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A Further Account of the Triassic Mammals

F. R. Parrington

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A FURTHER ACCOUNT OF THE TRIASSIC MAMMALS

By F. R. PARRINGTON, F.R.S.
University Museum of Zoology, Cambridge

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[Plates 1–3]

CONTENTS

The very contentious 'facts', and their possible interpretations, concerning the Triassic mammals are re-examined and new data are brought forward. The most important matters concern the structures of the lower jaws; the details of the two jaw hinges; the facts concerning tooth replacement; the possibility of epipubic bones having been recognized; the nature of the roots of the postcanine teeth; the relations of the upper and lower molars during biting; and the taxonomic results of these considerations.

1. Introduction

In 1971 two papers were published on the Triassic mammals *Eozostrodon* and *Kuehneotherium*. The first, by Parrington, gave, in an introduction, a somewhat detailed account of earlier work, together with a general account of the head and dentition of *Eozostrodon* as far as could then be ascertained from the Cambridge collection. The second, by Mills, was devoted almost entirely to the dentition of the former animal, but put forward a classification placing the various Triassic mammals into families. Since then several papers have been published. Parrington (1973) discussed the different claims made in his paper and in that by Mills. Also in 1973, Kermack, Mussett & Rigney gave a very beautifully illustrated account of the lower jaw of *Eozostrodon* (figured by them as *Morganucodon*) but some of their interpretations are incorrect. Crompton (1974) has given a much fuller account of the dentitions of the South African forms *Erythrotherium* and *Megazostrodon* after further, difficult preparation. And Jenkins & Parrington (1976) have described the post-cranial skeletons of *Eozostrodon*, *Erythrotherium* and *Megazostrodon*. Further good specimens of *Eozostrodon* have since been obtained from the clay stored in Cambridge and these add information, some of which is new, some of which throws light on points under dispute, and some of which lends support to claims previously based on less substantial evidence. Moreover, it is necessary that errors now in print should be corrected; and some of the statements in print are, at least, highly controversial.

2. The structure of the lower jaw

(*a*) *The dentary*

In 1971 Parrington called attention to the considerable variation of the shape of the dentary of *Eozostrodon*. A plate was published showing something of this variation, most notably the fact that the condyle could be about in line with the alveolar border, or slightly below it, but in a specimen figured by Kermack & Mussett (1959) it was in a very high position as it is in the Symmetrodonta. The posterior part of a dentary of *Eozostrodon* now in the Cambridge collection (D 245) also shows that the condyle was in a very high position. This is of interest since various palaeontologists believe that the symmetrodonts evolved from the triconodonts while others do not.

Again it was shown that the one then available top of a coronoid process would not fit the best preserved hind end of the dentary at any magnification. Kermack *et al.* (1973) describe and illustrate (fig. 14) a dentary which has the coronoid process complete dorsally and it has a posteriorly directed horn at the tip. This is quite unlike the fragment figured by Parrington; it is quite unlike four more apparently reasonably well preserved tops of coronoid processes recovered subsequently (D 214); and, moreover, it is quite unlike what appears to be a reasonably well preserved coronoid process also figured by Kermack *et al.* (1973, fig. 19). Two interpretations are possible. The first is that the horn only developed at a late stage and this possibility may be held to accord with the presence of five rather than four lower molars as the figure shows, the fifth molar also being held to develop at a late stage. Against this interpretation lies the fact that the first lower molar is not greatly worn, nor is the second (though the posterior accessory cusp has apparently been broken). Another objection to this interpretation lies in the fact that Crompton (1964) showed that the allied form *Erythrotherium* also has a posteriorly directed horn on the coronoid process and this specimen is undoubtedly the remains of an immature animal. The second possible interpretation is that these Welsh animals are at least dimorphic, as suggested by Parrington (1971), the presence of only four lower molars being associated with a rounded coronoid process. The importance of the discovery lies in the fact that here, for the first time (owing to the very scrappy nature of the available material), two pairs of varying characters may prove to be associated.

Similar hooked coronoid processes have been shown to exist in the later triconodonts *Amphilestes* and *Amphitherium* and also in the pantotheres *Amblotherium* and *Phascolotherium* (Simpson 1928, 1929).

(*b*) *The splenial and coronoid*

Kermack *et al.* (1973) say that seven specimens in the London collection give information about the accessory bones of the lower jaw, two showing the coronoid. Of the remaining five, three show pieces of bone in the internal mandibular groove and two show fragments in the trough. They go to considerable trouble to support their claim that only one bone is present in the groove. By the simple expedient of cutting sections through two such specimens (more than a dozen have been found in Cambridge) it is possible to be quite sure that they are right in claiming the presence of only a single bone in the groove (as would be expected), but they identify it as the prearticular.

When they first observed fragments of bone in the internal mandibular groove Kermack & Mussett (1958) said, 'We owe to Professor D. M. S. Watson the suggestion that this is the anterior end of the prearticular or angular'. At no time do they consider the possibility of it being the splenial though the fragments lie in the position of that bone. For a time this was thought to be a lapse and when he figured the internal view of the dentary Parrington (1971) called the bone the splenial as had Patterson & Olson (1961) when they described the Upper Triassic animal *Sinocondon* (be that animal what it may) and thought that the bone had become fused to the dentary. Krebs (1971) also found evidence of a bone in the internal mandibular groove of a dryolestid pantothere and identified it as the splenial.

Kermack *et al.* make no reference to these identifications and now claim that the bone is the prearticular which must, therefore, if they are right, have grown forward and replaced the splenial. They do not discuss the matter nor do they give reasons for their identification. In order to show that such an unexpected happening took place it is necessary to show continuity between the prearticular, conjoined with the articular (forming the condyle) and the bone in the internal mandibular groove. Their two specimens showing bone in the trough of the dentary (M 24829, their fig. 34*c*; C.U.P. 2320, their fig. 31) alone might show this. Neither does.

Specimen M 24829 shows broken pieces of bone in both the groove and the trough but there is no continuity. Moreover the larger, apparently double, fragment in the trough with the upper component labelled surangular, has a lower component, which if their interpretation of the upper component be correct, must be identified as the prearticular. It is quite free from the more anterior fragments in the groove and is lined above them. The necessary continuity is by no means demonstrated. Their best specimen is undoubtedly the Chinese one C.U.P. 2320. The inner face of the right mandible is beautifully illustrated in their fig. 31. In this specimen, by far the most complete, the surangular is seen lying above the articular–prearticular rod which reaches forward to the position at the front of the trough where Kermack *et al.* recognize a facet for its reception as in cynodonts. Below this they figure the angular, again a rod reaching forward to the front of the trough. Below this yet again, but only at the front of the trough, lies a fragment of yet another rod. It lies below the front of the prearticular and angular bones, and in line with the internal mandibular groove. Clearly it should be identified as the splenial; it is labelled prearticular.

There is no evidence whatsoever that the prearticular has grown forward and replaced the splenial; the Chinese specimen, in fact, denies that this happened.

Loss of the splenial in the early triconodonts would, of course, debar them from the ancestry of the trituberculate mammals and so support the view of Kermack and his associates, because Krebs (1971) has shown that the Jurassic dryolestid pantotheres still retained the splenial and the pantotheres are generally regarded as the ancestors of the Theria.

It should be noted that the prong supposed to exist by Kermack *et al.* on the coronoid is not shown by the well preserved Chinese specimen any more than it is shown by the two specimens they illustrate (fig. 34) or by the three well preserved specimens in the Cambridge collection (D 64, D 105, D 143). Because the relatively huge cynodont from the lower Trias, *Cygnognathus*, possesses such a flange it does not follow that the Upper Triassic, comparatively minute, mammal *Eozostrodon* did.

The two slight depressions in the dentary at the front of the trough are often represented by a single depression which is sometimes poorly formed. It is interesting that the Chinese specimen, where the prearticular and angular rods extend to the front of the trough, no trace of a flange is seen to develop as shown by Kermack *et al.* in their restoration. Better material would be very helpful in these matters.

(*c*) *The retroarticular process*

In their account of the articular region of the cynodont *Cygnognathus* Kermack *et al.* (1973) call a downward and recurved process of the articular bone 'the infra-articular process' and a slight boss on the surangular 'the retroarticular process'. They do this quoting Watson (1948) and Janensch (1952), and in the case of the former identification noting that they differ from Westoll (1945), Crompton (1963*a*) and Hopson (1966). They make no mention of the work of Parrington (1955) where the mechanics of downturned retroarticular processes are discussed, nor that of Crompton (1972) where the evolution of the boss on the surangular is described and shown to form a secondary articulation in Middle Triassic cynodonts.

If the primitive pelycosaurs *Varanosaurus*, *Varanops* and *Ophiacodon* are examined (Romer & Price 1940, fig. 3) it will be seen that their occiputs slope upwards and somewhat forwards, the modest retroarticular processes (for the depressor mandibuli muscles) project backward as in crocodiles and varanid lizards, and there are no significantly enlarged anterior maxillary teeth. But in the best known pelycosaur, *Dimetrodon*, the occiput is more vertical, considerably enlarged anterior caniniform teeth had been developed and the retroarticular process is downturned as Romer & Price show (1940, fig. 16). Watson (1948) accepted this interpretation and their figure which shows mesial rugosities identified as serving for the attachment of pterygoid muscles. Watson then turned to the Dinocephalia and first discussed the lower jaw of *Ulemosaurus*. Of this he wrote (p. 837, last line), 'The musculus pterygoideus posterior certainly existed, being attached to the lower part of the apparent retroarticular process . . .' and, on page 383, 'A musculus depressor mandibuli may well have existed in *Ulemosaurus* . . . inserted into the upper surface of the retroarticular process'. Was there, or was there not, a retroarticular process? And has this process ever served for the attachment of any pterygoid muscle? Next

Watson discussed *Titanosuchus*, illustrating a specimen from the British Museum (Natural History) and labelling the downturned, laterally situated process, which surely compares strictly with the retroarticular process of *Dimetrodon*, as the processus musculus pterygoideus posterius. He also wrote, 'There is no indication in Efremov's figures that a retroarticular process occurred in *Titanophoneus*, and it is possible that the muscular depressor mandibuli had vanished . . .'.

In his account of the dicynodonts, and in his illustrations, the downturned process of the articular is called the process for the posterior pterygoideus muscle (as Watson remarks, 'it has many names'). Yet Watson's fig. 16 is eloquent in this matter. It is of a form called *Oudenodon* because it lacked tusks and is often held to be the female. Not only does it lack tusks but it also lacks any downturned retroarticular process. This is in contrast to what Watson had said of the lower jaw of a *Dicynodon* in 1911 when he remarked on the downturned process that it was ideally situated for the insertion of the digastric muscle. Substitute 'depressor mandibuli' for 'digastric' and the matter resolves itself. The tusked form needed a good gape and had a downturned retroarticular process; the tuskless form did not need the same gape and lacked the downturning of the retroarticular process.

Among the goronopsids the canine teeth are huge in the upper jaw and large in the lower jaw. Such creatures had to have a huge gape if they were to use the teeth and they have very large retroarticular processes which are not only downturned but also turned forwards. This was necessary if, with more or less vertical occiputs they were to achieve huge gapes (Parrington 1955). Moreover, if the depressor mandibuli muscles were attached to the ends of the processes in certain cynodonts in which the processes turn forwards and even upwards, the tendons had been led to a position below the lower jaws where, by joining onto a slip of a mylohyoid muscle, the mammalian digastric muscle could have come into existence quite simply (Parrington 1974).

The argument against Parrington's interpretation is that the tensor tympani muscle of mammals is innervated by the trigeminal nerve and is attached to the malleus. It cannot be derived from the depressor muscle of the reptile which is innervated by the seventh nerve, but is a derivative of the pterygoideus muscle. But the posterior pterygoideus muscles of reptiles are attached to the lower surfaces of the hind end of the lower jaw and the tensor tympani muscles of mammals are attached to the medial surface of the hind end of the *shaft* of the malleus (the posterior angular process) and stretch forward as did the pterygoid muscle which gave rise to it. This has been shown, e.g. by Edgeworth (1935) in *Ornithorhynchus*, by Parker (1886) in a wide range of mammals including *Erinaceus*, *Sorex*, and *Galeopithecus*, and by Gray in *Homo* (Gray's *Anatomy*, any edition). Thus Goodrich wrote (1930, p. 466), 'The malleus is provided with a muscle (m. tensor tympani) attached to its medial surface and passing forwards towards the base of the skull'. In contrast the manubrium of the malleus, which Kermack *et al.* accept as the relic of their 'infra-articular' process, lies buried in the tympanum in all mammals. The depressor mandibuli muscle of theriodonts was attached to what became the anterior end of the *manubrium* in mammals.

Finally, by no stretch of the imagination does it seem possible to attach a depressor mandibuli muscle to the boss on the surangular where, it appears clear, Kermack *et al.* would place it. It is indeed strange that they should have interpreted this structure thus since K. A. Kermack (1972) reviewed an article by Crompton (1972) on the evolution of this structure and correctly reported his views. K. A. Kermack's summary of Crompton's article reads as follows: 'He describes a surangular–squamosal articulation developed in cynodonts to supplement the normal reptilian articulation (articular–quadrate). The former he considers the precursor of the mammalian dentary–squamosal articulation.' It is indeed very difficult to imagine how this boss on the upper surface of the surangular and lateral to the outer condyle could subsequently (in May 1973) be interpreted as a point of insertion of the tendon of the depressor mandibuli muscle. Apart from being crushed against the squamosal, in what direction could the tendon pull the lower jaw to open it? The boss lies alongside the lateral condyle and pulled in any direction (even downwards) would tend to disrupt the hinge and not to open the jaws.

3. THE TWO JAW HINGES

(*a*) *The condyle on the dentary*

It has long been known that in the Triassic triconodonts the mammalian squamoso–dentary hinge had been evolved while the reptilian quadrate–articular hinge still functioned. Such a stage must theoretically have existed if the quadrate and articular bones were to be incorporated in the mammalian ear, but details of the latter hinge in particular have so far not been described.

The dentary condyle has been well figured by Kermack *et al.* (1973), three specimens being shown each in several views. Also photographs have been published by Kermack & Mussett (1959) and Parrington (1971). It is an oval knob at the end of the articular process of the dentary which is strengthened by a ridge running across the trough which housed the post-dentary bones. The condyle itself is ovoid with its long axis running anteroposteriorly and the bearing surface itself faces upwards and backwards at an angle which varies in different specimens; no doubt this variation is in accordance with the varying height of the condyle above or below the line of the alveolar border (Parrington 1971). Condyles are common among the debris but are almost always broken off and appear as the sort of fragments figured by Kermack *et al.* (1973, fig. 22 and 23).

(*b*) *The squamosal*

About 40 squamosals have been found but only about six are helpful in understanding the whole, complex structure.

Medially the bone has two processes. The uppermost is a rather thin, rounded plate of dense bone which must surely have served for an attachment to the parietal since it stretches upwards and somewhat forwards. Below it is a process of rugose bone which projects medially and is of about the right size to have been attached to the relic of the paroccipital process described by Kermack (1963) on the periotic bone. It is here called the otic process. Between these two processes is the post-temporal fossa (figure 1*a*). It is possible that part of the rugose area made contact with the exoccipital but the material available does not permit a decision on this matter.

Ventrally the main transverse component of the squamosal is swollen and the bone is rugose. Moreover, it is hollow (as broken specimens show) and is pierced by a large opening which itself cuts back into the posterior wall of the bone to form an incision (figure 1*c*). The shape of this opening is difficult to ascertain because what is probably its true border is well shown medially but not laterally, but it appears to be approximately round. This opening surely housed the dorsal process of the quadrate which has part of its dorsal process reflected and this portion must, it seems certain, have been housed in the posterior incision much as happens in cynodonts (Parrington 1946, fig. 5). The swollen part of the bone is visible from above and below (figure 1*a*, *b*). Laterally to the quadrate pit the ventral surface becomes smooth and expands and has an oval-shaped, shallow depressed area which plainly invites interpretation as the surface against which the new dentary condyle articulated, that is the glenoid cavity. But one specimen, CR 11, has a flattened piece of bone broken only anteriorly, lying ventrally to this area and has itself an oval-shaped area which might be the glenoid. This underlying fragment of bone invites interpretation as the posterior extension of the jugal which may have extended sufficiently far posteriorly to form the glenoid. As is well known the jugal of the marsupials extends posteriorly and usually forms a part of the glenoid. Whether the 'dished' area of the squamosal normally forms the glenoid, and CR 11 (figure 2*c*) is an exceptional happening, cannot be ascertained with the material available.

Seen from behind (figure 1*a*) the proximal half of the transverse component has its uppermost part turned backwards forming a surface for the attachment of part of the temporalis muscle. Laterally to the quadrate incision the bone is slightly hollowed to house the external auditory meatus. What may be termed the zygomatic component of the squamosal becomes flattened with its uppermost border tiled slightly medially and the process is tapered and finally truncated (figure 1*b*, *c*).

(*c*) *The quadrate*

Only one quadrate has been found; the bone fragment tentatively assigned as a quadrate in 1971 is not one: it may be a fragment of a neural arch. The bone itself is a very small one and it is possible that if enough time were devoted to examining the finest sievings another might be found, but the work is both tedious and tiring and there is no certainty of success.

The quadrate consists of a cylindrical transverse condyle, measuring 0.90 mm in length, and a somewhat complex dorsal process (figure 1). Of the condyle itself there is little to be said except that it appears to be slightly tapered medially. The dorsal process is a blade of bone which arises from the top of the condyle and arches upwards and forwards and finally curves backwards (figure 1*d*). For some distance above the condyle the process is deeply recessed, a modification which allows the rather high posterior border of the articular to pass over the quadrate condyle and so retain a firm grip while allowing a wider gape (figure 1*d*). Medially the dorsal process turns forwards and expands and becomes higher than the transverse component. The position and form of this flange are important because together they allow the position of the bone in the squamosal to be determined and so indicate to which side of the skull it belongs. The flange must surely have fitted into the somewhat curved incision in the squamosal which is situated medially to the incipient glenoid cavity. If the bone was like that of the cynodonts the forwardly directed process arose medially, for in the cynodonts the quadratojugal was sited above the lateral condyle of the quadrate. If the incision in the squamosal was deep enough the condyle of the quadrate could have been in line with the new squamoso-dentary hinge.

That part of the dorsal process of the quadrate which runs more or less at right angles to the line of the condyle would be expected to be the part which lay in the incision in the squamosal. This flange must therefore be posterior and the part more or less in line with the condyle would be anterior to it. Next, since the incision in the squamosal lies laterally to the main part of the cavity (for the dorsal process) so must the reflected part of the dorsal process. This is as happens in the cynodonts (see, for example, Parrington 1946, fig. 5). But there are two principal differences between the mammal and the cynodont. First, in the cynodonts the dorsal process of the

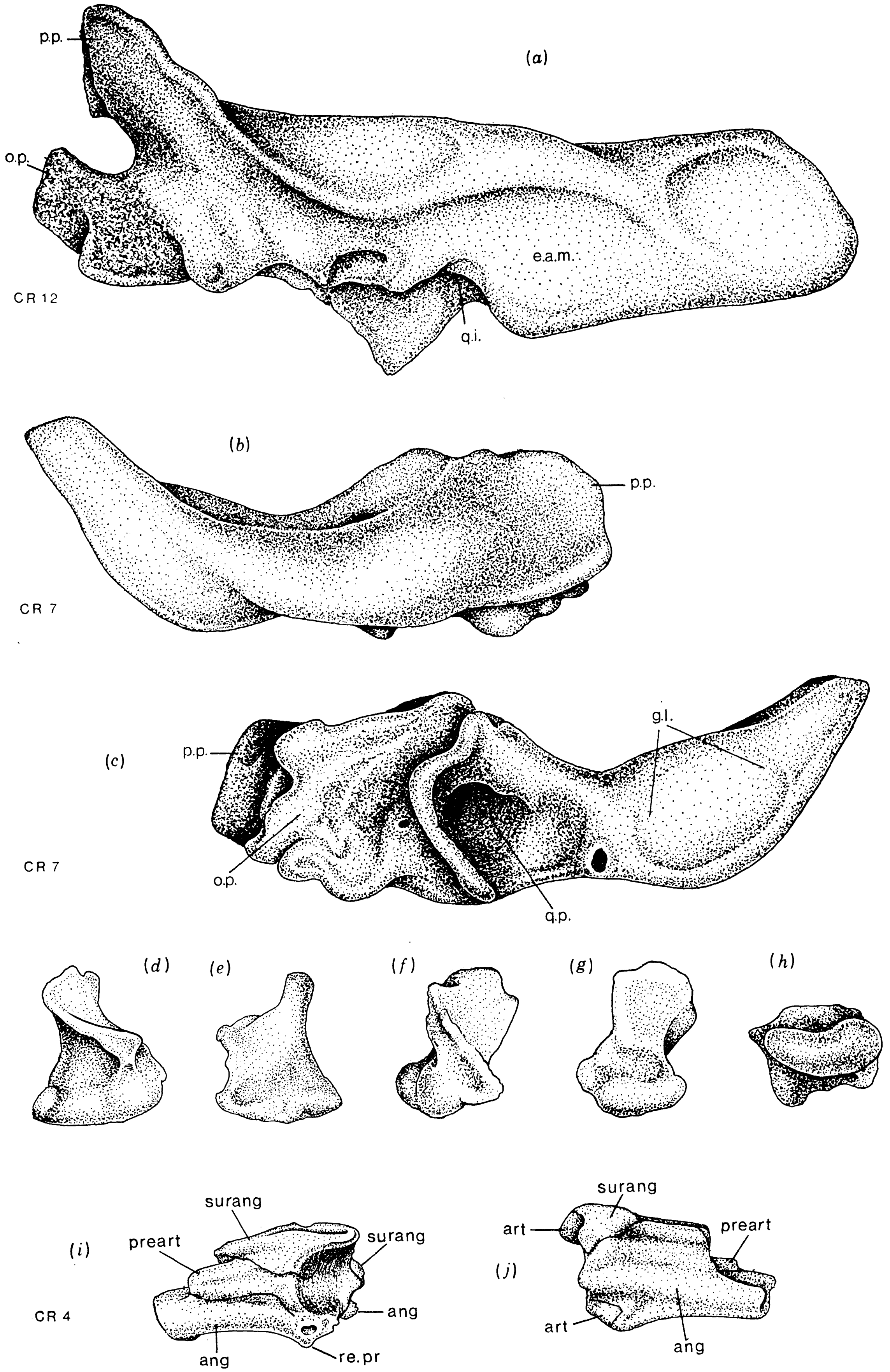

FIGURE 1. *Eozostrodon parvus*. (*a*) Posterior view of a rather large right squamosal. (*b*) Dorsal view of a well preserved left squamosal, drawn somewhat tilted. (*c*) The same specimen in ventral view. (All magn. × 30 approximately.) (*d*) Anterior view of a right quadrate, (*e*) posterior view, (*f*) median view, (*g*) lateral view, (*h*) ventral view. (All magn. × 25 approximately). (*i*) Internal view and (*j*) external view of a right articular and associated bones. (Magn. × 25 approximately). Ang, angular; art, articular; e.a.m., external auditory meatus; g.l.,? glenoid cavity; o.p., opisthotic process; p.p. parietal process; preart, prearticular; q.i., quadrate incision; q.p., quadrate pit; re.pr, retroarticular process; surang, surangular.

quadrate lies against the front face of the squamosal whereas in the mammal it is housed within a cavity in the bone. Secondly, while in the cynodont there is a reasonable part of the condyle lateral to the reflected wing on which the quadratojugal rested, in the mammal there is no clear evidence of this having occurred. If a quadratojugal was in fact present it must have been a very tiny bone and it has not been recognized. By reason of the foregoing arguments the quadrate is interpreted as a right quadrate. An oval-shaped boss lying above the lateral part of the condyle may have been for the articulation of the quadratojugal.

Tragically this unique bone was unaccountably lost during the simple process of washing it to remove 'Carbowax' which had been used to support the bone in various positions while it was being drawn.

(*d*) *The articular complex*

Three further articulars have been found since one (CR 2) was figured in 1971. They have been numbered CR 3, 4, and 8. These tiny bones (two measure only 1.55 mm in length) are extremely difficult to study, not only on account of their size, but also because cracks can be misinterpreted as sutures and the use of even thin layers of 'Alvar' to preserve them obscures difficult sutures.

One of the shortest specimens (CR 4) is probably the most important, as pointed out to me by J. A. Hopson, for the specimen appears to consist not only of the articular and conjoined prearticular but also of part of the angular and surangular.

The most striking feature of these bones lies in the extent to which the articular, together with part of the surangular, clasped the quadrate condyle forming a tight hold. This is in contrast to the very loose squamoso-dentary hinge which is much larger (figure 1*i*). Such a well developed articulation makes the continued association of the quadrate and articular in the mammalian ear understandable. Further development of the squamoso-dentary hinge would seem necessary before the post dentary bones could be abandoned as a hinge. In lateral view (figure 1*j*) the complex consists largely of the angular with the surangular forming the top of the structure as a fine ridge, but this bone deepens posteriorly to form a part of the articulating surface. Also a part of the articular appears laterally. In medial view the surangular forms about one third of the complex and lies across the top of the condyle. The articular forms most of the glenoid cavity but a small portion of the surangular and also a very small piece of the angular is visible lower down on the edge of the articulating surface. Most of the suture between the angular and prearticular is clear but posteriorly its position is obscure. What appear to be the base of the retroarticular process, with a clear hole in it, must surely be formed by the articular, forming, as it later does, the manubrium of the malleus, yet the suture between the angular and prearticular appears to continue posteriorly across the top of the stub. Great difficulty has been experienced in ascertaining the sutures of this tiny bone and the whereabouts of the posterior part of the angular and prearticular suture must be left uncertain.

4. TOOTH REPLACEMENT

It has been shown that in the theriodont reptiles tooth replacement was reptilian and the terms premolar and molar cannot therefore be used (Parrington 1936*a*, *b*; Crompton 1955, 1962, 1963*b*; Osborn & Crompton 1973; and others). Because both *Eozostrodon* and *Kuehneotherium* have their postcanine teeth clearly differentiated into premolariform and molariform types it was important to find out if the replacement was mammalian. If this turned out to be so it might well be possible to proffer an explanation of the great reduction of tooth replacement in mammals.

Mills (1971) claimed that the replacement was like that of the marsupials and some other mammals, only the last milk molar being replaced. He made this claim because the workers studying these animals under K. A. Kermack's leadership had found only one case of replacement among the many hundreds of specimens studied, and he cast doubts on the work of Crompton (1964) who had formed the opinion that in the South African form *Erythrotherium*, which is an immature animal, the first incisor and possibly the second postcanine were undergoing replacement.

On the other hand Parrington (1971) argued that, though one case of replacement of the fourth postcanine tooth had been found and no case of certain molariform teeth being replaced had been seen (among hundreds of specimens) the negative evidence became important because of the fact that 14 cases of the development of an additional molariform tooth at the back of the jaw *had* been found. These 14 cases, between them, showed every stage in the development of a new tooth from the formation of a very shallow depression to deep crypts, to crypts with partly or fully developed crowns, to partly erupted teeth. The position of these developing teeth, below the front of the coronoid process, preclude the possibility of precursors, and Compton's groove, which presumably held the dental lamina, had been seen in many specimens, but never developed pits for replacing teeth as it does in the cynodont *Thrinaxodon*. This explained the occasional presence of extremely worn molariform teeth. They came from old animals which were unable to replace them. It was then pointed out that it had become important to seek evidence relating to the more anterior, premolariform teeth in the rare, small and so delicate specimens; and how a lower premolar (either a first or a second) and an upper canine had been found which were undergoing replacement in very tiny jaws. The conclusion that the tooth replacement in this animal was diphyodont as in typical modern placental mammals was inescapable and accorded with Crompton's findings, and also with the long known classical case of the replacement of the lower canine and the molariform fourth deciduous postcanine in the triconodont *Triconodon mordax*, an interpretation which has never been challenged (Simpson 1928).

Contrary to what stands in print, Kermack *et al.* (1973, p. 107) state that Mills had shown that in the tooth replacement of *Eozostrodon* (called by him *Morganucodon*) was 'not of the therian pattern', which he did not. Mills likened the replacement to that of the marsupials and certain other mammals, and the marsupials are Theria by all classifications, including those published by K. A. Kermack. Kermack *et al.* (1973) do not make any mention of the work on tooth replacement by either Crompton or Parrington, leaving their readers in total ignorance

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DESCRIPTION OF PLATE 1

FIGURE 2. *Eozotradon parvus*. (*a*) Part of a right dentary showing the second, third and fourth incisors diminishing in size posteriorly. The socket for the first molar, and other material, show that the first incisor was the largest. (Magn. × 10.) (*b*) Two supposed epipubes. The rod of the specimen on the right is complete. (Magn. × 10.) (*c*) A right squamosal in ventral view. It shows the parietal lappet, the otic process, the pit for the quadrate filled with white matrix and a piece of bone overlying the glenoid region and complete except anteriorly. It may be the jugal which reached the glenoid region and formed it. (Magn. × 10.) (*d*) A small dentary with the first premolar loose in a large socket. (Magn. × 20.) (*e*) A small dentary with the fourth premolar developing in its socket. (Magn. × 15.) (*f*) A worn lower molar photographed over a grid. (Magn. × 30.) (*g*), (*h*), Stereophotographs of a left maxilla and the associated dentaries. (Magn. × 12.) The very small fourth upper molar was lost when the specimen was being remounted for further preparation.

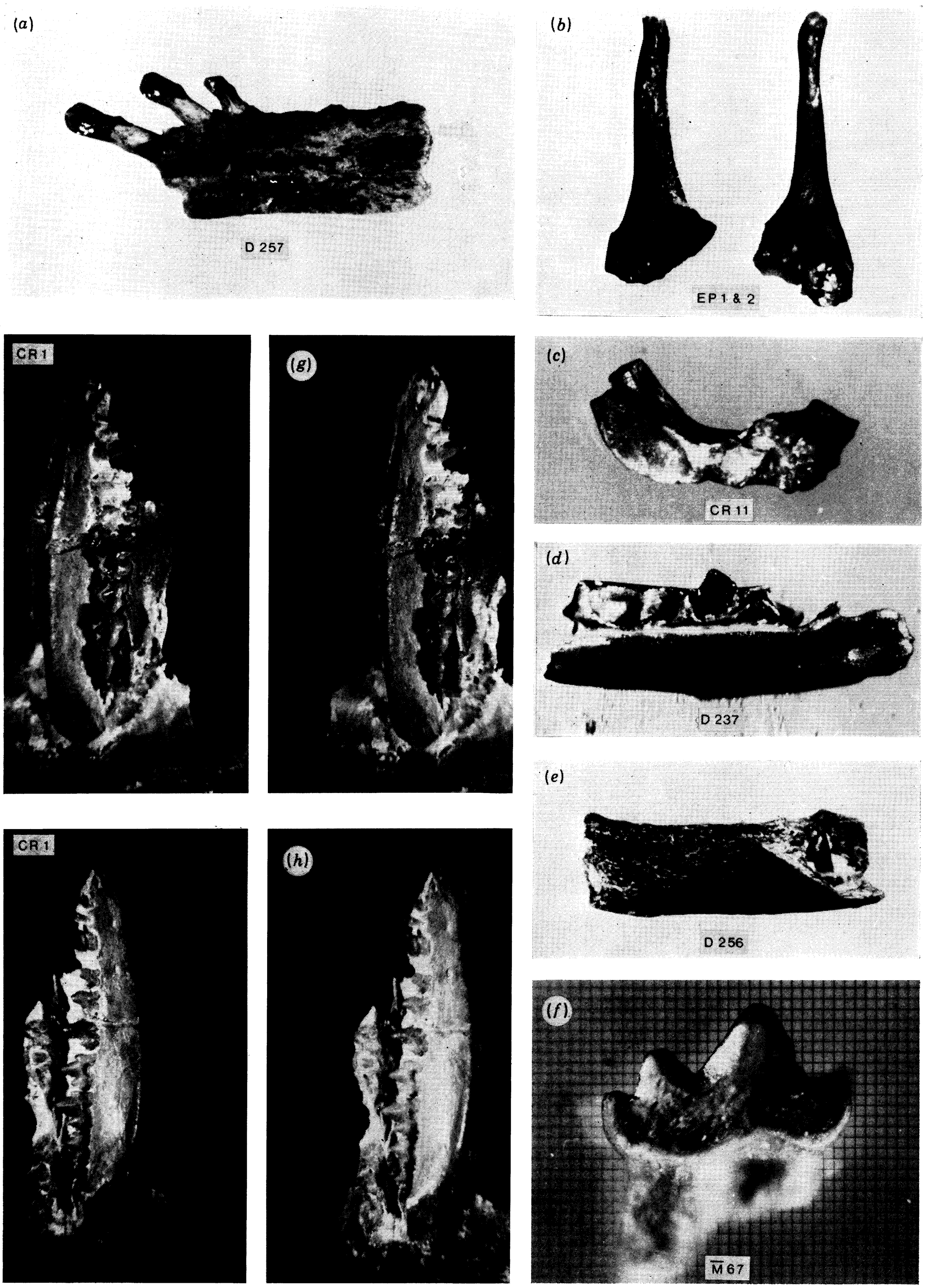

FIGURE 2. For description see opposite.

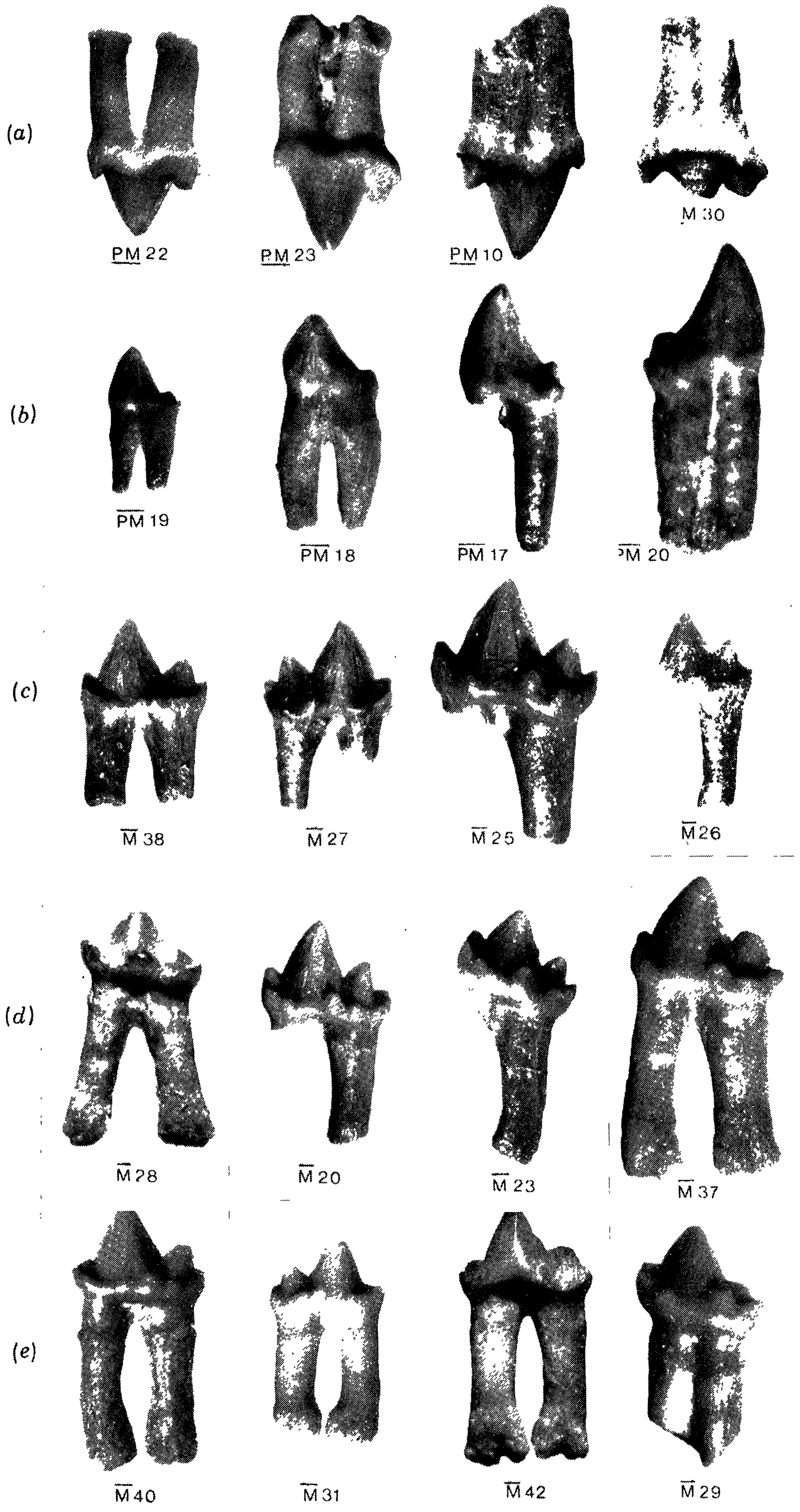

FIGURE 3. For description see opposite.

Description of plate 2

Figure 3. *Eozostrodon parvus*. (*a*) Three upper fifth premolars showing something of the variation of root form and an upper molar with the roots coalesced. (*b*) Four lower premolars showing that the roots can be tapered and incurved or coalesced. (*c*) Four lower molars with incompletely grown roots which can be parallel sided or tapered. (*d*) Four lower molars showing that the roots can be very widely separated or incurved. (*e*) Three lower molars with one root curved and the other straight and one with the roots coalesced. (All magn. × 15.)

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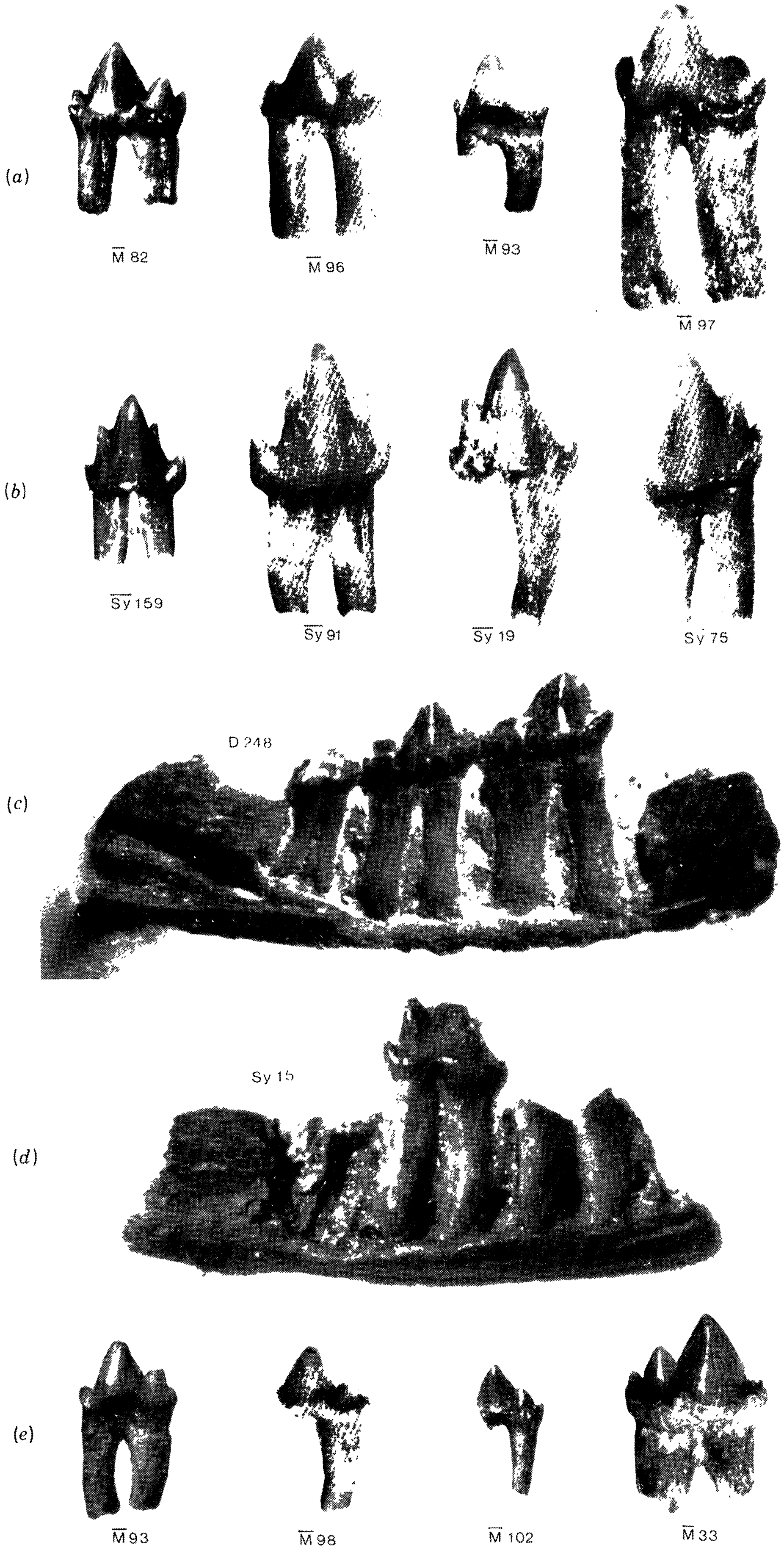

FIGURE 4. For description see opposite.

of it. Recently Crompton (1974) has redescribed the dentition of *Erythrotherium* after further, difficult preparation and shown that the second right and fourth left lower incisors were undergoing eruption as was the fourth right premolar, while the fourth left lower postcanine appears to be a molariform milk tooth.

Three further cases of erupting lower premolars have been found in the Cambridge material. One (D 237) shows the eruption of a first lower premolar which is very loose in a large socket (figure 2*d*, plate 1). Another (D 243) shows the shining tip of a tooth deep in the socket for the third lower premolar. The third (D 256) shows a developing tooth in the fourth postcanine socket which is partly damaged (figure 2*e*). All three cases are in very small dentaries.

For Mills to have concluded that because Kermack and his associates had found only a single tooth undergoing replacement none of the others was replaced was a *non sequitur*. If in fact the tooth replacement was nontherian (whatever that may be) it would still not necessarily be evidence supporting the view; held by Kermack and by Mills, that the triconodonts were not related to the trituberculate mammals from which modern marsupial and placental mammals arose. In fact there is now ample evidence that in the Triconodonta tooth replacement was diphyodont as it is in typical modern placental mammals.

5. POSTCRANIAL REMAINS

The postcranial skeletons of the Triassic triconodonts have been described by Jenkins & Parrington (1976) but two matters remain to be discussed. It has long been held that epipubic bones may well have been present in the earliest mammals (Jenkins 1971). They are known not only in the monotremes and marsupials but have recently been discovered in the multituberculates (Kielan-Jaworowska 1969) and in the tritylodontids, advanced mammal-like reptiles which, though very specialized, have many characters in common with the eozostrodonts (Fourie 1962). Moreover, Vaughn (1956) has argued from the anatomy of the living forms that epipubes must have evolved quite early in mammalian history. They are not known in any cynodonts (the ancestors of mammals) nor could they be found in the skeletons of *Erythrotherium* or *Megazostrodon* where, however, the pubes themselves are only very poorly known. The pubis of *Eozostrodon* itself is known only by a fragment contributing to an imperfect acetabulum (Jenkins & Parrington 1976).

Certain bones found among the thousands of scraps from Pont Alun quarry may be epipubes. The best reasons for suspecting this are the facts that epipubes are to be expected and that certain paired bones, which are of variable size, cannot otherwise be accounted for in the skeletons of either the mammals or the contemporaneous lizards, the remains of which are abundant.

DESCRIPTION OF PLATE 3

FIGURE 4. *Eozostrodon parvus* and *Kuehneotherium praecursoris*. (*a*) Four lower molars of the Welsh triconodont showing varying root form. (*b*) Four lower molars of the Welsh symmetrodont *Kuehneotherium* with roots matching those of the triconodont. (*c*) A dissected dentary of the Welsh triconodont showing that though the leading molar is very worn there are no significant terminal expansions. (*d*) A dissected dentary of *Kuehneotherium* to show the roots which are parallel sided and not tapered. (*e*) Four lower molars of the Welsh triconodont which contradict all that has been claimed about them. $\overline{\mathrm{M}}$ 93 has both roots incurved while the valley behind the centre cusp is high. $\overline{\mathrm{M}}$ 98 has the posterior root tapered and curved. $\overline{\mathrm{M}}$ 102 matches the tooth called *Eozostrodon problematicus* in having the posterior valley high, the cingulum weak and the root tapered. It is different in being much smaller. The tooth $\overline{\mathrm{M}}$ 33 shows that large lower molars of the Welsh form can have high posterior valleys. (All magn. × 15.)

Each of the bones in question consists of a thin plate from which projects a rod with a blunt end (figure 2*b*). The plate of bone is of uncertain shape since in no specimen is it complete. On one side the plate is shallowly depressed and the resulting depressed area is lightly striated in the same direction as the rod. Lying with the striated surface of the expanded area uppermost the whole bone is moderately arched. These bones are asymmetrical and right and left forms have been found and so they must be regarded as paired structures.

If these bones are epipubes and the rods projected anteriorly, as must be expected, then the basal plate is equivalent to the expanded and sometimes somewhat forked structure found among some of the monotremes and marsupials. It would seem possible that in these extremely early mammals the basal plate overlapped the pubis, this accounting for the thin striated area. Also it suggests that if this was so then the pubis itself may well have been a very thin plate where it was overlapped, this accounting for the absence of a single well preserved pubis. R. Presley has observed (personal communication) that there is an overlap between the pubis and epipubis in a newly hatched platypus.

But because neither the proximal part of the expanded plate nor the pubes of the eozostrodonts are properly known, it is by no means sure that the identification is correct. But if it is incorrect what are these bones? They do not resemble any bone in a lizard skeleton as represented by the varanids, generally regarded as among the most primitive of modern lizards, nor can they be matched except as epipubic bones, among mammals, and the epipubic bones are very variable in shape, differing in this respect even between the two monotremes, though each consists essentially of a rod with an expanded proximal portion.†

The other matter of interest in the postcranial skeleton lies in the tails of the eozostrodonts. First it must be recalled that their ancestors, the cynodonts, had short tails (Jenkins 1971). It is a point of agreement among all those who have studied these animals and is surely concerned with the change from the reptilian condition with powerful caudofemoralis muscles to mammalian gluteals. This is shown by the great expansion of the ilium, especially its forward development. Yet the eozostrodonts, the earliest mammals in which the postcranial skeleton is known, have long tails. As is shown by Jenkins & Parrington (1976), they have well developed proximal caudal vertebrae, with typical neural arches and zygapophyses, and centra of moderate length. In contrast the more distal vertebrae have progressively reduced neural arches and zygapophyses but considerably longer centra which sometimes are more than twice the length of the proximal centra. This suggests that these animals could bend their tails through a greater angle proximally than distally. If so, such a tail would be of value as a balancing organ, much as an acrobat uses a pole when walking on a tight-rope. This conclusion agrees with the other reasons given by Jenkins & Parrington (1976) that these early mammals were creatures which scrambled about on rough ground, in bushes and climbed trees. This sort of tail is found today in the tree shrews, various small carnivores and also small primates. It is of interest that Kühne (1956) has shown that the tail of the therapsid *Oligokyphus* was of the same form.

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† Since the foregoing was written epipubic bones have been reported in a Jurassic mammal. (Henkel, S. & Krebs, B. 1977 Der erste Fund eines Säugetier-Skelettes aus der Jura-Zeit. *Umschau* **77**, 217–218).

6. Taxonomy

(*a*) *General*

The whole history of the genera *Eozostrodon* and *Morganucodon* has been a sort of palaeontological gavotte.

Taxonomy is a difficult matter since it is largely one of opinion and this often varies among biologists. In palaeontology it becomes even more difficult since seldom is more than a part of a vertebrate skeleton found and among the rare Mesozoic mammals little has been known until recently about anything except the dentition and dentaries. But because teeth, being made of the hardest substances, survive when little else does, and because dentitions, especially of mammals, are often eloquent about the feeding habits, and also provide good evidence of relations, genera have been established on single teeth or on two teeth. Thus the theriodont reptile *Oligokyphus* was established on two teeth, as was the triconodont *Eozostrodon*, while the genera *Morganucodon* and *Aegialodon* have been established on single teeth.

The problematical little animals of the Upper Trias, the Haramiyidae, are known only from their teeth, though some dozens of these have been recovered. The problem of when to make a species or a genus was well stated by Simpson (1928) when he wrote (p. 56) of these animals, 'It is a legitimate criticism that classification on the basis here adopted may lead to placing different teeth of the same dentition in different species if they happen to be unlike. Convenience, however, demands that each type be given a name by which to call it. If other similar animals were known, it might be possible to unite these teeth into probable broad genera by analogy, but the Microcleptids are too isolated for this.' The writer faced this problem when describing the haramiyid teeth collected by Kühne in the late thirties (Parrington 1947). Several teeth were of a form quite distinct from any described before. Thus specimens H 7, H 15, and H 19 could each have been made into genotypes, judging from the genotypes then existing. But H 19, a large tooth with the rows of cusps compressed together and which could be matched by a poorly preserved specimen in the Moore collection, suggested the formation of a tooth of the type found amongst multituberculates in their lower posterior premolars. Again the features of H 7 suggested that it might be a posterior molar and a tooth of the same sort has recently been described by Hahn (1973) from Halberstadt in Germany. The writer's decision was to describe and discuss the new teeth but not to add to the generic or specific names. When Kühne started collecting these haramiyid teeth the writer felt that if a sufficient number could be found it might be possible to place them in rows suggesting the possible arrangement of the animal's dentition. Thus the broader teeth might be upper teeth and the narrower ones the lower teeth after the manner of tritylodonts and multituberculates. However, the collecting was stopped before the necessary quantity had been obtained.

Contrary to what stands in print (Parrington 1947), Kermack *et al.* (1973, p. 105) say of Kühne's collection, 'The whole collection was sold to Parrington who named the two teeth in question *Eozostrodon parvus* and *E. problematicus*'. This statement is both erroneus and irrelevant. If they had read Parrington's (1947) account of Kühne's material they would have learned that the tooth with the field number H 3 was sold to Bristol University while the tooth numbered H 11 was sold to the Bristol Museum and lost in the air attack on that city during the 1939–45 war. Nine of Moore's specimens have been lost (Simpson 1928) and it is not desirable that the Curators of the Cambridge University Museum of Zoology should some day be held to have lost two specimens which were never in their possession except for description (H 3).

The problem met with in the study of the haramiyids in the matter of establishing species and genera is met with in even greater measure when dealing with the very abundant triconodont teeth from Pont Alun. It soon became apparent that there appeared to be major and minor forms but the very scrappy nature of the material prevented any conviction being achieved. There are dentaries with only four molars, the last being very small. In contrast there are larger dentaries with five molars to judge by their sockets but the last tooth was clearly a very small tooth and such lower molars are found loose as Mills pointed out. Also, beyond question the size range is very great. Are there two distinct forms? It appears to be so but it does not follow that there were two species. When he collected two beautiful specimens of the reptile *Procolophon* Watson (1914) found that while they were about the same size, one was more heavily built than the other. After a discussion with Boulenger, Watson decided to regard the two as male and female. When Kühne made his magnificent haul of the theriodont reptile *Oligokyphus* and found that among his hundreds of pieces there appeared to be two forms, the one larger and with a greater number of postcanine teeth than the other, he made two species, *O. major* and *O. minor*. But it is common experience that two allied forms of somewhat different sizes do not usually congregate together. If the insectivores *Sorex araneus* and *S. munutus* are put into a cage together the smaller form lives only as long as it can keep running. The writer might have regarded Kühne's two species as male and female of the one form. For this reason it was decided not to make two species or genera of the Welsh triconodont. But to some workers many 'species' could be made on isolated teeth. Thus the lower molars with accessory cuspules on the buccal side could be differentiated on that single character: a number of such specimens have been found since two were figured (Parrington 1971, figs. 9*d*, *e*). Again the curious three rooted premolariform tooth described and figured in 1971 (fig. 9*g*) could be made into a type because several more have been found, one in the premolar region of a piece of a dentary. Yet again the two tall lower molars numbered 70 and 71 (figure 8*b*) might be regarded as sufficiently different from the average lower molars to warrant a new species, if doing so would serve any useful purpose. This applies also to the amphilestine-like teeth figured in 1971 (fig. 9*i*), a third having now been found: they might be made into a new genus and referred to that group, but at least until the dentition of the trituberculate *Kuehneotherium* has been described it seems wiser to call attention to such teeth and make no further names until better material has been obtained.

Mills (1971) considers that in *Morganucodon* the hindmost of the three principal cusps of the lower molars is an enlarged cingulum cusp and that these teeth are biconodont and not triconodont. It was pointed out by Parrington (1973) that this interpretation was not likely in view of the many theriodonts which have triconodont lower molars while none are known which have triconodont upper molars and biconodont lower molars. On this matter something further may be said. Referring to Eocene mammals Gregory (1934, p. 189) says, '. . . the structures called cingula are sharply ridged rims on any of the four sides of the crown'. And also 'The power of the cingulum to give rise to new cusps when it occurs is not different in kind from the power of other parts of the crown to do the same thing . . .'. In short the cingulum can produce cusps which in no way differ from those produced by the crown itself.

In the course of his discussion Mills (1971, p. 49) comments on the two types of Triassic mammals having comparatively simple molars with, more or less, three cusped crowns, which he rightly says is a common condition in both the early mammals and in mammal-like reptiles. He then makes a strange remark: 'Apart from this resemblance their teeth seem almost as unlike as one could imagine.' Not only does this ignore the cusp for cusp and sometimes cuspule for cuspule comparison emphasized by Crompton & Jenkins (1967, 1968), Hopson & Crompton (1969) and re-emphasized by Crompton & Jenkins (1973) and Crompton (1974) but it overlooks the contemporaneous Haramiyidae and the later docodonts and multituberculates.

(*b*) *Eozostrodon and Morganucodon*

It is convenient next to deal with the associated faunas. It seems to be accepted that the Bridgend quarries in Glamorgan, S. Wales, including Pont Alun and Ewenny, are situated on what, in late Triassic and early Liassic times, became an island with the transgression of the Mesozoic sea (Robinson 1957). The mammalian remains in the crevices of these quarries are found together with abundant lacertilian and, much more rare, archosaur bones and teeth. The haramiyid teeth collected by Moore in the last century and the haramiyid and triconodont teeth collected by Kühne in the thirties, from Holwell quarry in Somerset in England, are associated with the teeth of such fishes as *Sargodon*, *Hybodus*, *Acrodus*, and other remains of marine animals. Kermack *et al.* (1973) lay emphasis on these different associations. But the Holwell animals were recovered from a Neptunian dyke. Unless one is to suppose that *Eozostrodon* lived, otter-like, on the fishes (and the haramiyids on seaweed?) it might be better to accept the opinion of Robinson (1957) who wrote that the mammalian teeth collected in Somerset were almost certainly derived Rhaetic remains redeposited in early Oolitic times. Against this neither *Eozostrodon* tooth appears to have been rolled. This applies also to the haramiyid teeth. It is easy to envisage the bones of terrestrial animals being entombed in a Neptunian dyke within a few hundred metres of where they lived. The associated faunas contribute nothing to help to solve the problem of the possible or probable synonomy of the genera *Eozostrodon* and *Morganucodon*.

Contrary to what stands in print Kermack *et al.* (1973, p. 106) make a very misleading statement. They wrote, 'Throughout Parrington seems to make two implicit assumptions: That there was only one Rhaeto-Liassic fauna containing mammals in Western Europe, and that that fauna could only contain a single morganucodont species . . .' But Parrington wrote (1971, p. 239) after a survey of earlier publications on these mammals, '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 a considerable size range, until the whole of the available material has been examined. But there is a real possibility of dimorphism.' And again (p. 256), '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 . . .' and five numbered reasons follow.

One of the facts that must be borne in mind when considering the identity of *Eozostrodon problematicus* is that since the posterior part of the crown of the type tooth shows no wear while the root below it is apparently developed to its fullest length, though it still lacked its terminal expansion, wear must have taken place during the stage of root 'penetration' and so must have been on the front of the crown. It is the first lower molar that is usually first subject to anterior wear by reason of the fifth upper premolar standing proud of all other upper postcanine teeth. Now since tooth replacement had become diphyodont it follows that in any mature animal it is the first lower molar which has been the tooth longest in wear. This greatly reduces the chances of obtaining an exact match – a tooth only recently erupted but with the root having reached its full length. Such teeth are, naturally, very rare. At the time the first molars are erupted the animals were plainly very immature and their dentaries delicate and subject to destruction, whereas more fully developed dentaries might have survived. An example of this condition is to be seen in Kermack *et al.* (1973). Their fig. 16*a* is a right dentary of an immature animal showing the molariform fourth deciduous molar and on the first and second molars erupted. The bone is seen in inner view and the two molars show no wear. The specimen below this fine specimen (their fig. 16*c*, *d*, *e*) illustrates well the wear at the front of the first molar in a jaw which had erupted five molars.

Two further points about the dentition of the triconodont can be added here. The front part of a recently recovered dentary (D 257) contains the second, third and fourth lower incisors (figure 2*a*). This, together with a previously studied specimen (D 87), establishes beyond any doubt that the first incisor was the largest, the second was rather smaller, the third smaller still and the fourth was the smallest of all. This is as was shown by Parrington (1971). It is of special importance in view of recent discoveries of later triconodonts. The second point lies in the recovery of a very small glass phial from among the scrap material collected by Kühne. In this phial is one of the tiny anterior upper premolars which are known in the maxillae of the Welsh form. This third triconodont tooth from Holwell has been given the number H 22.

(i) *The roots*

It must be borne in mind when reading the following section that the number of isolated premolar and molar teeth which have both roots preserved is very small and even the number of those with one of the two roots preserved is small, the roots being preserved most frequently in those specimens having the cementum still on the roots. This somewhat obscures the form of the root but cannot entirely hide it. However, sufficient teeth with the roots bare are available to demonstrate that they vary in both the triconodont and the trituberculate to such an extent as to make them useless for taxonomic purposes.

Both Mills (1971) and Kermack *et al.* (1973) first claim that the tooth called *Eozostrodon problematicus* differs from the lower molars of the Welsh triconodont in having a long, tapered curved root. Mills says (p. 32) of the teeth of *Morganucodon*, 'The roots of the lower premolars are similar to those of the molars . . . and are quite striking'. Also, 'Unlike recent mammals they do not taper towards their ends. Their sides are parallel until near their end, when they dilate, giving a shape reminiscent of a blunderbuss.' Examination of figure 3, plate 2, shows that these statements are not even widely true. It is characteristic of many lower premolars of the Welsh triconodont that whatever their size their roots are long, tapered and sometimes curved. That Professor Mills could have been so mistaken suggests that the sample available to him was much too small (Parrington 1973). Kermack *et al.* (1973, p. 105, *et seq.*) also discuss this matter starting with the roots. 'The first clear difference lies in the root.' Of Parrington's (1973) remark, 'while the roots are penetrating they are tapered . . .' they say, 'They are not: they have nearly parallel sides and in no way match the long curved tapering roots of *E. problematicus*', and later, 'It is not a valid taxonomic procedure to postulate that if *E. problematicus* had this character it would be "about identical" with *Morganucodon*, because *E. problematicus* palpably has not the character'. It was not claimed that it had; what was claimed was that *if* it was tapered during growth (and plenty of such teeth are available, some being shown in figures 3 and 4, plates 2 and 3) the sectioned specimen which has been figured would have passed through a stage very like that of *E. problematicus*. The London collection of teeth from Glamorgan would seem to be curiously limited in its variation when compared with those in the Cambridge collection. Thus the fifth upper premolar can have its roots divergent, both can be recurved, or they can be coalesced as can the roots of the upper molars which are themselves peculiar in that the anterior root is compressed along the line of the jaw while the posterior root is compressed across the line of the jaw (Parrington 1973). In this character they resemble the upper molars of *Kuehneotherium* where, however, the anterior root may be somewhat rounded and is compressed only in the well angled teeth as is the posterior root. This is seen in the roots of the upper molar SY 130 where they lie partly across the line of the jaw approaching each other at nearly a right angle.

The roots of the lower molars of *Eozostrodon* can be parallel sided and blunt as they grow (Parrington 1973, fig. 3, A) or they can be divergent to a large degree (figure 3). But it is not hard to find teeth with roots which are curved and tapered (figures 3 and 4). Mills claims that the roots of *Kuehneotherium* lower molars 'taper towards their ends, they diverge and are usually slightly curved' and in this respect he regards them as nearer to the therian condition than are those of *Eozostrodon* (his *Morganucodon*). When the roots of the trituberculate lower molars in the Cambridge collection are studied it is seen that the majority of reasonably well preserved ones are straight and parallel sided – 12 roots – while only nine are of the shape claimed by Mills. Figure 4*a* and *b* show that each kind of tooth found in *Kuehneotherium* can be matched by one from the triconodont and, moreover, the four teeth shown in figure 4*e* contradict everything that has been claimed about the triconodont lower molars. It seems clear that Mills had a far too restricted sample to study.

The roots of the teeth of the Triassic mammals are of no value taxonomically except that those of each of the two forms, that is the triconodont and trituberculate, vary in much the same way. This might be considered as further evidence in support of the view that they are closely allied.

(ii) *Mills's comments on the crowns*

In the course of his discussion of the tooth called *Eozostrodon problematicus* Mills claims that the valley between the main, centre cusp and the posterior accessory cusp is unusually high. There is something to be said for this, but it is by no means unknown in the Welsh triconodont. No increased precision of measurements can help in this matter since Mills refers to the height of the valley above the gum line – a line which might well be placed somewhat differently by two people. In fact it is easy to find teeth with the valley at about the same height above the gum line as in *E. problematicus*. Usually the two anterior molars have higher crowns than the third and fourth and it is these low crowned teeth which have high valleys (figure 8*a*) measuring about 60 % of the total height of the crown. In contrast tall teeth (figure 8*b*) tend to have lower valleys and in one of the abnormally tall and large molars ($\overline{\text{M}}$ 71) the valley behind the centre cusp is only about 40 % of the height of the crown. But as Mills has commented (1971, p. 35) the crowns of the lower molars are very variable in their form and plenty of examples of molars with high valleys can be demonstrated (figure 4). Variability of the crown structure is well illustrated by the two molars $\overline{\text{M}}$ 70 and $\overline{\text{M}}$ 71. These two teeth are exceptional in their proportions and are very large. They were picked out of some debris at the same time and both are dark coloured whereas the other teeth in the sample were brown, and they may well have come from the same animal. It will be seen that $\overline{\text{M}}$ 70, a left lower molar, has the posterior accessory cusp distinctly higher than the anterior accessory cusp whereas in $\overline{\text{M}}$ 71 the reverse is true (figure 8*b*).

Many more molars show the same Mills's factor as the type called *Eozostrodon problematicus* (e.g. $\overline{\text{M}}$ 33, $\overline{\text{M}}$ 78 and $\overline{\text{M}}$ 102) but it may be argued that since these are single teeth they might be posterior molars. However, for example, D 217 and D 230 have the first molar in place in their dentaries, and again the posterior valley behind the main cusp is as high as in the type – about 60 % of the total height of the crown above the gum line.

Finally the cingulum can be strongly developed or quite weak as in the type *E. problematicus* (e.g. $\overline{\text{M}}$ 66 and $\overline{\text{M}}$ 102) and there can even be two equal sized, large kühnecones ($\overline{\text{M}}$ 63 and $\overline{\text{M}}$ 92) Indeed, Mills was right when he claimed of the lower molars of the Welsh triconodont 'The most striking feature of these is the marked variation in crown pattern' and he might have included also their roots. Furthermore, he wrote (1971, pp. 49 and 50) of *E. problematicus*, 'It could well belong to *Morganucodon*'! He should have written, of course, *Morganucodon* could well belong to *Eozostrodon* since the latter was the first to be described.

The great variability of the lower molars remarked by Mills does not depend on size (figures 3 and 4). It can be illustrated by many more specimens if it were worth the time required to pick them out and the cost of illustrating them. In view of these observations Mills's position seems untenable. It is to be hoped that further prevarication on this matter will not be published.

(iii) *The statistical analysis*

In an appendix to their 1973 paper Kermack *et al.* return yet again to the question of the synonomy of *Eozostrodon* and *Morganucodon*, and in doing so Kermack achieves his second *volte-face* in this matter. Having said originally that the two were probably the same and, later, that they certainly were; he next denied that the tooth called *Eozostrodon parvus* could be distinguished from one of the premolars of the trituberculate *Kuehneotherium* (a matter which must remain in abeyance until this latter form has been studied and described) and said that the tooth called *E. problematicus* was so badly preserved as to be useless, and he made no reference to its existence in his next publication on the matter (see Parrington 1971, p. 239). In 1973, however, he claims that the useless tooth called *E. problematicus* can be examined metrically and treated statistically! This approach is based, curiously enough, on Mills's claim that the valley between the two main cusps is situated high above the gum line. It has already been shown that this character is not uncommon in the Welsh triconodont.

It was for a short time difficult to follow just what Kermack had been measuring, but after some discussion with colleagues it was concluded that he measured the vertical height of the valley behind the main cusp (i.e. the height of the restored main cusp above the bottom of the valley) and divided this distance into the amount by which the posterior accessory cusp fell short of this amount. (Kermack *et al.* call this the D/V ratio.) It will be seen that these figures have no bearing on Mills's point.

The first problem was how to draw a vertical line down what may be called the posterior valley. After some trials it was decided to drop a perpendicular from the tip of the main cusp (as best this can be done), draw a line at right angles to this through the bottom of the posterior valley and another through the tip of the main cusp and then from this drop a perpendicular through the tip of the posterior accessory cusp.

An attempt to do this was made on a well preserved lower molar crown ($\overline{\text{M}}$ 64, figure 5*a*). But it was at once apparent that a slight deviation in the choice of the vertical line gave D/V ratios of considerable difference (0.84–0.75). These drawings were made on tracing paper and so two fresh drawings were made on Bristol board for publication. Two more values now appeared! They were 0.91 and 0.82 (figure 5*b*). It was realized that when drawn a second time the tooth had lain at a slightly different angle. Not a promising start.

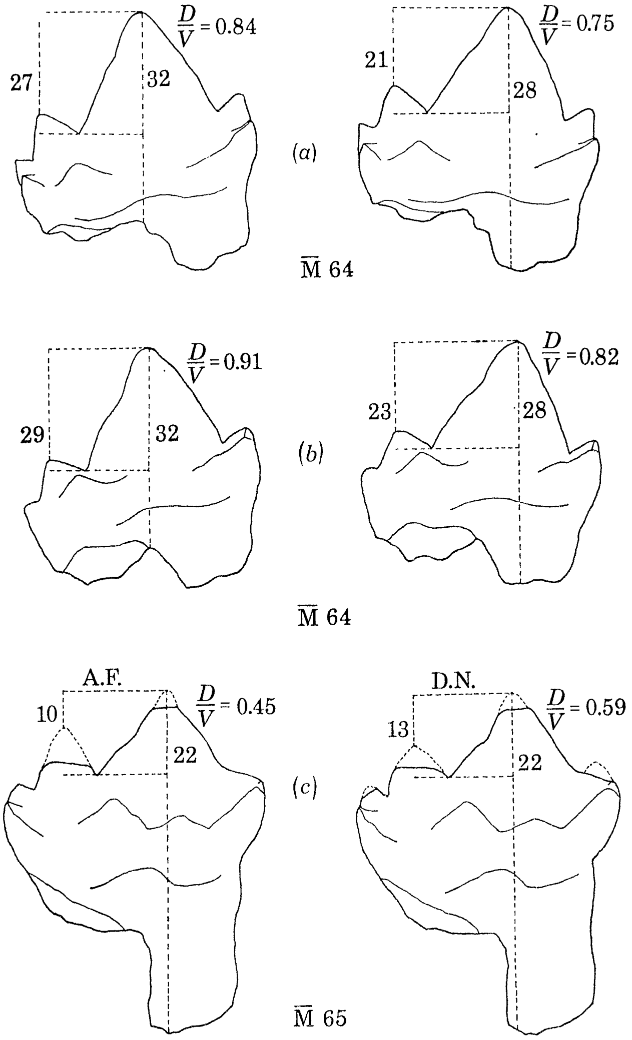

FIGURE 5. *Eozostrodon parvus*. (*a*) A typical left lower triconodont molar from Wales showing the variation in the D/V figures according to somewhat different verticals. (*b*) The same tooth drawn when slightly tilted showing two further D/V figures. (*c*) The damaged molar $\overline{\mathrm{M}}$ 65 as restored by two different people (A.F. and D.N.) who are reasonably familiar with these teeth. The same perpendicular has been used on both restorations. (All magn. × 25.)

After some thought it was recalled that Kermack *et al.* had in some cases given D/V figures for four molars in the one jaw (their group 2). But by the time the fourth molar had erupted the first two had usually undergone considerable wear. Some of these specimens, listed in group 2 of their appendix, bear British Museum numbers (M) but, on inquiry it was found that they had not yet reached that museum. However, it was recalled that many superb figures had been published – they give every impression of being accurate – and so group 2 numbers were sought among the figures. The result was illuminating. Thus their fig. 13 shows the dentary numbered M 24560. All four molars are given D/V figures in group 2 yet the first two molars are plainly very worn. Again in fig. 16 of dentary M 22679 the first and second molars are shown together with part of the third. The crown of the fourth is missing. In the list group 2 D/V values are given for the third and fourth molars; plainly this is an error, perhaps in the typing, and they must refer to the first and second molar both of which are seen to be very worn. Fig. 18 shows specimen U 25 and a D/V figure is given for a very worn molar which is distinctly tilted. Perhaps the worst example is to be seen in their fig. 19 showing specimen U 6 which has the first three molars very worn or damaged. Yet D/V figures are given for all four molars!

As a result of the foregoing, group 1 of the appendix was examined. This is headed as 'Isolated well-preserved lower molars of *M. watsoni*'. Sixty consecutively numbered teeth are given. Yet two are premolars, three are described as having 'heavy damage' and seven others lack either one or both the D/V figures. Well preserved lower molars indeed! It must surely be that these lower postcanines were numbered as they were recovered; but unworn molars are not very common and plainly here again worn teeth have been given D/V ratios. In order to explore the effects of using worn teeth an accurate outline drawing of a molar lacking the tips of the two main cusps, magnified 50 times ($\overline{\text{M}}$ 65), was given to each of two people who are reasonably familiar with these teeth and they were asked to restore the worn cusps. The same vertical (as far as was possible) was applied to the resulting drawings (figure 5*c*) and two D/V ratios were obtained: 0.45 and 0.59.

The explanation of appendix 1 of Kermack *et al.* (1973) was then reread when it was realized that the D/V figures were not obtained from carefully made, enlarged drawings, but by putting a graticule in the eyepiece and measuring imagined complete cusps and unworn valleys! Anyone who cares to try this will soon realize that it is impossible to feel satisfied with such measurements (figure 2*f*).

Finally the type tooth was restudied. A first attempt had resulted in a figure of over 0.6 in contrast to Kermack *et al.*'s figure of 0.4375. Drawings, enlarged 50 times, were then submitted

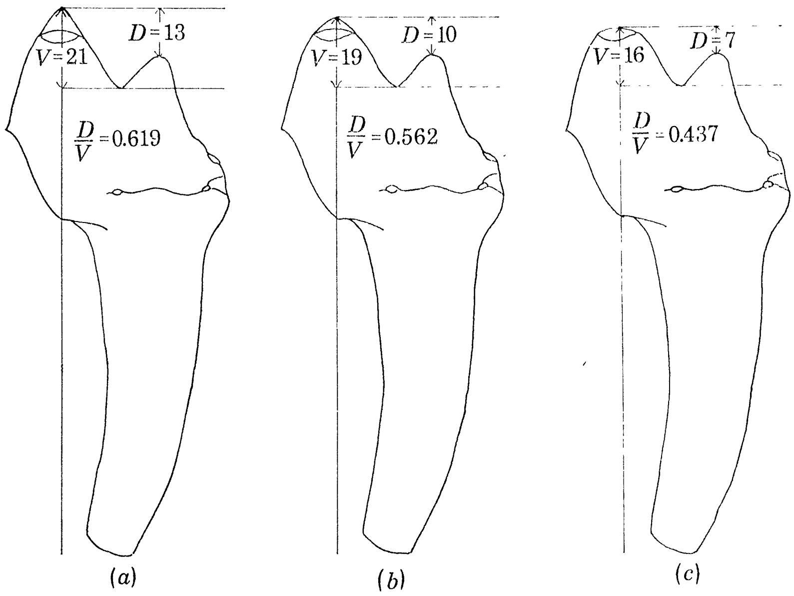

FIGURE 6. (*a*) The type tooth *Eozostrodon problematicus* with the centre cusp restored as many would restore it. The D/V figure is well within the range of the Welsh material. (*b*) With the centre cusp restored as low as reasonable. The D/V ratio is still within the range of the Welsh material (specimen U.20 $\overline{\text{M}}$ 1). (*c*) Only when the centre cusp is not restored can the figure of 0.4375 of Kermack *et al.* be matched. The third and fourth places of decimals can be altered by the thickness of a line. (Magn. × 25.)

to three people who are familiar with these teeth and they were asked to restore the broken main cusp. The same vertical was applied to the three drawings and the following figures were obtained: A.F., 0.60; B.C., 0.56; D.N., 0.62.

Next the type tooth, enlarged 50 times, was restored with what the writer considered to be a reasonable restoration of the centre cusp (figure 6*a*), with the lowest possible restoration (figure 6*b*) and, finally, without the main cusp being restored (figure 6*c*). Plainly the figure published by Kermack *et al.* was derived from measurements made *without* the centre cusp being restored, and the conclusion drawn in their appendix 1 is null and void. It has been a waste of everybody's time. Moreover, no knowledge of statistical methods is needed to reduce this impressive looking exercise to nothing. It may be noticed that the third and fourth decimal places are of no value since it has been shown how easily the first decimal place can be changed.

Although the statistical analysis is useless for taxonomic purposes their figures are not without interest. According to their group 2 the D/V figures for the first lower molar range from 0.56 to 0.92, a range of 0.36. When their D/V figures for the second lower molar are studied it is seen that they range from 0.67 to 0.92, a range of 0.25. The range for the third lower molar is from 0.78 to 0.89, a range of only 0.11. The range for the fourth molar is based on only two teeth and so is of no help. These figures arise, probably, from two things. They arise partly from the crude method of measurement (estimation?) adopted; but largely from the amount of wear to which these molars, erupting successively, have been subjected.

It is a pity that Kermack *et al.* did not check their student's figures by referring to Parrington's (1941) photographs and drawings.

(iv) *Summary*

The evidence for regarding the name *Morganucodon* as a junior synonym of *Eozostrodon* can now be summarized as follows. First the new genus was established on the supposed lack of tilting of the crown seen by Kühne in the two teeth called *Eozostrodon*. It is understandable that Kühne, who made the first discovery of Triassic triconodonts when his studies had been interrupted, having resumed his studies, should regret having sold the first triconodonts for someone else to name. The now extensive collection from Glamorganshire provides many examples of teeth with greatly tilted crowns. Next Kühne himself believed that, despite the supposed difference, the two forms were very close as is shown by the fact that he put all three teeth into the same dentary, the tooth called *E. problematicus* anterior to his new tooth. In this he was almost certainly right, *E. problematicus* very probably being a first molar and his *Morganucodon* a posterior molar. Next Kermack, who was allowed to study the two teeth called *Eozostrodon* in his own laboratory for some six months or so, stated that the two forms were probably the same and, later, that they were certainly so (Parrington 1971). Next he changed his opinion and claimed that the upper premolar *E. parvus* could not be distinguished from similar teeth belonging to the contemporaneous trituberculate *Kuehneotherium* and that the lower molar *E. problematicus* was so badly preserved as to be worthless. Next Mills claimed that the root of *E. problematicus*, in being long and tapered and curved, was quite different from the straight sided and straight roots of *Morganucodon*. He also claimed that the valley between the centre cusp and the posterior accessory cusp was very high. It has been shown that the form known as *Morganucodon* can have long, curved and tapered roots and that the trituberculate *Kuehneotherium* often has straight and parallel sided roots. Finally Kermack *et al.* (1973) supported Mills's contentions and also claimed that the once despised lower molar (*E. problematicus*) could be studied metrically and examined statistically, and claimed, in a most misleading appendix to their paper, that they had proved the two genera to be distinct. It has been shown that their conclusions are based on serious methodological errors.

There are no grounds whatsoever for maintaining the genus *Morganucodon*. It is a junior synonym for the genus *Eozostrodon*.

(*c*) *Mills's families*

Mills (1971) claims that the Triassic triconodonts can be put into two families, the Morganucodontidae and the Sinoconodontidae. He writes (p. 42), 'The occlusal relations of *Morganucodon* are quite constant; as constant as those of any therian mammal'. He maintains, first, that the centre cusps of the upper molars wear down the valley between the centre cusp and the posterior accessory cusp of the lower molars. This claim is far from being well established. As is shown by the first three teeth in figure 7 the wear *can* start as Mills claims. But another 12 teeth show the wear starting in the valley between the posterior accessory cusp and the posterior cingulum cusp. Many more examples could be illustrated if it were necessary. It is worth noting that in specimen M̄ 46 wear starts at the front of the first molar, this because the large fifth upper premolar is quite the highest of the upper postcanines. Occasionally wear is not present in this position due, probably, to the milk molar (which, it may be, was small) not having been shed or to the incomplete eruption of the fifth premolar at the time of death. The occurrence of

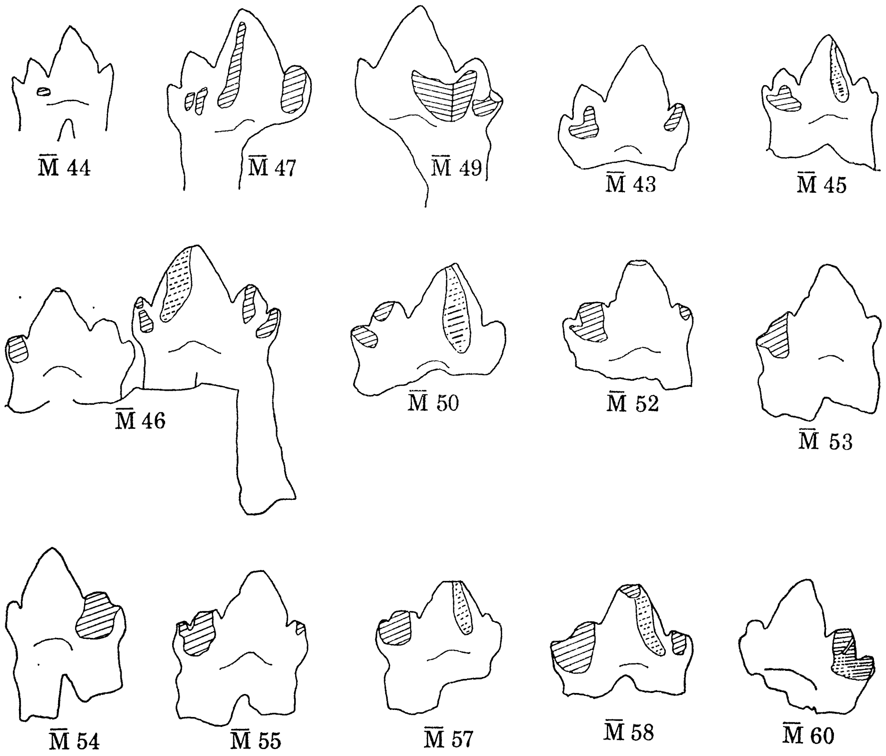

FIGURE 7. *Eozostrodon parvus*. The first three lower molars (M̄ 44, M̄ 47 and M 49) show stages in the start and development of wear between the centre and posterior accessory cusps as claimed by Mills for the family Morganucodontidae. Twelve other lower molars show the start of wear between the posterior accessory cusp and the 'fourth' cusp as claimed by Mills for his family Sinoconodontidae. Specimen 46 shows the onset of wear at the front of the first molar resulting from the fifth upper molar being the tallest upper postcanine. Where broken cross hatching is shown the wear is very slight or uncertain and may result from abrasion *post mortem*. (All magn. × 25.)

wear in the valley behind the posterior accessory cusp denies that this feature is characteristic of the family Sinoconodontidae.

The second character used by Mills to establish his families lies in the relations of successive lower molars to each other. He maintains that in the Morganucodontidae successive molars override the posterior cuspule of the preceding molar and he demonstrates this with a beautiful stereophotograph (Mills 1971, pl. 1 A). Material in the Cambridge collection in part supports Mills's claim but a number of specimens are different (D 117, D 134, D 217, D 248, etc.), either lacking the override or the overlap claimed by Mills to be characteristic of his Sinoconodontidae. Some specimens of the Welsh triconodont illustrated by Kermack *et al.* (1973) support Mills (in particular their fig. 13) but others do not (e.g. their fig. 19) and their restorations of *Morganucodon* (figures 7 and 8) lack both the characters used by Mills to establish the Morganucodontidae, and to distinguish it from the Sinoconodontidae. Mills wishes to place *Eozostrodon problematicus* in the Sinoconodontidae but gives no reasons for doing so. It may be that he is depending on the high valley behind the centre cusp but, as has already been shown, this feature is easily matched among the teeth from Wales. He also suggests the inclusion of Peyer's Hallau specimens numbered 1, 56, 64 and 65. It is shown quite clearly in figure 8 that Peyer's specimens 1 and 65 are easily matched by specimens from Wales and this is true of specimen 56. Only specimen 64 cannot be matched by teeth from Pont Alun.

Mills's families are not well established and it is likely that much more knowledge is required before Triassic triconodont families can be established.

With regard to what has been said above, the best specimen of the triconodont in the Cambridge collection consists of a pair of dentaries together with the left maxilla (CR 1, figure 2*g* and *h*). The distance between the centre cusps of the four upper molars was measured as 3.4 mm under a binocular microscope by means of a calibrated scale in the eyepiece. It is not possible to remove the left maxilla to see the underlying molars but those of the right dentary can be studied and measured. Totally against expectation the distance between the valleys behind the first and fourth lower molars measures 3.6 mm. The teeth shown in figure 7 would lead one to expect the posterior valleys of the lower molars to be slightly closer together – rather than further apart – than the centre cusps of the upper molars. It will be suggested, perhaps, that the proportions of the left and right molars may well be different, and this is true. Tragically the crown of the fourth upper molar was lost during the remounting of the specimen for further preparation. However, photographs were taken in various views before this accident happened.

(*d*) *The Docodonta*

In his classical monograph on the American Mesozoic mammals Simpson (1929), referring to the molars of the Docodontidae, wrote as follows. 'Their molars are much the most complicated structures of the Jurassic, or, indeed, with the possible exception of some of the Cretaceous multituberculates, from the entire Mesozoic.' Kermack (1963, p. 98) agreed with this opinion in that he wrote, referring to *Docodon*, 'The molariform teeth of this animal are the most advanced of any Jurassic mammal'. Yet having followed Patterson for many years in claiming that *Eozostrodon* (*Morganucodon*) was a docodont (see Parrington 1971, Introduction) in 1973 he gave way to Mills in saying that these Triassic teeth were those of a triconodont (a matter which was clear from the first) and proceeded to make the docodonts a mere suborder of the triconodonts! That what he claimed were the most advanced teeth in the Jurassic should now put into the same *order* as what must surely be agreed are the simplest teeth is curious.

In the course of his three classifications K. A. Kermack has put forward names for two subclasses, one infraclass, one order and five suborders – all new (the two names for subclasses refer to the same animals). His five varying opinions on the nature of *Eozostrodon*, the last the most seriously questionable, leave one supporting his remark (1967), 'Rather, a worker in this field may be gratified if his concepts are still regarded as valid five years after he put them forward'.

(*e*) *Peyer's material from Hallau*

In the course of their discussion of the synonomy of the genera *Eozostrodon* and *Morganucodon* Kermack *et al.* (1973) state, '*E. problematicus* can be matched closely by some of the teeth from Hallau in Switzerland (Peyer 1956), as Parrington (1946) himself showed'. Here's prescience indeed! In 1947 Parrington had only an upper premolar and a lower molar from Somerset and models of an upper molar and a lower premolar from Hallau. That they were correctly identified has been shown by the now extensive material from Wales, but it could not be established against any reasonable doubt that they belonged to the same species or even genus. All that it was possible to say was that they were probably from very similar animals. It must be stated here that the writer has not seen the material collected by Peyer after 1956 but which he did not describe.

Kermack *et al.* do not state which teeth from Hallau match the type tooth called *E. problematicus* and the writer has been unable to find at all a close match. But Peyer's tooth numbered one, the upper molar described by Parrington in 1947, can easily be matched by Welsh material such as $\underline{\text{M}}$ 47 from Wales (figure 8*d*) and Peyer's lower molar tooth numbered 65 is closely matched by the lower molar $\underline{\text{M}}$ 47 from Wales (figure 8*c*). Again the lower premolar from Hallau numbered 4 is easily matched by $\overline{\text{PM}}$ 25 from Wales and the upper molar from Hallau numbered 56 is a good match with $\underline{\text{M}}$ 33 from Wales. The very curious tooth Peyer numbered 64 is only approached by a number of lower molars from Wales which have two or three external cuspules (quite a number of these teeth have now been collected). But these teeth have a well developed internal cingulum which is cuspidate and has a kühnecone, while Peyer's tooth has only a partially developed internal cingulum. W. A. Clemens, who has studied the Hallau material, has informed me that the space between what is here called the internal cingulum and the main posterior accessory cusp is, in fact, the result of wear. It is noteworthy that three of Peyer's teeth, numbered 5, 21, and 33 resemble the 'claw-like' tooth from Somerset numbered H 14.

At a meeting of the Society of Vertebrate Palaeontology held in Harvard in 1975, Clemens, who has seen Peyer's entire collection, expressed the view that the upper molars of the Hallau collection were somewhat narrower than are those from Wales. However, the Welsh upper molars are variable in this respect. The four upper molars seen in crown view in figure 8*e* are all distinctly too large to match any fourth upper molar in the Cambridge collection and are, therefore, almost certainly one of the first three upper molars. Yet there are four different shapes. One is very narrow, one very broad, one is narrowed anteriorly and the fourth is narrowed posteriorly. These are unworn crowns. The upper molars of the Welsh triconodont are distinctly variable as are the lower molars.

(*f*) *The Triconodonta and Trituberculata*

It was claimed long ago by H. F. Osborn that the trituberculate mammals evolved from the triconodont forms. Much new evidence supporting this claim is now available, due to the discovery of many more theriodonts and of many Triassic mammals, and due to the invention of new apparatus and new techniques. It can be summarized as follows:

1. As has been repeatedly emphasized by Crompton (e.g. Crompton & Jenkins 1968; Crompton 1974) the cusps of the molars of the triconodont *Eozostrodon* and the trituberculate

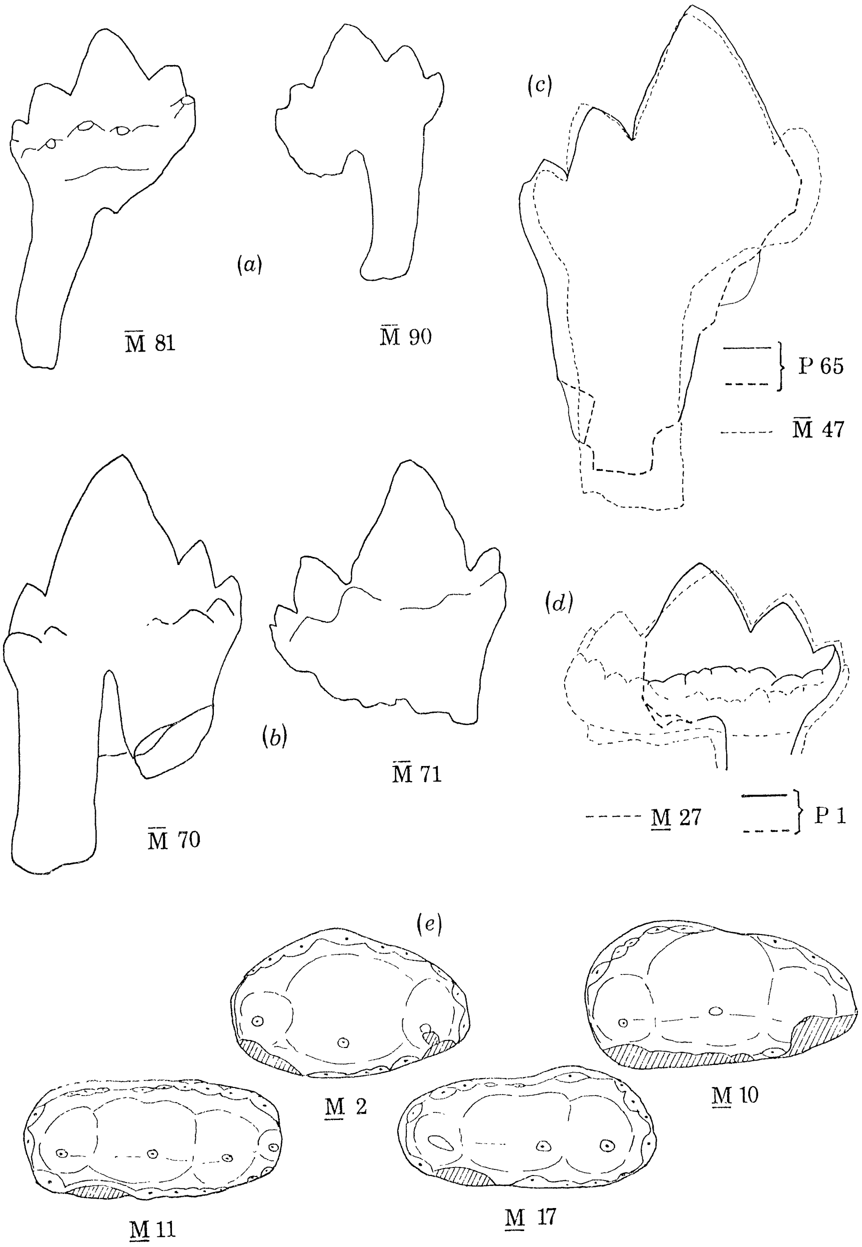

FIGURE 8. *Eozostrodon parvus*. (*a*) Two left lower molars of the Welsh triconodont with high valleys behind the centre cusp. Note that the posterior accessory cusp can be higher or lower than the anterior accessory cusp, note also the roots. (*b*) A large right ($\overline{\text{M}}$ 70) and a large left ($\overline{\text{M}}$ 71) lower molar each with a low valley behind the centre cusp. Again note the different heights of the accessory cusps. These two teeth may well have come from the same animal. (*c*) A comparison of Peyer's lower molar 65 with $\overline{\text{M}}$ 27 from Wales. (*d*) A comparison between Peyer's upper molar numbered one with $\underline{\text{M}}$ 27 from Wales. (*e*) Crown views of four left upper molars from Wales. The crown can be swollen medianly ($\overline{\text{M}}$ 2), tapered posteriorly ($\overline{\text{M}}$ 10), narrow and parallel sided ($\overline{\text{M}}$ 11), or tapered anteriorly ($\overline{\text{M}}$ 17). All four teeth are far too big to be fourth upper molars. (All magn. ×25.)

Kuehneotherium, and in many cases the cuspules, can be matched closely. The absence of a kühnecone in the trituberculate is a clear difference; it is, however, nearly always missing in the later triconodonts. This claim has never been contradicted.

2. It has been shown by Parrington (1971) that the linear, anterior molars of *Kuehneotherium* grade into the acutely angled posterior molars as in other symmetrodonts (Crompton & Jenkins 1967). If there is any significance in dental 'merism' (or serial homology as in vertebrae) this must be of importance. It has been pointed out that if, in fact, the cusps of a triconodont moved relative to each other as claimed by Osborn, there should also occur examples of teeth where the cusps moved in what might be called the 'wrong' direction, but, giving a less effective bite, they would be selected against and so be rare. Such teeth were found by Parrington (1971) and, furthermore, it has now been shown (Crompton 1974) that the first and second upper molars of *Megazontrodon* are clearly angulated in the 'wrong' direction. Merely to stigmatize Osborn's theory as 'spurious' is to blackguard it and not to answer the evidence. Such writing serves to call attention to the lack of any evidence against the theory.

3. It has been claimed that the roots of the two forms are different. It has been shown that the evidence for this statement was based on too small a sample. It should be added that the roots of the upper molars of the two types of Triassic mammals are very similar, the anterior root being compressed along the line of the dentary and the posterior root across it. This condition is less clearly developed in the anterior root of *Kuehneotherium* than in that of *Eozostrodon*.

4. Both mammals have lower molar teeth with comparatively tall crowns and long roots in contrast with their upper molars.

5. As Moss & Kermack (1967) claimed, the enamel of the teeth of *Eozostrodon* and *Kuehneotherium* differs from that of the theriodonts but is not the same as that of true Theria.

6. As shown by Pamela Gill (1974) the premolars of *Kuehneotherium*, like those of *Eozostrodon*, are liable to be shed, their roots absorbed and the alveoli filled with bone which is, at first, vascular. Gill claims that this is unknown in modern mammals.

7. With the exception of K. A. Kermack and some of his coworkers, students of the origins of mammals are now generally satisfied that the cynodonts, and the cynodonts alone, could have been their ancestors. Cynodonts have been known and studied for over a century and they have been collected in great numbers from South Africa, and have been collected also in Central and East Africa, South America, Europe, Asia and even Antarctica. Many forms have been described with what are essentially triconodont teeth (though single rooted). None is known to the writer which has teeth of such a form that by adding cusps in an appropriate 'rotated' or 'angled' position could give rise to tritubercular teeth.

8. As has been shown by Parrington (1971, fig. 17) the position of the condyle of the dentary of *Eozostrodon* varies very considerably. It may lie more or less in line with the teeth, as in other triconodonts, or it may be in a very high position as in symmetrodonts.

9. It must be repeated that the two critical mammals, the triconodont and trituberculate, are of the same order of size, and lived in the same part of the world at the same time. Kermack *et al.* (1973, p. 165) scorn this comment by saying that it needs no answering. In so far as it is a statement of facts it cannot be answered. Would Kermack *et al.* prefer to ally two animals of disparate sizes, living in different parts of the world at different times?

10. Finally it can now be said that the roots of the triconodonts and trituberculates from the Trias vary in the same way, though carved and tapered roots are more common in the trituberculate than the triconodonts.

In conclusion it must be repeated that the Triassic eozostrodonts were very variable and very widely distributed. Their likenesses to the trituberculate *Kuehneotherium* are significant and a common ancester may well have lived in the early Upper Trias. Simpson (1975) has written, 'The fact is that within every population studied hereditary variation has been found to occur and moreover that it is a necessary condition for the evolution of a population'.

7. Summary

It is concluded that the splenial bone existed in a reduced state in *Eozostrodon*; that the ventrally recurved process of the articular was a true retroarticular process; that the tooth replacement, at least in the triconodonts, was diphyodont as in typical mammals today; that epipubic bones have probably been identified (and the properties of the re-elongated tail are discussed); that the genus *Morganucodon* is a junior synonym of *Eozostrodon*; and that the proposed families Morganucodontidae and Sinocondontidae are not well established. Finally it has been argued that the trituberculates were descendants of the triconodonts as H. F. Osborn claimed long ago.

I am indebted to various colleagues and friends for assistance in completing this work. Dr K. A. Joysey and Dr A. E. Friday devoted considerable time to discussing doubts and difficulties and finding troublesome sutures. For photography I am indebted to Mr R. D. Norman, Mr G. G. Runnalls and Mr M. J. Ashby. I am grateful to Mr J. W. Rodford who made the drawings for figure 1 in spite of much other pressing work. Finally, I am deeply indebted to the Leverhulme Trust whose generous support enabled me to have the assistance of Miss J. A. Papworth who patiently undertook the tedious work of extracting the debris from the clay.

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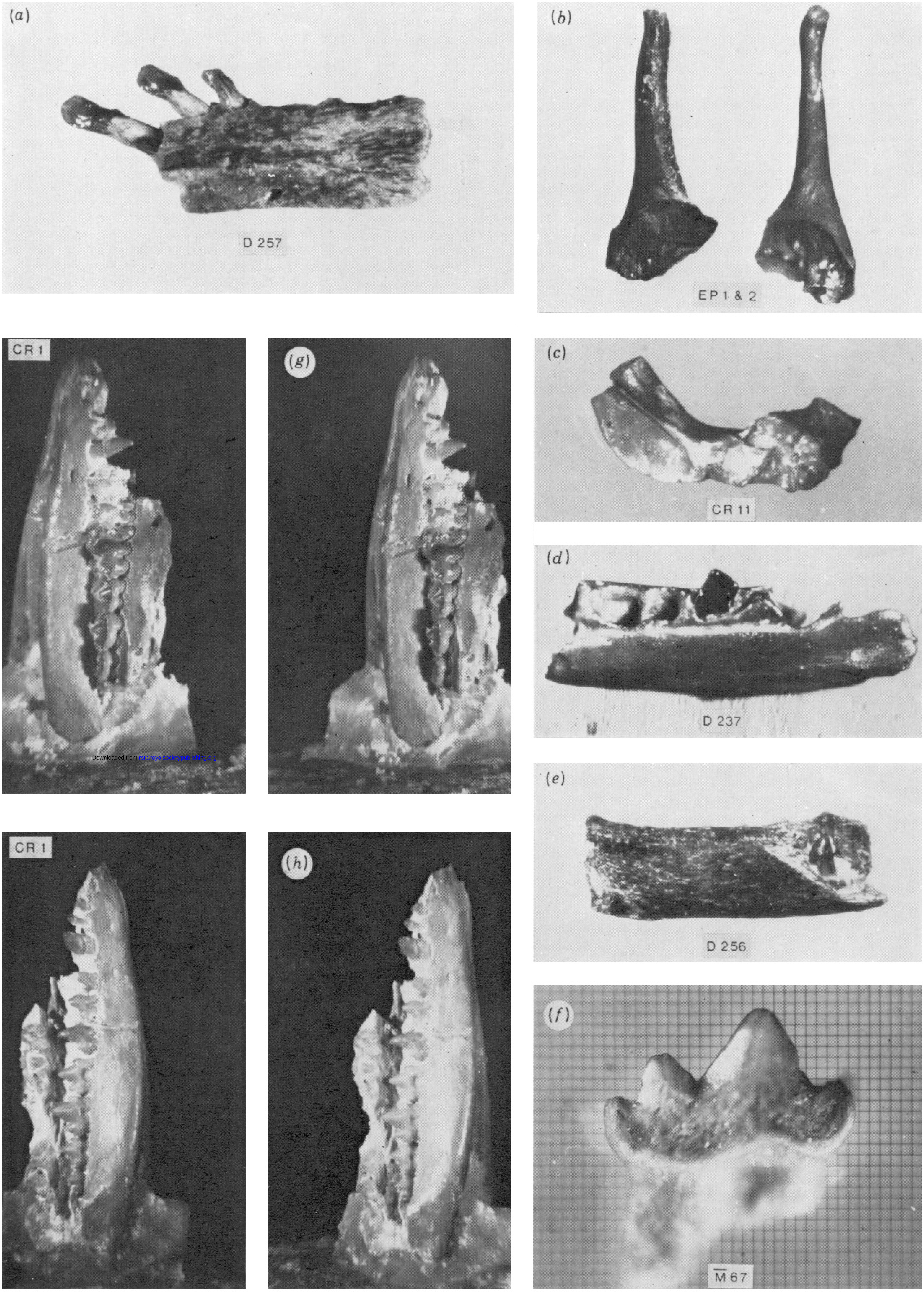

FIGURE 2. For description see opposite.

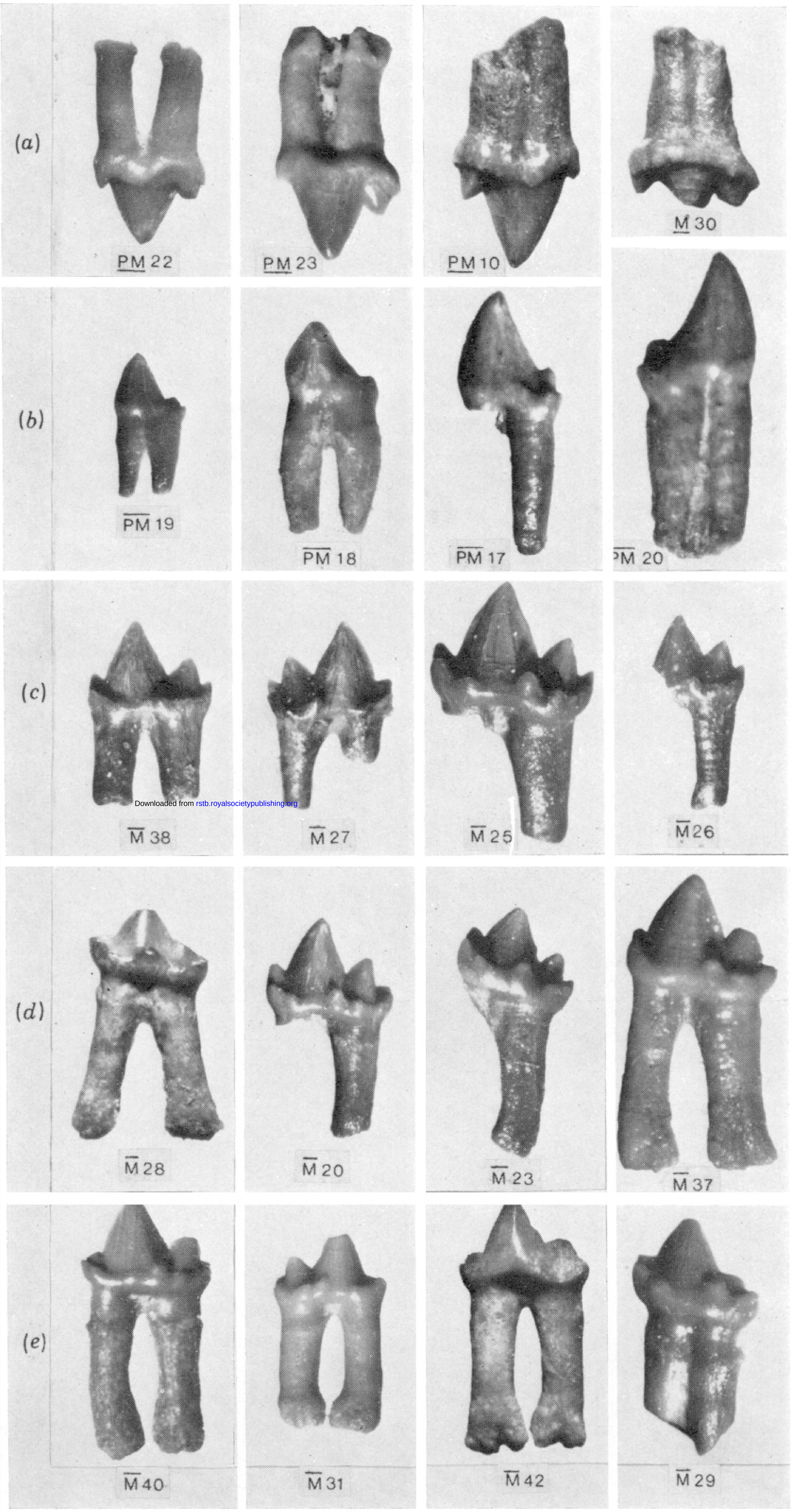

FIGURE 3. For description see opposite.

FIGURE 4. For description see opposite.