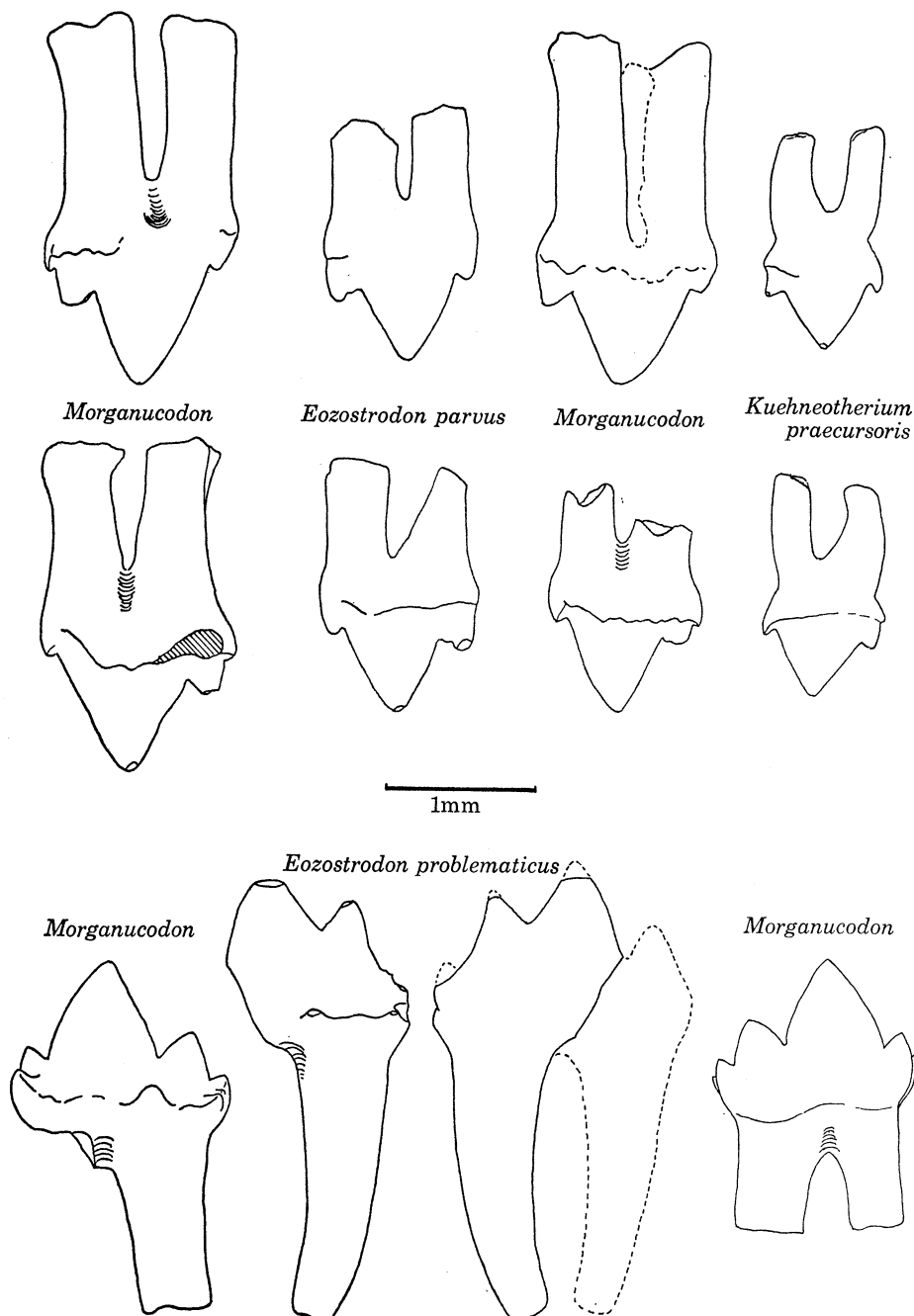

FIGURE 1. The original drawings of *Eozostrodon parvus* and *E. problematicus* for comparison with examples of '*Morganucodon*' and the tooth identified as belonging to *Kuehneotherium praecursoris*. Upper row external views of right premolars, in the case of *Eozostrodon* the fifth. Centre row internal views of the same teeth except in the third example. Bottom row internal and external views of *E. problematicus* with examples of similar teeth from Glamorgan: The drawings of *Kuehneotherium praecursoris* and the third tooth from the left in the centre row have been reversed; the former from D. M. Kermack *et al.*

constriction at the base of the crown, not seen in *E. parvus*, and that the principal cusp is proportionately larger and dominates the crown more completely. It is perhaps these features that give it a different appearance and so enable them to identify it as a premolar of *Kuehneotherium*.

The statement by D. M. Kermack *et al.* (1968) that upper and lower premolars cannot be distinguished from each other is strange for only in very rare cases can the one be confused with the other. As was recognized when the type tooth was described, the upper premolars are only a little asymmetrical; in contrast the lower premolars are markedly so. The large, last upper premolar is essentially a twin cusped tooth with small cingulum cuspules added anteriorly and posteriorly, the former being the larger and giving the tooth a triconodont appearance. The tip of the large cusp is slightly, but only slightly, behind the centre line of the tooth and it has its anterior edge somewhat more curved than the slightly shorter posterior edge. Anteriorly it gives way to the cingulum cuspule. These are features which allowed the tooth to be orientated in 1941 when it was said to be slightly recurved. The internal cingulum is complete; the external cingulum is incomplete but may be more extensive than in the type and is occasionally crenulated. In contrast typical lower premolars are markedly recurved (figure 16*a*, plate 45). In these teeth the apex of the principal cusp usually lies anteriorly and the anterior slope of this cusp swells out and bulges far ahead of the front edge of the leading root and there is no anterior cingulum cuspule, features in which they differ radically from upper premolars. The comparatively small, leading upper premolars lack both the outer cingulum and the cuspules, but in only rare examples can their lack of symmetry cause confusion with the small, leading lower premolars. Among the thousands of teeth examined several large lower premolars have been found in which the centre cusp lacks the usual anterior bulge and has developed an anterior cuspule on the cingulum and such teeth resemble upper premolars (figure 9*h*). But they are easily distinguished from the posterior upper premolars (the only ones with which they could reasonably be confused) by the absence of an external cingulum. Such teeth are, moreover, very rare. In fact the same comparative asymmetry of lower premolars is seen in other triconodonts, in symmetrodonts and in pantotheres.

Wear by the scimitar-like posterior lower premolar can eventually remove the leading cuspule of the last upper premolar (figure 16*e*, *f*, plate 45), so causing it to resemble the larger lower premolars. But this wear cannot produce the forward bulge of the lower premolars. Moreover, such worn teeth retain the external cingulum never found on lower premolars.

Next, D. M. Kermack *et al.* make no mention of the second tooth, found at the same place, at the same time, and described (together with the first tooth) as *Eozostrodon problematicus*. This use of a second specific name to distinguish the distinctly different second tooth followed the example of Hennig (1912) when he described the first two teeth of the form *Oligokyphus* under the names *O. biserialis* and *O. triserialis*, suspecting them to be a premolar and a molar of the same animal (they proved to be lower and upper postcanine teeth). It does not justify the statement by Kermack *et al.* 'the single tooth from Holwell Quarry in Somerset which constitutes the type and total hypodigm of *Eozostrodon parvus*'—a statement which is most misleading. Such is the reasoning which satisfies D. M. Kermack *et al.* that *Eozostrodon* is indeterminable. The specimen called *E. problematicus* has most of the crown preserved and one of the roots. Except for the somewhat large size of the posterior accessory cusp the crown shows all the characters of a typical lower molar of the sort called '*Morganucodon*'. As in typical '*Morganucodon*' lower molars there was a fair-sized posterior cingulum cusp, followed lingually by a similar cusp and two smaller ones (the second of these a mere uprising of the cingulum) and finally,

in the correct position, a modest Kühnecone. The small size of these cingulum cusps can easily be matched in specimens of '*Morganucodon*' from Wales. The crown view conforms to their pattern, and the restoration, attempted in 1940 with no other evidence available, shows the missing anterior part of the crown restored too large but nevertheless is reasonably close to the now well-known pattern (figure 1). Fresh, totally unworn crowns of lower molar teeth have the roots only half developed indicating that the penetration stage of root development had not begun. The root of *E. problematicus* which is preserved has developed its full length but was not, apparently, locked in place by a cement 'shoe'. There is no obvious wear. Had this been a second or third molariform tooth the posterior accessory cusp would have been expected to show wear by this stage of root development. But wear starts on the first molar tooth at the
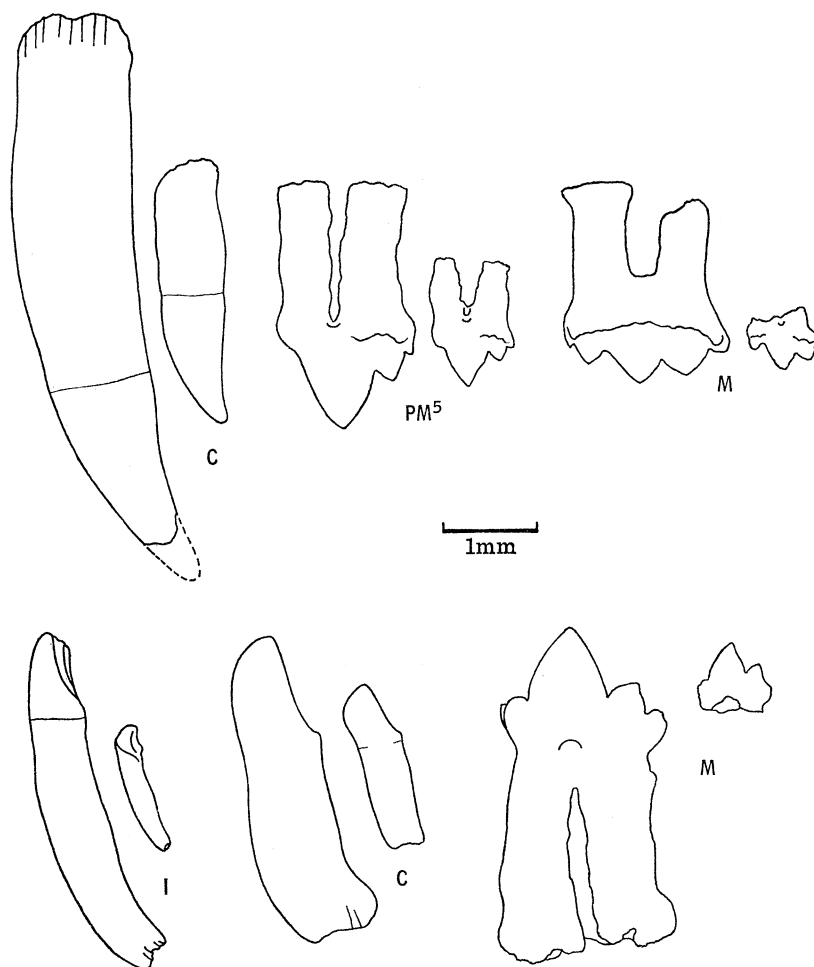
FIGURE 2. Isolated teeth of *Eozostrodon parvus* showing the size ranges of identifiable teeth.

front (figure 5b) a region missing in this specimen. The form suggests it was not a fourth molar tooth. It seems therefore to have been a first molar, occupying a position in the lower postcanine series as correctly determined by Kühne as long ago as 1949. K. A. Kermack's view that the tooth is indeterminable is not well founded.

In a recent account of the Triassic mammals Mills (in press) called attention to differences in the roots of *Eozostrodon problematicus* and *Morganucodon watsoni*, pointing out that whereas the root of the former was slender, a dissection had shown him that those of *Morganucodon* were
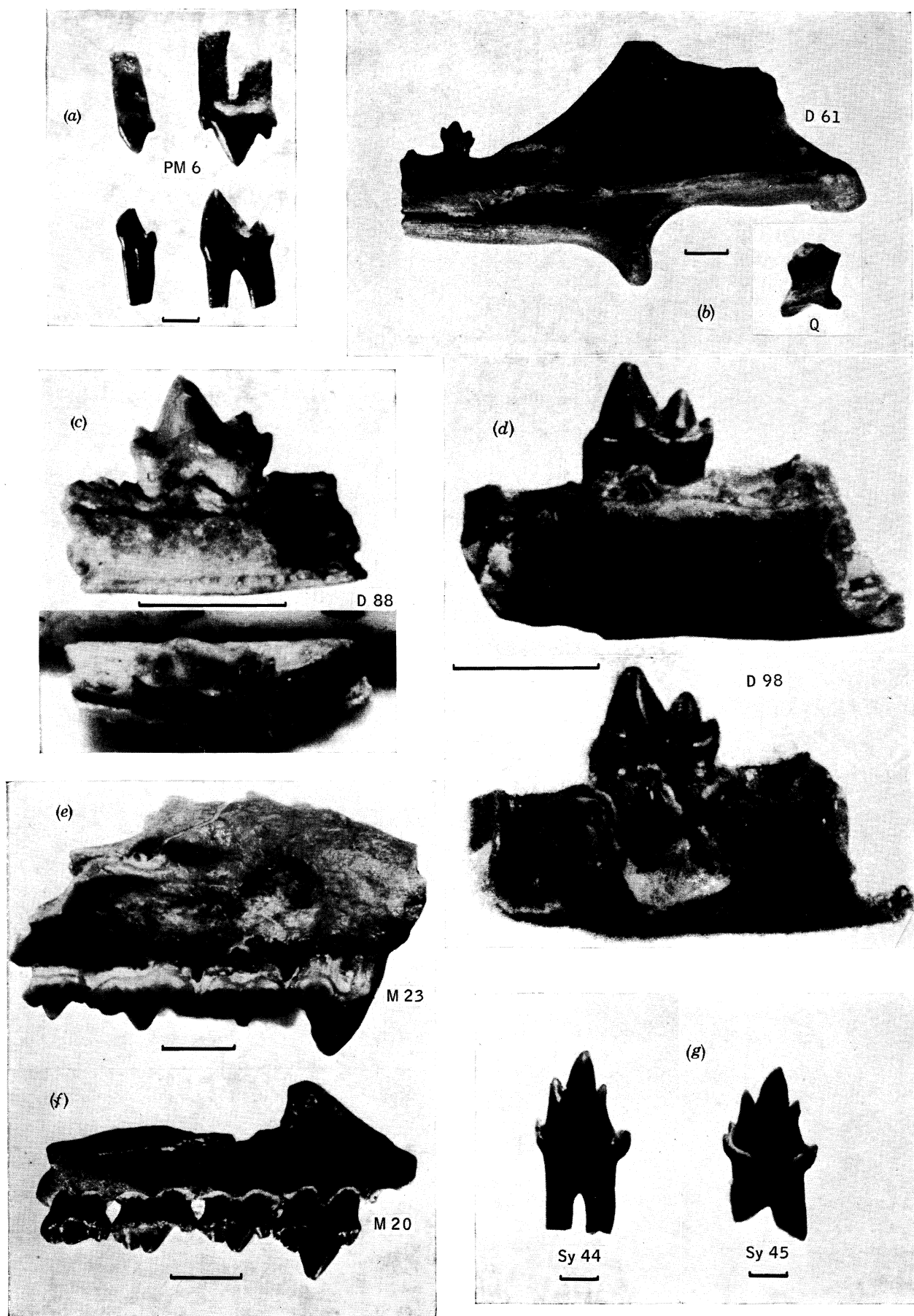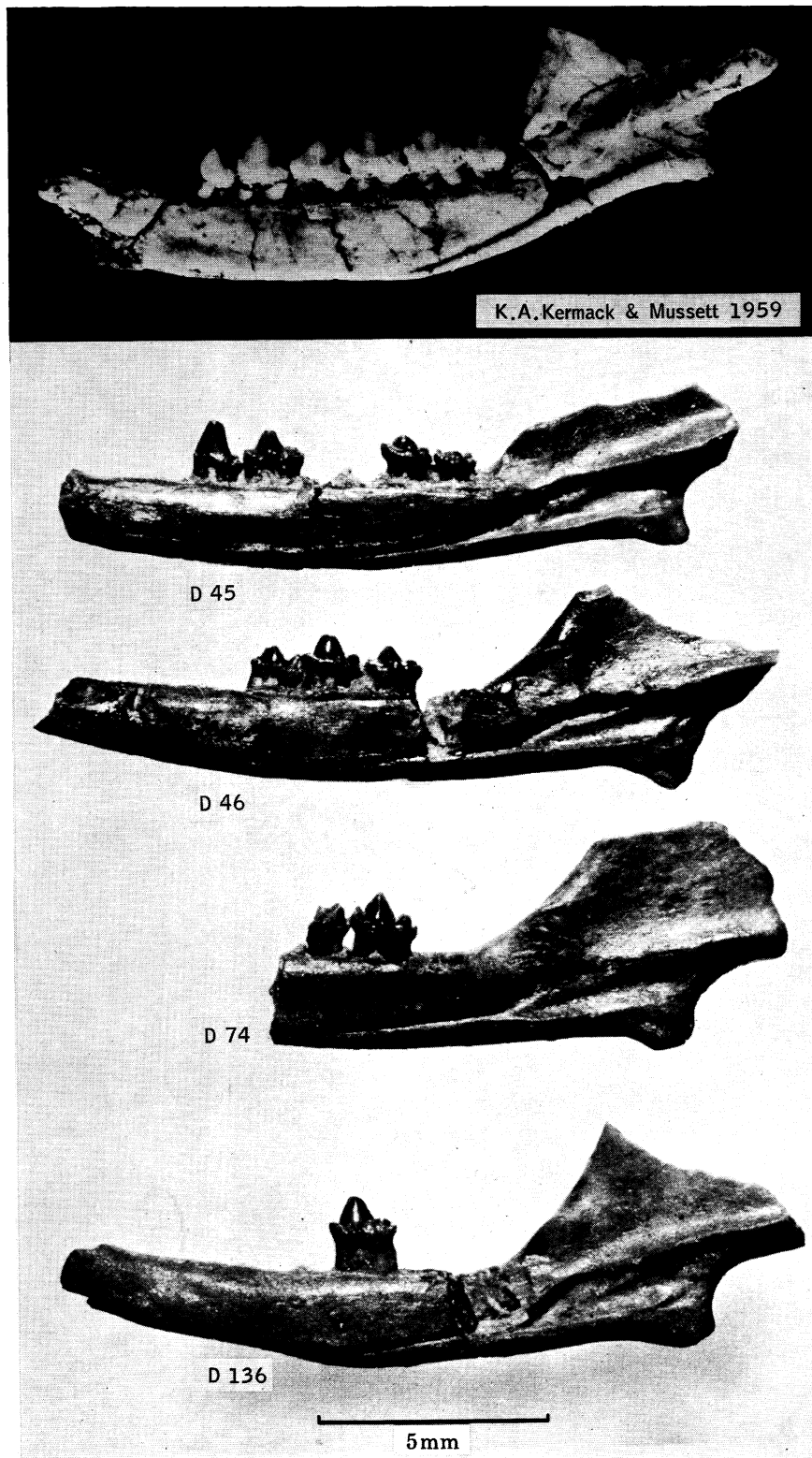
FIGURE 16. (a) Anterior and posterior upper and lower left premolars of *Eozostrodon parvus*. (b) Hind end of dentary, lacking only the top of the coronoid process, and a quadrate. (c) Milk molar in a dentary showing a pit in Crompton's groove. (d) A replacing tooth below a milk molar, before and after dissection. (e) A maxilla with parts of lacrimal and jugal. The teeth are severely worn. (f) A maxilla with the teeth moderately worn. (g) Two left lower molars of *Kuehneotherium praecursoris* probably from the same dentary, the second having a complete outer cingulum. Markers indicate 1 mm.

K.A.Kermack & Mussett 1959

(a)

D 45

D 46

(b)

D 74

D 136

5mm

FIGURE 17. (a) Dentary of *Eozostrodon parvus* figured by K. A. Kermack & Mussett showing high positions of the angular and articular processes. (Reversed.) (b) Four dentaries of *Eozostrodon parvus* showing the varying form.

stout and terminated in a club foot. He also claimed that while the roots of *Morganucodon* were long those of *Kuehneotherium* were more 'therian'. The study of thousands of specimens of isolated teeth, together with the dissection of about 100 fragments of dentaries, and one or two fragments of maxillae, show beyond much doubt that the differences seen by Mills between *E. problematicus* and '*Morganucodon*' are but growth stages, while those claimed between the two Triassic mammals are confined to the final club-rooted stage of *Eozostrodon*.

Beautifully preserved molar crowns of *Eozostrodon* are found, with the cusps extremely sharp, and the enamel shining, but having no roots. In a few cases these crowns are largely hollow, a condition which first invited the interpretation that perhaps the softer dentine had been partly dissolved during preservation. But further considerations led to the obvious conclusion that the very perfection of these rootless crowns indicated that they were those of developing teeth and the roots had either not started to grow or, where the crown had only a moderate pulp cavity, were but partly developed at death. Very beautiful teeth are occasionally found with short roots which may be well preserved or one may be broken (figure 1). These can only reasonably be interpreted as teeth which were either only partly or recently erupted at death. The state of the crown and the total absence of wear urge this explanation. Once the crowns of teeth come up against the opposing tooth further eruption becomes impossible and the stage of penetration starts, that is the roots start to grow down deeply into the dentary. In *Eozostrodon* they reach about the level of the dental canal. While the roots are penetrating they are tapered and such is the condition in the tooth called *Eozostrodon problematicus*. In these conditions the teeth are easily lost from the dentary or maxilla and, losing the protection of the bone and having no hard enamel coat, they are usually broken and complete specimens are rarely found. Once penetration is complete the root enlarges by further thickening of the dentine and finally cementum, or bone of attachment, develops round the apices of the roots giving them the typical clubbed appearance observed by Mills. This condition locks the teeth into the bone of the jaw and the tooth can now be lost only by the breakage of the roots, which has happened in the great majority of specimens, or by the smashing of the bone. This is why nearly all teeth found *in situ* have clubbed roots and only very few isolated teeth have their roots at all well preserved. It should be noted that lower molar teeth have distinctly longer roots than upper molars, the maxillae not being developed to accommodate long roots. The premolars have much the same properties except that the small anterior premolars have room for comparatively long roots and seem much less inclined to develop clubbed apices to their roots, though these do occur on the posterior premolars. While the material available of *Kuehneotherium* is much less abundant than that of *Eozostrodon*, it conforms to the same interpretation, the upper teeth having shorter roots than the lowers, beautifully preserved unworn lower molars having short, tapered roots, and those which are worn are, usually, in the dentary and have comparatively long roots. It is quite impossible, in the writer's opinion, to use the forms of their roots which are mere growth stages to distinguish the two Triassic mammals. This is to be expected if, as the writer believes, the two forms are closely related (p. 269).

The various attempts to derogate *Eozostrodon* have been ill founded. It is quite clear that the two teeth from Somerset match the last upper premolar and a lower molar, probably the first molar, of the form collected in Glamorgan. The name *E. parvus* has priority and the names *E. problematicus* and *Morganucodon watsoni* are synonyms.

As in other Mesozoic mammals, comparatively well-preserved dentaries are far more common than premaxillae and maxillae, for the dentary being the stouter bone and lying more or less in

244   F. R. PARRINGTON

one plane is less likely to be broken. Because of this it can be described more fully, and with greater confidence, than the maxilla, and its dentition can be used to some extent in restoring that of the upper jaw. For this reason it is described first.

(b) The lower jaw

The dentary of *Eozostrodon* was first described by K. A. Kermack & Mussett (1959) who showed that proximally it had three processes; a coronoid process, a condylar process with a well-formed articulating condyle, and an angular process. But the most important discovery was the presence of a well-developed medial trough running posteriorly from behind the position of the last tooth, which was rightly assumed to have held comparatively well-developed postdentary bones, and also a groove running forward from the front extension of the trough, where the dental foramen opens. In this groove fragments of bone were observed which were interpreted as the remains of the prearticular. The likeness of this dentary to that of *Docodon* has been one reason for the belief that the animal was a docodont and not a triconodont.

One of the most interesting features of the dentary is its variation in shape. In 1959 K. A. Kermack & Mussett published a photograph of a dentary which has its lower border strongly curved posteriorly and the angle (which does not seem to have a distinct process) is about in line with the alveoli. The trough for the postdentary bones is large posteriorly and the result is that the process for the articulating condyle is carried high above the line of the teeth as the condyle itself must have been. The anterior border of the coronoid process rises sharply making an angle of about 80° with the line of the teeth. No dentary has been found which matches this one, though the general form and the dentition leave no doubt about the identity. In contrast the posterior part of the lower border is usually only moderately curved, or is even almost straight, with the result that the angular process usually lies below the lower border (D 46) or but little above it (D 45). In one specimen (D 136) the posterior border is straight but makes a distinct angle with the anterior part which rises anteriorly to the second molar. In this specimen the anterior border of the coronoid process rises sharply, though not as strongly as in the specimen figured by K. A. Kermack & Mussett, whereas in others (e.g. D 74) the angle is nearer 40° or even 50° (figure 17, plate 46). The attempted restoration (figure 8) is a compromise between such conflicting data. Kermack & Mussett (1958) seem to have met this difficulty since their restoration of the hind end of the dentary has distinctly different proportions to those of their photographed specimen.

The great variation in form of the hind end of the dentary is of special interest in view of the relationships claimed to the symmetrodonts and the Upper Jurassic triconodonts. In the former group, as in the dentary of '*Morganucodon*' figured by Kermack & Mussett (1958), the front border of the coronoid process rises steeply, making an angle of about 90° with the line of the teeth (Simpson 1929, Figure 15) and the condyle is situated in a high position. In the Upper Jurassic triconodonts, on the other hand, as in the other dentaries shown in figure 17, the anterior border of the coronoid process slopes much more gradually, in one case making an angle of only about 50° with the horizontal and the condyle lies in line with the teeth or even below it (figure 16) (Simpson 1928, Figure 19). A rounding off of the angular process or a straightening of the lower border is all that is necessary to produce the two types of dentary from those found in *Eozostrodon*. The mechanical effects of such modifications have been discussed by Parrington (1960).

The coronoid process is not preserved in at all a complete state in any specimen. The most

perfect specimen of the hind end of the dentary (D 61, figure 16b) shows much of the base of the process and it is difficult to restore it without making it a tall structure. But the top part of a coronoid process, which had part of the coronoid boss preserved (D 132, figure 8) shows the blade as a much shorter structure, resembling more the reconstruction of *Kuehneotherium* made by Kermack *et al.* (1968). It may belong to that form, or this may well be yet another example of the variability of *Eozostrodon*.

The condyle is shown in one good specimen (figure 8) and many fragments. It is somewhat variable in shape when viewed from above but is a rounded knob which faces both upwards and backwards. A flange which is developed above the centre region of the trough for the post-dentary bones is clearly seen when the dentary is viewed from above (figure 8).

The symphysis is but poorly developed, the opposing surfaces being remarkably smooth and the edges often weakly defined. It seems clear that the two halves of the lower jaw were only loosely attached to each other. Specimens showing this region are not common and are usually ill preserved anteriorly. This adds to the difficulty of determining the number of incisors.

The coronoid boss is shallow and is recessed by a wedge-shaped, horizontal depression for the coronoid bone. This has a thin base, of irregular outline, but it is raised centrally into a kidney-shaped boss of some size (D 64, 95). There would seem to be a possibility of some form of pterygoid process having existed for the boss to act against, but no evidence of this has been found.

The splenial is preserved, usually as a few fragments, in a number of specimens. Anteriorly the bone reaches almost to the front of the groove where this reaches the bottom of the dentary, a position which may be below the first or the second molar, but appears to be comparatively shorter in the deeper, and presumably older, dentaries. The posterior extension of the bone is uncertain, but it may terminate just inside the anterior part of the trough.

Two specimens of what are probably the articulars and their associated bones have been found. These tiny fragments comprise the articulars, which form articulating condyles, together with the prearticulars and, possibly, the angulars and surangulars, but they are imperfectly preserved. No retroarticular process has been seen (figure 8). I am indebted to Dr J. A. Hopson, who is familiar with the postdentary bones of the tritylodonts, for his opinion of these difficult fragments. He informs me that 'the similarity is amazing considering the phylogenetic distance between the two'.

A very small bone which lacks marked features may be the quadrate (figure 8). It is a slightly tapered bone with the larger end forming a somewhat screw-shaped but cylindrical articulating condyle, separated from the thinner dorsal component by a slight neck. This bone has some resemblance to the quadrate of such a cynodont as *Thrinaxodon liorhinus* (Parrington 1946). Another, but much less well-preserved specimen has been found.

Plainly the quadrate-like bone and the articular are of different sizes, the former being distinctly too large to accommodate the latter; the size ranges of the different samples available suggest that this objection may not carry significant weight.

If correctly identified these small fragments confirm the announcement of Kermack & Mussett (1959) that two jaw hinges were functional in this animal.

In the course of his studies of acid prepared specimens of the cynodont *Thrinaxodon liorhinus* Crompton (1963) observed a shallow longitudinal groove lingual to the alveolar borders of the canines and postcanines in both upper and lower jaws. These grooves he correctly interpreted as accommodation for the dental lamina because pits containing developing teeth appeared in the floor of the groove. Similar, but much less strongly developed, grooves have been found

in the majority of the dentaries lingual to the alveolar borders of the molars, but in only a few, small dentaries lingual to the premolars (D 71). Crompton's groove can be seen entering a developing crypt at the back of the molar series in at least one specimen (D 24) and in two others a pocket was found opening into the groove in the fragments of small dentaries (D 88, 181; figure 10). These were dissected and found to be filled only with matrix, but in a third specimen
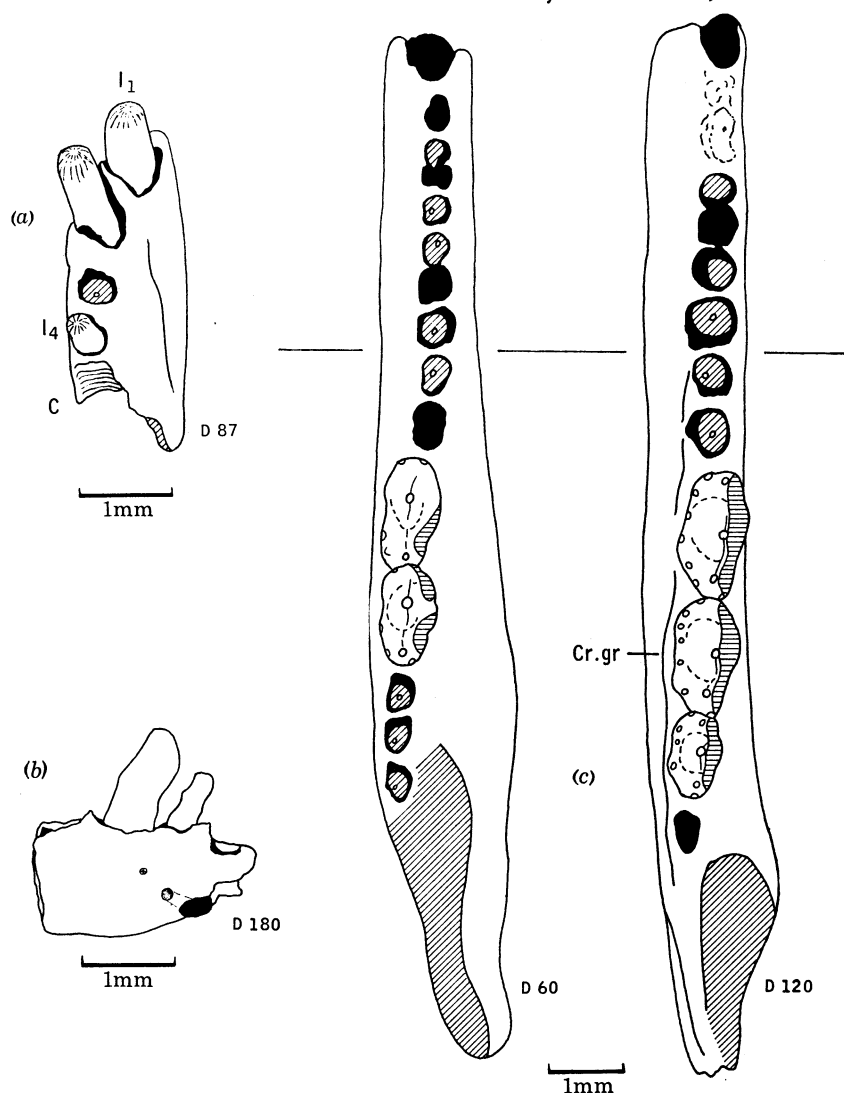

FIGURE 3. *Eozostrodon parvus*. (a) The fragment of a dentary showing four incisors and the socket for the canine. The crowns of the teeth are severely worn. (b) A fragment of a very small dentary with the last incisor and the canine. These may be milk teeth. (c) Two dentaries viewed from above. Four premolars were originally present and five molars. The marker indicates the change of root socket size, and Crompton's groove is present in one specimen. The left specimen (D 60) had all four premolars at death, the first single rooted. The right specimen (D 120) had lost the first two molars and plugged their sockets with vascular bone. It is not uncommon in this animal for the sockets of neighbouring teeth to be closer together than are the two sockets of either tooth.

(D 98) the groove disclosed the tip of a replacing tooth (p. 258). The fact that the groove has been lost in the premolar region of all moderate sized and large specimens seems to indicate that replacement may have been complete in this region and the dental lamina lost. The absence of the groove in some of the larger specimens is open to two explanations. The groove may have

been obliterated by *post mortem* abrasion, or it may have disappeared in older animals when tooth development had been completed and the dental lamina lost. Evidence of the presence of such a groove in the upper jaw is far from satisfactory. But well-preserved maxillae are rare and it may be present in a number of specimens (MX 16, 20, 58).

For a time it was not possible to determine the premolar–molar junction unless both the last premolar and the first molar were present. Eventually it was realized that there are three tests which can be applied to find the junction. First, the distance between the back of the canine socket to the back of the posterior root of the last premolar varies between 3.0 and 3.7 mm (no doubt these measurements will eventually be extended); next, and most helpful, the socket for
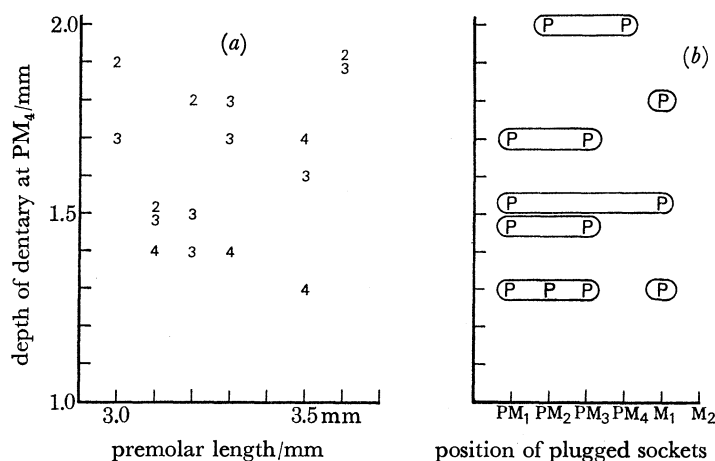
FIGURE 4. *Eozostrodon parvus*. Figures showing the occurrences of losses of premolars and molars and the plugging of their sockets. (*a*) Shows the relations of the numbers of premolars to the premolar length and the depth of the dentary. In all cases it is the first or the first and second premolars which have been lost and their sockets plugged. (*b*) Shows examples of irregular plugging. Individual specimens are indicated by looping.

the posterior root of the last premolar is nearly always distinctly larger than that for the anterior root of the first molar; finally, in all but very small specimens, Crompton's groove, when visible, starts below the first molar. Two of the three tests are quite commonly available and all three are not rare (figure 3). Once they are understood many otherwise troublesome fragments become intelligible.

As the collection of fragments of the dentary mounted it became clear that in the premolar region teeth were sometimes missing and the space occupied by vascular bone. It seemed likely that teeth might have been shed, possibly by resorption at the neck of the crown as suggested by Kermack for the canines of the gorgonopsids (K. A. Kermack 1956), and the socket plugged by bone which, for a time at least, was cancellous. This happening, it seemed, might well be concerned with tooth replacement, and specimens were examined by dissection and by X-ray. One specimen (D 90) which was dissected from above showed the presence of a pair of roots and X-ray has shown their presence in some other cases. In many specimens, however, no certain evidence of a root could be found and in no case has the crown of a tooth been found. The conclusion is that teeth are lost in this manner and not replaced, an interpretation which conforms to the suggestion put forward by Crompton (1963) that the anterior postcanines of the cynodonts were probably lost and not replaced. The fact that this plugging can occur in an irregular fashion, and can occur in the region of the last lower incisor (D 150) and the first lower molar, added greatly to the difficulties in working out a credible interpretation of the

premolar region (figure 4b). The histology of this plugging is at present being studied by Dr J. W. Osborn.

At an early stage in the study of this material it was observed that quite a number of teeth had a constriction, or neck, below the crown and the possibility seemed to be that resorption had started and that eventually the crown would be shed. It was thought that this might be concerned with replacement, but the idea was abandoned because the condition was found in a wide range of both worn and unworn teeth. The alternative interpretation was that the neck resulted from *post mortem* abrasion by mineral particles where the tooth was protected neither by hard enamel nor by the jaw bone. It would seem not unlikely, however, that the phenomenon is in fact due to resorption, at least in some cases, but that it is concerned with 'plugging' and not replacement.

The anterior end of the dentaries are seldom at all well preserved and this may account for differences of opinion as to the number of lower incisors present. Kermack & Mussett (1959) claimed five while Mills (in press) claimed the number could be four, five or six. The material available to the writer shows four lower incisors of which the anterior ones are the largest. These teeth are subject to very considerable wear (figure 3a) and in one case the posterior incisor has been so worn that it has become an anteriorly directed spike (D 209). The canine tooth is spatulate, resembling those of other non-multituberculate mesozoic mammals, and it becomes worn on its postero-external face by contact with the upper canine. This tooth is received into a pit in the maxilla (or in the maxilla and premaxilla, the junction of these two bones not having been seen).

The poor quality of the available material, and the claim that there could be either two or three premolars but only seven postcanine teeth, caused considerable difficulties in determining the dental formula. Thus the third dentary to be registered had sockets for nine postcanine teeth but none was present and the specimen might well have belonged to the symmetrodont which was known to be present, or to some new form. Eventually specimens having sockets for eight and nine postcanine teeth were found which had one or more identifiable *Eozostrodon* molars present.

The number of premolar teeth was finally determined only when those specimens having the posterior border of the canine socket, the last premolar and the first molar tooth present, were studied alone. It was found that if the premolar length was plotted against the depth of the dentary (as an approximate indication of the animal's age) and the number of premolars (or their sockets) was indicated, then it appeared clear that the smallest, and so youngest, animals usually had four premolars, the majority three, and the largest and so presumably oldest, but two (figure 4a). The position of the missing second premolar was nearly always occupied by somewhat vascular bone, as was occasionally the position of the first. Since dissection of many specimens, and the examination of about sixty by X-ray, failed to show any evidence of tooth replacement it seemed highly probable that, as suggested in the case of the cynodont *Thrinaxodon* by Crompton (1963), the anterior postcanines tended to be lost with age. The picture was much more complex than might appear from this solution. Thus it will be seen that one shallow dentary has but two premolars while a much deeper one has four. But the premolar lengths indicate that the former specimen is a small animal while the latter is a large one and so the depths of the dentaries if taken alone could be misleading. Also one or two specimens appear to show little if any room for four premolars (D 191). The picture was still further complicated by the presence of specimens which appear to have lost premolar teeth in a distinctly irregular manner and,

furthermore, even the first molar can be lost and its sockets filled by bone (figure 4 b). Irregular loss of premolars occurs in some living animals, notably in the Ursidae. This tendency for irregular loss of teeth accounts for the discovery of teeth showing unusual wear, abnormalities which were at first very puzzling.

The lower premolars have a characteristic form. In the case of the last premolar a strongly recurved principal cusp dominates the crown and bulges forward beyond the line of the leading root. This cusp is distinctly compressed and the leading edge normally divides and curves lingually and forms an internal cingulum. Posteriorly there is a small accessory cusp and lingual to it a small cuspule. These two latter structures give the appearance of a heel to the tooth. The height of the main cusp varies somewhat, some giving the tooth a tall appearance while others are somewhat squat though these latter may be, to some extent, worn teeth. The premolars diminish in size anteriorly (figure 8) but apart from a diminution of the accessory cusps, the appearance remains much the same (D 121, 138). Very occasionally the last premolar develops a small (usually extremely small, D 93) cusp anteriorly (D 196; figure 9 h). This cuts back the anterior bulge normally present at the front of the lower molars and gives the tooth a resemblance to the last upper premolar. As previously stated such exceptional teeth can be distinguished from the fifth upper premolar (the only tooth with which they might be confounded) by the absence of an external cingulum. In general these lower premolars are trenchant teeth and the compression of their crowns is reflected in their roots.

As K. A. Kermack & Mussett (1959) claimed, there can be either four or five molars. There seem to be two possible explanations of this fact; either the fifth molar is added at a late stage of development, or the form is dimorphic. The former interpretation is supported by the fact that the specimens with five molars are distinctly large, and the latter by specimens with quite small fourth molars and the occurrence of two different sorts of upper canines. The molar teeth each have a large centre cusp with anterior and posterior accessory cusps, the latter being the larger, and a small fourth, cingulum, cusp added at the back. Internally there is a cingulum bearing cuspules which vary in both number and size (Parrington 1967). Commonly there are two cuspules between the 'fourth' cusp at the back of the tooth and an enlarged cuspule, the 'Kühnecone' which is about in line with the posterior half of the centre cusp. Anteriorly the cingulum usually bears two cuspules, but there may be three. Normally the cingulum is continuous but the centre cusp may bulge lingually and divide it into anterior and posterior portions. Perhaps the most interesting variation is a tooth having the cuspules of relatively huge size (figure 1, bottom left).

Normally, it seems, the second molar is the largest (crown length) but in one specimen (D 50) the third is longer than the second and in two others the second and third are the same length. The first molar may be larger than the third or, rather more usually, the third is somewhat larger than the first. The fourth is always the smallest of these four, the fifth probably smaller still, but it has not been seen in the dentary.

It is of interest that, just as in the Upper Jurassic triconodonts (e.g. Yale Peabody Museum no. 10359) the palatal components of the maxillae have pits, tending to run together, for the reception of the second and third lower molars (figure 7).

Specimens interpreted with confidence show the first molar varying between 1.0 and 1.4 mm, the second between 1.2 and 1.6 mm and the third between 1.0 and 1.5 mm though several specimens suggest that the crown length of the third molar may only be 0.9 mm. The fourth molar shows a greater range of size if certain rather poor specimens have been correctly

interpreted (D 30, 63, 119). In these specimens the crown length of what appear to be the fourth molars measures between 0.4 and 0.6 mm, whereas several specimens have the crown length of 1.1 mm. Sockets for a fifth molar are present in five specimens and crypts for the development of a fifth molar are present in two others, but in no case is the tooth itself preserved. Specimens having sockets for five molars show a molar length (measured from the front of the leading socket of the first molar to the back of the posterior root of the fifth) of 5.1 to 6.1 mm
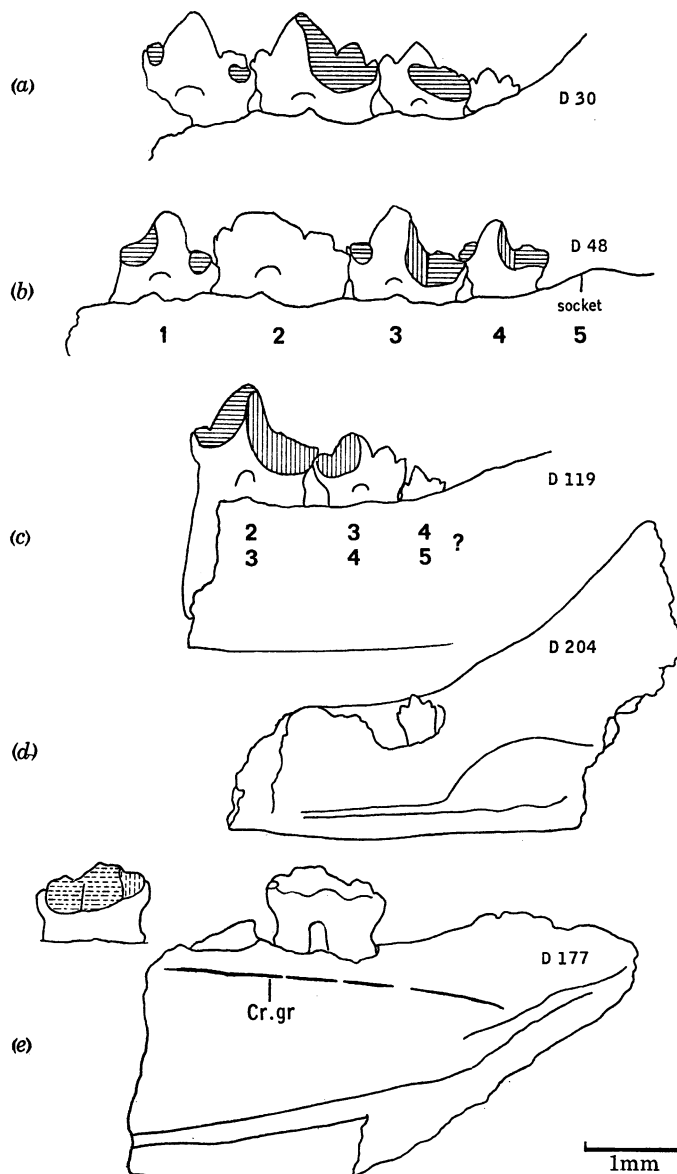
FIGURE 5. *Eozostrodon parvus.* Examples of wear of lower molars. (*a*) A normal example in which wear has started at the front of the first molar and the back of the second and third. The fourth tooth, imperfectly erupted, is unworn. (*b*) A specimen with five molars, the fifth missing. The first molar is worn anteriorly, the second not at all, and the third and fourth are severely worn posteriorly in the usual manner. (*c*) A specimen which can be interpreted as having either the second, third and fourth molars or the third, fourth and fifth. Neither interpretation agrees with the two specimens (*a*) and (*b*) in the wear of the teeth. (*d*) A moderate sized dentary showing the last molar of small size and imperfectly erupted. (*e*) A fragment of one of the largest dentaries obtained. The last molar is of very large size and Crompton's groove clearly visible. In neither (*d*) nor (*e*) is it possible to identify the teeth as the fourth or the fifth molars. (*a*) and (*d*) are reversed.

and the depth of the dentary in the region of the fourth and fifth molars of 1.5 to 2.0 mm, whereas specimens which certainly had only four molars have a molar length of from 4.1 to 5.2 mm and the dentary a depth below the fourth molar of from 1.0 to 1.7 mm. It seems therefore very likely that the fifth molar is added only when the dentary reaches a depth of at least 1.5 mm in this region, the overlap in measurements being accounted for by the considerable size range of the animal. Specimen D 204 is a fragment of a very delicate and shallow dentary, having a depth of only about 1.1 mm below the penultimate molar and a last molar with a crown length of rather less than 0.5 mm. This is not surprising since, for example, D 176 has the last molar with a crown length of 0.5 mm. These teeth must surely be fourth molars since they are at the base of the coronoid process and no example of the third molar had been positively identified, or even suspected, which has a crown length of this small size, the smallest being 0.9 mm. Yet specimen D 177, a fragment of a huge, substantial dentary, measuring 2.3 mm below the penultimate tooth, has the last, very worn tooth, with a crown length of at least 1.15 mm. The explanation which immediately presents itself to one's mind is growth and replacement. But this is completely denied by other evidence on replacement, which is quite strong, and only size range and possible dimorphism remain to explain these occurrences. In one case (D 48) where the original presence of a fifth molar is certain because four molars have been preserved in place, the socket for the last tooth measures only 0.5 mm and the tooth must surely have been rather small. In another case (D 190), where the identification is less certain, the last socket measures about 0.9 mm.

The crown lengths of lower molars which have been identified with some confidence are as follows:

M1 1.0–1.4;   M2 1.2–1.6;   M3 1.0–1.5; M4 0.8–1.1 mm.

However posterior molars which may be either fourth or fifth molars may be as small as 0.4 mm. The difficulties arise from the very imperfect nature of so much of the material. For example specimen D 119 has three consecutive posterior molars with crown lengths measuring 1.3, 0.9 and 0.4 mm. These may well be the second, third and fourth molars but may also be the third, fourth and fifth. The dentary measures only 1.3 mm below the second molar and this is small, and so the former identification is the more likely and this indicates that the fourth molar may vary in crown length from 0.4 to 1.1 mm, an enormous range. The sizes of the molar teeth tend to vary to some extent with the sizes of the dentaries. Thus seven dentaries measuring from 1.9 to 2.1 mm in depth have second molars with crown lengths varying from 1.3 to 1.6 mm and three of these show the fourth molars as having crown length of 1.0 or 1.1 mm. In contrast, if the teeth have been correctly identified, seven small dentaries with depths of only 1.2 to 1.3 mm have the second molars varying from 1.2 to 1.5 mm in crown length and the fourth only from 0.45 to 0.6 mm. It will be shown in a later section that it is not possible to account for the enormous size range of the fourth molar by supposing that it had been replaced in the larger specimens. Like the variation in premolar length these measurements indicate the great size range of the animal and emphasize the possibility that it may be dimorphic.

(c) The upper jaw

Few specimens of premaxillae have been collected, all in a poor state of preservation. The best specimen, M 60, is illustrated in figure 6 a. In side view the bone shows a shallow depression, which is found also in other specimens, and which is taken to show the region of overlap of the maxilla. The bone shallows anteriorly, perhaps forming the border of the nares though a
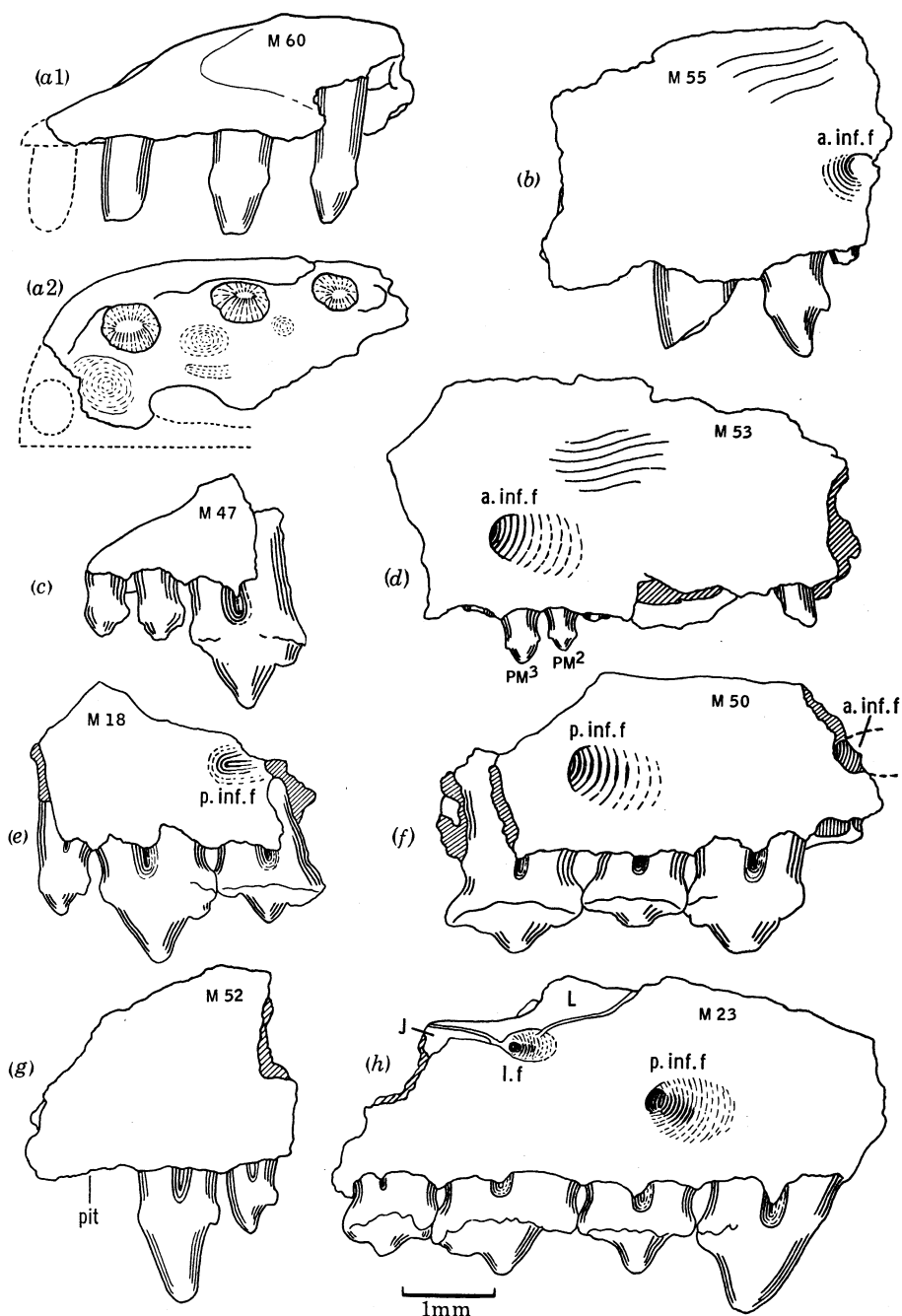
FIGURE 6. *Eozostrodon parvus* (a1), (a2). Side and palatal views of a premaxilla with three incisors preserved. The depression for overlap of the maxilla is seen and also most of the border of a palatine vacuity. (b) A fragment showing the base of an upper canine and a well preserved first premolar. The anterior extension of the anterior infraorbital foramen extends above the root of the second premolar which is very small. (c) A typical last upper premolar preceded by two small premolars. (d) A large fragment of a maxilla showing a badly preserved precanine tooth, the root of the canine, the first four premolars. The second and third premolars are well preserved but the first and fourth are represented only by their roots. The anterior infraorbital foramen is shown above the second and third premolars. (e) A fragment showing a typical fifth premolar preceded by a small fourth premolar and followed by the first molar. (f) A fragment showing the posterior infraorbital foramen above the first and second molars and the posterior part of the anterior infraorbital foramen extending above the root of the fourth premolar. (g) A specimen showing the special form of upper canine preceded by the pit for the reception of the crown for the lower canine and followed by a typical small premolar. (h) The best preserved fragment of the skull obtained. The fifth premolar is well worn anteriorly and the molars are strongly worn. Part of the lacrimal is preserved, with the lacrimal foramen, and the anterior extension of the jugal.

septomaxilla may have been present. Anteriorly the bone is broken but what remains suggests that there was no internarial process. The palatal component shows shallow depressions, presumably for the crowns of the lower incisors. The bone is too badly preserved to show the relations with the maxilla in the region of the pit for the lower canine and all the three teeth present appear to belong to the premaxilla. A fourth incisor must surely have been present anteriorly. What appears to be the true border of the anterior palatine notch is present.

The maxilla has several points of importance. There are two anteriorly directed, infraorbital foramina, the posterior borders of which are sharply marked while anteriorly they fade out into shallow grooves. These foramina help in reconstructing the premolar region, the posterior foramen having its posterior border above the front of the second molar in M 50, and above the centre of the first molar in M 23. The anterior foramen has its posterior border above the front of the fourth premolar and its anterior depression extends to a position above the second premolar (M 55, 53). The best fragment of the upper jaw (M 23) shows part of the orbit bordered by the lacrimal and a thin wedge of the jugal extending forward between the maxilla and lacrimal up to the position of the foramen for the lacrimal duct which lies outside the orbit (figure 6h). The palatal components of the maxillae are poorly preserved; though several specimens appear to show a true border posteriorly no attempt has been made to reconstruct the palate on the available evidence. The maxilla has a pit for the reception of the lower canine, in front of and slightly lingual to the upper canine and, immediately in front of this pit, there is a small tooth which Mills (in press) regards as a maxillary tooth (figure 7b). However, the suture between the maxilla and premaxilla has not been seen and the tooth may be the last incisor. As in the Upper Jurassic triconodonts there are pits for the reception of the lower molars; these are most marked lingual to the first and second upper molars but posterior to these pits there is a groove. The root of the zygomatic arch is present in a number of specimens but is poorly preserved and seems to arise opposite either the third or the fourth molar (figure 7d, f). Specimen M 48 shows the suture with the jugal and what is the best preserved base of the zygomatic arch. This appears to stand away sharply from the line of the molars.

Few upper incisors have been found in position. One in specimen M 60, presumably the second, is worn and rounded. What are taken to be the third and fourth are less simple having small cuspules at the base of the crowns posteriorly. This makes these teeth almost indistinguishable from the anterior premolars (figure 6b, d).

The upper canine is normally a reasonably proportioned tooth of the type common among carnivorous and omnivorous animals. There is usually a wear facet down the inner face of the front of the tooth resulting from wear against the lower canine, and occasionally it is severe. A substantial number of similar, but on the whole smaller, canines were found, which differ in having a small cuspule added to the base of the crown at the back. These teeth are far too numerous to belong to the comparatively rare trituberculate which is found with these remains of *Eozostrodon* and they suggest that *Eozostrodon* may well be dimorphic (figure 6g). The possibility of two canines being present, or of the first premolar being very large and caniniform is ruled out by specimen M 52 where the canine of this special form is preceded by the pit for the lower canine and followed by a normal first premolar (figure 6g).

The number of upper premolars was at first difficult to determine. One specimen (M 18, figure 6e) shows that only one large premolar of the form of the type of *E. parvus* is present since such a tooth is in this case preceded by a small premolar and followed by a molar. Another specimen (figure 6c) has a typical last premolar preceded by two small premolars. Finally

a large piece of maxilla was found (M53) which has the root of the canine followed by the root of one small premolar, two well-preserved small premolars, and the root of a fourth small premolar. Using infraorbital foramina as guides, and taking into account the fact that four small upper premolars and one large, upper premolar, have been demonstrated, it becomes clear that there were five upper premolars in normal forms. They are comparatively simple
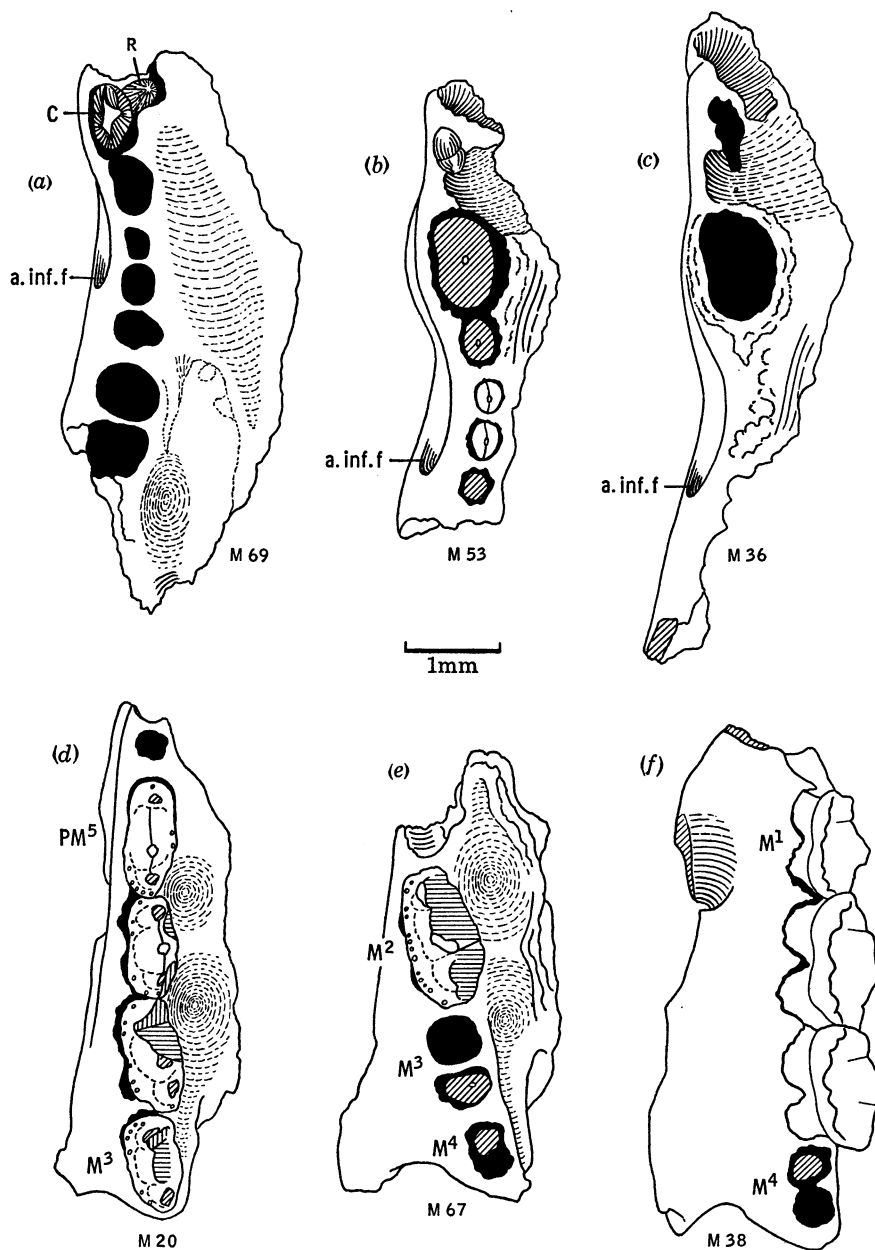

FIGURE 7. *Eozostrodon parvus.* (a) Palatal aspect of a small maxilla with a small, worn canine and a replacing canine developing alongside it and the sockets for the five premolars the last with two roots. (b) Maxilla with a poorly preserved precanine tooth in front of the pit for the reception of the crown of the lower canine and the root of the canine followed by remains of four small premolars. (c) Part of a large maxilla in which the sockets of the first three premolars have been plugged by bone. (d) Palatal aspect of a maxilla with the fifth premolar and first three molars in place with pits for the reception of the crowns of the first and second lower molars. The zygomatic arch arises near the third molar. (e) and (f) Maxillae showing the zygomatic arch arising near the fourth molar.

teeth (except the last) with a small posterior cuspule and, sometimes, a slight anterior swelling at the base of the crown. They do not have external cingula as does the last however. These upper premolars are in nearly all cases easily distinguished from the lower premolars by their comparative symmetry, at the most bulging but slightly over the line of the front root. As described in 1941, the fifth premolar is a slightly recurved tooth with an internal and part of an external cingulum, this last varying in extent and sometimes being distinctly crenulated (see Crompton & Jenkins 1968, Figure 1A). It has an anterior cingulum cuspule, a posterior
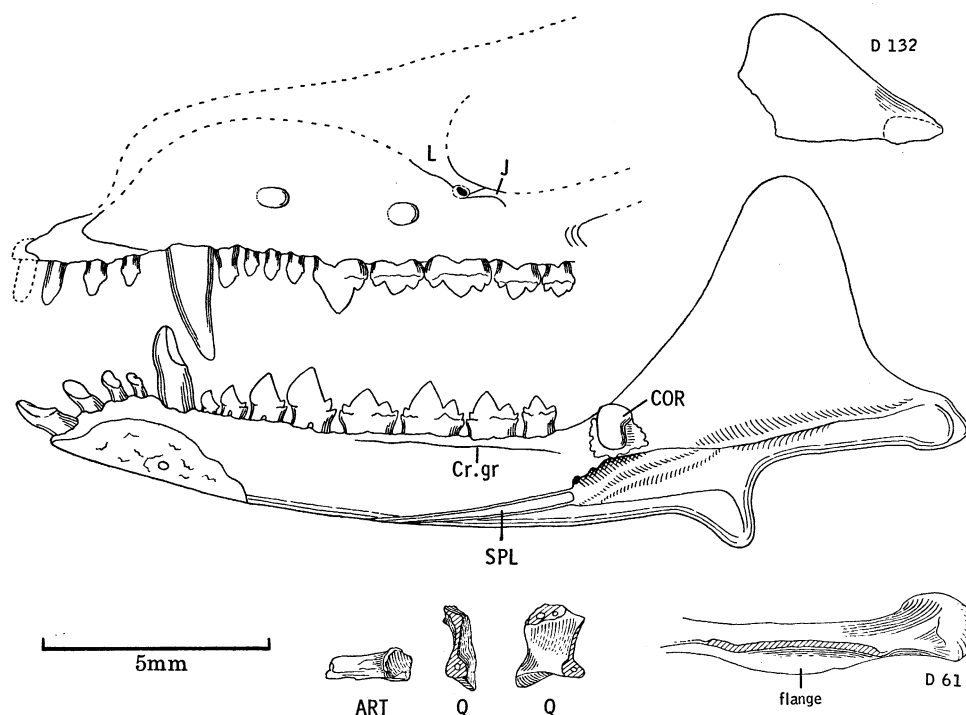
FIGURE 8. Attempted restoration of the left upper jaw, external view and the right dentary, internal view. Fragments of the apex of a left coronoid process, inner view, and the dorsal aspect of the hind end of a right dentary are shown together with the outer and anterior views of a presumed quadrate, and the dorsal view of an articular and its associated bones.

accessory cusp and a posterior cingulum cuspule. The tooth is an important one, not only because it is the type tooth of the genus, but because it is in fact a carnassial tooth, standing clear above the small anterior premolars and also above the first, much lower, molar, and cutting against the back of the similarly enlarged last lower premolar (figure 8). The interaction of these two teeth seems to be a good example of the mutual sharpening called 'thegosis' by Every & Kühne (in press).

With rare exceptions, there can be no difficulty in distinguishing these upper premolars from the lowers (figure 16(a), plate 45, and figure 8).

The molars, of which there appear to have been four, are of much the same pattern but differ in size and in the details of their cusps. There are both internal and external cingula which join behind at the back of the tooth and sometimes also at the front. There are three main cusps in line, the centre one being the largest and the posterior accessory cusp the second largest. An enlarged cingulum cuspule is added to the row at the back of the tooth and very occasionally there is a small cuspule on the cingulum at the front of the line. Each cingulum

is cuspidate but the number of the cusps, or cuspules, seems to vary quite considerably. The cuspules on the outer cingulum are usually but not always smaller and more numerous than those on the inner cingulum. These latter are the first part of the crown to become worn by the opposing lower dentition. The second molar is the largest tooth and is usually about 1.0 to 1.5 mm in crown length. The shape of the crown varies somewhat; it may be oval, parallel sided or slightly tapered towards the front. The crown of the first molar varies from 0.9 to 1.4 mm in length, that of the third from 0.9 to 1.3 mm while the only certainly identifiable fourth upper molar measures 0.9 mm in crown length. No evidence of a fifth upper molar has been found.

As might be expected when thousands of teeth of an animal have been examined some interesting variations have been found. As was pointed out in 1967 the shapes of the crowns and the number and size of the cuspules on the cingula vary quite considerably, though there is a fairly standard normal. Some of the most interesting variations are illustrated. First there is the upper molar tooth shown in figure 9a. This is remarkably like the teeth of *Megazostrodon*, particularly in the symmetrical cusping on the incomplete outer cingulum, though it is much smaller than that form. Figure 9b is perhaps the most interesting of the unusual forms. It is a small tooth (and might be a milk molar) with an incomplete cingulum. But the most important feature is the triangulation of the principal cusps for they make an angle of about 155°. Now the importance of this tooth lies in the fact that the centre cusp has moved outwards and not inwards. A watch was kept for such a tooth because the theory suggested by the writer in 1967, that triangulation would reduce wear and so might be advantageously selected, demands that teeth with the centre cusps moved away from the opposing tooth-line must also have occurred but, producing a less effective bite, would be selected against. Figure 9c shows an upper molar in which the centre cusp bulks large and has, as it were, obliterated the centre region of the outer cingulum; this tooth could be held to be slightly triangulated. A series of about seven lower molars have been found which have from one to three cuspules developed on the outer face of the tooth. Such teeth may well have been more common than is apparent since the outer face of the lower molars is subject to severe wear and so evidence of the existence of such cuspules would soon have been removed (figure 9d, e). Such teeth as these suggest the manner in which the Multituberculata might have acquired their specialized dentition.

What appears to have been a developmental abnormality is shown in figure 9g, a tooth found by Dr Anne Howie. It is one of a series having the appearance of being the product of two lower premolars which have fused, an interpretation which received support when an example was found in a dentary. However, the discovery of a canine tooth which also has the twinned appearance suggests that developing teeth may have partly divided. It is very doubtful if such teeth have any evolutionary significance.

Finally a small and remarkably symmetrical tooth, with three principal cusps together with an anterior and a posterior cingulum cuspule, may represent an amphilestine, resembling those forms in the symmetry, and *Amphilestes* itself in the rising of the lingual cingulum near its centre (figure 9i). There appears to be a hint of triangulation by the three principal cusps and, in the writer's opinion, such a slight triangulation is to be seen in the American amphilestid *Phascolonodon*. K. A. Kermack (1967b) described such a tooth.

It will be seen from the foregoing account that *Eozostrodon*, as known from a large collection of fragmentary remains, is a very variable form and may be dimorphic or even polymorphic. The reasons for this opinion are as follows:

(1) The great size range shown by what are apparently mature animals.

(2) The fact that the zygomatic arch may apparently arise from opposite the third or the fourth molar.

(3) The varying form of the dentary where, for example, the condyle may be well above the line of the dentition or below it.

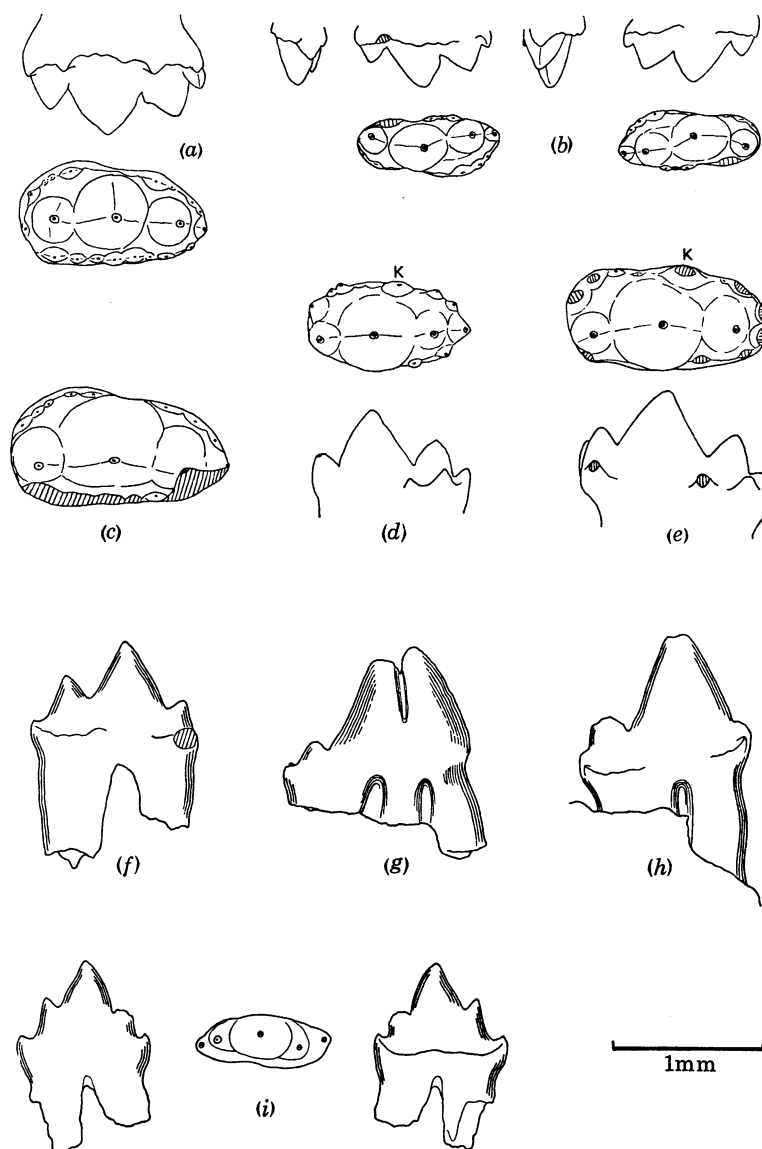(4) The presence of two distinct forms of upper canine, the one averaging distinctly larger than the other.

FIGURE 9. Abnormal teeth. (a) Crown and outer views of an upper molar resembling those of the South African form *Megazostrodon*. (b) A small right upper molar showing the start of wear. The cusps are somewhat triangulated but with the primary cusp moved outwards. (c) A large upper molar with the outer cingulum partly obliterated by the enlarged primary cusp. (d, e) Two lower molars with accessory cusps on the outer face. (f) A small lower tooth with, apparently, a pressure wear facet. Probably a lower milk molar. (g) An abnormal right lower premolar with three roots. Several such forms have been found. (h) An abnormal posterior lower premolar with a slight anterior cusp development. It has no outer cingulum. (i) A small amphilestine-like tooth. Possibly a milk tooth of the trituberculate *Kuehneotherium*.

18-2

(5) The possibility that some forms may have only four lower molars while others certainly had five.

(d) Tooth replacement

Perhaps the most interesting of the still unresolved problems concerning the origin of the mammalian state of organization on which *Eozostrodon* might have been expected to throw some light was that of the origin of the mammalian diphyodont dentition. The reptilian poly-phyodont condition, which is known to have survived among the Theriodontia at least as late as the Lower Triassic cynodont *Thrinaxodon* (Crompton 1963), would appear at first sight to be the more effective, the animal maintaining the ability to replace its teeth far into old age. Yet the mammals have flourished with only a milk dentition followed by a permanent one, and in those modern forms in which abrasion is serious, hypsodonty or some other modification has been achieved and not a return to a multiple succession.

The very mammalian appearance of the dentition of *Eozostrodon*, especially the clear distinction of the postcanines into premolariform and molariform teeth, tempts one to the immediate assumption that the replacement may well have been diphyodont. But the provision of the evidence for a reasonably well-established case proved to be a long task.

Four lines of evidence must be taken into account when considering the nature of the tooth replacement in *Eozostrodon*. These are:

(1) The direct evidence afforded by specimens where replacement is actually taking place.
(2) The negative evidence of the great mass of the available material.
(3) The state of wear of many teeth.
(4) The ranges of size in the different sorts of teeth.

The first apparent find of tooth replacement occurred in specimen D 35 where a molariform crown was found partly erupted in a dentary in which more anterior and posterior tooth sockets were preserved. The crown was askew and not in an open socket but clasped by spongy bone and X-ray examination disclosed that the roots were fully formed, extending to the bottom of the dentary and having swollen apices. Since typical mammalian teeth erupt before the roots are more than half grown, and this condition can be shown to take place in *Eozostrodon*, it must be concluded that this specimen is abnormal and that no further eruption could have taken place had the animal continued to live. I am indebted to Professor A. D. Hitchen for his opinion of the nature of this tooth.

One specimen was found, a fragment of a small dentary (D 88, figure 16c, plate 45) in which Crompton's groove was well developed and enlarged into a pit below a small molariform tooth. This was dissected but only matrix was found in the pit. A subsequently discovered specimen (D 181) is similar (figure 10a).

The first specimen to be discovered showing a replacing tooth *in situ* was specimen D 98 (figure 16d), the product of a year's searching. This specimen consists of a fragment of a small dentary carrying a modest-sized molariform tooth below which was seen the tip of a replacing tooth rising from an enlarged hollow in Crompton's groove (figure 10b). The specimen was dissected but it was found that the crown of the replacing tooth was only partly developed, and it is not possible to be sure whether it is molariform or premolariform, though the appearance rather suggests the latter. The molariform tooth has an estimated crown length of 1.0 mm and it is peculiar in having no anterior accessory cusp, but instead there is what seems to be a wear patch. This wear patch would appear to be the result of pressure wear against the neighbouring tooth since it is partly lingual and so cannot have resulted from the action of the upper

teeth. This tooth is unusual and has only very small cingulum cuspules and it can be matched by very few others. Because the dentary is shallow, and so probably young, the possibility is that it is a molariform milk molar. If so the size suggests that it is the fourth since the fourth
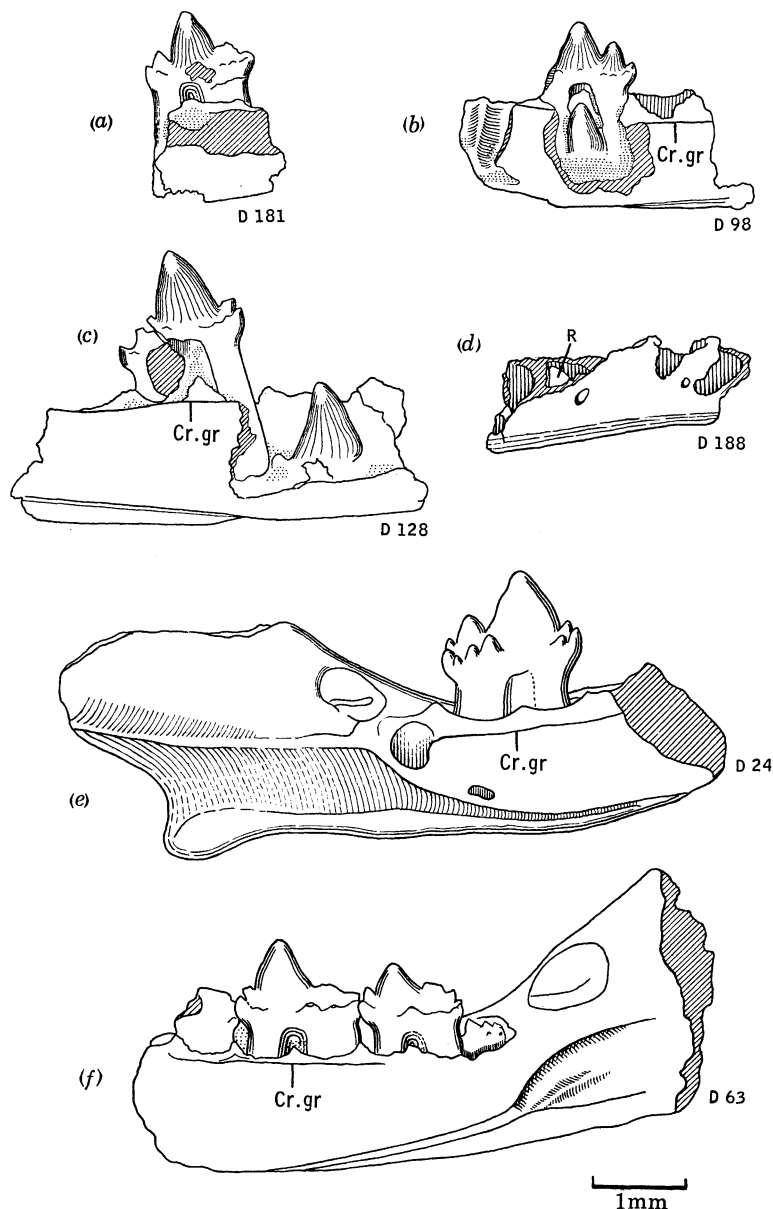

FIGURE 10. *Eozostrodon parvus*. Specimens showing evidence bearing on the problem of lower tooth replacement. (a) A milk molar below which was found an empty pocket developed from Crompton's groove. (b) A milk molar with the crown of a premolar developing below it. (c) The developing crown of the fourth premolar followed by the first molar. (d) A replacing tooth developing in the second postcanine socket. (e) Part of a small dentary with a freshly erupted molar, possibly the third molar, with Crompton's groove leading into a crypt for the development of an additional molar. (f) A specimen in which a last, possibly fourth, molar is developing in a crypt behind the last functional molar.

premolar varies in crown length between 0.8 and 1.24 mm, the third between 0.6 and 0.9 mm and the others are smaller.

The second specimen to be discovered showing a replacing tooth was D 128. Here an erupting tooth was seen within the socket which lies immediately in front of a somewhat damaged molar

tooth (figure 10c). Dissection showed that, beyond doubt, the developing tooth had a premolariform crown. The molar tooth has a crown length of 1.0 mm, has small cingulum cuspules, and shows wear only on the outer side of the anterior accessory cusp, and so must be regarded as the first molar; the erupting tooth is certainly, therefore, the fourth premolar.

After about two and a half years searching, no further examples of replacement having been found, the position was reviewed. By this time many hundreds of jaw fragments had been examined and about 150 fragments of dentaries had been registered as being of interest in one way or another. In addition to the examination of probably well over 500 fragments of dentaries, of which more than 100 contained premolar or molar teeth, or both, nearly sixty had been examined by X-ray and about 100 dissected. Yet only the two cases of tooth replacement had been found. Meanwhile a series of specimens had been noted which showed various stages in the formation of a crypt behind and below the last erupted molar. These ranged from the slightest of depressions to enormous caverns. In what appears to be a pair of dentaries (D 123) large crypts are present and in one, the right, the primary cone of a developing tooth was found. A series of five specimens have the crowns of developing molars within these posterior crypts (figure 10f) and in one an almost fully erupted tooth is present. All stages in the formation of a posterior crypt and the development of an additional molar are represented by more than a dozen specimens. In the face of this evidence the complete absence of evidence of the development of a replacing tooth below an unquestionable molar becomes overwhelming. The conclusion, that the molariform teeth were not replaced, accords with the not infrequent occurrence of severely worn molars; it is difficult to believe that such teeth would have been retained could they have been replaced. It remains to consider whether or not the molariform teeth themselves replaced predecessors. This seems very unlikely in view of the small size of the dentaries in which molars with fresh, unworn crowns and short roots occur (e.g. figure 10e). The conclusion that these molar-like teeth are true molars appears to be inescapable.

If it is accepted that in the great bulk of the specimens true molars are present, then it appears reasonable to expect that the premolariform teeth might well be premolars, a conclusion in accord with the by now extensive evidence that they too were not replaced. But it carries with it the implication that the premolars themselves might well have replaced milk molars and this conclusion receives the support of the two specimens, one showing, apparently, the replacement of a molariform milk molar and the other the late eruption of the fourth premolar. The next logical step was, therefore, to search for dentaries of smaller size in the hope of finding supporting or contradicting evidence. The methods of extracting the remains from the bulk clay were therefore reviewed by Dr K. A. Joysey and stringent steps were taken to reduce to the absolute minimum any actions which tended to break small, delicate specimens. This imposed considerable restraint on the extracting processes and so slowed up the supply of material for study. An occasional fragment of a very small dentary was found but always lacking teeth until, after about 6 months further work, a fragment of a very tiny dentary was recovered in which the shining enamel cap of a replacing tooth was visible (figure 10d). The specimen (D 188) measures less than 3 mm long and less than 1 mm in depth (the borders of the tooth sockets are poorly preserved and this makes measurement difficult) and shows part of the symphysis. The replacing tooth lies within what appears to be the second postcanine socket, but is just possibly the first.

Finally, after about three and a half years work, and still employing the most gentle methods of extraction, a small maxilla (M 69) was obtained which has the most extensive palatal component of any such specimen yet collected. Sockets for all the premolars are present but in

addition the bone contains a very small and badly worn canine (the crown length is about 0.65 mm) and, lingual and anterior to it, the crown of a replacing canine (figure 7*a*).

The discovery of two cases of replacement among anterior teeth within a period of less than a year, despite the slowness of the new techniques employed (and the demands of other work) seems to justify the conclusion that tooth replacement in the anterior region took place when these animals were very small, and this can be taken as indicating that they were young. It seems clear that sufficient data have been obtained, both positive and negative, to justify the conclusion that *Eozostrodon* had the mammalian diphyodont condition.

The conclusion reached above is in accordance with observations on *Erythrotherium*. In this form, which is small, there is a replacing incisor present and one of the premolariform teeth appears to have been incompletely erupted at a time when the crown of the most posterior molar had not been fully formed (Crompton 1964). Professor Crompton informs me that he is of the opinion that the specimen is that of a juvenile animal, a conclusion which may well account for the slenderness of the dentary and the absence of an angular process and of a coronoid boss. These are features which might well have changed in a fully grown animal.

The well-known dentary of *Triconodon mordax* in the British Museum (Simpson 1928, Figure 24), showing a replacing canine and a premolariform tooth replacing a molariform tooth immediately in front of a molar tooth, also conforms to the evidence of *Eozostrodon*.

Finally the observed facts about Crompton's groove are in accordance with the proffered interpretation, the replacement of the milk dentition normally being complete in mammals before the posterior molar erupts.

If the foregoing interpretation is accepted then the great size range of the isolated teeth shown in figure 2 can be accounted for as a combination of the existence of two dentitions in a form having a great size range. Thus the minute lower incisors and very small canines would appear to be milk teeth, whereas the range in size of the molars can be accounted for as a combination of the known considerable range of size within any one jaw together with the great variation in size of adult animals and of their teeth (D119, 120).

It may be pointed out that the diphyodont condition in *Eozostrodon* conforms to the writer's view, held also by Crompton, Jenkins and Hopson, that the form lies close to the base of the mammalian stem. The view that only one tooth is replaced (Mills, in press) is against this interpretation but it is ill founded.

Crompton & Jenkins (1968) have pointed out that the tooth wear in *Eozostrodon* resulted from closer interaction between the teeth of the two jaws, more efficient biting being achieved than occurred, for example, in *Thrinaxodon*, a cynodont with very similar teeth which, however, show no such wear. Yet while this latter animal replaced its teeth frequently (Crompton 1963), *Eozostrodon* had reduced its dentition to the mammalian condition. Such developments appear to be completely contradictory for the teeth of *Eozostrodon* are sometimes worn to mere stumps (Parrington 1967), and the question arises as to why the change came about. Only one supposition appears to be able to account for the change.

Because the eozostrodonts were very widespread, occurring throughout the length and breadth of the Old World, and, locally at least, were very abundant, and because they appear to have been ancestral to a wide variety of forms, it must be concluded that their dental equipment was efficient for their needs. The development of further sets of teeth would, therefore, have been a waste of materials and energy. The known eozostrodonts are very small animals, comparing in size with the shrews, among the smallest of living mammals. This must surely be

taken to indicate that their life cycle was brief, as it is in shrews, their teeth providing for their needs until the breeding cycle was either complete, or at least adequate for the animals to remain abundant. It is doubtful if any large animal could have afforded to have worn its teeth at a high rate and at the same time have reduced the dental succession, since its size would require a comparatively long life. It may be noted that while *Thrinaxodon* was a small cynodont, nevertheless it was a giant compared with *Eozostrodon*. The immediate descendants of the eozostrodonts were all small animals which modified their teeth in a variety of ways which reduced the rate of wear (p. 268). The question of the appearance of the hard, thick, prismatic enamel of the mammals has interested several people. Poole (1956) has shown that the enamel of the synapsid reptiles differs from that of other reptiles but is not mammalian. Moss & Kermack (1967) claim that the enamel of *Eozostrodon* and *Kuehneotherium* is different again, but still not mammalian. The optical properties will, no doubt, eventually be of use to taxonomists but what would be of the greatest interest would be a scale of hardness, like that used by geologists when testing minerals. If this could be achieved it might show progressive hardness of the enamel as the mammalian condition was approached and, together with increased thickness, it may have permitted a longer life for the teeth.

Tertiary mammals prolonged the lives of their teeth by keeping the incisors growing, as in the rodents; by hypsodonty, as in the perissodactyls and artiodactyls; or by using enormously enlarged teeth one at a time, as in the elephants. Small mammals usually fed without subjecting their teeth to undue wear, as in the insectivores, and were short lived. It is of special interest that rodents, while maintaining the growth of their gnawing teeth, did not greatly modify their molars which are only moderately hypsodont and no rodents are large.

The loss of the primitive, multiple tooth succession appears to be an interesting example of the supposed irreversibility of evolution.

(e) *Postcranial material*

Little usable material of the postcranial skeleton has been obtained, and it appears probable that useful accounts of this are likely to come from the types of the South African forms *Erythrotherium* and *Megazostrodon*. However some points can be made. Fragments of the shoulder girdle confirm the claim by K. A. Kermack & Mussett (1959) that the precoracoid, while excluded from the glenoid cavity, retains a sutural connexion with the scapula.

It is clear from the shape of the narrow, trihedral, preacetabular ilium that the leg musculature was essentially mammalian (figure 11*b*). The head of the femur (figure 11*a*) makes a distinct angle with the shaft and other fragmentary pieces show that the distal articulating condyles were more or less terminal and not ventral (as in tritylodonts and monotremes), but the appearance is not as mammalian as the Purbeck femur figured by Simpson (1928, Figure 49). The major and minor trochanters make a wider angle with the condyle when viewed from the proximal end than might have been expected from the writer's interpretation of the cynodont femur (Parrington 1961), but the appearance can be matched among small living mammals such as *Phascogale* (figure 11*e*). At one time it was thought that the femur of *Sinocondon*, variously interpreted as a triconodontine and as an eozostrodont, was distinctly different, but comparison with a bone having the trochanter minor broken in a similar way suggests that this is not so (figure 11*c, d*).

No other useful postcranial remains have been studied though parts of the humerus are reasonably well preserved as are pieces of epipodials.
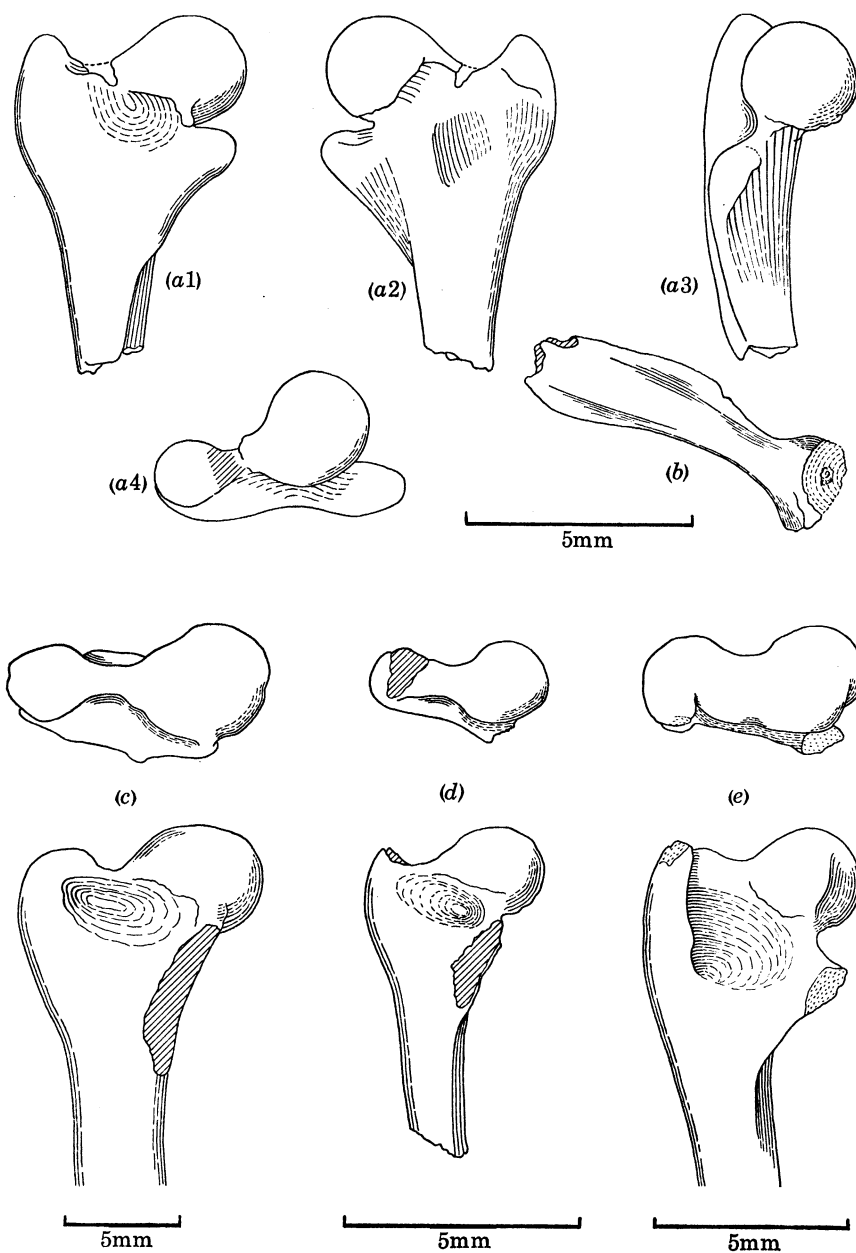
FIGURE 11. (a) Four aspects of the proximal end of the left femur of *Eozostrodon*. (a1) Posterior view; (a2) anterior view, (a3) internal view, (a4) proximal view. (b) Outer view of left ilium. (c) Posterior aspect of the femur of *Sinoconodon* (drawn from a cast) for comparison with (d) a fragment of a femur of *Eozostrodon* (d) with the lesser trochanter broken in a similar way. (e) The head of the femur of the marsupial *Phascogale* for comparison.

3. *KUEHNEOTHERIUM PRAECURSORIS* KERMACK, KERMACK & MUSSETT

In the course of three and a half years work rather more than 100 trituberculate teeth have been found, ninety or so in good or fair condition. Only two teeth have been found in pieces of dentaries, but half a dozen or so other dentaries seem to be represented by fragments. These are identified on the grounds of the wide spacing of the premolar sockets; by the lack of an angular process in dentaries of fair size; and by the thickening of the bone in the molar region which accompanies a form of triangulating of the teeth sockets (not seen in *Eozostrodon*); and

a thickening of the dentary posteriorly together with a deepening of the trough for the post-dentary bones. The most interesting fact acquired (Sy 15) is that Crompton's groove can be recognized.

D. M. Kermack *et al.* (1968) claim that the form *Kuehneotherium praecursoris* is a pantothere.
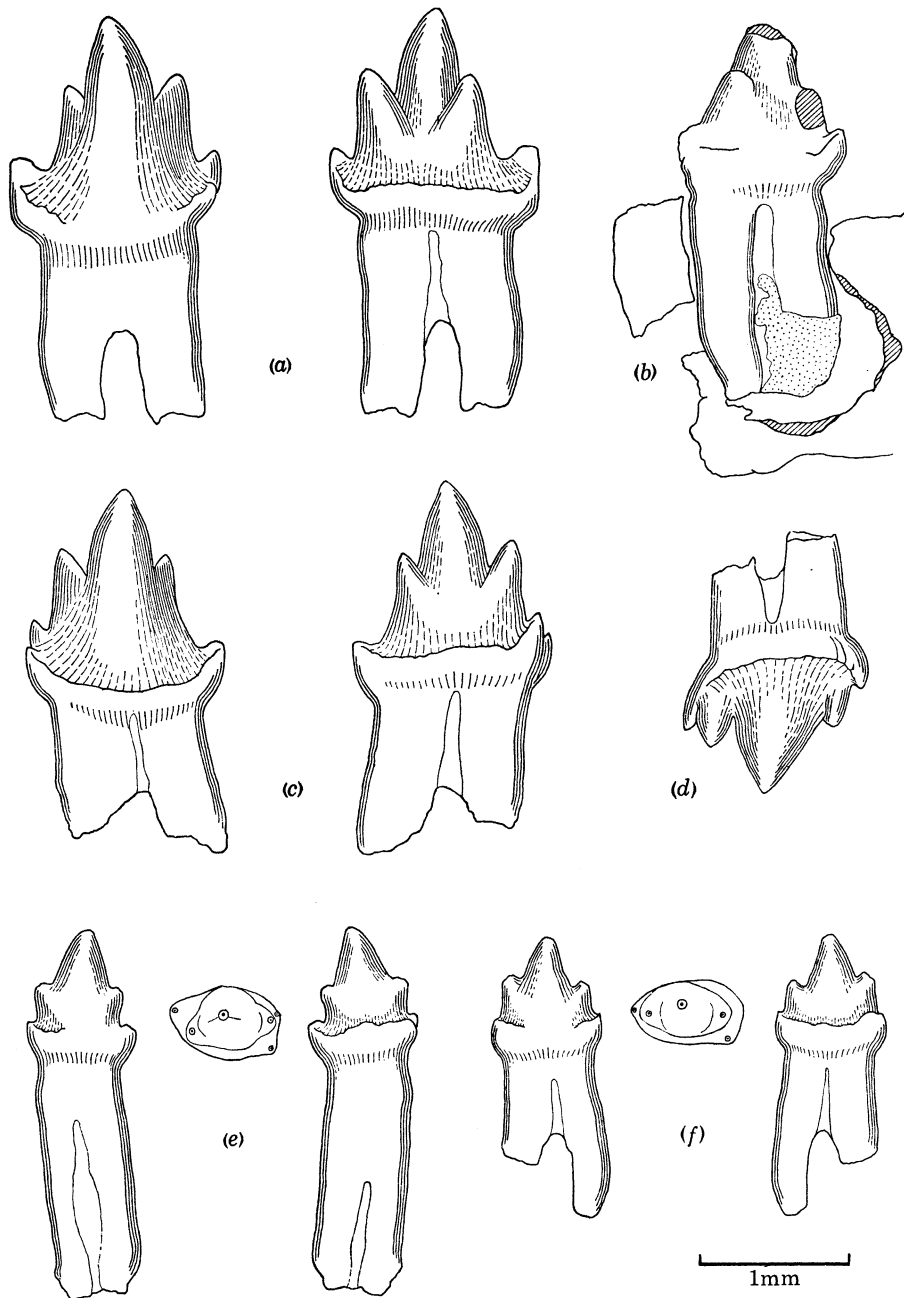
FIGURE 12. Various trituberculate teeth. (*a*) A typical right lower molar of *Kuehneotherium* with an unworn crown and incompletely developed roots. (*b*) An old right molar tooth, somewhat damaged but showing the long roots achieved with age. The dotted region may be formed of cementum which has been partly removed. (*c*) A left lower molar differing from other similar teeth in the complete outer cingulum. In this the tooth resembles the symmetrodont *Spalacotherium* very closely. (*d*) A typical right upper molar of *Kuehneotherium*. (*e,f*) Two small teeth which may be posterior molars. Their identification remains uncertain.

But their classification is different from that used through many decades and itself has undergone changes which are difficult to accept as useful. As Crompton & Jenkins (1967) have shown, the teeth of this animal match those of the American symmetrodonts *Tinodon* and *Eurylambda* remarkably closely. It can now be said that *Kuehneotherium* resembles *Spalacotherium* even more closely, the lower molar tooth Sy 45 (figure 12*c*) even having a complete outer cingulum as do most of those of *Spalacotherium*. This tooth was found together with Sy 44, in the same handful of concentrate, at almost the same moment. Both come from a left dentary and both are beautifully preserved and have only partly grown roots. The great rarity of these trituberculate teeth in the clay available to the writer make it almost certain that these teeth came from the same dentary, and the tooth Sy 44 is a typical *Kuehneotherium* molar as the form has been described. In *Spalacotherium*, as in *Kuehneotherium*, the posterior accessory cusps of the lower molars retreat further across the crown than do the anterior accessory cusps, the degree of angulation increasing posteriorly to about the fifth molar but opening slightly in the seventh, as far as can be judged from the rather poorly preserved material available (figure 14). The external cingulum is better developed though it is not present on M_7 and damage to the anterior three molars makes it impossible to be sure if it was complete on these teeth. The cingulum appears to enlarge rather more anteriorly than posteriorly but the preservation and successive layers of preservative make it impossible to determine this point with certainty. To obtain a tooth of the type found in *Spalacotherium* from that of the type found in *Kuehneotherium* all that is necessary is to reduce the anterior and posterior cingulum cusps. But to obtain a panto-there tooth it would also be necessary to reduce the anterior cusps; to rotate the posterior accessory cusp until it is in line with the primary cusp; and to enlarge greatly the 'tiny talonid' of Kermack *et al*. Taken in conjunction with the symmetrodont-like upper molars (figure 12*d*) and the absence of an angular process these facts will not allow the statement that *Kuehneotherium* can about equally easily give rise to a symmetrodont or a pantothere. Plainly, as Simpson foresaw, the symmetrodonts are more primitive than the pantotheres (unless the meanings of these words are changed) and it is plain today that, as Osborn foresaw, the trituberculates came from the triconodonts (figure 16*g*, plate 45).

The claim by Mills (in press) that the roots of *Kuehneotherium* do not develop the swollen apices to their roots as seen in *Eozostrodon* is supported by the rather meagre evidence available, but the view that the roots are more therian-like is difficult to understand. As in the case of the triconodont, teeth of *Kuehneotherium* are occasionally found with perfect crowns and short but apparently perfect roots (figure 12*a*). These are surely freshly erupted teeth which have not been subjected to wear and which have not developed their roots fully. Worn molars found in the dentary have long roots—at least as long as those of *Eozostrodon* (figure 12*b*).

A point of interest in the crowns of the trituberculate teeth is that in nearly all cases the posterior accessory cusp of the lower molars and the anterior accessory cusps of the upper molars have moved further across the crown than the other accessory cusps (figure 13). This accords with the suggestion that the process of triangulation results in a better fit between opposing teeth and so a reduction of wear (Parrington 1967; Crompton & Jenkins 1968). A further point of interest lies in the fact that while most lower molars have two small anterior cingulum cusps, some teeth have only one. The molars of a specimen of *Spalacotherium tricuspidens* Owen in the Sedgwick Museum, Cambridge (J 11378) shows something of the tendency of the posterior accessory cusp to rotate further than the anterior one, and an increase in the angulation in the more posterior teeth, the seventh excepted (figure 14). But the teeth are not
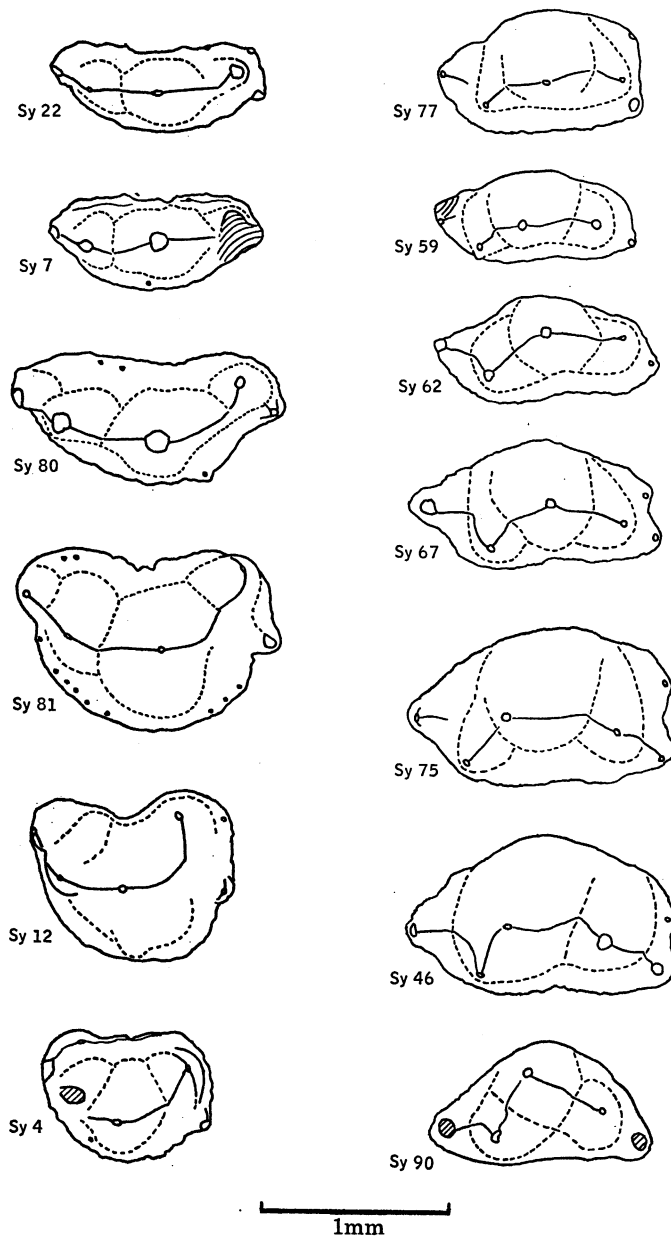
FIGURE 13. *Kuehneotherium praecursoris*. Upper (right) and lower (left) crown views of molars showing the varying angulation and the movement of the anterior accessory cusp of the upper molars and the posterior accessory cusps of the lower molars. Some of the upper molars have only single leading cingulum cuspules while others have two. Additional small cingulum cuspules occur sporadically on the upper molars. Teeth numbered 12, 4, 75 and 90 are reversed.
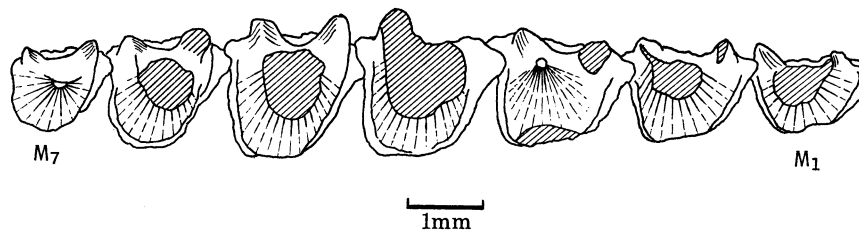

FIGURE 14. The crown view of the lower right molars of *Spalacotherium* from a specimen in the Sedgwick Museum (J 11378).

well preserved and various strengthening substances have been used which tend to obscure details.

Two small teeth which show little or no angulation and very long roots may be posterior lower molars, but they are different somewhat from each other, and the shorter of the two might be a posterior upper molar. But it should be noted that these two teeth (figure 12 e,f) are remarkably symmetrical; they were for a time regarded as possible members of the Amphilestinae. Until the London collection has been described there appears to be little point in trying to separate such teeth taxonomically.

4. The relationships of early mammals

K. A. Kermack (1967) has claimed that the class Mammalia should be divided into the therian and non-therian mammals according to the relations of the mandibular branch of the trigeminal nerve to the alisphenoid (foramen ovale) or the periotic (foramen pseudovale). This is in disregard of the suite of characters shared in common by the Triassic triconodont and trituberculate forms (Parrington 1967; Crompton & Jenkins 1967; Hopson & Crompton 1969). He supposes that when found, the brain case of *Kuehneotherium* will not show the formation of a foramen pseudovale and holds that the two kinds of Triassic mammals arose independently from different therapsid reptiles and belong to the two quite different sorts of mammals. It has been the experience of zoologists that major groupings of animals on single characters are seldom reliable and this one must be regarded as suspect.

Kielan-Jaworowska & Kermack (in press) have recently shown that the anterior flange of the periotic of *Eozostrodon* (*Morganucodon*) *oehleri* has captured the mandibular nerve, thus forming a foramen pseudovale as in the monotremes. But, unlike those forms, *Eozostrodon* has an expanded alisphenoid of mammalian pattern and not a mere ventral slip of bone. Whichever view is taken about the origin of therian mammals one of two assumptions must be made. Either it must be supposed, as Kermack would suppose, that when found the brain case of *Kuehneotherium* will show the mandibular branch of the trigeminal nerve leaving the brain case between the periotic and the alisphenoid (as in cynodonts), or that it has already formed a true foramen ovale through the alisphenoid; or it must be supposed that, though captured by the forward growth of the periotic flange in both *Eozostrodon* (and its allies) and presumably also in the allied trituberculate *Kuehneotherium*, the nerve later migrated forward into the alisphenoid in the true therian line of evolution. Either happening is possible. Some will think that Kermack *et al.* are right in seeing nothing in common between the dentitions of the two sorts of Triassic mammals and accept the proposition that, when found, their brain cases will also be found to be different. Others, accepting the fact that the known Triassic mammals have much in common, notably in their dentitions, will expect that the periotics will eventually be found to be essentially similar and they will prefer to suppose that in the enormous expansion of the brain, the outstanding feature of therian evolution, the mandibular nerve escaped from the periotic flange and penetrated the alisphenoid. This interpretation finds some justification in the considerable variation in the position of the nerve exit within modern mammals (MacIntyre 1967).

As has already been stated *Eozostrodon* must be regarded as a triconodont because it has a dentition which is very close to that of the, typical, Upper Jurassic members of the order, differing largely in the unevenness of the molar cusping and the more numerous cuspules on

19-3

the cingula. This claim remains unrefuted (K. A. Kermack 1967 b, p. 243). The form of the lower jaw, with its large trough for postdentary bones, is that of a primitive mammal and, as Kermack has realized, it is a condition through which various early mammals are likely to have passed (e.g. *Kuehneotherium*). The reason for the persistence of this primitive condition in *Docodon*, with its highly specialized molar teeth, remains unknown. Crompton & Jenkins (1967) and Jenkins (1968) have shown how, by very considerable developments, the molar teeth of *Eozostrodon* may have been transformed into those of *Haldenodon* and *Docodon*, but hold, rightly, that these modifications are such as to prevent the inclusion of such bizarre forms within the order Triconodonta (Crompton & Jenkins 1967; Hopson & Crompton 1969). Kermack (1967 b) has illustrated an amphilestine-like tooth from the Triassic fissures and like Patterson & Olson (1961) has expressed doubts about the relationships of these forms. The likeness of the tooth to the amphilestines, as shown by another specimen (figure 9 e), lies in the symmetry of the five cusps and in the rising of the internal cingulum at its mid-point. But the reason against including the amphilestines within the Triconodonta lies, in the writer's opinion, in a slight tendency for the three main cusps of *Phascolonodon* and perhaps *Amphilestes* towards triangulation.

That the trituberculate animal *Kuehneotherium* is properly regarded as a symmetrodont has been shown quite clearly by Crompton & Jenkins (1967) whose views receive strong support from the tooth illustrated in figure 12 c, and the collection of Triassic trituberculate teeth in general, and their claim can only be denied by making considerable changes in the meanings of the words symmetrodont and pantothere, changes which have never been defined and which, in the writer's opinion, serve no useful purpose.

If, as the writer holds, the tricondont tooth, as represented by *Eozostrodon*, is the basic type from which those of other mammals evolved, and if, as has been demonstrated, the dentition is diphyodont yet subject to severe wear, then it is reasonable to imagine various changes which would reduce the rate of wear (and so increase the life of the tooth and potentially of the individual) and such modifications should be known. The first change would be to even the sizes of the three principal cusps, thus spreading the area of wear at the start of the life of the tooth, and so prolong its life. This change occurred in the typical tricondonts of the Upper Jurassic, though something of the original inequality of the cusps is still to be seen in the lower molars of *Priacodon*. The second wear-reducing modification is to move the opposing cusps until a better fit is achieved despite the unevenness of the cusps. This happens in *Kuehneotherium* where the leading accessory cusp of the upper molars and the posterior accessory cusp of the lower molars retreat away from the large principal cusp of the opposing tooth. Two developments take place from this stage. Triangulation is more fully and evenly developed and the small 'fourth cusp', Kermack's 'tiny talonid', is reduced, thus presenting a series of opposed shearing surfaces and a long zig-zagged cutting line. This results in the later and but little different symmetrodonts. Alternatively the retreating leading and trailing accessory cusps can continue their movements ahead of those of the other accessory cusps, allowing for the formation of a full talonid against which the opposing tooth can crush food which has already been cut. In this way the pantotheres evolved towards the formation of the typical tribosphenic molar itself. Finally wear could be reduced by opposing the crowns of the teeth, broadening them in the process. This occurred in the development of *Docodon* (Crompton & Jenkins 1968) and it occurred also in the Multituberculata, if they too are of triconodont origin.

It has sometimes been stated by writers that they do not support the theory of the rotation of the triconodont cusps into the triangle (see, for example, Simpson 1928, 1929; Patterson 1956).

The implication behind this view is that in the trituberculate ancestor accessory cusps were added to single cusped teeth in the triangular position and never passed through the triconodont stage. One argument which has been used to support this view was that no intermediate stage was known. This argument has lost its force both by the demonstration of the varying degrees of angulation of the cusps in such symmetrodonts as *Kuehneotherium* and *Tinodon*, and by the probability that the amphilestines, long regarded as triconodonts, have in fact slightly angulated cusps. Also against this view is the fact that no Triassic cynodonts are known which have single-cusped postcanines and the only theriodonts from the Trias which do so, a few therocephalia from the basal Trias, are quite unsuited as mammal ancestors.

In view of these facts, and of the obvious resemblances between the dentitions of *Eozostrodon* and *Kuehneotherium*, particularly between the molar teeth of the former and the non-angulated, and only slightly angulated, molars of the latter, the Triconodonta must be regarded as ancestral to the Trituberculata as Osborn claimed long ago. Crompton & Jenkins (1968) have shown how, by somewhat extensive modifications, the teeth of the Docodonta can also be derived from those of the early triconodonts but hold, rightly, that their dentitions have become so highly modified that they cannot be placed in the same order. Finally the discovery of lower molars of *Eozostrodon* which have developed a series of small cusps on their outer faces (figure 9*d, e*) lends some support to the view that the Triconodonta might also be ancestral to the Multituberculata, a view already made possible by the teeth known as haramiyids.

As has been emphasized the numerous resemblances between the dentitions of *Eozostrodon* and *Kuehneotherium* must surely indicate a fairly close relationship. This conclusion receives some support from the facts that the two animals are of the same size and lived at the same period of time in the same part of the world, and that the known postcranial remains, albeit poor, do not indicate the presence of two distinct forms. Furthermore, eozostrodonts are now known from China and from South Africa, showing that they were very widespread indeed. This fact, together with their abundance in South Wales and their observed tendency to vary at least their dentitions, is consistent with the view that they can be regarded as having been near the basal stock from which mammals as a whole evolved.

Rightly, Crompton & Jenkins (1968) have retained the orders Symmetrodonta Simpson and Pantotheria Marsh, pointing out that the classification proposed by Kermack *et al.* (1968) places such different animals as the symmetrodonts and the dryolestids within one order. But the inclusion of the two orders within a Superorder Trituberculata would restore the coherence of these animals properly claimed by Osborn who used this term in 1893. Thus Simpson wrote (1929, p. 45): 'Despite some rearrangement of their contents the orders Pantotheria Marsh and Trituberculata Osborn are synonymous.' And, as rightly foreseen by Simpson when he established the order, the Symmetrodonta represent a more primitive stage of organization of the trituberculates than the Pantotheria (Simpson 1928, Figure, p. 183).

The large number of publications in which the classifications of *Eozostrodon* and *Kuehneotherium* have been debated will cause some to ask why there should have been such difficulty about two animals which can clearly be placed within long established orders. Why should *Eozostrodon*, an obvious triconodont, ever have been called a docodont? Why should *Kuehneotherium*, clearly a symmetrodont, ever have been called a pantothere? When the reasons are sought they are not to be found in the sum of the characters of the animals, nor in insufficient data, but in an overwhelming desire to place them at the root of the great evolution of the therian mammals (at the time *Eozostrodon* was transferred to the Docodonta these were regarded

as Pantotheria). It is ironical that when their true natures are accepted they lie closer than any other known animals to that important event.

It will be seen that the foregoing conclusions are very close to those advanced by Crompton & Jenkins (1968) and by Hopson & Crompton (1969). They are summarized in figure 15.
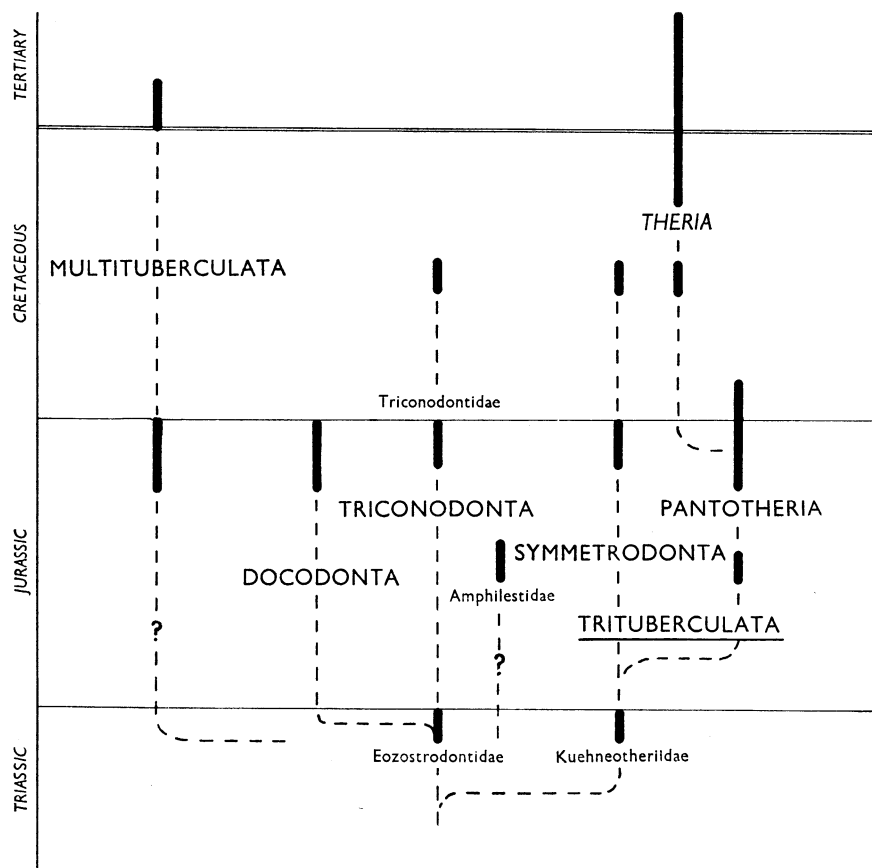

FIGURE 15. The relationships of the Mesozoic orders of mammals. These are largely as expounded by Simpson (1928, 1929), but with the addition of more recent discoveries in the Trias and Cretaceous and also the addition of the Order Docodonta and the Superorder Trituberculata.

LIST OF ABBREVIATIONS USED IN THE FIGURES

ART	articular and associated bones	l.f.	lacrimal foramen
a.inf.f.	anterior infraorbital foramen	M	molar
C	canine	p.inf.f.	posterior infraorbital foramen
COR	coronoid	PM	premolar
Cr.gr.	Crompton's groove	Q	quadrate
I	incisor	R	replacing tooth
J	jugal	SPL	splenial
L	lacrimal		

REFERENCES

Bohlin, B. 1945 The Jurassic mammals and the origin of the mammalian molar teeth. *Bull. geol. Inst. Univ. Upsala* **31**, 363.

Crompton, A. W. 1963 Tooth replacement in the cynodont *Thrinaxodon liorhinus* Seeley. *Ann. S. Afr. Mus.* **46**, 479.

Crompton, A. W. 1964 A preliminary description of a new mammal from the Upper Triassic of South Africa. *Proc. zool. Soc. Lond.* **142**, 441.

Crompton, A. W. & Jenkins, F. A. Jr. 1967 American Jurassic symmetrodonts and Rhaetic 'pantotheres'. *Science, N.Y.* **155**, 1006.

Crompton, A. W. & Jenkins, F. A. Jr. 1968 Molar occlusion in Late Triassic mammals. *Biol. Rev.* **43**, 427.

Hopson, J. A. 1966 The origin of the mammalian middle ear. *Am. Zool.* **6**, 437.

Hopson, J. A. & Crompton, A. W. 1969 Origin of mammals. *Evolutionary Biol.* **3**, 15.

Jenkins, F. A. 1969 Occlusion in *Docodon. Postilla* no. 139.

Kermack, D. M., Kermack, K. A. & Mussett, F. 1956 New Mesozoic mammals from South Wales. *Proc. geol. Soc. Lond.* **1533**, 31.

Kermack, D. M., Kermack, K. A. & Mussett, F. 1968 The Welsh pantothere *Kuehneotherium praecursoris*. *J. Linn. Soc. (Zool).* **47**, 407.

Kermack, K. A. 1956 Tooth replacement in mammal-like reptiles of the Suborders Gorgonopsia and Therocephalia. *Phil. Trans. Roy. Soc. Lond.* B **240**, 94.

Kermack, K. A. 1963 The cranial structure of the triconodonts. *Phil. Trans. Roy. Soc. Lond.* B **246**, 83.

Kermack, K. A. 1965 The origin of mammals. *Sci. Jnl* **1**, 66.

Kermack, K. A. 1967*a* Molar evolution in Mesozoic mammals. *J. dent. Res.* **46**, 792.

Kermack, K. A. 1967*b* The interrelations of early mammals. *J. Linn. Soc. (Zool.)* **47**, 241.

Kermack, K. A. 1967*c* In *The fossil record* (ed. W. B. Harland *et al.*), p. 763. London: Geological Society.

Kermack, K. A., Lees, P. M. & Mussett, F. 1965 *Aegialodon dawsoni*, a new trituberculo-sectorial tooth from the Lower Wealden. *Proc. Roy. Soc. Lond.* B **162**, 535.

Kermack, K. A. & Mussett, F. 1958 The jaw articulation of the Docodonta and the classification of Mesozoic mammals. *Proc. Roy. Soc. Lond.* B **149**, 204.

Kermack, K. A. & Mussett, F. 1959 The first mammals. *Discovery* **20**, 144.

Kretzoi, M. 1946 On Docodonta, new order of Jurassic mammals. *Ann. Hist.-Nat. Mus. Nat. Hungarica* **39**, 108.

Kühne, W. G. 1947 The geology of the fissure-filling 'Holwell II'; the age-determination of the mammalian teeth therein; and a report on the technique employed when collecting the teeth of *Eozostrodon* and Microcleptidae. *Proc. zool. Soc. Lond.* **116**, 729.

Kühne, W. G. 1949 On a triconodont tooth of a new pattern from a fissure-filling in South Glamorgan. *Proc. zool. Soc. Lond.* **119**, 345.

Kühne, W. G. 1950 A symmetrodont tooth from the Rhaeto-Lias. *Nature, Lond.* **166**, 696.

Kühne, W. G. 1958 Rhaetische Triconodenten aus Glamorgan, ihre Stellung zwischen den Klassen Reptilia und Mammalia und ihre Bedeutung für die Reichastsche Theorie. *Paläont. Z.* **32**, 197.

Kühne, W. G. 1968 Origin and history of the Mammalia. *Evolution and environment*. A symposium presented on the occasion of the 100th Anniversary of the foundation of the Peabody Museum of Natural History at Yale University (ed. Ellen T. Drake). New Haven: Yale University Press.

MacIntyre, G. T. 1967 Foramen pseudovale and quasi-mammals. *Evolution* **21**, 834.

Moss, M. L. & Kermack, K. A. 1967 Enamel structure in two Triassic mammals. *J. dent. Res.* **4**, 745.

Parrington, F. R. 1941 On two mammalian teeth from the Lower Rhaetic of Somerset. *Ann. Mag. nat. Hist.* 11, **8**, 140.

Parrington, F. R. 1946 On the cranial anatomy of cynodonts. *Proc. zool. Soc. Lond.* **116**, 181.

Parrington, F. R. 1947 On a collection of Rhaetic mammalian teeth. *Proc. zool. Soc. Lond.* **116**, 707.

Parrington, F. R. 1960 The angular process of the dentary. *Ann. Mag. nat. Hist.* Ser. 13, **2**, 505.

Parrington, F. R. 1961 The evolution of the mammalian femur. *Proc. zool. Soc. Lond.* **137**, 285.

Parrington, F. R. 1967 The origins of mammals. *Advmt Sci., Lond.* **24**, 1.

Patterson, B. 1955 A symmetrodont from the early Cretaceous of Northern Texas. *Fieldiana, Zool.* **37**, 689.

Patterson, B. 1956 Early Cretaceous mammals and the evolution of mammalian molar teeth. *Fieldiana, Geol.* **13**, 1.

Patterson, B. & Olson, E. C. 1961 A triconodont mammal from the Triassic of Yunnan. Int. Colloq. on the Evolution of Lower and non-specialized Mammals. *Kon. Vlaamse Acad. Wetensch. Lett. Sch. Kunsten Belgie.* no. 129.

Peyer, B. 1956 Über Zähne von Haramiyden, von Triconodonten und von Wahrscheinlich synapsiden Reptilian aus dem Rhät von Hallau Kt. Schaffhausen, Schweiz. *Schweiz. paläont.* **72**, 1.

Poole, D. F. G. 1956 The structure of the teeth of some mammal-like reptiles. *Q. Jl. micr. Sci.* **97**, 303.

Rigney, H. W. 1963 A specimen of *Morganucodon* from Yunnan. *Nature, Lond.* **197**, 1122.

Romer, A. S. 1966 *Vertebrate Palaeontology*, 3rd ed. University of Chicago Press.

Simpson, G. G. 1928 *A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum.* London: British Museum (Natural History).

Simpson, G. G. 1929 *American Mesozoic Mammalia.* New Haven: Yale University Press.

Simpson, G. G. 1945 The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* **85**, 1.

Simpson, G. G. 1961 Evolution of Mesozoic mammals. Int. Colloq. on the Evolution of Lower and non-specialized Mammals. *Kon. Vlaamse Acad. Wetensch. Lett. Sch. kunsten België*, Pt 1. 57 Brussels.

Watson, D. M. S. 1916 The monotreme skull: a contribution to mammalian morphogenesis. *Phil. Trans. Roy. Soc. Lond.* B **207**, 311.
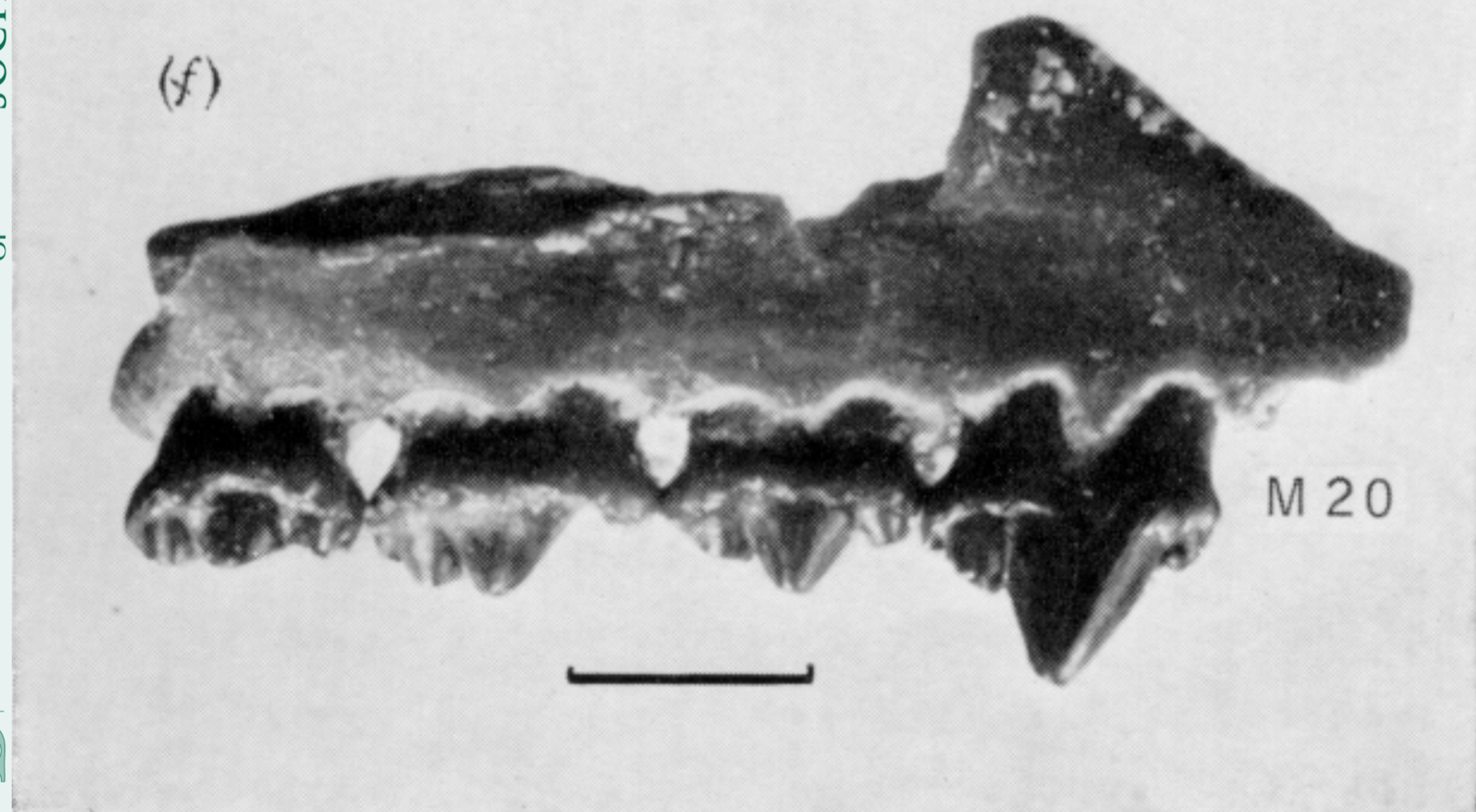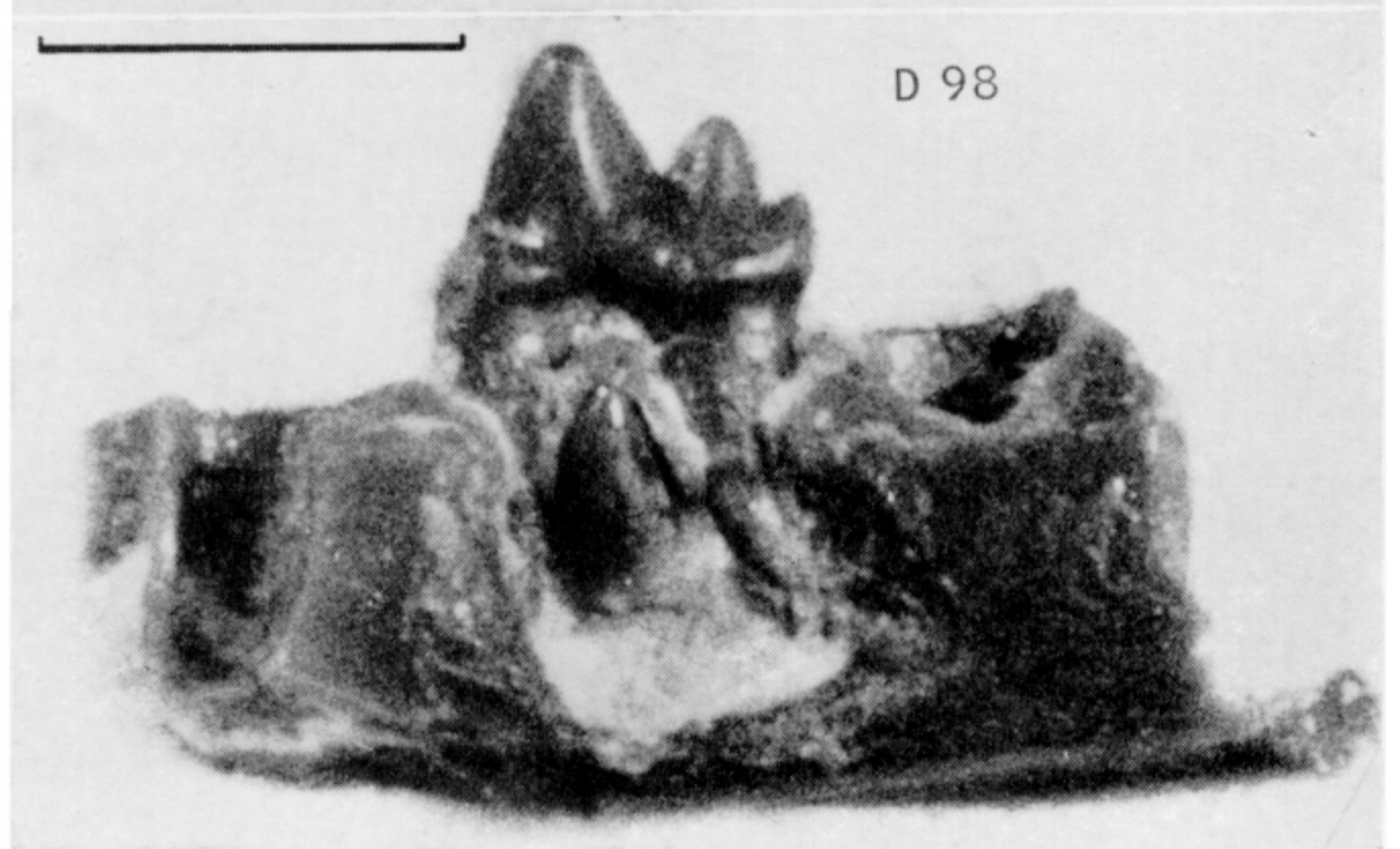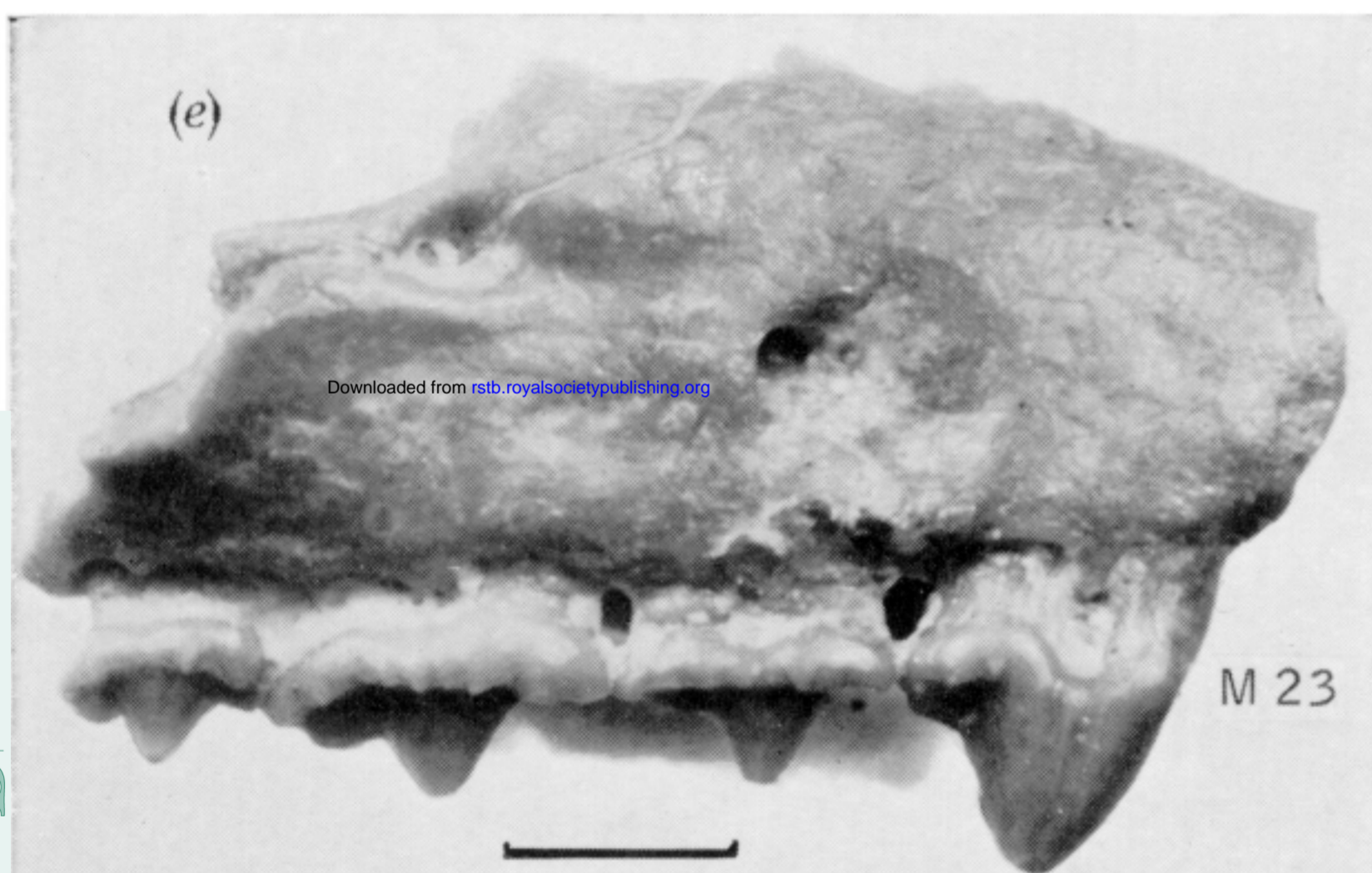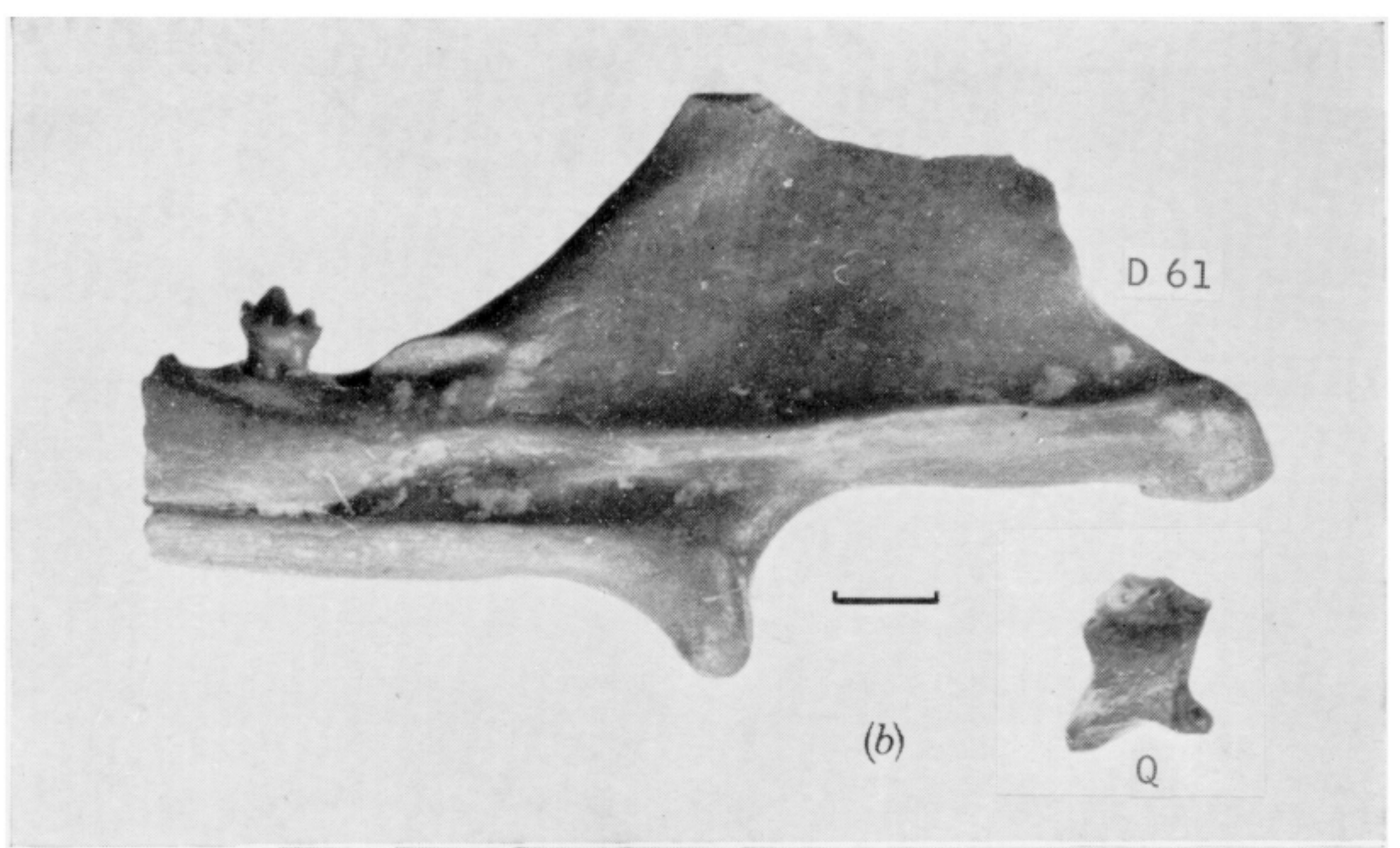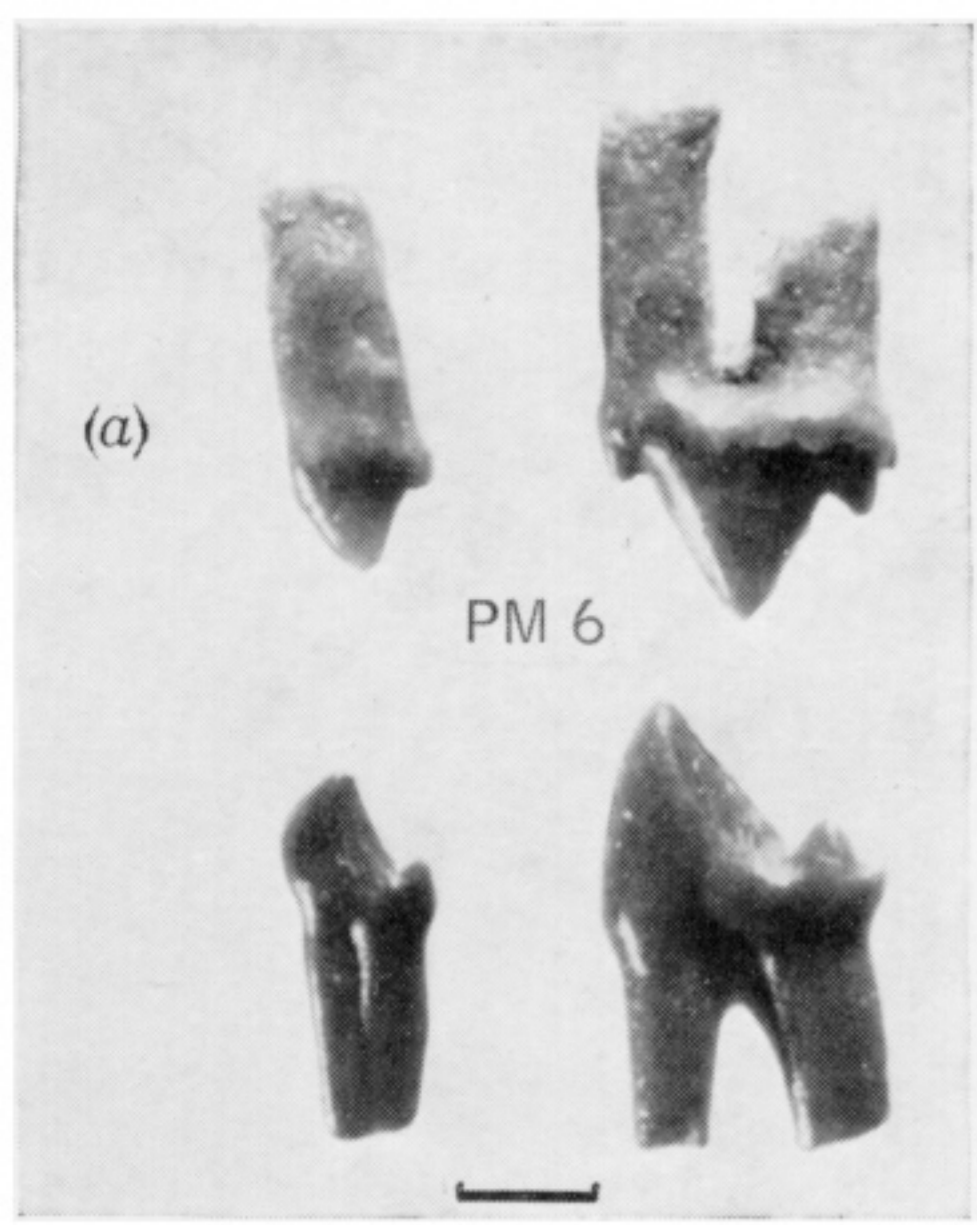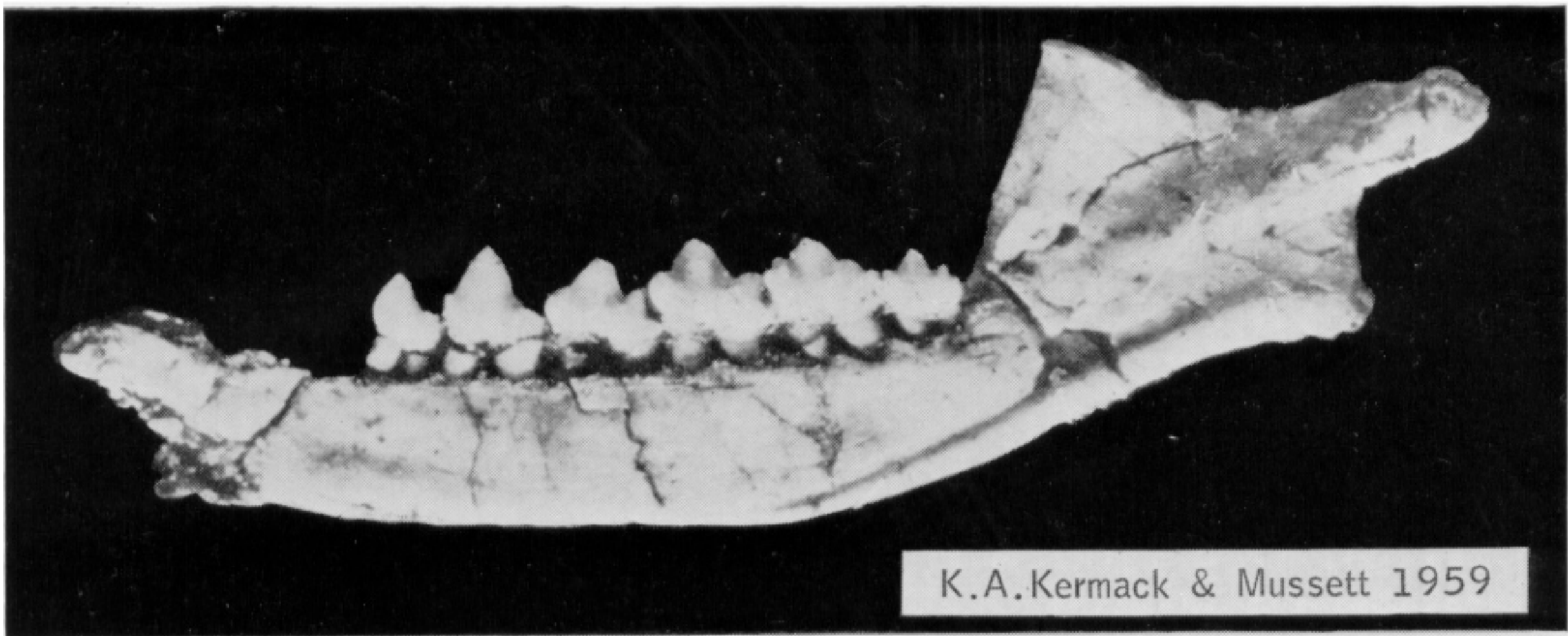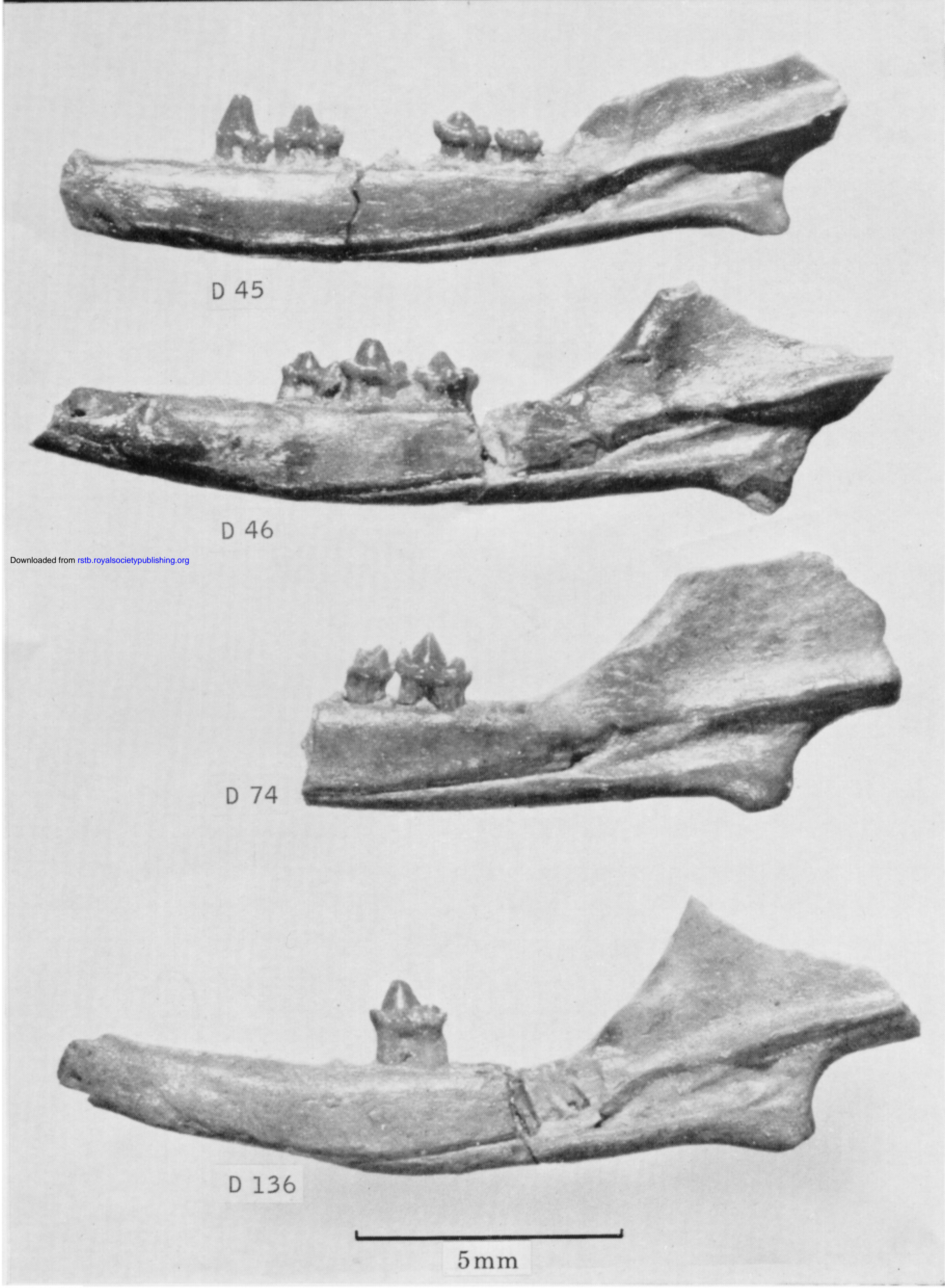
FIGURE 16. (a) Anterior and posterior upper and lower left premolars of *Eozostrodon parvus*. (b) Hind end of dentary, lacking only the top of the coronoid process, and a quadrate. (c) Milk molar in a dentary showing a pit in Crompton's groove. (d) A replacing tooth below a milk molar, before and after dissection. (e) A maxilla with parts of lacrimal and jugal. The teeth are severely worn. (f) A maxilla with the teeth moderately worn. (g) Two left lower molars of *Kuehneotherium praecursoris* probably from the same dentary, the second having a complete outer cingulum. Markers indicate 1 mm.

D 45

D 46

D 74

D 136

5mm

FIGURE 17. (a) Dentary of *Eozostrodon parvus* figured by K. A. Kermack & Mussett showing high positions of the angular and articular processes. (Reversed.) (b) Four dentaries of *Eozostrodon parvus* showing the varying form.