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ON A TETRAPOD ASSEMBLAGE FROM A MESOZOIC FISSURE-  
FILLING IN SOUTH WALES.

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ABSTRACT

An account is provided of a new assemblage of small tetrapod remains from a Mesozoic fissure in a quarry in South Glamorgan. Other fissures in the same quarry have previously yielded remains of small tetrapods belonging to the Hirmeriella association, generally considered to be of Rhaetic or Rhaeto-Liassic age. On geological grounds the new assemblage -which comprises many thousands of disarticulated skeletal elements -cannot be younger than basal Sinnimurian, but the only way in which its age can be determined at all approximately is on the basis of faunal correlation. The fossils are little mineralised, and generally poorly preserved, identified specimens consisting predominantly of teeth. The following forms are represented: (1) Three new species of sphenodontid. Two are congeneric and belong to a new genus. The remaining form also belongs to a new genus. Both genera are closely related to the Late Norian genus Glevosaurus; (2) A non-squamate pleurodont lepidosaur. This form is also a component of the Hirmeriella association; (3) Several species of archosaur; (4) Five distinct forms of the tritylodont Oligokyphus. Three of these are conspecific with the forms which occur at Windsor Hill in Somerset. The remainder -which are probably growth stages -are new; (5) A species of the karmiid Thomasia; (6) Five species of morganucodont. One is Morganucodon watsoni. A second is congeneric with the molar from Holwell in Somerset called Eozostrodon problematicus. The three remaining species are new, and all belong to new and different genera; (7) One, or several closely related species of a new type of triconodont; (8) The early therian Kuehneotherium praecursoris. In addition to the identified material of the above mentioned forms, there are a few mammalian-type teeth of uncertain affinities. It is argued on faunal grounds that the age of the assemblage is most probably Lower Liassic. It is further argued that the faunal components of the assemblage are contemporaneous with those of the Hirmeriella association, and have hence been drawn from the same terrestrial biota.





INTRODUCTION

Mesozoic fissures of terrestrial origin in a small cluster of five quarries in Glamorgan, South Wales have yielded elements of a unique faunal and floral association, which Kermack, Mussett & Rigney (1973) have called the Hirmeriella association after its most widespread component, the fossil conifer Hirmeriella muensteri. The age of the association is generally considered to be Rhaetic (Kermack & Mussett, 1967; Parrington, 1971) or Rhaeto-Liassic (Lewarne & Pallot, 1957; Kermack, et al, 1973), and it includes several species of small tetrapod, the remains of these forms affording an exceedingly rare, and hence invaluable glimpse of the small tetrapod life of this remote period. The only relatively abundantly represented Hirmeriella tetrapods are an unnamed pleurodont lepidosaur, the early triconodont Morganucodon watsoni, and the earliest known therian Kuehneotherium praecursoris, the remains of these three species together constituting an enormous assemblage of disarticulated bones, of which the lepidosaur accounts for about 60% and the mammals (predominantly Morganucodon) 40%. None of the three species is found anywhere else in the world. The Hirmeriella association also contains two other small tetrapod species -an unnamed archosaur and an unnamed amphibian -each of which is represented by a single specimen. Its only other faunal components are a gastropod and a beetle (Kermack, et al, 1973).

The first fossils from the Hirmeriella fissures were discovered by the distinguished palaeomammalogist W. G. Kühne. Following the Second World War, Kühne had begun a systematic search for the remains of Mesozoic mammals in fissures in the numerous quarries of South Glamorgan. In the summer of 1947, on the floor of Dutchy quarry, he found a small quantity of fossiliferous fissure material which came from a fissure that had been quarried away prior to his visit. This material subsequently yielded the first specimens of Morganucodon (Kühne, 1949 & 1958) and Kuehneotherium (Kühne, 1950; Kermack, Kermack & Mussett, 1967). In a second Hirmeriella quarry -Cnap Twt- Kühne discovered a fissure containing abundant plant remains, whilst in a third -Pant- he found a fissure which yielded scraps of bone. In 1951 Kühne returned to Germany having emphasised "the desirability of strict surveillance of all quarries in the Carboniferous Limestone of Somerset and South Glamorgan. As quarrying continues, new fissures

may be revealed at any time... If not detected and duly exploited at once these fissures will disappear, some very soon after their exposure, some a short time later." (Kühne, 1947). The vital work of keeping the quarries of South Glamorgan under surveillance was taken up by K. A. Kermack, D. M. Kermack and F. Mussett of London University, who were later joined by P. M. Lees. Over the ensuing years the London University team made important discoveries of Hirmeriella tetrapod remains in Dutchy, Pant, Pontalun and Eweny quarries. Until relatively recently, all of the tetrapod assemblages obtained by these workers from fissures in the Hirmeriella quarries consisted exclusively of the remains of components of the Hirmeriella association (see Kermack et al, 1973, p.98). In 1968, however, routine quarrying operations in one of the quarries began to expose a new fissure which, in 1971, yielded a few specimens of a tritylodontid and a sphenodontid. Between 1971 and 1974 a large quantity of fossiliferous material from the fissure was collected and removed to University College, London, where I had the opportunity to break down a substantial portion of it in order to extract and study the contained fossils. The remains which I obtained from this material constitute a new type of small tetrapod assemblage which is faunally far richer and more diverse than any of the Hirmeriella assemblages. The three principal Hirmeriella tetrapod species are represented within it, but the majority of species are either new to science or have never before been found at any Welsh locality. The new assemblage, which has not hitherto been described, forms the subject of this thesis.

## GEOLOGY

### Background

The Hirmeriella quarries are situated on a low Carboniferous limestone plateau, a few square miles in extent, which lies about two miles to the south of the town of Bridgend. The plateau, which has a maximum height of 300 feet, is bordered on its north-western flank by the river Ogmore, which enters the Bristol Channel adjacently.

Structurally, the plateau is part of the western half of the Cardiff-Cowbridge anticlinal fold belt (George, 1933). Except along its border with the river Ogmore, it is surrounded by Lower Liassic deposits which rest directly upon Carboniferous limestone (Strahan & Cantrill 1904; Trueman, 1922). The youngest of these deposits are basal Sinemurian (bucklandi zone); no younger Mesozoic deposits are present in the Vale of Glamorgan, owing to erosion in late Tertiary times (George, 1970). In the walls of Longlands quarry, which is situated on the north-eastern edge of the plateau, the Lower Liass can be seen transgressing over the Carboniferous limestone. A hundred yards to the east of this quarry is the site of Brocastle pit, a small quarry from which Moore (1867) obtained Liassic corals.<sup>1</sup>

In his classic study of the Liassic rocks of Glamorgan, Trueman (1922) has shown that the plateau formed part of a small, progressively contracting island - which Robinson (1971) has called St. Brídes island - throughout the Hettangian. The reader is referred to his paper for a full account of the pertinent geological evidence. At the end of angulata times the greater part of St. Brídes island lay on what would now be the eastern side of the river Ogmore (figure 1) and the shoreline of this part of the island appears to have corresponded approximately to the outline of the plateau. Only part of the shoreline of the remainder of the island can be plotted as only a small part of the littoral Liassic deposits which once bordered it are now preserved. These are exposed in the immediate vicinity of Merthymawr, and in a number of localities between the last named town and Tythegston (see Trueman, 1922, page 270). With the close of the Hettangian, the contraction of St. Brídes island continued and, as Trueman's investigations have shown, it finally submerged

<sup>1</sup> Although Brocastle pit has long been disused and is now very overgrown, I was recently able to find several loose fragments of Liassic limestone on its floor which are packed with ammonites.

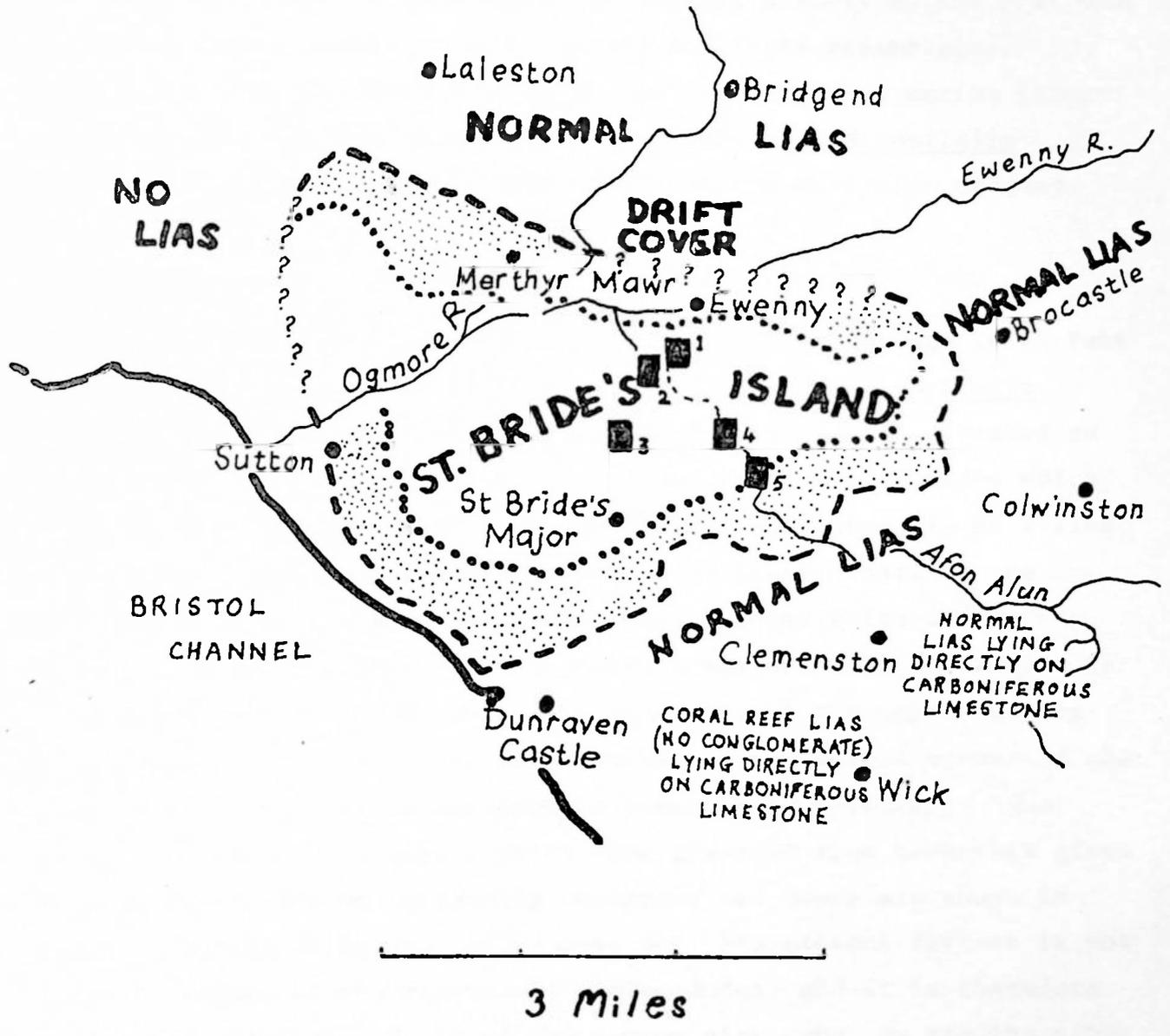


Figure 1. St Brides Island.

- ..... Probable outline of Island at the end of angulata times.
- Existing outcrops of on-shore deposits (Sutton stone facies) of angulata age.
- - - - - Approximate seaward limit of on-shore deposits (Sutton stone) of angulata age.
- Hirmeriella quarries; 1 = Ewenny quarry, 2 = Pontalun quarry, 3 = Pant quarry, 4 = Dutchy quarry, 5 = Cnap Twt quarry.

(From Robinson, 1971, with minor modifications).

beneath the sea in upper bucklandi times. The minimum possible age of the tetrapod assemblages from the Hirmeriella quarries is therefore basal Sinemurian. The pre-Liassic geological history of the area does not fix a credible maximum possible age for these assemblages.

Strahan & Cantrill (1904) have shown that there was no marine transgression over the area of the plateau on which the Hirmeriella quarries are situated between the Liass and the Hercynian orogeny.

The fissure

The fissure which has produced the new tetrapod assemblage is in Pant quarry. This quarry - which is one of the only two Hirmeriella quarries still working (the other one is Pontalun) - is situated on the western flank of the narrow dry valley of Pant St. Brides which dissects the Carboniferous limestone plateau approximately on a line between Bridgend and St. Brides Major. The eastern part of the quarry stands entirely on the clean, well jointed white oolite of the caninia oolite zone. On the quarry's western side, this zone is overlain by the crinoidal dolomitic limestone of the upper caninia oolite zone. The fissure is situated in the south-west corner of the quarry and it runs in an approximately east-west direction. The other fissures in the quarry which have produced bone have been given numbers by the London University workers, and these are shown in Kermack, Mussett & Rigney, 1973, page 98. The present fissure is not a branch of any of the previously numbered ones, and it is therefore designated 'Pant 4'. It is of the narrow slot type, as are the other fissures in the quarry, and most of those in Pontalun quarry, half a mile to the north. These fissures represent a very immature stage of the karstification process; they were formed by weakly acidic rain-water draining away from the original Mesozoic land surface along joints in the limestone. The original width of the currently exposed part of Pant 4 - which was variable - never exceeded four feet, and it was normally much narrower, being of the order of one to one and a half feet. About 120 feet of the fissure have been exposed as the southern part of the west wall of the quarry was blasted back over a period between 1968 and 1975. Blasting progressively removed sections of the southern wall of the fissure to expose its contents and its northern wall, the fissure thereby being bisected along its length. With the removal of each new section of southern wall, the freshly exposed fissure filling collapsed to the quarry floor leaving the northern wall largely bereft of material. Distinctive

flutings, etched by the passage of water through the fissure, can be observed in many places on this wall. Some of the flutes are clearly asymmetrical in cross-section, with their steeper slopes lying east. The steeper slopes of such flutes are generally taken to lie in the upstream direction (Kermack, et al, 1973), so that the direction of water flow through the fissures would appear to have been east-west. This is the same as the direction of the water flow through the fissure which is situated at the northern end of the quarry, from which the abundant remains of the Hirmeriella tetrapods were obtained in 1955 (Kermack, Kermack and Musset, 1956).

The fissure filling

The lithology of the fissure filling is very similar to that of some of the fissure fillings which have been obtained from the Hirmeriella fissures (cf Kermack, Mussett and Rigney, 1973, page 102). It is not lithologically uniform, being locally variable in the mean size and in the composition of its constituent particles, and also in its colour. It varies in texture from a plastic clay to a relatively hard, concretionary material which consists mainly of granules of very coarse sand grade. Some 75% of the fissure filling is ochre-red in colour, and almost all of the remainder grey. Because, during the course of quarrying, the bulk of the exposed fissure filling inevitably collapsed to the quarry floor, no detailed account can be given of the spatial relations of its various constituent sediments when they were held in situ. However, from a study of the residual material which still adheres to parts of the northern wall of the fissure, and also of the collapsed material on the quarry floor, it is possible to build up a general picture of these spatial relations. The mean grain size of the sediments varied both vertically and horizontally throughout the length of the exposed part of the fissure, progressively graded stratification being strictly confined to local pockets. Thus, layers of a particular grain size of material very frequently passed horizontally, and abruptly into strata of a different texture, and layers of relatively fine material were often sandwiched between layers of coarser sediments, and vice versa. From this it is evident that sediments were washed into the fissure on very many separate occasions, these in-washings very probably taking place after heavy rain storms during a wet season. The pockets of progressively graded

11.

strata represent the local settlings of particular in-washings of sediments, in water that was only slowly moving through the fissure, or which was stationary. The presence of some layers of extremely fine sediments demonstrates that deposition took place, at least occasionally, in water that was standing within the fissure for some time.

The fissure filling was not colour stratified to any significant extent. Instead, the grey deposits occurred as irregular shaped pockets of varying sizes within the red ones and these pockets occurred at all levels. This situation effectively precludes the possibility that either of the principal colours of the infilling was the result of a chemical change effected in situ by water percolating through the fissure. If this had been the case, distinct colour stratification would inevitably have resulted, as it did, for example, in the infilling of the Norian aged fissure in Slickstones quarry in Gloucestershire, which is described by Halstead and Nicoll (1971). The composition of the different coloured deposits also precludes the possibility that either colour was determined after the deposition of the sediments, as will be appreciated from the following description.

The composition of the red deposits:

The red deposits vary from a soft clay to a relatively hard, coarsely granulated material,<sup>1</sup> which consists essentially of a mass of small pellets of amorphous haematite, cemented into a clay matrix. This coarsely granulated deposit accounts for by far the largest proportion of the red fissure filling. The pellets at the surface of a nodule of the deposit may be abraded off with the fingers, although even quite small nodules are difficult to break by hand. The cement is vigorously attacked by dilute hydrochloric acid, indicating that it is of a calcareous nature. Calcareous cementation is clearly the result of the fissure being developed in limestone; weakly acidic drainage water percolating through the fissure would have acquired

<sup>1</sup> This or an almost identical material obtained from some of the Hirmeriella fissures, has been referred to by Kermack, et al (1973), as a red 'marl'. Whilst the term 'marl' is often used in a very loose sense, its application in the present instance is - I think - both inappropriate and misleading. A marl is essentially a mixture of clay and limestone particles. The material in question here does not fall into this category.

dissolved calcium bicarbonate, this subsequently becoming precipitated within the sediment as the insoluble carbonate. The haematite pellets constitute between 70 and 80% of the deposit.<sup>1</sup> They are sub-spherical in shape, and are hard and shiny at the surface. Many are broken and their breakage surfaces are clearly water-worn, showing that they were transported for some distance prior to their deposition in the fissure. The diameters of the pellets vary between 0.1 and 3.0mm, although the majority have a diameter between 0.4 and 0.7mm. Their internal structure is oolitic, although in some instances the concentric shell pattern has been obscured by in situ silicification, the silica taking the form of a micro-crystalline mosaic. Calcite crystals and rounded quartz grains are present in the coarsely granulated deposit in small quantities, and there are also a few angular fragments of limestone. The latter were probably derived from the walls of the fissure or from the immediate neighbourhood; they rarely exceed 10mm in length. The only other components of the coarse deposit are fossils. Derived crinoid ossicles account for about 0.5% of it. These are normally water-worn, and they are sometimes stained with haematite. Bone is almost invariably present. It is never very concentrated, and it normally constitutes between 1 and 2% of the material. It is fragmentary, fragile and white, although occasionally it may be stained with haematite. Bone fragments rarely exceed 10mm in length. Carbonised plant remains intermittently occur, and these are always very sparsely concentrated.

In addition to the coarse deposit, the red fissure filling includes pockets of material in which the average grain size of the haematite pellets is rather smaller than that described above, and there are also pockets in which the concentration of pellets is less. These deposits are generally less well cemented than the coarse one, and they break down slowly in water. Bone is normally rare, and consists only of very small, unidentifiable fragments. A few sparse plant remains are occasionally found. The fine grained deposits intergrade with red clay in which there are few - if any - haematite pellets. The red colour of the clay is due to finely divided haematite, very probably derived from pellets which disintegrated

<sup>1</sup> The percentage abundance estimates of the components of particular deposits have been made by the application of Pettijohns grid analysis to small samples of the deposits (cf Pettijohn, 1949).

during the course of their journey to the fissure. The clay is very weakly cemented, and, upon immersion in water, it collapses almost instantaneously into a sludge. This relative lack of cementation may be correlated with the impermeability of the clay when it was held compact within the fissure. The clay is effectively barren of bone and plant remains.

The composition of the grey deposits:

There are two types of grey deposit: a plastic clay and a soft marl. The marl - which makes up the greater part of the grey fissure filling - is rather less well cemented than the coarse red deposit. It consists predominantly of calcareous siliceous micro-particles, which, unlike the haematite pellets, are not oolitic in structure. The grain sizes of the principal components of the marl rarely exceed those of a medium grade sand. In addition to these components, the marl contains a few heavy mineral grains, quartz grains, calcite crystals, unworn pieces of Carboniferous limestone (some of which may exceed 20mm in length), and fossils. Derived crinoid ossicles are generally more common than they are in the coarse red deposit, sometimes constituting up to 3% of the marl. Bone occurs very patchily, and it rarely accounts for more than 1% of the marl. As in the red fissure filling, it is fragmentary and fragile. In this case, however, the colour of the bone is light grey or grey-black. Plant remains are generally more common than in the red fissure filling, although their local density is very variable. A few nodules of marl contain plant in such abundance that the marl appears to be almost black, the concentration of plant rivalling that in the plant-rich fissure material from Cnap Twt and Ewenny quarries which was described by Harris (1957). It is noteworthy that these plant-rich nodules contain virtually no bone fragments. Some nodules of marl contain very thin layers of amorphous, finely divided limonite, and some bone fragments are coated with it. This has quite clearly formed in situ as a result of oxidising water percolating through the fissure, quite possibly in recent times. The grey clay is very little cemented, and it is barren of bone. Plant remains occur rather rarely, and in relatively low concentrations.

#### The origin of the fissure deposits

The grey deposits almost certainly originated as weathering products of the Carboniferous limestone of the plateau when the latter formed

a Mesozoic karst land-surface. Their date of origin probably does not predate that of the formation of the fissure to any significant extent - if at all. This, however, is of little value in dating the infilling of the fissure, as the Carboniferous limestone formed a karst land-surface in the immediate area of the plateau throughout Norian and Rhaeto-Liassic times. The origin of the red deposits is less immediately obvious. In colour they resemble the local Keuper Marls, but they are lithologically quite distinct from them. The haematite (or gothite) in the Keuper Marls forms a coating around the rock particles of which the marls are composed; it does not constitute the major part of the sediment as it does in the present case. The extremely high concentration of haematite in the red fissure deposits suggests that the latter are essentially reworked haematite ore, which formed originally by the metazomatic replacement of limestone. Such ores are common in veins and large pods in the Carboniferous rocks of the region, especially along the south-east crop of the nearby South Wales coalfield. At Llanharry, a few miles east of Bridgend, haematite ore is mined on a large scale, and I have found small veins of the ore in the Carboniferous limestone above Ogmores beach. The iron in these ores is probably ultimately derived from the pyrite in the Coal Measure Shales which once overlay the Vale of Glamorgan (Jones, 1930). The dates of formation of these ores probably varied considerably, and they could, quite conceivably, have been spread over the interval between the Hercynian orogeny and the ultimate submergence of the Vale in Liassic times. The lithology of the red fissure deposits, as in the case of the grey, is thus quite useless for determining the date at which the infilling of the fissure took place. The only way in which this date can be determined at all approximately is from a study of the plant and tetrapod remains which have come from the fissure. The plant material has unfortunately not yet been positively identified. The evidence afforded by the tetrapods will be discussed after the faunal composition of the new assemblage has been described.

THE EXTRACTION OF THE TETRAPOD FOSSILS FROM THE FISSURE FILLING

This was basically a two-fold procedure, comprising:

- (a) the breakdown of the cement which binds together the macroscopic components of the fossiliferous fissure filling.
- (b) the removal of the bone from the residual, uncemented particulate matrix.

Approximately one and one quarter tons of fossiliferous fissure filling was broken down during an initial nine month period following its collection in 1972, this allowing the compilation of an extensive collection of fossils. The breakdown of small amounts of fissure filling was continued throughout the duration of the present study, however, a procedure to which I owe the discovery of several unique specimens.

The calcareous cement of the bulk of the fossiliferous fissure filling - the relatively coarsely granulated red deposit - was broken down by application of the acid technique, after the manner described by Toombs (1948). Since its inception, this technique has had a wide application where vertebrate fossils are preserved in a calcareous material. Acetic acid in strengths of 15% or less is normally used, although formic acid is sometimes substituted where the cement of the fossiliferous material to be broken down is particularly resistant, as, for example, in the case of a dolomitic marl. Formic acid is less pungent than acetic, and it has a faster action. It also has the advantage that its calcium salts are more soluble than those of the latter, and they are hence more easily washed away. Unfortunately, formic acid - even in very dilute strengths - soon begins to attack fragile bone, and it was therefore unsuitable for use in the breakdown of the Pant 4 fissure filling.

The principal advantage of the acid technique is in the saving of time and labour. In the present case, considerable time and effort would have been required for the manual removal of the fossils from the untreated fissure filling, instead of which the breakdown of the fissure filling was able to proceed largely unattended.

Because of the fragility of the fossil material, care had to be taken to ensure that the reaction between the acid and the cement

did not proceed too vigorously, thereby risking damage. 10% acetic solution proved optimal for the bulk of the red fissure material. Prior to treatment with the acid, each nodule of fissure filling was carefully examined under a binocular microscope and any visible bone coated with poly-butylmethacrylate lacquer, in order to protect it from possible mechanical injury. Poly-butylmethacrylate is unaffected by acid in the concentration which was used, and it could be removed later by application of ethyl acetate solution. After examination, and the coating of any exposed bone, each nodule was placed in an acid bath and left for 24 hours, the acid bath being placed in a fume cupboard because of the pungency of the fumes. The acid was not normally exhausted during this period, and the cement of the fissure filling was generally completely broken down. The resultant breakdown material was repeatedly hand washed in copious amounts of water, and the very fine sediments which were released into suspension poured off. These sediments consisted mainly of silt, calcium acetate and other breakdown products of the cement. When no further fine sediments could be removed by washing, the material was left overnight with a gentle inflow of water into the containing vessel so that there was a continuous decantation. This normally served to remove the last of the fine sediments, although occasionally the washing process had to be repeated. The complete removal of all potentially adhesive fine sediments was essential to the subsequent sorting of the residual matrix.

Finally, the residual, uncemented matrix was drained and dried thoroughly in a hot air oven at 15<sup>o</sup> centigrade for a further 24 hours, prior to the extraction of the bone. In the few cases where a nodule of fissure filling was not completely broken down, the whole procedure was repeated.

The soft grey marl was not broken down in acid because even at a dilution of 10%, acetic acid effected its almost instantaneous collapse into a sludge, with the consequent danger of serious damage to any contained fossils. Immersion in cold water proved a suitable method of breaking down the cement, the procedure being otherwise the same as in the case of the coarsely granulated red deposit.

After the breakdown of the cement, the residual matrix - which consisted predominantly of haematite pellets or of calcareous fragments, according to which type of infilling had been broken down - had a

particle size range which varied from that of a fine sand to that of a very coarse one, with, frequently, the presence of a few larger particles of up to about 10mm diameter (mainly bone fragments and crinoid ossicles). Because the bone which was being obtained after the breakdown of the fissure filling cement was very fragmentary, one nodule of each type of fossiliferous deposit was dissected manually with the aid of a fine needle held in a pin chuck, to establish that the condition of the bone was not the result of some rigour of the breakdown techniques. The bone obtained by this laborious method compared exactly with that obtained after the application of the normal breakdown methods. The survival of a few very delicate specimens, such as the slender teeth of a pleurodont lepidosaur, and some tiny mammalian and tritylodont icisors also provided evidence that the breakdown techniques employed were not significantly hazardous to the fossil material.

Prior to the removal of the bone, the dried residual matrix was separated into five size categories of particles, by passing it through a stack of sieves of mesh British Standard Units 12 (0.055 inch mesh), 18 (0.033 inch mesh), 25 (0.023 inch mesh) and 36 (0.016 inch mesh). Each category was then sorted by hand. This was done by spreading a small quantity of the material at a time onto a grided dish, surveying this through a binocular microscope, and removing the fossils with the moistened tip of a fine paint brush (No. 1). Any cracked specimens or broken surfaces were lacquered to prevent any further deterioration. Sorting was by far the most time consuming and laborious phase of the extraction procedure, and attempts were made to reduce the effort involved. Unfortunately, the use of the heavy liquid technique described by Lees (1964) to concentrate the bone prior to sorting was found to be of little value in the case of the bulk of the matrix (i.e. that consisting principally of haematite pellets), as the specific gravities of the bone fragments and haematite pellets are too close together to effect a good separation. The haematite pellets were found to be weakly magnetic, but passing unsorted matrix through a magnetic separator did not effect more than a minimal separation, and this technique was not, therefore, used extensively. After about one cwt. of the dried residual matrix had been sorted it was concluded that the two categories of smallest sized particles did not yield sufficient fossil fragments of a recognisable character to justify the considerable time required for their sorting. On sub-

sequent sievings, this fraction of the matrix was stored in an unsorted condition for possible later reference.

Once the fossils were removed from the matrix they were stored in individual specimen tubes and they were examined in a sand tray. Particularly fragile specimens were finely coated with lacquer.

THE GENERAL CONDITION OF THE TETRAPOD REMAINS

The tetrapod remains from Pant 4 consist of bone fragments, isolated teeth and teeth which are ankylosed to bone. Teeth constitute about 5% of the remains. To date no two bones have been found in association, although thousands of bone fragments have been obtained from the fissure filling. This implies that all the bones that are represented in the collection were fully macerated prior to their transportation to the fissure; if they had not been one would naturally expect at least a few associated skeletal elements to occur. The identified remains of all the tetrapod species which occur most commonly in the assemblage were spread fairly evenly throughout the fossiliferous part of the fissure filling. It is therefore clear that all of the primary aggregations of bones and teeth which are represented in the collection had an essentially similar faunal assemblage. Although the remains which have been obtained from the red and grey deposits differ in their colour, they do not appear to differ to any significant degree in their state of preservation.

The general condition of the tetrapod fossils is poor, the majority of elements having undergone both fragmentation and water-wear. Almost all of the teeth have their crowns damaged, and substantially preserved roots are rare. The bones are still more poorly preserved than the teeth, a situation which is understandable in view of the fact that bone is softer - and hence less resistant to impactation and abrasion - than enamel and dentine. No bone is complete and few specimens are even substantially intact. Bone fragments vary in size and condition from minute chips and fragments of no discernible character of 0.5mm or less in length to substantial sections of dentary which attain up to 13mm in length. The bulk of the bone is of no morphological value. Some 50 to 60% of fragments are of a completely unidentifiable nature, and much of the remainder can only be ascribed to a general category of bone, such as longbone.

The fracture edges on the bones and teeth are generally water-worn, although this is not always the case. Evidence of breakage during deposition within the fissure itself is, however, very rare. Where the fracture surfaces of the bones have not been heavily abraded, they are almost invariably found to be fibrous. In this respect they resemble the fracture surfaces of Recent bones. When fossil bones are broken, their fracture surfaces are, by contrast, normally flat

(Reif, 1970). The nature of the fracture surfaces of the bones from Pant 4 thus suggests that these bones were broken prior to fossilisation. In the case of the majority of bone fragments, the degree of water-wear of all the fracture edges and surface structures is approximately uniform. In some instances, however, a bone possesses one or more fracture edges which are noticeably less worn than the other parts of the fragment. Such fracture edges are clearly the result of breakages which have occurred during the course of the bones' journey to the fissure. It should be emphasised that there is no evidence that all breakages are the result of the rigours of transportation; where all the fracture edges on a bone have been equally abraded, it is perfectly possible that the specimen was broken before it became waterborne.

It is noticeable that the fragments of those morphological types of bones and teeth which had a relatively large intact size are, on average, less complete than the fragments of those where the intact size is small. This state of affairs is well illustrated by the following data, which relates to some of the different morphological types of tritylodont incisor which are present in the assemblage:

<u>Tooth type</u>	<u>Estimated average length of intact tooth</u>	<u>Average length of preserved fragments</u>	<u>% of specimens comprising <math>\frac{1}{2}</math> tooth or more</u>
I <sub>1</sub>	17mm	3.10mm	6%
I <sub>2</sub>	15mm	3.80mm	8%
I <sub>3</sub>	11mm	3.00mm	11%
A	8mm	3.20mm	18%
I <sup>1</sup>	6mm	2.70mm	20%

As large, relatively robust teeth were obviously not more prone to fragmentation than smaller, more delicate ones, it is apparent that the currents which carried the tetrapod remains to the fissure must at some stage have acted selectively, transporting a greater percentage of the smaller elements that were available than of the larger ones.

The level of water-wear exhibited by the majority of bones and teeth is consistent with their having been transported for some distance prior to deposition in the fissure. Sharp edges have normally been smoothed and fine surface details eliminated, but major morphological features are generally discernible. In some instances, however, elements exhibit very little water-wear, whilst in other instances

their morphology has been substantially obliterated. In a minority of cases, specimens have been worn into rounded, featureless pebbles. Bones and teeth exhibiting differing levels of water-wear were normally found intermixed in the same pocket of fissure filling. The variations in the level of water-wear indicate that these specimens were transported from a number of sites which were situated at different distances from the fissure.

As stated earlier, the bones and teeth from Pant 4 are very fragile; they are also very brittle. Specimens break easily, and upon breakage readily disintegrate. Their condition compares closely with that of recent bones which have had their organic content removed by burning, and it is apparent that they have been very little mineralised. In their present condition, the bones and teeth would have been quite unable to have withstood the rigours of their fluvial transportation without disintegrating. It is therefore obvious that they must have been washed into the fissure whilst they still retained their organic content, and hence their elasticity. In other words, the fissure is their primary place of sedimentation. The conclusion that the tetrapod fossils are not derived accords with the fibrous nature of the fracture surfaces of the bones referred to above.

The texture of the bones and teeth is variable. The non-impact surfaces of many specimens are smooth and the specimens have a compact internal structure. Others, by way of contrast, have rough exfoliated surfaces and a relatively porous internal structure. These textural differences are independent of the colour of the bones and also of the level of abrasion to which they have been subjected. Relatively porous, exfoliated bone fragments have been obtained from the same nodules and pockets of infilling as the smooth compact surfaces ones. It is therefore apparent that the textural differences are not due to differential fossilisation of the bones; they must have existed prior to their transportation to the fissure. They are most plausibly accounted for by postulating that the different textured specimens were subjected to differing lengths of sub-aerial weathering before they became water-borne, the exfoliated bones thereby having their organic content more dehydrated than the smooth surfaced ones. This hypothesis is supported by the observation that exfoliated teeth have been split, prior to deposition, much more frequently than smooth surfaced ones. Splitting is known to be a frequent occurrence amongst bones and teeth which have been subjected to partial dehydration (Behrensmeyer, 1974).

THE FAUNAL COMPONENTS OF THE ASSEMBLAGE

In the following account of these components, descriptions are almost entirely confined to isolated teeth and dentitions. This is simply because - as stated earlier - the teeth on the whole survived the rigours of their journey to the fissure much better than the bones. In describing teeth I have followed the now not infrequently adopted practice of employing the terms used in dentistry, as these are devoid of ambiguity. In this terminology the tooth surface which faces towards the lips is the buccal surface and that which faces towards the tongue the lingual surface. The surface which faces towards the jaw symphysis is the mesial surface of the tooth, whilst that which faces towards the jaw articulation is its distal surface. The tooth surface which opposes the corresponding tooth in the other jaw in biting is the occlusal surface. The end of the root furthest from the crown is the apex, and the root meets the crown at the cervix.

Class	<u>REPTILIA</u>
Subclass	<u>LEPIDOSAURIA</u>
Order	<u>RHYNCHOCEPHALIA</u>
Suborder	<u>SPHENODONTIA, Cope 1890</u>
Family	<u>SPHENODONTIDAE, Cope 1890</u>

Sphenodontids are, in terms of numbers of individuals, the most abundantly represented tetrapods in the assemblage. Identified material consists of numerous fragments of maxilla dentaries and palatines - most of which have teeth ankylosed to them - and isolated teeth which have been broken away from bones.

Sphenodontids are most clearly distinguished from other reptiles by the nature of the dentition, which is unique. All the teeth are acrodont and relatively broad based, and few, if any, are replaced. The palatine bone is raised laterally into a narrow, elongated ridge which bears a well developed tooth row. This lies parallel to the maxillary tooth row, the teeth of the dentary biting between the two. Some early sphenodontids also bear other palatine tooth rows, but these are never borne on prominent ridges, and they never approach the lateral palatine teeth in size. The juvenile premaxilla bears a few teeth of relatively small size. During the course of ontogeny, these may become united by downgrowths of bone into a single, chisel-shaped structure. In the maxilla and dentary, the teeth of the very young juvenile are distinguishable from the teeth which erupt sequentially behind them by their smaller size and also by their morphology. Following the terminology of Robinson (1973) these small maxillary and dentary teeth may be called the 'juvenile' teeth, and the teeth which erupt posterior to them the 'additional' teeth. The juvenile teeth invariably alternate between small and very small specimens. There is little or no alternation in the size of the additional teeth. In some forms, such as Sphenodon, the anterior juvenile teeth are replaced by larger 'successional' teeth, but there is never any replacement of the more posterior juvenile teeth. In consequence it is always possible, where the juvenile dentition has not been too heavily worn, to recognise at least two distinct dental regions in the mature maxilla and dentary.

The Welsh material consists almost entirely of the remains of one species. Two other species are also represented. All are new and all are morphologically quite distinct from the only living

member of the family, the New Zealand tuatara, Sphenodon punctatus. In the following descriptions the new species will be referred to by letters. Their relationships within the Sphenodontidae will not be considered for the time being.

#### 1. SPHENODONTID A

This is by far the most abundantly represented animal in the assemblage. Its bones and teeth constitute between 65 and 70% of all identified tetrapod remains. The lateral palatal tooth row and every part of the marginal dentition is represented. In addition there are sizeable fragments of dentaries, maxillae and premaxillae. The ages of the represented individuals varies considerably. There are, however, no dentitions which consist exclusively of juvenile teeth.

In the following account I will be mainly concerned with the dentition, but the morphology of the dentary, maxilla and premaxilla will be briefly considered. The majority of the upper and lower marginal teeth of Sphenodontid A exhibit occlusal wear, as do the upper and lower jaw bones. Wear and occlusion are most conveniently considered together, and this will be done after the morphology of the teeth and identified bones has been described.

#### The morphology of the dentition

Although there are more than 2800 fragments of tooth rows, only one specimen comprises as much as half the intact row. The majority of fragments are only two or three teeth long, and the majority of teeth are damaged. No evidence of non-lateral palatal tooth rows has been found. There is also no evidence, amongst the enormous numbers of tooth row fragments which are available, of any tooth which has been lost prior to its fusion to the bone. It is therefore clear both that the growth of the animals was very slow - tooth eruption being in consequence a relatively rare event - and that eruption and ankylosis was a rapid process.

All of the in situ teeth are broadly ankylosed to the bone and their bases are almost invariably sheathed by bone of attachment. Near its junction with the exposed portion of the tooth the bone of attachment appears thin and spongy and the junction is normally irregular. Away from the junction, the bone of attachment becomes thicker and its texture more compact, so that it forms a continuous layer with the

underlying bone surface. In the case of teeth which are situated near the distal end of mature maxillary and dentary tooth rows, the bone of attachment frequently extends half way up the body of the tooth, and it sometimes extends almost to the tooth's apex.

The enamel surfaces of the teeth are generally smooth, although in some instances they are slightly wrinkled. Fine sub-surface cracks, which have formed through posthumous drying of the enamel, can normally be seen. In the case of the teeth which have been obtained from the red fissure deposits, the enamel is invariably olive green in colour, in striking contrast to the white colour of the bone and non-sphenodontid teeth. This green colour is probably due to mineral replacement during the fossilisation process. It indicates that the enamel structure of the teeth differs significantly from that of the other teeth in the collection.

(a) The dentary teeth

The dentary tooth row is clearly divided into juvenile and additional tooth regions. The total length of the dental ramus of any one mandible is not known, but it would appear that the juvenile teeth generally account for between 20 and 25% of the length of the fully mature tooth row. There are no spaces between any of the dentary teeth, except at the extreme distal end of the tooth row of old individuals.

The juvenile teeth:

More than 90 fragments of dentaries have part of the juvenile dentition preserved, but only about a quarter of these possess the whole of it. In many cases the juvenile teeth have been severely worn, often to the level of the bone. There is never any evidence of replacement of the juvenile teeth and, in the light of the number of fragments of this part of the dentition which are available, it is thus apparent that there was none. This differs from the situation in Sphenodon where the anterior juvenile teeth are replaced by a large caniform successional tooth. The juvenile teeth are morphologically uniform, and there is no variation between those which belong to different individuals. As can be seen from table 1, there is no significant variation in the sizes of the members of each of the alternating size series, so that the juvenile dentition very probably corresponds to the hatchling dentition. Figure 2 shows a specimen of the anterior part of the dentary (T37) which bears the

TABLE 1

Lengths (mm) of juvenile dentary teeth

SPECIMEN

T.45	0.35	0.2	0.35	0.2	0.4	0.2	0.4	0.2	0.35
T.49	0.35	0.2	0.4	0.2	0.4	0.25	0.4	0.2	-
T.54	-	0.25	0.4	0.2	0.35	0.2	0.4	0.2	0.4
T.41	0.4	0.25	0.4	0.25	0.4	0.2	0.35	0.2	0.4
T.39	0.4	0.25	0.4	0.25	0.4	0.2	0.4	0.25	0.4
T.37	-	0.2	0.4	0.2	0.4	0.25	0.4	0.2	0.35
T.43	-	-	-	0.2	0.4	0.2	0.35	0.2	0.4
T.235	-	-	-	0.2	0.25	0.25	0.4	0.2	0.35

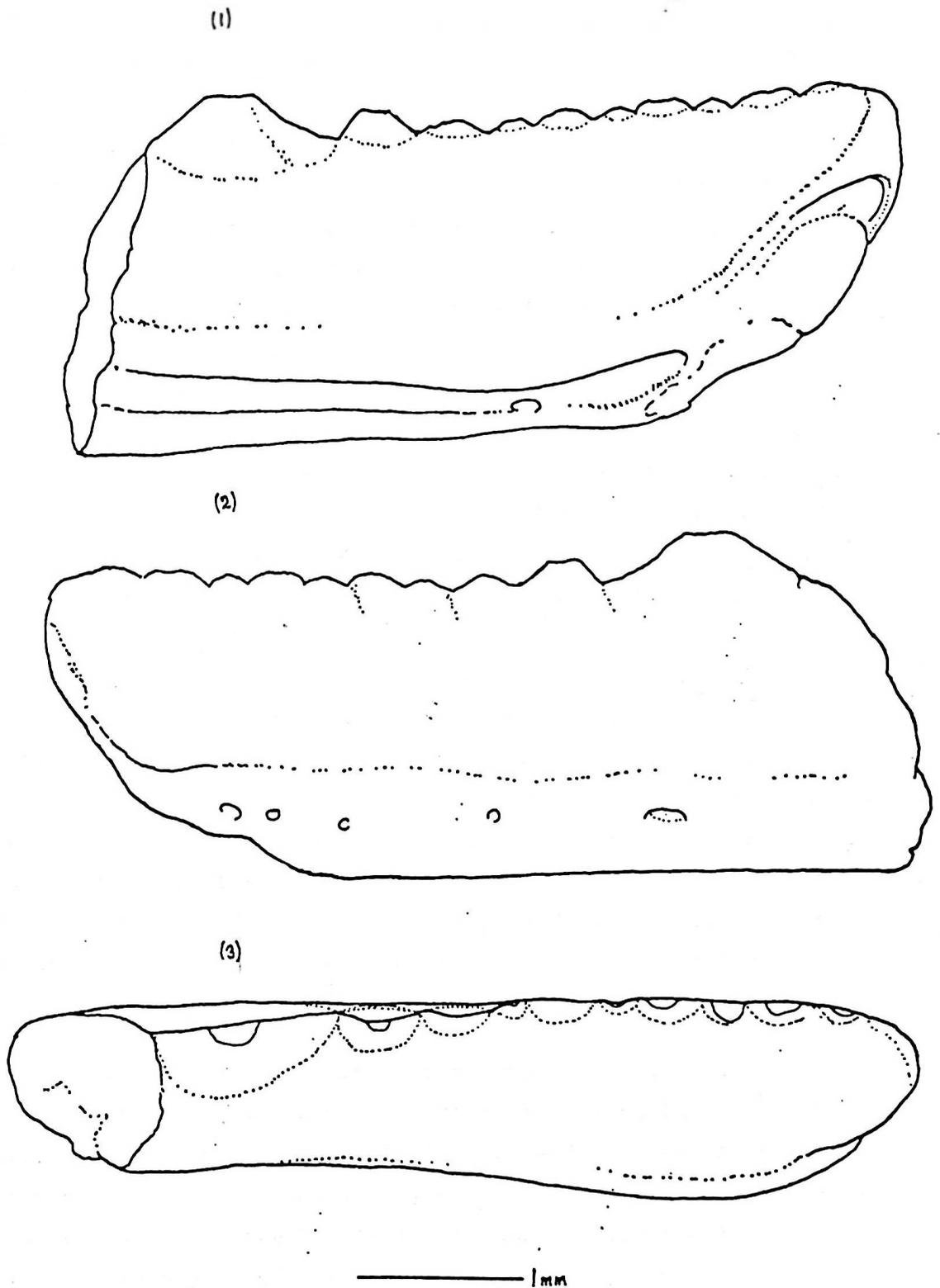


Figure 2. Sphenodontid A. Incomplete left dentary bearing the juvenile dentition and the first two additional teeth, specimen T.37. (1) Medial, (2) lateral, and (3) dorsal views. The teeth and the ventral part of the symphysis are damaged, Note the foramen in the lower border of the meckelian groove (medial view).

juvenile dentition, followed by the first two additional teeth. The juvenile teeth, of which eight are preserved, are unfortunately all slightly damaged, as they are in every other specimen. As can be seen, the last of the juvenile teeth is one of the larger ones, and this is almost invariably the case.

Figure 3 shows the most completely preserved juvenile dentition (T41). As with some of the other relatively well preserved specimens there are nine juvenile teeth, and this appears to be the full complement. The teeth are not very dissimilar to the juvenile dentary teeth of Sphenodon. Each tooth is low and broadly fused to the jaw and in lateral view, the profile of each resembles an isosceles triangle; its mesial and distal edges are straight, or very slightly convex, and of about equal length, and its height is only about half the length of its base. In horizontal section the lingual surface of each tooth is markedly convex, whilst in vertical section it is nearly straight and makes an acute angle of about 40 degrees with the vertical axis of the jaw. The buccal surface of each tooth is almost straight in both horizontal and vertical sections. In the latter section it is nearly vertically orientated, and it is confluent with the buccal surface of the bone immediately below it. In consequence each tooth has the appearance of a half cone in occlusal view, its buccal surface being almost indiscernible (figure 3 ). The half cones are slightly elongated mesio-distally. The buccal and lingual surfaces of the teeth meet to form sharp, well defined crests. There is no overlapping between adjacent teeth so that their mesial and distal crests form a single continuous, serrated cutting edge.

Figure 4 shows the estimated lengths of the juvenile tooth row in 21 dentary fragments which have the whole of this region preserved. The agreement in length between the longest and shortest specimen is extremely close, being approximately equivalent to the length of one of the larger juvenile teeth. There is thus no evidence for dimorphism in this part of the dentition.

The additional teeth:

The more anterior and the middle additional teeth increase in size passing backward. The largest tooth is normally situated about three quarters of the way along the length of the fully developed dentary tooth row.

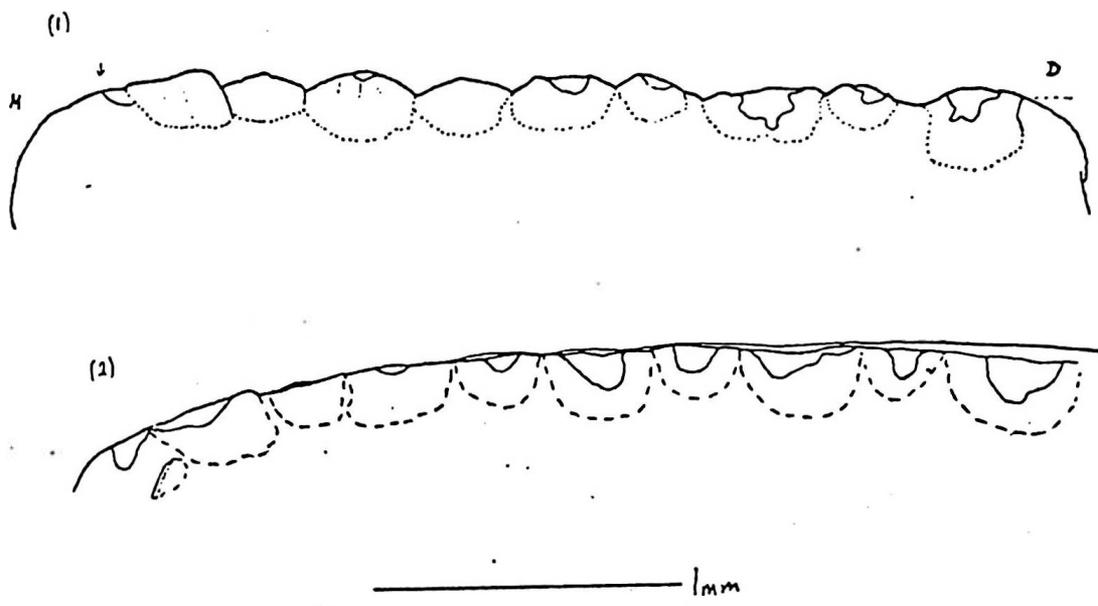


Figure 3. Sphenodontid A. The mandibular juvenile dentition, specimen T.41. (1) Lingual, and (2) Occlusal views. M denotes the mesial end.

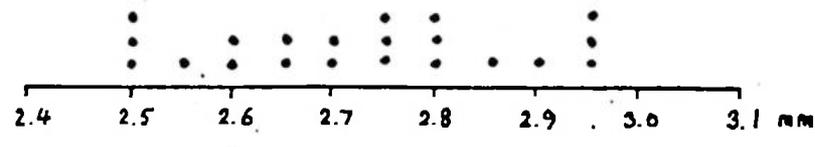


Figure 4. Sphenodontid A. The lengths of 21 mandibular juvenile dentitions.

There are some 320 fragments of dentaries which bear four or more relatively large additional teeth, although these are well preserved in less than one quarter of this number. As in the case of the juvenile teeth, there was clearly no tooth replacement. The precise dental positions of additional teeth are only obvious in those dentary fragments which retain at least the posterior part of the juvenile dentition. None of these fragments possesses more than five preserved additional teeth although the number of the intact mature dentary exceeds this. Fortunately, the dental positions of more posterior teeth can normally be identified when they occur in fragments which bear the third additional tooth ( $A\bar{3}$ ) as this tooth is normally sufficiently morphologically distinctive to be recognisable. From a study of all those dentary fragments in which the dental positions of the additional teeth can be worked out it has been possible to deduce the following general facts concerning the additional teeth in fully developed tooth rows: the first four teeth invariably increase in size passing posteriorly; the  $A\bar{5}$  is the largest member of the series or is subequal to the  $A\bar{4}$ ; the  $A\bar{5}$  is followed by one or two teeth of slightly smaller size; the latter are followed by from one to three very much smaller teeth. The difference between the dentaries in the numbers and size sequences of their additional teeth do not divide them into two distinct groups so that they cannot be wholly due to sexual dimorphism. There are no significant differences between dentaries in the morphology of the first five additional teeth ( $A\bar{1}$  -  $A\bar{5}$ ). The morphology of the more posterior teeth, by contrast, varies somewhat from specimen to specimen. This variation is largely correlated with the variation in the relative sizes of the teeth.

Figure 5 shows the best preserved specimen of the anterior part of the additional tooth region (T.425). The first five additional teeth are present, together with the last of the juvenile teeth. The apices of all of the teeth are damaged, but they are otherwise largely intact. The first two additional teeth are slightly worn, disto-lingually, and the remainder unworn. Unlike the situation in Sphenodon, the basic morphology of the first five additional teeth is similar to that of the juvenile teeth, each tooth having what is essentially<sup>a</sup> half cone structure. The teeth are not, however, morphologically uniform, as will be seen from the description given below. The enamel of the lingual surfaces of the teeth is thick whilst that

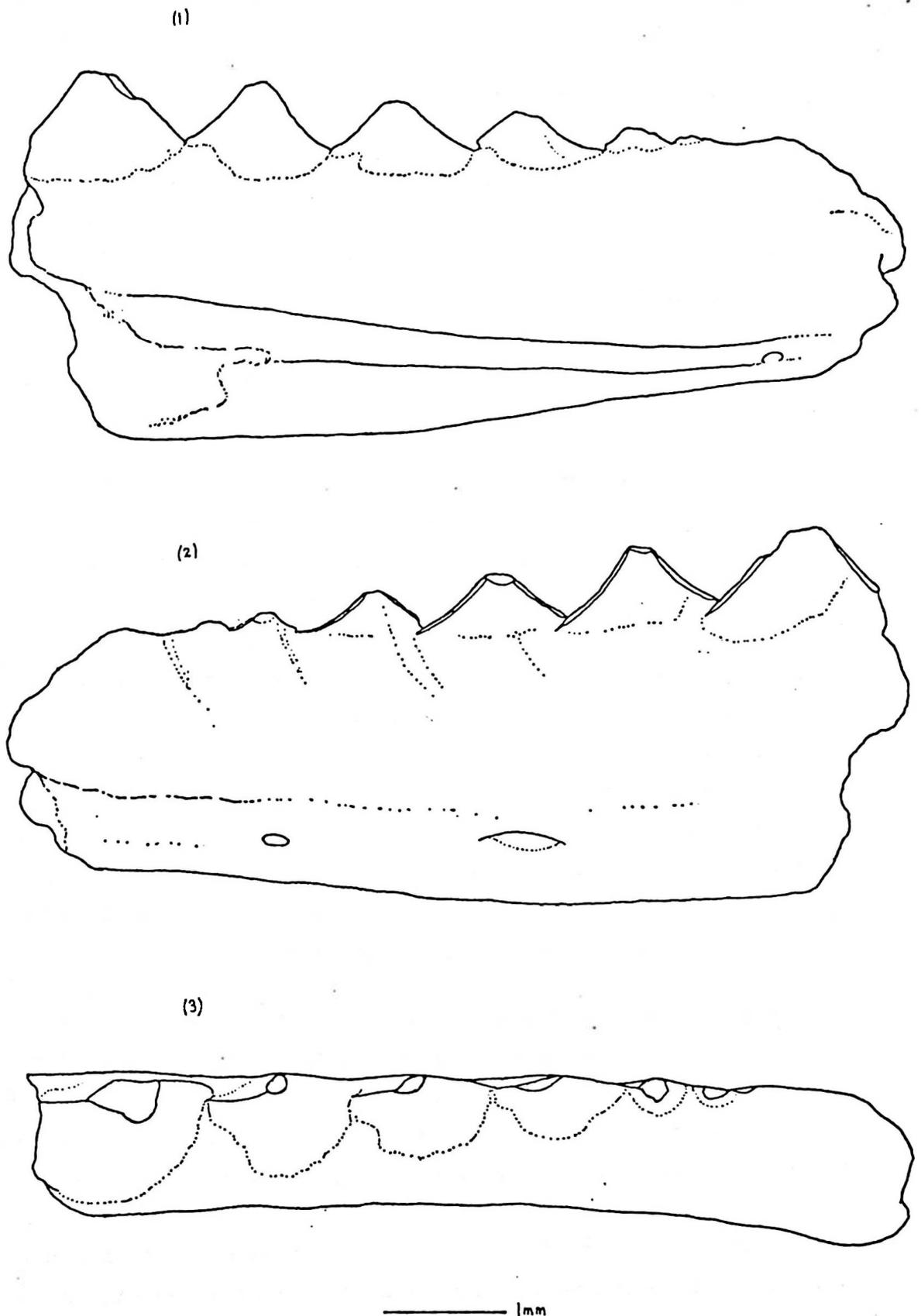


Figure 5. Sphenodontid A. Incomplete left dentary bearing the first five additional teeth (A1 - A5) - specimen T.425. (1) Medial, (2) lateral and (3) dorsal views.

of their buccal surfaces is sufficiently thin for the lingual enamel to be clearly discernible through it.

The  $\bar{A1}$  is about twice the size of the last of the juvenile teeth. Its intact height would have been less than half of its basal length. In contrast to the situation in the juvenile teeth, the mesial crest of the tooth is distinctly longer than the distal crest, and it is also very slightly concave. The distal crest is also very slightly concave, except immediately above its junction with the surface of the bone where it is straight, turning sharply downward and fractionally mesially. The tooth is perfectly in line with its neighbours.

The  $\bar{A2}$  is approximately twice the size of the  $\bar{A1}$ . It differs from the latter in that it appears to be incipiently divided into two portions. The main part of the tooth consists of the 'normal' half cone. This is preceded by a small, relatively narrow, flange-like portion, the free edge of which extends downwards and forwards from near the apex of the half cone. As a result, the mesial crest of the tooth - which is uninterrupted - is proportionally longer than in the  $\bar{A1}$ . In horizontal section, the lingual surface of the anterior 'flange' is slightly concave, and it merges smoothly into the convex surface of the half cone. The buccal surface of the flange is continuous with, and in the same plane as the rest of the tooth's buccal surface. The base of the 'flange' accounts for about a third of the basal length of the tooth. The distal crest of the tooth is perfectly in line with the mesial crest of its successor.

The  $\bar{A3}$  is slightly taller and broader than the  $\bar{A2}$ . It lacks an incipient mesial flange, but its mesial crest is slightly longer than its distal one. The intact height of the tooth was a little under half of its basal length. The  $\bar{A4}$  is a little taller and broader than the  $\bar{A3}$ . Its intact height would have been approximately half of its basal length, and the tooth has a symmetrical appearance, its mesial and distal crests being of about equal length. In contrast to all of the preceding teeth, it is very slightly obliquely orientated, relative to the long axis of the jaw. The distal part of its base slightly overlaps the mesial part of the following tooth, lingually. The latter tooth is slightly larger than the  $\bar{A4}$ , the difference in size being of the order of about 1/7th. It is identical to the  $\bar{A4}$  in shape, and it is also slightly obliquely orientated in the jaw, its distal extremity (which is broken off basally) being lingual to its mesial one.

Figure 6 shows a well preserved specimen of the posterior part of the additional tooth region (T.463). The first preserved tooth is the  $\overline{A3}$ . As in a number of other specimens of this dental region, the  $\overline{A4}$  and  $\overline{A5}$  are not obliquely orientated in the jaw as they are in T.425. The  $\overline{A6}$  and  $\overline{A7}$  are completely intact and are unworn. The  $\overline{A6}$  is a little smaller than the  $\overline{A5}$  and fractionally smaller than the  $\overline{A4}$ . It is symmetrical in lateral view, and its height is approximately half of its basal length. The distal half of the tooth is bilaterally symmetrical, the distal part of the buccal as well as that of the lingual surface being markedly convex in horizontal section. There is no distal crest, the two surfaces merging smoothly into one another behind the crown apex. The mesial half of the buccal surface of the tooth is less convex in horizontal section, than the distal half, and there is a prominent mesial crest. This is in line with the distal crest on the preceding tooth. Although the majority of  $\overline{A6}$  resemble the present specimen, some are morphologically identical to the  $\overline{A5}$ . In those dentaries where the  $\overline{A7}$  is of similar size to the  $\overline{A6}$  it usually resembles the latter morphologically. In the present instance, however, the tooth is of very much smaller size and it is separated from the  $\overline{A6}$  by a small space. It bears no crests and is perfectly conical in shape. In dentaries where still more posterior reduced teeth are present these are morphologically similar to the present specimen. In some instances they are of even smaller size.

Table 2 gives the lengths and heights of relatively large, well preserved additional teeth. In the majority of cases, the latter measurement is an estimate, as the apices of the teeth have normally been damaged. Both dimensions have been measured on the buccal side of the teeth. There is a fairly close agreement in size between the  $\overline{A1}$  and  $\overline{A2}$  belonging to different dentaries. The more posterior teeth, by contrast, exhibit a considerable degree of variation. It has not, however, proved possible to separate this material into more than one discreet size group on the basis of the sizes of these teeth.

(b) The premaxillary teeth

There are 43 premaxillae in the assemblage although only one of these possesses more than a vestige of the teeth. The specimen (T.667) is shown in figure 7. The ventral edges of the teeth have been

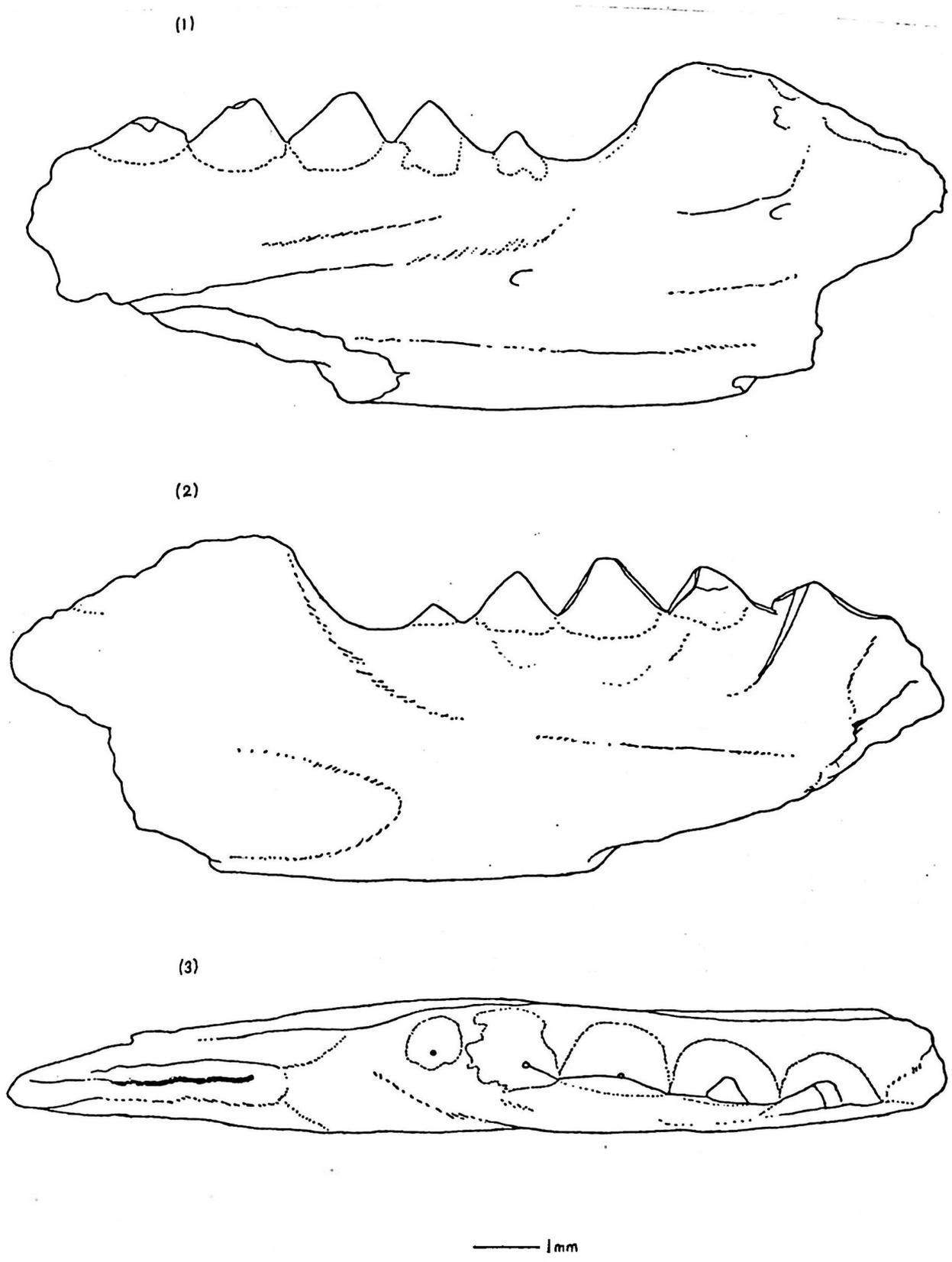


Figure 6. Sphenodontid A. Incomplete right dentary bearing the posterior end of the tooth row (A3 to A7 inclusive) - specimen T.463. (1) Medial, (2) lateral and (3) dorsal views.

TABLE 2

Lengths & heights (mm) of lower additional teeth belonging to 29 fragments of dentaries

SPECIMEN	<u>TOOTH</u>							
	A1	A2	A3	A4	A5	A6	A7	A8
T.38	0.55 x 0.2	1.1 x 0.4	1.25 x 0.6	1 x 0.4				
T.47	0.5 x 0.2	1 x 0.3	1.2 x 0.4	1.3 x 0.6				
T.36	0.45 x 0.2	1.1 x 0.25	1.25 x ?	1.4 x 0.7				
T.43	0.6 x ?	1.1 x 0.3	1.25 x 0.5	1.4 x 0.6				
T.42	0.5 x ?	1.1 x 0.3	1.2 x 0.5					
T.46	0.6 x 0.3	1.05 x ?	1.15 x 0.45					
T.56	0.65 x 0.1	1.25 x 0.3	1.2 x 0.4					
T.227	0.5 x 0.25	1 x 0.5	1.3 x 0.6					
T.222	0.6 x ?	1.1 x 0.55	1.2 x 0.6	1.3 x 0.8				
T.425	0.5 x 0.25	1 x 0.4	1.15 x 0.5	1.20 x 0.6	1.4 x 8			
T.253	0.5 x 0.25	1 x 0.5	1.2 x 0.7	1.4 x 1				
T.254	0.5 x 0.25	1.2 x ?	1.25 x 0.6	1.4 x 0.7				
T.228	-	1.1 x 0.4	1.3 x 0.5					

continued overleaf...

SPECIMEN	A1	A2	A3	A4	A5	A6	A7	A8
T.428	-	1.2 x 0.4	1.25 x 0.5	1.6 x 0.9	2 x 1			
T.223	-	1 x 0.4	1.25 x 0.5	1.3 x 0.6	1.4 x ?			
T.468	-	0.8 x 0.4	1.2 x 0.5	1.4 x 0.7	1.5 x 0.7			
T.470	-	1 x ?	1.4 x 0.4	1.4 x ?	1.4 x 0.6			
T.471	-	1 x ?	1.2 x 0.45	1.3 x 0.6	1.3 x 0.6			
T.472	-	1.2 x ?	1.2 x ?	1.4 x 0.8	1.6 x 0.9			
T.483	-	1 x 0.3	1.1 x 0.5	1.3 x 0.6	1.3 x 0.55			
T.487	-	1 x ?	1.2 x 0.5	1.4 x 0.8	1.4 x ?	0.6 x 0.3		
T.527	-	1 x ?	1.15 x 0.6	1.2 x 0.7	1.4 x 0.8			
T.460	-	1.1 x ?	1.3 x 0.6	1.7 x 0.9	1.6 x 0.7	1 x 0.3		
T.459	-	-	1.4 x ?	1.8 x ?	1.6 x 0.8	1 x 0.4		
T.461	-	-	1.2 x 0.3	1.4 x 0.8	1.6 x 0.8	1 x 0.5	1 x 0.4	0.4 x 0.2
T.462	-	-	1.4 x 0.6	1.5 x ?	1.6 x 0.9	1.2 x 0.6	0.8 x 0.4	0.3 x 0.2
T.463	-	-	1.3 x 0.5	1.5 x 0.75	1.55 x 0.8	1.3 x 0.7		
T.512	-	-	1.35 x 0.5	1.5 x 0.7	2 x 1			
T.507	-	-	1.4 x 0.6	1.8 x 0.8	1.9 x 1			

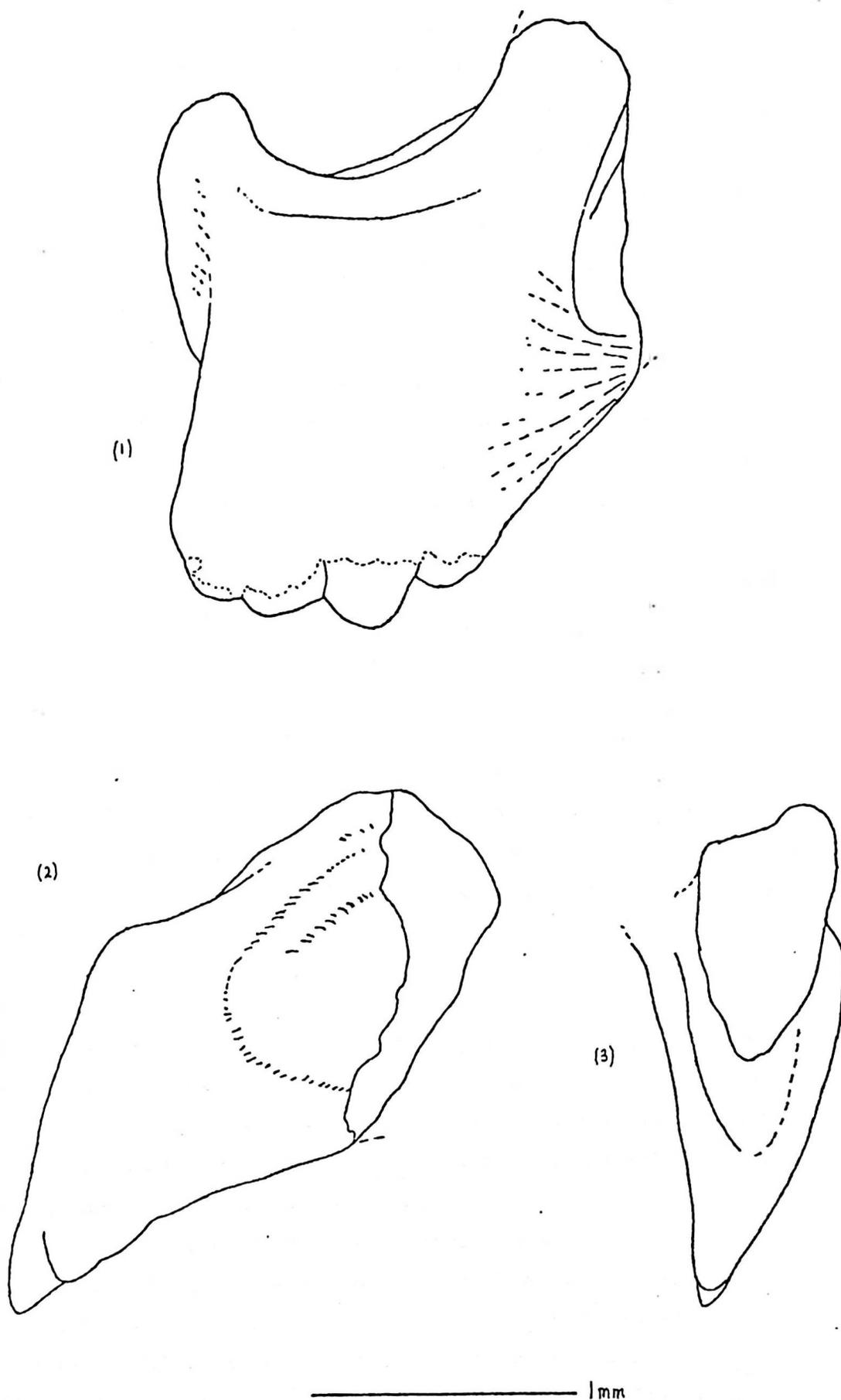


Figure 7. Sphenodontid A. Premaxilla, specimen T.667.  
(1) Frontal, (2) lateral and (3) saggital views.

posthumously abraded, but their crowns are otherwise intact. They are four in number and they are borne on the ventral edge of the anterior facing part of the bone. Each tooth abuts with its neighbour, the four forming a shallow arc. They are very small in size, the two central specimens - which are larger than the lateral ones - being only slightly larger than the juvenile dentary teeth. In occlusal view, each tooth has the appearance of a half cone, as in the case of the majority of dentary teeth. Here, however, the relatively flat surface of the crown faces lingually, rather than buccally. T667 is regarded as a relatively juvenile premaxilla both because of its size (see table 14) and because of the fact that the teeth have not been substantially worn. In many of the premaxillae the teeth have been completely worn away so that only a bony ridge remains as an occlusal surface. In no case have the teeth been united by the downgrowth of bone into a single chisel-like structure comparable to that found in mature Sphenodon premaxillae.

(c) The maxillary teeth

The material of the maxillary dentition is less abundant and qualitatively inferior to that of the dentary dentition. As in the latter, the tooth row is clearly divided into an anterior juvenile tooth region and a more posterior additional tooth region. There are no spaces between the teeth except at the extreme distal end of the mature tooth row.

The juvenile teeth:

There are twelve fragments of the anterior part of the maxilla but only three of these possess relatively well preserved teeth. In none of these specimens have the anterior juvenile teeth been replaced by successional teeth as in adults of Sphenodon and, to judge from the situation in the lower juvenile dentition, there was probably no replacement. There are no differences between the specimens in the form and sizes of the juvenile teeth. Figure 8 shows the best preserved juvenile dentition (T.539). There are eight juvenile teeth followed by two additional teeth. The bone is broken off anteriorly so that it is possible that the original number of juvenile teeth slightly exceeded eight. The apices of the teeth are damaged and their lingual surfaces are slightly worn, but they are otherwise intact. They are almost identical in morphology and size to the juvenile teeth of the dentary. As in the case of the premaxillary

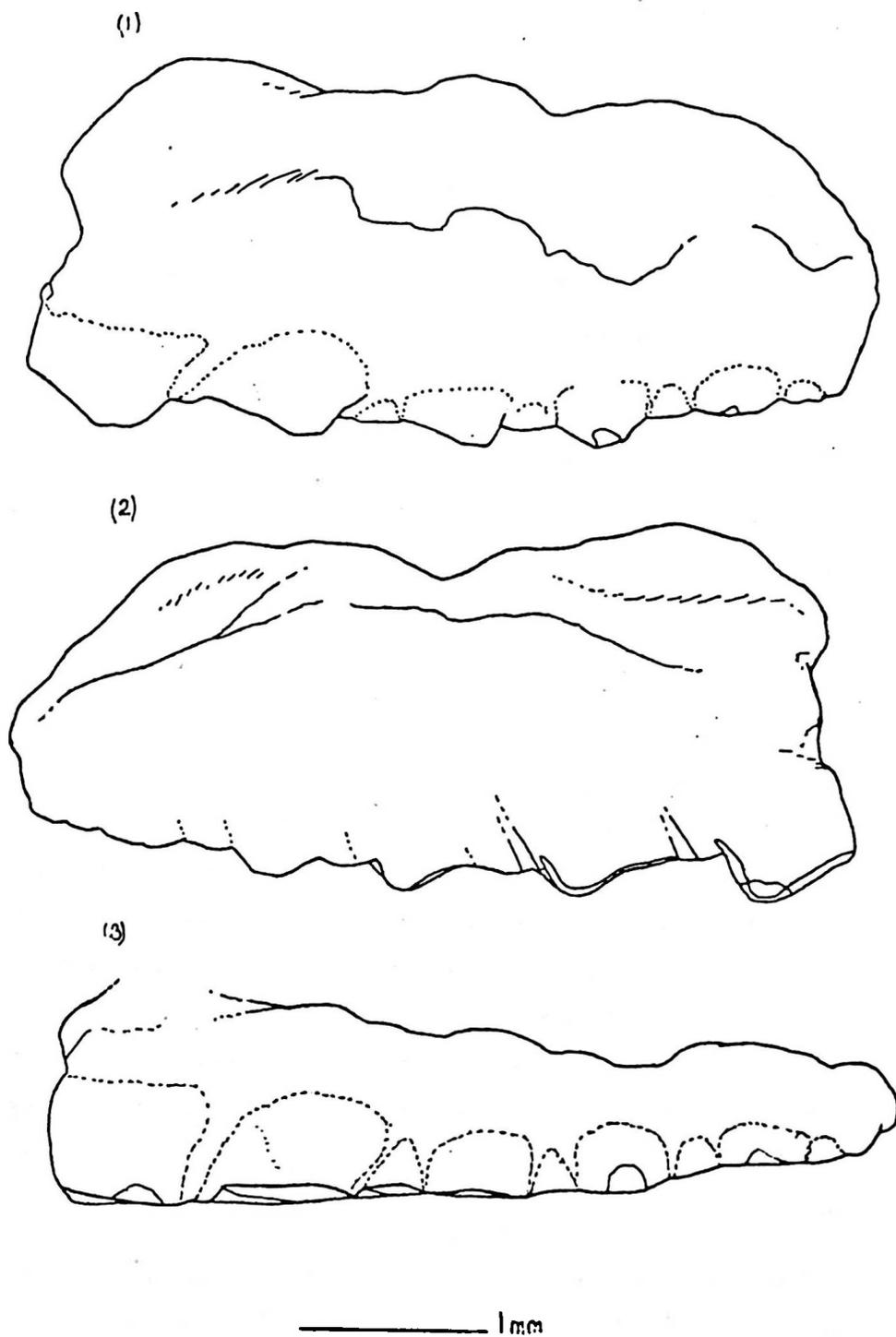


Figure 8. Sphenodontid A. Incomplete right maxilla bearing juvenile teeth and the first two additional teeth - specimen T.539. (1) Lateral, (2) medial, and (3) ventral views.

teeth, the flat surfaces of the 'half cones' face lingually instead of buccally. It may be noted that the last of the juvenile teeth is one of the smaller ones, in contrast to the situation in the dentary. This is also the case in the other maxillae where the posterior end of the juvenile dentition is preserved. The last of the larger juvenile teeth differs from the other members of the dentition in that the half cone of the crown is followed by a very small, flange-like portion. There is no overlapping between adjacent teeth, their mesial and distal crests forming a continuous cutting surface.

The additional teeth:

As in the case of the dentary the fully developed additional tooth region consists of series of relatively large teeth which are followed by a few teeth of comparatively reduced size. None of the additional teeth were replaced. The anterior additional teeth do not alternate in size as they do in the tuatara.

There are slightly over seventy fragments of maxillae which bear three or four relatively large additional teeth, although in only a very small proportion of cases are those teeth well preserved. No fragment bears more than four large additional teeth. As a result of the very poor quality of the material it has not proved possible to determine the dental positions of teeth from the more posterior part of the additional tooth region. It is clear from the way in which the marginal teeth worked however, that the number of large additional teeth in any given maxilla must have been the same as that in the corresponding dentary, as will be appreciated in due course.

So far as can be ascertained, the first five additional teeth always increase in size passing posteriorly. In the majority of cases the lingual parts of these teeth have been considerably modified by wear, and in no case is the crown preserved in its pristine condition. Nevertheless it is apparent that the basic morphology of the teeth is uniform, and that there are few differences between specimens belonging to different individuals. The A<sub>1</sub> to A<sub>5</sub> are quite different from the juvenile teeth, but they are not very dissimilar to the additional teeth of Sphenodon. Their basic morphology is most clearly illustrated by the most posterior of the three teeth which are preserved in the maxillary fragment shown in figure 9. The ventro-lingual edge of this tooth - which is identified as an

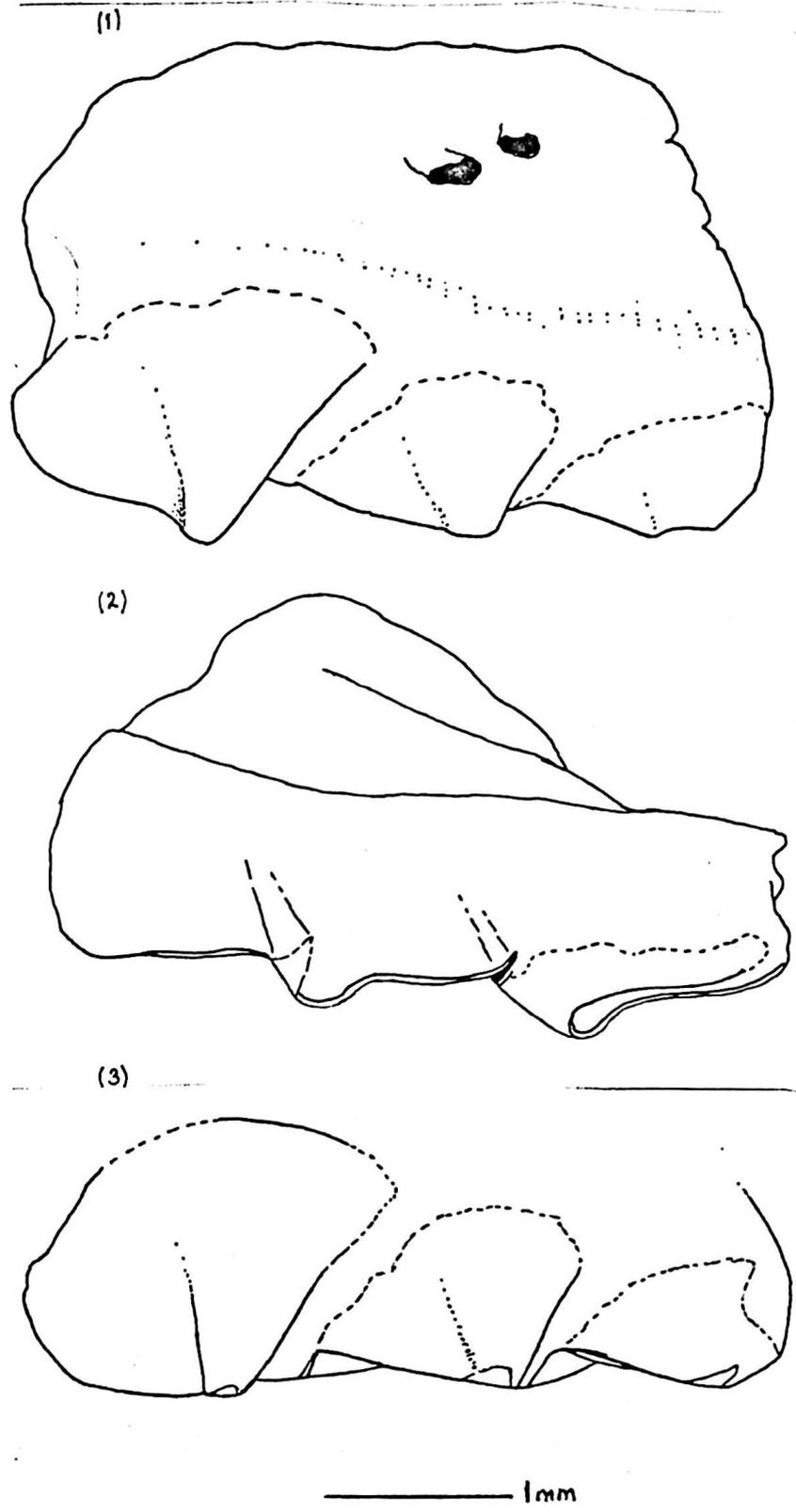


Figure 9. Sphenodontid A. Incomplete left maxilla bearing three additional teeth - specimen T.565. (1) Lateral, (2) medial and (3) ventral views.

A<sub>4</sub> has been worn to expose the dentine, but the enamel is everywhere else intact. The mesial part of the crown comprises a slightly laterally compressed cone, and this is followed by a prominent flange. The latter is much more prominent and clearly differentiated from the rest of the tooth than is the flange of the A<sub>2</sub>. Mesially, it extends for the full height of the cone shaped portion of the tooth, and its free edge slopes gently dorsally as it passes backward. The flange is situated lingual to the midline of the cone, so that the lingual surface of the tooth is flat, distal to the latter. The tooth leans distinctly lingually on the maxilla, its free ventral edge overhanging its base. The cone also leans slightly backward. The exposed buccal surface of the tooth extends much further dorsally than the lingual surface, most of the base of the tooth being buccal to the ventral-most extremity of the maxilla. As in the case of the lower additional-most extremity of the maxilla. As in the case of the lower additional teeth, the buccal and lingual enamel surfaces of the tooth are not of equal thickness. Here it is the buccal surface which is the thicker one.

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Figure 10 shows one of the best preserved specimens of the anterior part of the additional tooth region. The first four additional teeth are present and each is morphologically typical. In the case of each specimen, the original lingual and linguo-ventral features of the crown have been effaced through use. The distal part of the A<sub>4</sub> is broken off. In lingual view the teeth all appear to be very similar, and there is only a slight increase in size passing posteriorly. In buccal view, on the other hand, there is a very marked increase in the dorso-ventral lengths of the crown surfaces passing from first to last, and the bucco-ventral length of the A<sub>4</sub> is more than twice that of the A<sub>1</sub>. The distal parts of the flanges of the A<sub>1</sub>, A<sub>2</sub> and A<sub>3</sub> are completely covered, buccally, by bone of attachment. The distal extremities of these flanges are also overlapped buccally by the mesial parts of the cone bases of the following teeth.

The best specimen of the posterior part of the additional tooth region is shown in figure 11. The first two preserved teeth are substantially worn, and the third is moderately worn. The more posterior teeth are unworn. The first tooth is either the A<sub>4</sub> or the A<sub>5</sub>. The following tooth, which is morphologically identical, is slightly larger. In both cases the distal part of the flange is covered buccally by bone of attachment. The cone of the next tooth is slightly smaller than those of its predecessors; and it is also distinctly laterally compressed, and bears a mesial crest. There is only a very incipiently developed flange. The tooth is separated from its predecessors by a very small space. Distal to this tooth

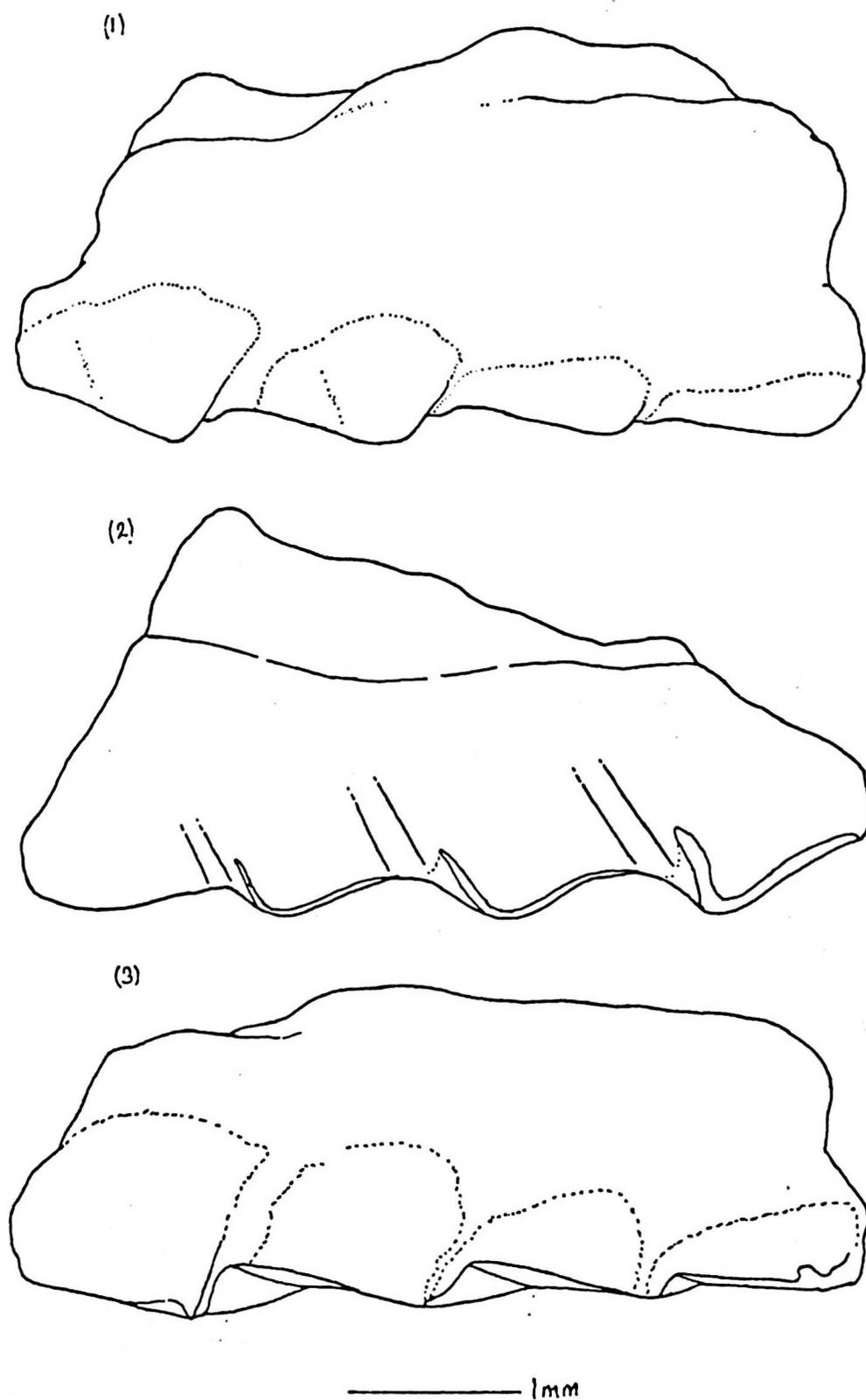


Figure 10. Sphenodontid A. Incomplete right maxilla bearing the first four additional teeth - specimen T.551. The teeth are all worn. (1) Lateral, (2) medial and (3) ventral views.

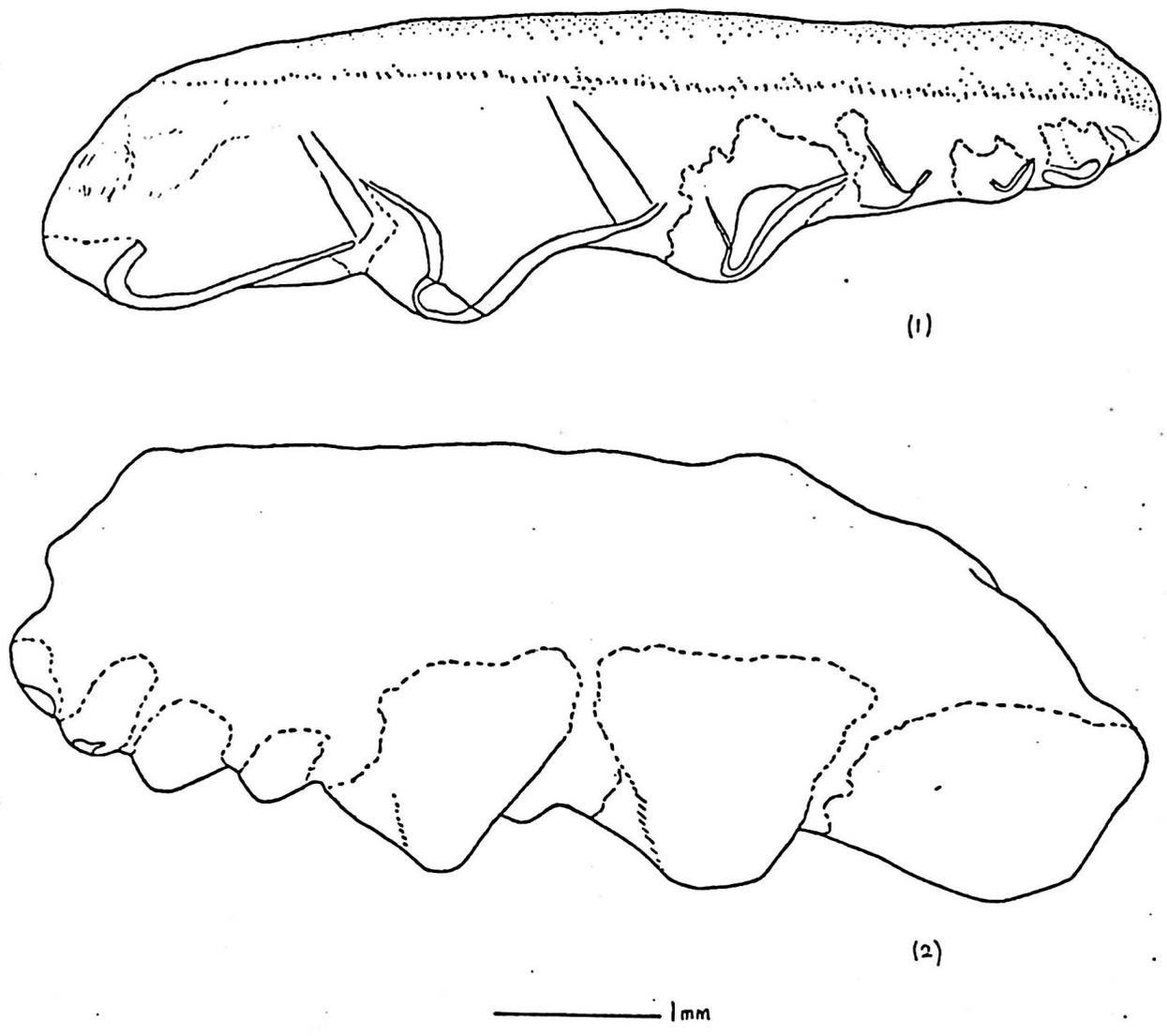


Figure 11. Sphenodontid A. Incomplete right maxilla bearing the posterior end of the tooth row - specimen T.1. (1) Medial and (2) lateral views.

TABLE 3

Basal lengths (mm) of additional teeth belonging to 13 fragments of  
maxillae

SPECIMEN	TOOTH			
	A1	A2	A3	A4
T.539	0.95	1.0	-	-
T.540	1.0	1.0	1.2	1.3
T.550	1.0	1.05	1.25	-
T.551	1.1	1.1	1.2	1.4
T.552	0.9	1.0	-	-
T.553	1.0	1.0	1.2	-
T.555	1.0	1.0	1.15	1.4
T.556	1.15	1.2	1.25	-
T.557	1.0	1.1	1.15	-
T.558	0.9	1.1	1.25	1.3
T.570	1.05	1.1	-	-
T.573	1.0	1.0	1.2	-
T.582	1.0	1.1	-	-

there are four very much smaller teeth, the posterior two of which are damaged. These teeth correspond to the reduced additional teeth which occur in the dentaries of old individuals. No maxilla possesses more than four of them, and the majority have less. They differ morphologically from the more anterior teeth. Each is sub-conical in shape, its buccal surface being more convex than its lingual surface in horizontal section. The first two illustrated specimens bear incomplete mesial and distal crests (the third and fourth specimens are too damaged to show whether crests were originally present). In some other maxillae the reduced posterior teeth are devoid of crests. Characteristically, the posterior teeth are separated from one another by spaces.

Table 3 gives the basal lengths of relatively well preserved additional teeth in fragments of maxillae. In each case the measurement has been made on the lingual side of the tooth. Only teeth belonging to the anterior end of the additional tooth region have been measured as these are the only specimens whose dental positions are known. As can be seen there is a reasonably close agreement in the sizes of teeth belonging to different maxillae.

(d) The palatine teeth

There are more than 200 fragments of the lateral palatine tooth row, almost all of which are very incomplete. The teeth are morphologically uniform along the tooth row, and there is little variation in their size. This contrasts markedly with the situation in the mature lateral palatine tooth row of Sphenodon where a large anterior successional tooth is followed by four or five small juvenile teeth of alternating size, which in turn are followed by a larger number of much bigger additional teeth.

Figure 12 shows the most substantial fragment of the lateral palatine tooth row of Sphenodontid A (T.572). The specimen comprises the posterior part of the intact tooth row, and probably accounts for about two thirds of its fully developed length. The three posterior teeth are rather badly damaged and the second and third preserved specimens have had their apices abraded away. As in other fragments of the tooth row, none of the teeth exhibits evidence of ante-mortem wear. The teeth are slightly larger than the reduced posterior additional teeth which occur in the maxillae of old individuals. They are perfectly conical in shape and are devoid of crests. Here again, the

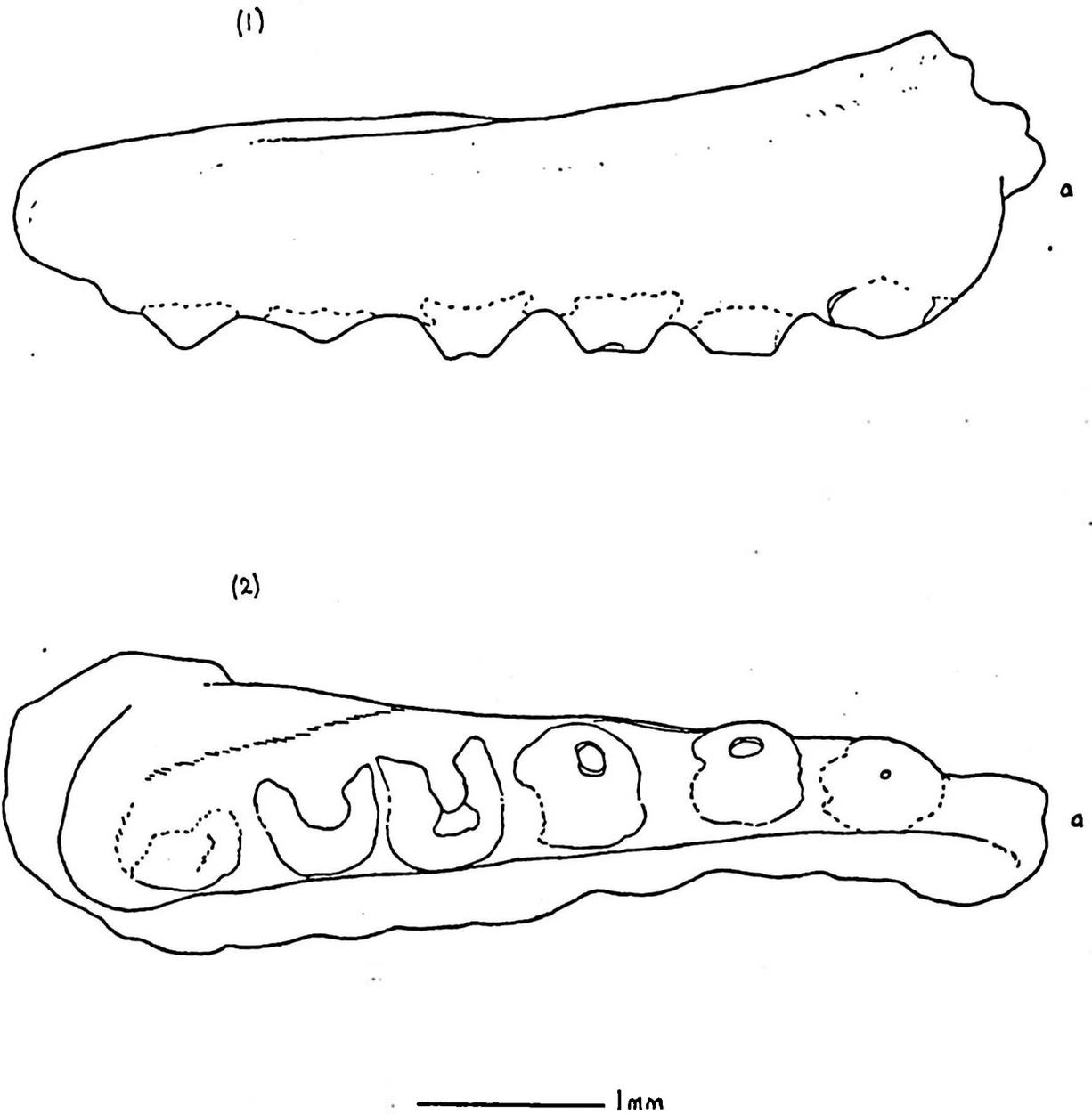


Figure 12. Sphenodontid A. Lateral palatine tooth row (posterior part) - specimen T.572 (1) Lateral and (2) ventral views. a denotes anterior end.

situation contrasts with that which pertains in Sphenodon where the more posterior palatine teeth are similar in size and morphology to the large additional teeth which lie opposite to them in the maxilla. The palatine teeth of Sphenodontid A are separated from one another by small spaces.

The dentary

The dentary is the only bone of the lower jaw which is preserved in a recognizable state. Although there is an extremely large number of specimens, none is more than about two thirds complete and the majority of fragments consist of only a short length of the tooth bearing portion of the bone. As in other sphenodontids, the bone made up almost the entirety of the tooth bearing portion of the intact mandible and it bears a well developed coronoid process posteriorly. It thus rivals the dentary of many advanced theriodonts in its relative size. The dorsal and posterior parts of the coronoid process and the posterior end of the horizontal ramus are not known. In life, the dentary probably extended back to contact the articular as it does in Sphenodon. The dentary is very similar to that of Sphenodon in its known morphology. It differs from the latter, however, in a number of details, apart from size, of which the following are the most noteworthy:

(1) The relative dorso-ventral depth of the tooth bearing portion of the bone. This is distinctly greater than in Sphenodon, the length of the mature tooth row relative to the maximum depth of the bone below it being of the order of 3.5:1 compared to about 4.5:1 in the latter genus. This difference reflects the fact that the mature mandibular tooth row of Sphenodontid A comprises many fewer functional additional teeth than that of Sphenodon.

(2) The relative height of the coronoid process. The relative height of the most complete fragment of this process (T.463, figure 6) slightly exceeds that of the process of Sphenodon. To judge from the shape of the fragment in question, the intact process of Sphenodontid A would have been substantially taller than that of the extant genus. It is unlikely that the coronoid bone originally projected above the level of the coronoid process, as it does in Sphenodon.

(3) The position of the posterior end of the mature tooth row

relative to the antero-posterior line of the coronoid process. In both Sphenodontid A and Sphenodon the middle part of the row is in line with the coronoid process. In the latter genus, the posterior end of the row is also in line with the process, but in the former genus it curves slightly medially as it passes backwards, so that the posterior additional teeth are situated medial to the line of the process.

(4) The presence of a small foramen which interrupts the lower border of the meckelian groove. This foramen is a constant feature of all those dentaries which have the relevant region preserved. In very small, and hence, very young dentaries, it lies beneath the middle of the juvenile dentition. As the dentary grows in size, it moves backwards until it comes to lie beneath the first or second additional tooth of the mature bone. The foramen serves as an anterior exit from the inferior dental canal and it has no homologue in the dentary of Sphenodon.

(5) The presence of a depression in the lower part of the lateral surface of the horizontal ramus, just posterior to the level of the ultimate tooth. This depression is well defined anteriorly and it passes back beneath the anterior part of the coronoid process before becoming indistinct. It clearly served as an area of insertion for an external part of the adductor musculature. There is no depression in the lateral surface of the horizontal ramus of the dentary of Sphenodon. In the latter genus the superficial temporalis inserts upon the lateral surface of the coronoid process and the laterally exposed part of the coronoid bone.

(6) The presence of a groove in the symphysis. This groove has the shape of an inverted U and it passes from the internal to the external margin of the symphysis, dividing its surface into a small dorsal and a large ventral component. When the dentary was ligamentously united to its antimere, the opposing symphyseal grooves must have formed a complete tube.

#### Measurements:

In order to compare the sizes of as many dentaries as possible the dorso-ventral depth of the horizontal ramus has been measured, immediately below the  $\bar{A}1$ . The resultant data has been plotted in figure 13. As can be seen, the size distribution of the measurable

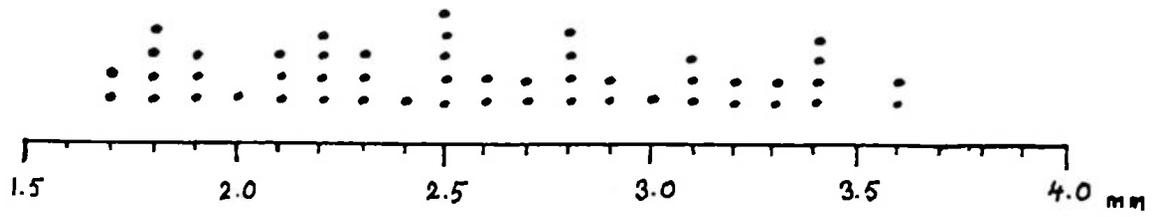


Figure 13. Sphenodontid A. Scale showing depth of dentary beneath the A1 in 50 specimens.

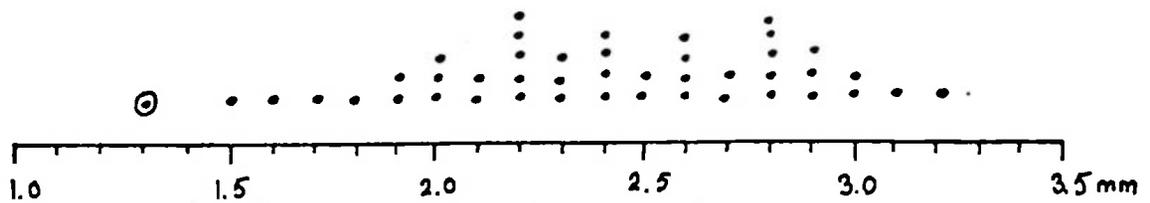


Figure 14. Sphenodontid A. Scale showing the depth below the external naris of the frontal portion of the premaxilla in 44 specimens ⊙ = T.667.

specimens is unimodal, and their size range very considerable (the largest specimen is actually about four times the size of the smallest). Dentary size is closely correlated with the degree of functional wear of the teeth and the upper part of the lateral surface of the bone; in the case of very small dentaries the wear is negligible or absent, whilst in the case of very large ones it is extremely heavy. It is therefore clear that the marked variation in the sizes of the dentaries is due largely or wholly to age. A wide, uninterrupted size spectrum in the sampled population of Sphenodontid A accords with the earlier deduction that growth in this species was very slow.

#### The premaxilla

No specimen of the premaxilla is intact. The best preserved and most informative specimen, T667, is shown in figure 7. It is morphologically quite different from the narrow, dorso-ventrally elongated premaxilla of Sphenodon. The bone is divided into a frontal, tooth bearing component and a well developed lateral component, which is broken off posteriorly - as in the case of every other specimen. The lateral component has no counterpart in the premaxilla of Sphenodon. Its preserved antero-posterior length slightly exceeds both its depth and the medio-lateral length of the frontal component. The lateral component is straight in both horizontal and vertical sections and its external surface faces slightly anteriorly as well as laterally. This surface bears a well defined depression posteriorly where it was overlain by the maxilla. The intact dorsal and ventral margins of the lateral component are both slightly concave in side view and they diverge slightly passing posteriorly. Passing anteriorly, the lateral component slopes downwards to make an angle of about  $45^{\circ}$  with the frontal component, so that the bone evidently formed a pronounced beak when it was in situ, its dental border overhanging the anterior part of the dental border of the maxilla quite markedly (the extent of this overhang is conjectural as the exact in situ orientation of the bone in lateral view is uncertain).

The depth of the frontal component of the bone slightly exceeds its length. It is distinctly curved in horizontal section and very slightly curved in vertical section, the convex side of the curve facing anteriorly in each case. The internal and external surfaces of the frontal component diverge slightly passing upwards from the

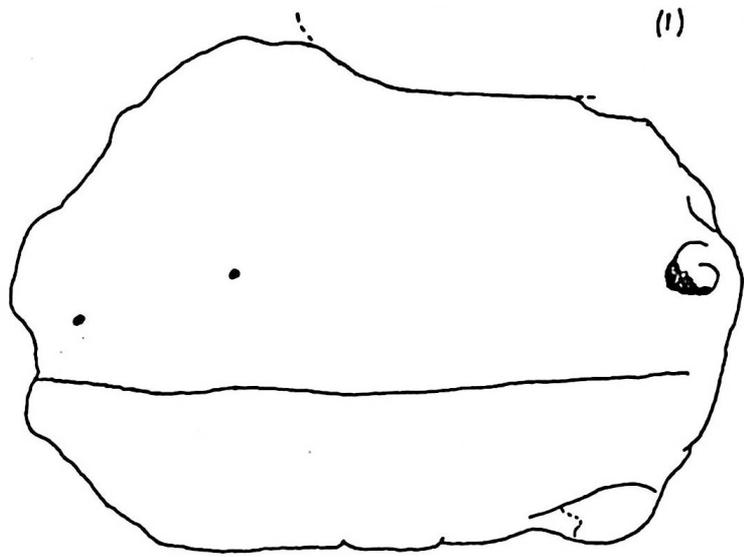
tooth row so that the outline of the saggital surface of the bone is triangular. This surface is divided into two articular surfaces by a U-shaped groove, the base of which is situated approximately midway between the dorsal and ventral margins of the bone. This groove is an almost perfect mirror image of the groove in the symphysis of the dentary. The medial, lateral and ventral margins of the frontal component of the bone are nearly straight in anterior view, and they form three sides of a rectangle. Its dorsal margin, by contrast, is markedly concave in this view, the deepest part of the curve being situated above the centre of the tooth row. The medial end of the dorsal margin rises smoothly to the tip of a short internarial process, which evidently contacted a ventral internarial process of the nasal. The whole of the intact dorsal margin of the bone from the tip of the internarial process to the broken posterior edge of the lateral component of the specimen clearly bordered the external naris, which therefore faced mainly anteriorly. The relation of the premaxilla to the external naris in *Sphenodontid A* thus contrasts markedly with that in *Sphenodon*, where the bone lies in front of the external naris and part of its postero-lateral margin forms the anterior border of the opening, the opening itself facing mainly anteriorly.

#### Measurements:

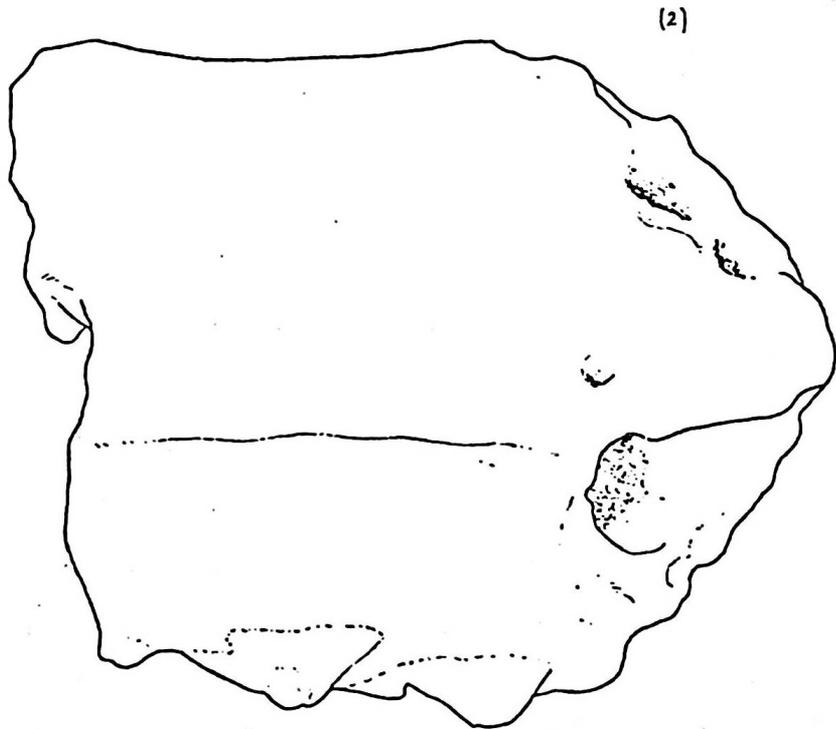
The only measurement which can be made on a majority of specimens of the premaxilla is the dorso-ventral depth of the frontal component of the bone immediately below the lowest part of its dorsal margin. The measurements have been plotted in figure 14. The premaxilla exhibit a considerable size range, in accordance with the size range exhibited by the dentaries. As in the case of the latter, the size distribution of the premaxillae is unimodal and, hence, affords no evidence of sexual dimorphism.

#### The maxilla

The maxilla is very incompletely known. With three exceptions, all the available specimens consist of narrow, rod-like fragments of the ventral part of the bone, which bear a few teeth and which are broken off anteriorly and posteriorly. The three exceptions are more substantial fragments, each of which preserves part of the dorsal as well as the ventral margin of the bone. All three specimens belong to the same region of the maxilla. Two of them, T.570 and T.582, are shown in figure 15. The whole of the ventral margin of the former specimen



— 1mm



— 1mm

Figure 15. Sphenodontid A. Maxillae. (1) Left maxilla, specimen T.582; (2) Right maxilla, specimen T.570.

accommodates the first two additional teeth, whilst the slightly longer ventral margin of the latter one has been rather abraded and bears only a part of a single tooth - the A<sub>3</sub> - which is situated posteriorly (the original positions of lost first and second additional teeth are indicated by wear facets on the medial side of the bone). Both specimens demonstrate that a substantial part of the maxilla underlay the orbit, as it does in Sphenodon, for in each case the intact part of the dorsal margin of the fragment forms part of the ventral border of the latter opening. In the case of T582 the orbital border begins to turn upwards anteriorly, just before it is broken off. This suggests that the maxilla formed at least a small part of the anterior border of the orbit, in contrast to the situation in Sphenodon, where the whole of this border is formed by the prefrontal. To judge from the dorso-ventral depth of T570 relative to the sizes of the teeth, the sub-orbital part of the maxilla of Sphenodontid A is proportionally rather deeper than that of Sphenodon.

#### Measurements:

The dorso-ventral depth of the maxilla beneath the lowest part of the orbital border in the three specimens which permit this measurement to be made is as follows -

T.582	-	4.25mm
T.570	-	3.65mm
T.553	-	3.95mm

#### Dental wear and occlusion

As dental wear and occlusion have not previously been described in the case of any fossil species of sphenodontid, their nature in Sphenodontid A is of particular interest. All of the marginal teeth of Sphenodontid A, except for some of the reduced additional teeth at the posterior end of the mature dentition, engaged in occlusion. The wear on the marginal teeth is confined to the lingual surfaces of the uppers and the buccal surfaces of the lowers and it is therefore clear that the latter teeth never contacted those in the lateral palatine row. The basic mode of occlusion can be deduced from the form of the wear on the additional teeth and bone surfaces of the incomplete maxilla and dentary which are illustrated in figure 16. The levels and patterns of the wear exhibited by these specimens are

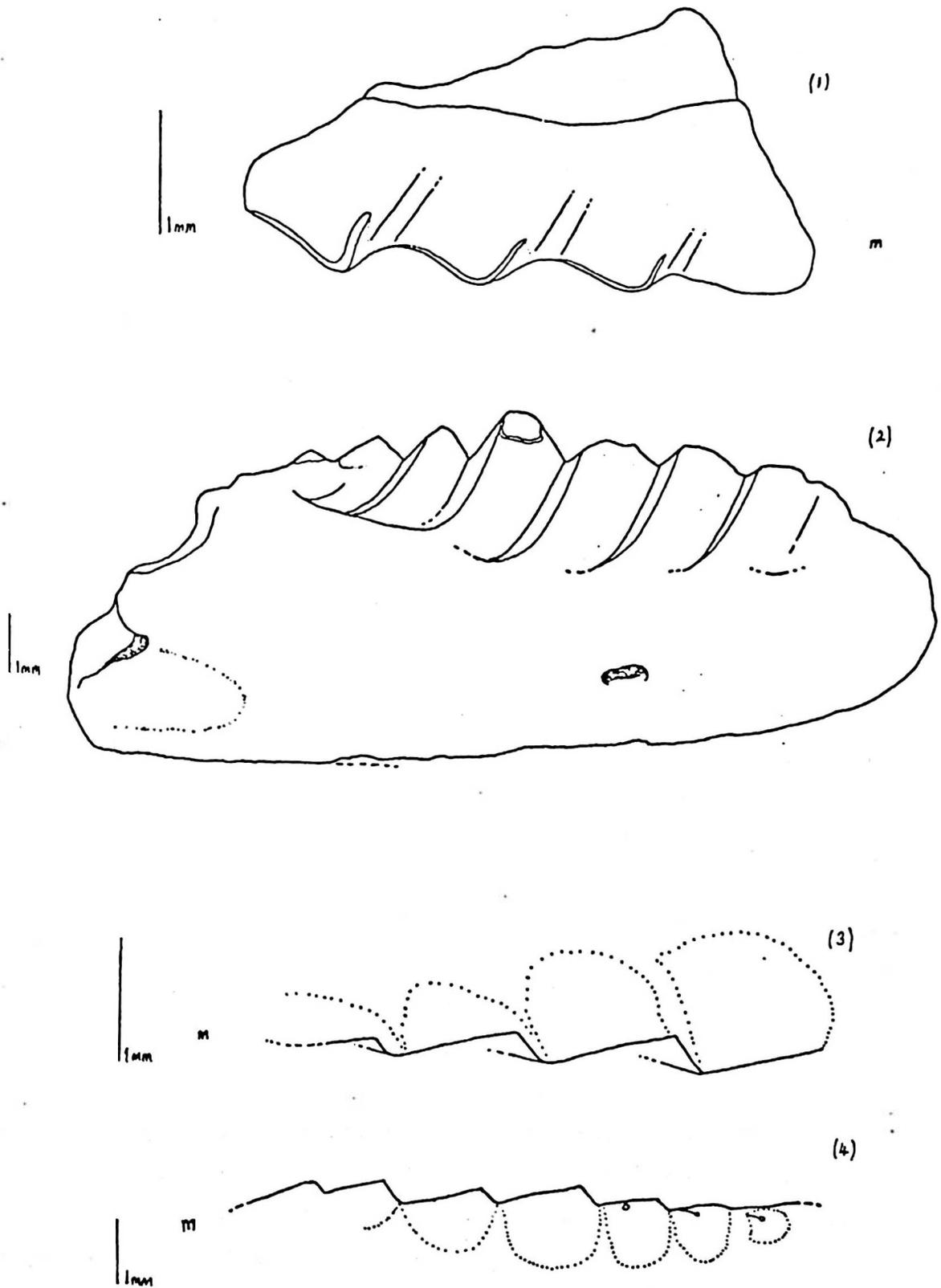


Figure 16. Sphenodontid A. Examples of specimens exhibiting functional wear. (1) Incomplete maxilla bearing well worn additional teeth - specimen T.551, medial view (the drawing has been reversed for comparative purposes) (2) Incomplete dentary bearing well worn additional teeth - specimen T.462, lateral view. (3) and (4) Occlusal views of the teeth of the two specimens (T.551 uppermost). Note the zig-zag edges formed by the edges of the adjacent shearing planes. m denotes the mesial end in each instance. (1)-(4) not to the same scale.

typical for the more posterior parts of mature upper and lower dentitions. A series of well defined grooves has been worn into the tooth row of each specimen by opposing additional teeth and in both instances these grooves continue for some distance into the surface of the bone. Each groove is made up of an anterior, disto-laterally facing wear facet and a posterior, mesio-laterally facing facet, the two meeting at an angle of about  $100^{\circ}$  in horizontal section. In the case of the maxillary grooves, the disto-laterally facing facet is very much broader (anterio-posteriorly) than the mesio-laterally facing one, whilst in the case of the dentary grooves the reverse is true. The maxillary grooves are substantially shorter (dorso-ventrally) than the dentary grooves owing to the differences in the shape of the two bones. The longest of the dentary grooves - which are those that were worn by the tallest teeth of the opposing maxilla - pass more than one third of the way down the lateral side of the bone indicating that the maxilla overlapped the dentary extensively, during the course of occlusion, as in Sphenodon. Both sets of grooves demonstrate clearly that the mandible moved predominantly orthally during occlusion, and that precise occlusal relations were maintained throughout the functional lives of the teeth. The basic mode of occlusion in Sphenodontid A was thus very different from that which Robinson (1976) has recently shown pertains in Sphenodon. In the latter form the mandible moves backwards and forwards during occlusion so that the lower teeth saw the food, and occlusal relations are, as a consequence, very imprecise. In order for precise occlusal relations to be maintained it is essential that opposing teeth maintain exact antero-posterior positions relative to one another. The fusion of the teeth to the jaw bones in Sphenodontid A ensured them against longitudinal drift. It also ensured them against cervical damage and lateral displacement whilst the food was chewed.

It will be observed that the grooves which have been worn into the teeth and jaw bones illustrated in figure 76 are, in each case, slightly obliquely orientated in lateral view; each groove slopes slightly forwards passing dorsally. The mandible must, therefore, have moved slightly palinally as well as orthally during occlusion. When the wear on the two specimens is considered in bucco-lingual cross-section it is found that the wear facets on each slope slightly medially passing upwards. This indicates that during

occlusion the movement of the mandible also included a small ectental component, as in many mammals. As Kallen and Gans (1972) have argued, a slight medial movement of the mandible during occlusion is advantageous as it conserves momentum. The cutting edges on the worn teeth of Sphenodontid A are formed by the thickest layers of enamel on the teeth. In other words they are formed by the buccal layers on the upper teeth and the lingual layers on the lower teeth. These edges are very sharp and they would have facilitated a highly effective double shearing action as the jaws were closed during occlusion. Deep, unidirectional striae in the enamel and dentine surfaces of the wear facets on a few teeth (eg those on maxillary fragments T579 & 572) provide direct evidence that the sharpness of the cutting edges was maintained by a periodic mutual whetting action of the opposing teeth, ie by thegosis (Every & Kuhne, 1971). Although evidence of thegosis has - as far as I am aware - only previously been documented in mammalian dentitions, its occurrence in a reptilian dentition is hardly surprising in view of the fact that this dentition was adapted to precision shearing. Thegosis is an essential concomitant of any mode of dental occlusion in which precision shearing is a significant element. In all of the dentitions of Sphenodontid A which are represented in the collection, the level of wear on the teeth diminishes passing posteriorly, as the more posterior teeth have - owing to the absence of any tooth replacement - inevitably been subjected to functional attrition for a shorter time than the more anterior ones. The juvenile teeth of mature animals have invariably been completely worn away to leave <sup>sharp</sup> reburnated edges of bone, and in some instances the first and even the second additional teeth have also been obliterated. During occlusion in these individuals the anterior edentulous regions of the upper and lower jaws acted like the blades of a pair of scissors so that food could still be sheared in the anterior part of the mouth.

Because the opposing surfaces of the unworn upper and lower juvenile teeth of Sphenodontid A slope slightly lingually, passing upwards, these surfaces largely anticipate the form of the shearing surfaces on the worn teeth. The opposing surfaces of the unworn functional upper and lower additional teeth, by contrast, do not at all anticipate the form of the shearing surfaces on the worn teeth owing to the fact that the upper additional teeth lean markedly lingually. Only the most lingually projecting parts of the freshly erupted functional upper additional teeth - the apices of the cones - con-

tacted any opposing element during occlusion and the remaining parts of these teeth were, in consequence unworn. The whole lingual surface of an upper additional tooth only became worn after that part of the tooth which overhung the tooth base had been completely obliterated. The shearing planes produced as a result of the mutual wearing of opposing additional teeth take the form of the disto-laterally and mesio-laterally facing wear facets described above. The relative positions of grooves formed by these facets show that the apices of the upper and lower additional teeth alternated at the outset of occlusion, and the same was true of the apices of the upper and lower juvenile teeth. Each functional tooth of Sphenodontid A contacted two opponents during the course of occlusion. It is very difficult to determine exactly the initial contact points between opposing juvenile teeth because of the fact that the wear on the juvenile teeth does not take the form of well defined grooves. In the case of the opposing additional teeth however, it is clear that the initial contact points were not quite the same in all individuals, or even, in some instances, along the length of a single dentition (as will be appreciated from the nature of the wear shown in figure 17 ). In the majority of cases the apex of the upper additional tooth commenced occlusion at the point where two adjacent lower teeth abutted, but in some cases it began to occlude against the distal edge of the more anterior of the two opposing lower teeth. This slight variation reflects the fact that the topography of the teeth themselves did not determine occlusal relations in Sphenodontid A.

In well worn dentitions, the grooves produced by opposing additional teeth are confluent with their neighbours, so that each series of grooves forms a continuous shearing surface which has a zig-zag shape when seen in occlusal view (figure 16 ). The cut inflicted by the opposing rows of additional teeth would thus have been a jagged one like that which is made by dressmakers' pinking shears. Interestingly, the shearing planes on a row of heavily worn Morganucodon watsoni molars also form a continuous zigzag shearing surface (cf. Crompton & Jenkins, 1968, figure 6), although the angles made by the juxtaposed shearing planes and the relative breadths of these planes are not the same in the two animals. The principal advantage which such shearing surfaces have over opposing shearing surfaces which run parallel to the long axes of the tooth rows is that they significantly increase the lengths of the opposing cutting edges.

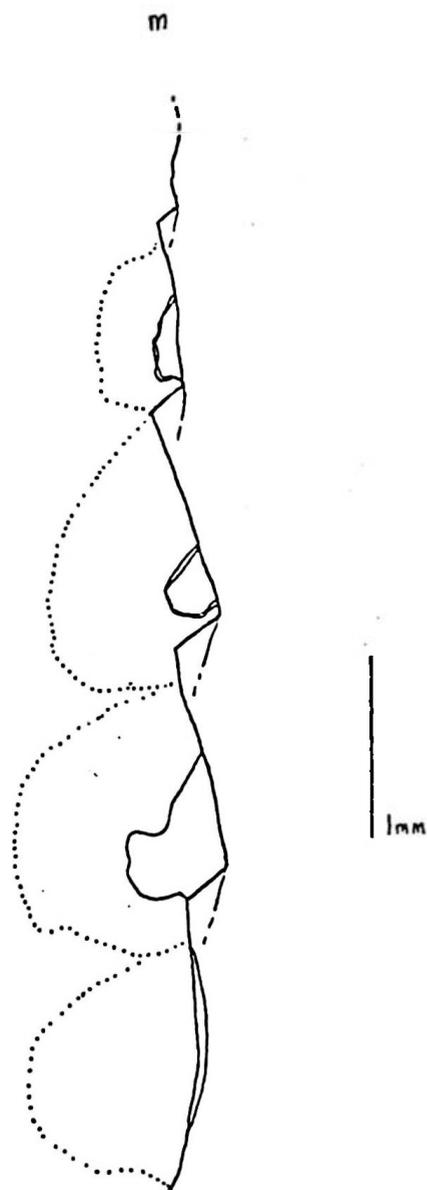


Figure 17. Sphenodontid A. Occlusal view of the cutting surface formed by the shearing planes of the worn additional teeth of dentary T.465. Note the relative mesio-distal positions of the shearing planes. m denotes the mesial end.

2. SPHENODONTID B

This species is represented by two left dentaries, T703 and T.539 (figures 18 & 19) which are broken off anteriorly and posteriorly. The two bones agree very closely in size and morphology and each bears a short series of four additional teeth, of which the penultimate is the largest. The corresponding teeth of the two specimens also agree very closely in size and morphology and there can thus be no doubt that they belong to the same dental positions. Both dentaries are broken off immediately anterior to the first preserved tooth. T.703 is broken off posteriorly just in front of the point at which the coronoid process would have attained its maximum height, and the preserved part of the leading edge of this process is separated from the last preserved tooth by a short space. The dorsal margin of the horizontal ramus is well preserved in this region and it is clear that the latter tooth was not originally succeeded by a still more posterior tooth. In the case of T.539 the bone continues for a slightly shorter distance behind the last preserved tooth before it is broken off. The dorsal margin of the dentary has been rather abraded here and there is no trace of the coronoid process. It is nevertheless clear from the shape of the trough for the accessory jaw bones behind the level of the last preserved tooth that this tooth was the ultimate of the intact bone. The buccal sides of the preultimate teeth of T.539 and the upper part of the lateral surface of the bone have been very heavily worn, the level of this wear indicating that the specimen belongs to an adult which was well past its prime. In the case of the other dentary the preultimate teeth and the lateral surface of the bone also exhibit wear, but this is much less marked, so that the specimen would appear to belong to a rather younger adult. Both of the represented adult animals must have been substantially smaller than any adults of Sphenodontid A: the <sup>maximum</sup> depth of T.703 and T.539 below the tooth row is only one third of that of a typical mature dentary of Sphenodontid A, and the largest tooth of each specimen is only the size of an A<sub>3</sub> of the latter form.

The morphology of the dentition:

The teeth of T.539 have been rather abraded. The first tooth of T.703 is badly damaged, but the remainder have suffered only apical damage. This is most marked in the case of the ultimate tooth. There are no spaces between adjacent teeth and they do not overlap.

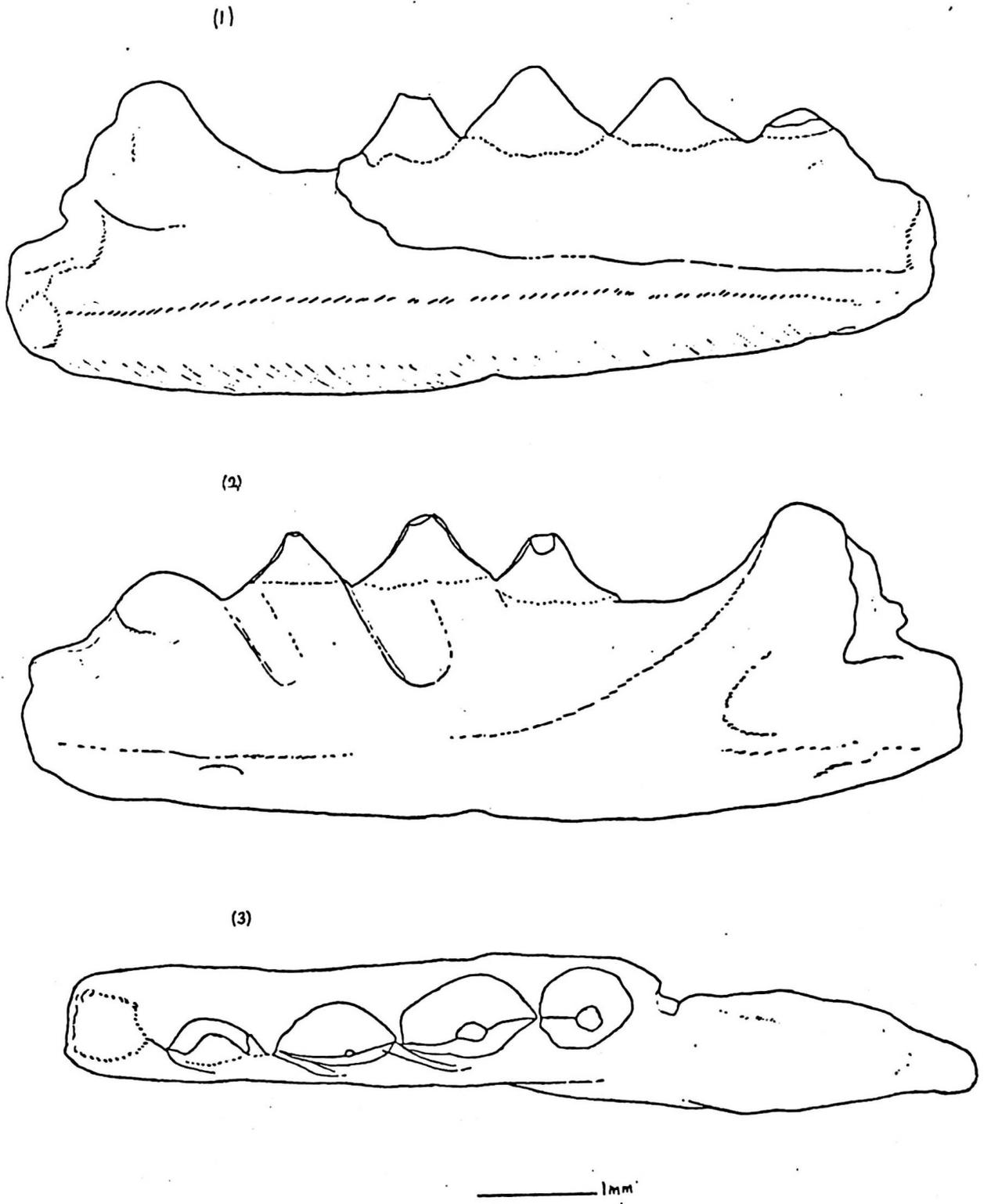


Figure 18. Sphenodontid B. Right dentary, specimen T.703. (1) Medial, (2) lateral and (3) dorsal views. Note shearing surfaces on teeth and bone.

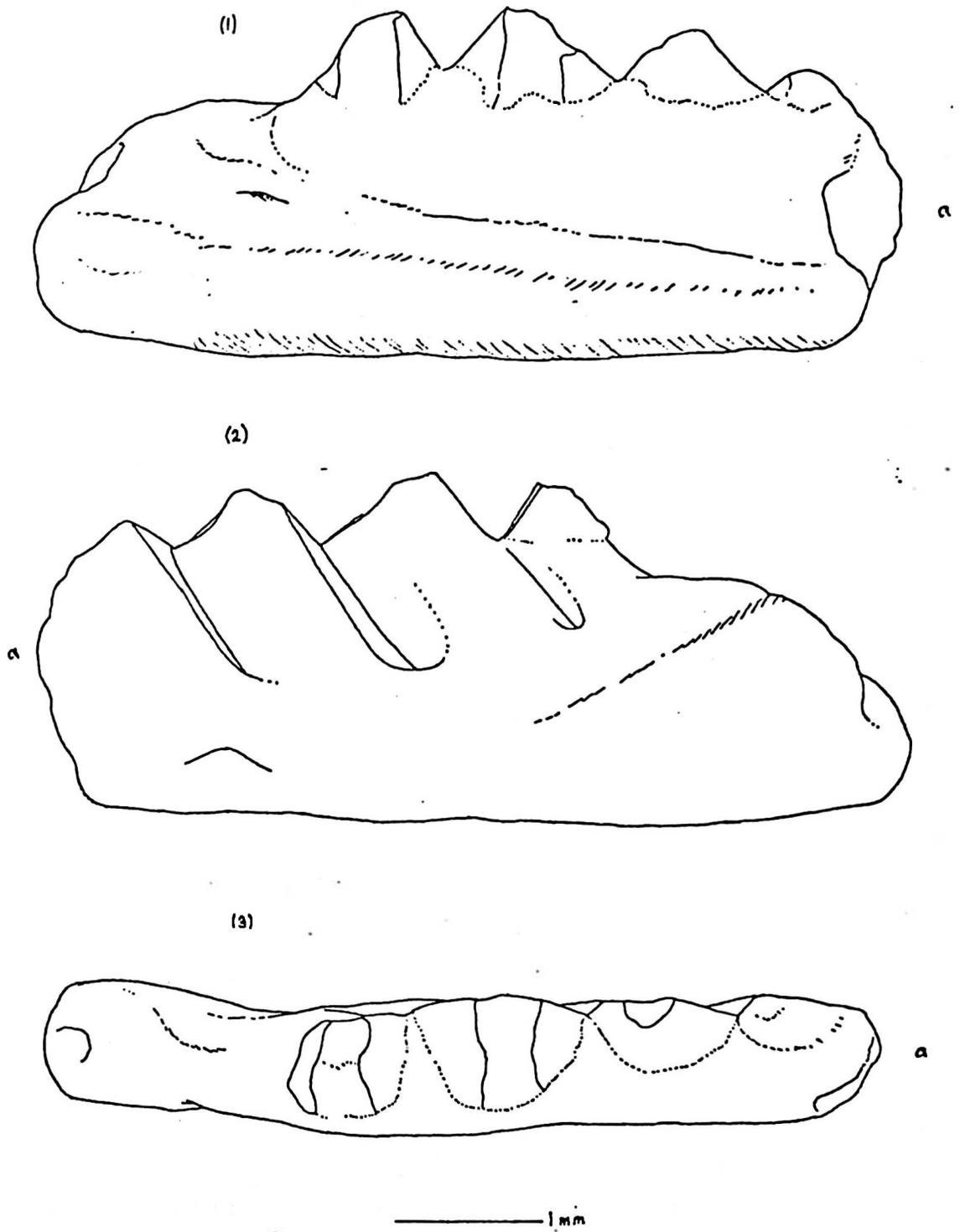


Figure 19. Sphenodontid B. Right dentary, specimen T.539. (1) Medial, (2) lateral and (3) dorsal views. Note the heavy level of wear of the teeth and upper part of the lateral surface of the bone. a denotes the anterior end.

The basic morphology of the first three preserved teeth is similar to that of the first five lower additional teeth of Sphenodontid A.

There is no way of knowing whether the first preserved additional tooth is the first of the intact mandible. This tooth has the form of a low, slightly elongated half-cone. The second preserved tooth is somewhat larger. It has the same morphology as the A<sub>3</sub> of Sphenodontid A. The third preserved tooth is slightly larger than the second and is morphologically identical to the A<sub>4</sub> and A<sub>5</sub> of Sphenodontid A. When intact, the ultimate tooth would have had about the same height as the second preserved tooth, but its basal length is inferior to that of the latter. It differs from its predecessors in being almost perfectly conical in shape and in lacking a distal crest. It is morphologically identical to the A<sub>6</sub> in a Sphenodontid A dentary such as T463 (cf. figure ).

The morphology of the dentary:

The tooth bearing portion of the dentary is rather shallower, relative to the large additional teeth, than that of Sphenodontid A. In all other respects, apart from size, the known part of the bone is closely similar to that of the larger species.

Measurements:

In the following table, the heights of the teeth, which are given after their basal lengths, are, of course, estimates. All measurements are given in millimetres.

	A'1'	A'2'	A'3'	A'4'
T.703	0.6 x -	1.1 x 0.4	1.2 x 0.7	0.8
T.539	-	1.0 x -	1.2 x 0.7	0.8 x 0.6

Greatest depth of tooth bearing portion of bone -

T.703 : 1.95mm; T.539 : 1.90mm

Wear and occlusion:

As can be seen from figures 18 and 19 the wear patterns on the teeth and lateral surfaces of the two dentaries are exactly the same as wear patterns which occur on the lower functional additional teeth and equivalent parts of the dentaries of Sphenodontid A. It is therefore clear that the mode of occlusion and the antero-posterior positions of the opposing additional teeth relative to one another

were the same in the two species. It is also apparent that the basic morphology of the unknown upper additional teeth of the present species must be similar to that of the equivalent teeth of the larger form.

3. SPHENODONTID C

This species is represented by a single right dentary of minute size, T.459 (figure 20), which is broken off anteriorly and posteriorly. The specimen consists of a fragment of the tooth bearing portion of the bone which bears a short series of four additional teeth, the last of which is the largest of the series. The dentary is broken off anteriorly along an oblique fracture line which passes postero-ventrally from in front of the first preserved tooth. Posteriorly, the bone continues for a short distance behind the last preserved tooth before it is broken off. There is a miniscule fragment of enamel immediately behind the latter tooth which indicates the original presence of a still more posterior tooth. Behind this fragment, the dorsal part of the dentary has been broken away to below the level of the tooth row, and there is no trace of a coronoid process. The buccal sides of the first three preserved teeth and the upper part of the lateral surface of the bone beneath them have been heavily worn, the level of this wear clearly demonstrating that the specimen belongs to an adult. This individual is by far the smallest adult animal which is represented in the assemblage, and one of the smallest adult tetrapods known. The maximum depth of T.459 is less than  $\frac{1}{4}$  of the depth of the tooth bearing portion of a mature dentary of Sphenodontid A, and the largest preserved tooth of the specimen is only the size of an  $A_1$  of the latter form.

The morphology of the dentition:

There are no spaces between the teeth and they do not overlap with one another. Their apices have been damaged, but, with the exception of the first preserved tooth, this damage is slight. The basic morphology of the teeth is the same as that of the first five lower additional teeth of Sphenodontid A.

As preserved, the first tooth has the form of a low elongated half cone. However, the leading edge of the half cone is damaged and there is some indication that a more mesial portion of the tooth has been broken away. This inference is supported by the fact that both

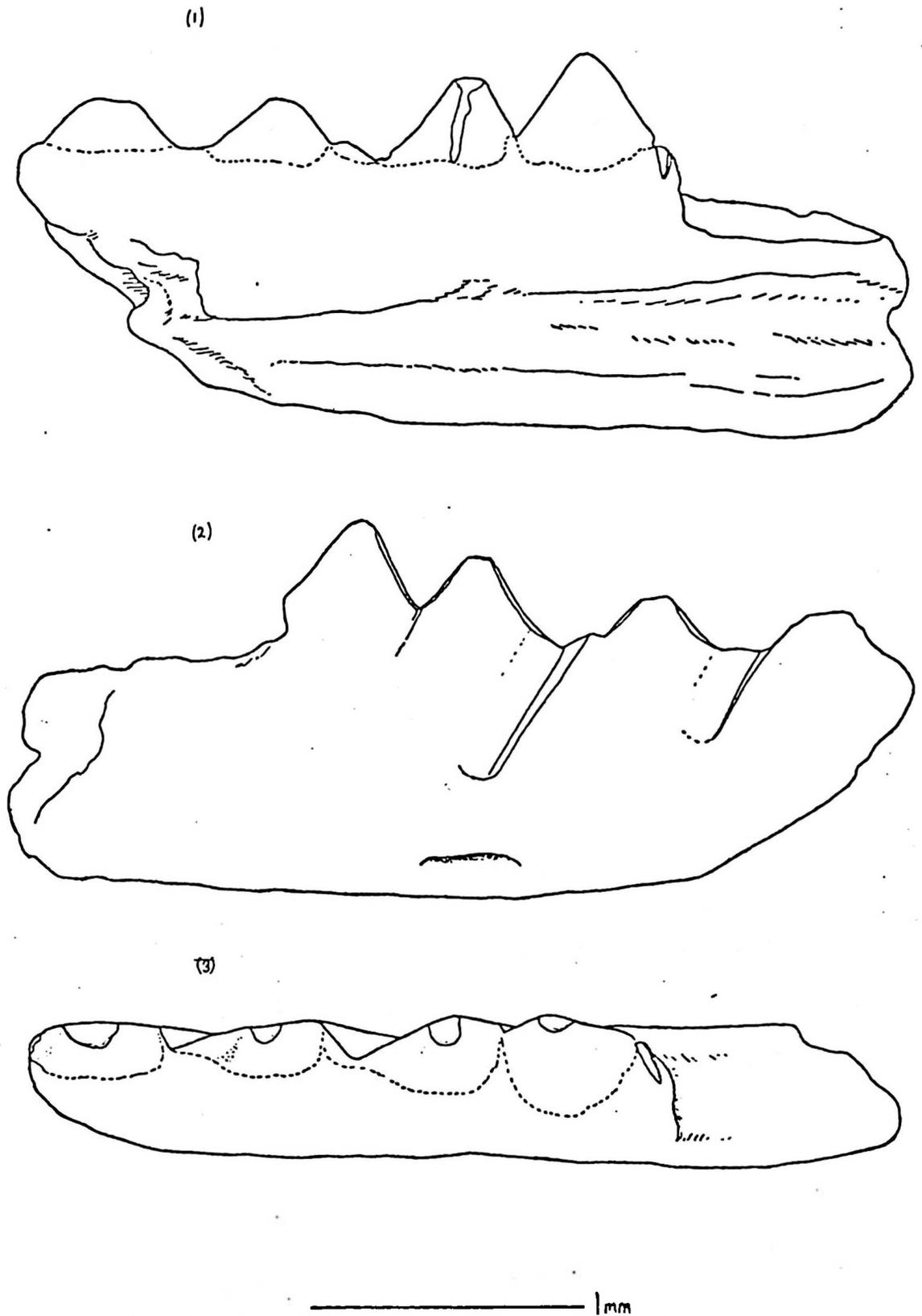


Figure 20. Sphenodontid C. Left dentary, specimen T.459. (1) Medial, (2) Lateral and (3) dorsal views. Note the heavy level of wear of the preultimate teeth and the upper part of the lateral surface of the bone. a denotes the anterior end.

of the succeeding teeth bear mesial flanges.

The second preserved tooth is morphologically very similar to the  $A_2^-$  of Sphenodontid A. The half cone main body of the tooth has the same size and proportions as that of its predecessor. The flange has been substantially worn away, especially anteriorly, so that in lingual view the tooth appears to be separated from the first preserved tooth by a short space. The flange accounts for about  $\frac{1}{3}$  of the tooth's total length. The third preserved tooth is a little larger than the second. It differs from the latter only in that the half cone is relatively slightly taller, and the flange proportionally slightly longer. As in the case of the second preserved tooth, much of the flange has been worn away. The last preserved tooth is devoid of a flange and has a symmetrical profile in lateral view. It is slightly taller than its predecessor, and it is morphologically closely similar to an  $A_4^-$  or  $A_5^-$  of Sphenodontid A.

The morphology of the dentary:

As in the small species described previously, the tooth bearing portion of the bone is proportionally narrower than in Sphenodontid A, although here the difference is more marked. Apart from this, the known part of the dentary exhibits no structural differences from the dentary of the large species. (It is true that there is no depression for the insertion of an external adductor muscle in the lateral side of the horizontal ramus, but the absence of such a depression can be adequately accounted for by postulating that this depression was originally situated behind the level of the preserved part of the bone).

Measurements:

As in the previous table, the heights of the teeth, which are given after the lengths are estimates. All measurements in millimetres:

A'1'	A'2'	A'3'	A'4'
0.5 x -	0.55 x 0.2	0.65 x 0.25	0.5 x 0.3

Greatest depth of the tooth bearing portion of the bone : 1mm.

Wear and occlusion:

The form of the wear on the first three preserved teeth and underlying lateral surface of the bone is very similar to that which

occurs on some of the more worn lower additional teeth and dentaries of Sphenodontid A. The mode of occlusion and the relative positions of the opposing additional teeth in the present species must, therefore, have been closely similar to those in the two previous ones. There was however, clearly one slight difference; at the outset of occlusion the apices of the more anterior upper additional teeth sheared against the flanges of the corresponding lower teeth rather than between two adjacent teeth as in the other forms. By contrast, the apex of the upper tooth which occluded with the last preserved additional tooth of T.459 must initially have sheared between this tooth and its predecessor, these occlusal relations being the same as those of the opposing additional teeth of Sphenodontid A and B.

#### The intra-familial positions of the Welsh Sphenodontids

It is appropriate to begin by considering the generic position of the most complete known of the three species - Sphenodontid A. In the morphology of its dentition this form resembles the late Norian species Glevosaurus hudsoni much more closely than any other Sphenodontid which has been described in the literature. No detailed account of the morphology of Glevosaurus hudsoni, which comes from fissures in the Bristol Channel area of Great Britain, has yet been published, but I have fortunately been able to study those specimens belonging to it which are housed in the British Museum (Natural History). This material, which comprises a few isolated and damaged jaw bones, vertebrae, limb bones and girdles, was the subject of a preliminary account by Swinton (1939), who established the genus and species upon it. A rather larger collection of G. hudsoni material has subsequently been compiled by Dr. P. L. Robinson, who in 1973, published a paper containing a brief description of the skull and a more thorough diagnosis of the genus and species than that given by Swinton. I have used the information provided in this paper, together with that provided by a photograph of a well preserved dentary in a more recent paper (Robinson, 1976, plate ) to supplement my own observations on G. hudsoni for the purposes of the following comparisons between the form and Sphenodontid A.

(1) Size - To judge from the incomplete but evidently relatively mature jaw bones of G. hudsoni in the B.M.N.H. collection, the two species are of closely similar size. The depths below the A  $\bar{1}$  of the

best preserved of the B.M.N.H. dentaries (R6102) is 4.1 mm, so that, in terms of this dimension, this specimen matches the largest specimens amongst the dentaries of Sphenodontid A (c.f. table ).

(2) The dentary - The tooth bearing parts of the dentaries of the two species are identical in every respect except that of their proportions, the dental ramus of G. hudsoni being shorter than that of Sphenodontid A. The G. hudsoni dentary also corresponds to that of Sphenodontid A in (a) the presence of a fossa in its lateral surface just posterior to, and below the level of the tooth row, and in (b) the fact that its coronoid process is distinctly taller than that of Sphenodon.

(3) The premaxilla - No specimen of the premaxilla of G. hudsoni is present in the B.M.N.H. collection, but the overall morphology of the bone is indicated in figures 4 & 5 in Robinsons 1973 paper. The bone is clearly very similar in its shape and relations with the maxilla to the premaxilla of Sphenodontid A.

(4) The maxilla - As the maxilla of Sphenodontid A is so poorly known there is little to be gained from a comparison of the bone in the two species. All that can be stated with certainty is that the known part of the maxilla of the Pant 4 form cannot be distinguished in any way from the equivalent part of the bone of G. hudsoni.

(5) The marginal dentition - There are no differences between the species in the nature of the juvenile dentitions of the upper and lower jaws. The maxillary and dentary juvenile teeth were not replaced in either species. In G. hudsoni the juvenile premaxillary teeth were superseded during the course of ontogeny by a boney chisel-like structure, in contrast to the situation in Sphenodontid A, where there was no replacement of the premaxillary dentition. The first four upper and lower additional teeth of G. hudsoni increase in size passing posteriorly, as in Sphenodontid A, and they share the same basic morphology as the equivalent teeth of the latter species. The first four upper additional teeth of the Norian form lean lingually, like their counterparts in the Pant 4 species, and they differ from these counterparts only in that their distal flanges are slightly more elongated. The corresponding lower additional teeth of G. hudsoni do not match their Sphenodontid A counterparts as closely. The first three bear distinctive mesial and very small distal flanges (the mesial flanges are in each case more prominent than the flange of the  $A\bar{2}$  of Sphenodontid A) and the fourth bears an incipient mesial flange. In G. hudsoni there are no functional teeth behind the largest upper and lower additional teeth (i.e. the  $A\bar{4}$  and  $A\bar{4}$ ) as there

are in Sphenodontid A. The mature maxilla of the former species bears two or three reduced additional teeth at its posterior end which closely resemble those in the mature maxilla of the latter one. In marked contrast to the situation in Sphenodontid A, however, there are no teeth at all behind the fourth additional tooth of the mature dentary of G. hudsoni.

(6) The palatal teeth - There are no morphological differences between the components of the lateral palatine tooth rows of the two species. The lateral palatine teeth of G. hudsoni are rather larger than those of Sphenodontid A. Robinson (1973) states that G. hudsoni also has a single tooth lying opposite to the anterior end of the lateral palatine tooth row, and several rows of very small palatal teeth. There is no evidence for the existence of such teeth in Sphenodontid A, but the possibility that they occur cannot be entirely ruled out.

(7) Dental wear and occlusion - In the case of one of the G. hudsoni dentaries in the B.M.N.H. collection (R6102) well defined grooves have been worn into the preultimate additional teeth and the upper part of the lateral surface of the bone below them. These grooves are identical in form and orientation to those worn by the upper additional teeth of Sphenodontid A, and their relative positions indicate that the occlusal relations of the opposing additional teeth were the same as those in some individuals of the latter species. The details of occlusion were thus identical in the two forms.

Of the differences between G. hudsoni and Sphenodontid A outlined above, those pertaining to the upper and lower functional additional teeth, the proportions of the flanges on the first four upper additional teeth and the relative sizes of the lateral palatine teeth, are of little or no taxonomic significance above the species level. Those pertaining to the detailed morphology of the first four lower additional teeth, the nature of the posterior parts of the upper and lower marginal dentitions, and the nature of the occlusal apparatus of the mature premaxilla, however, are rather more important, especially when taken together. They fully warrant the separation of the forms at generic level. In spite of this, the similarities between G. hudsoni and Sphenodontid A are, within the content of the Sphenodontidae as a whole, more extensive and impressive than the differences between them, and there can be no doubt that the genus to which the Pant 4 species belongs is closely related to Glevosaurus.

On the evidence of their known morphology and the details of their dental occlusion, the two remaining Sphenodontids from Pant 4 are closely related to Sphenodontid A. Sphenodontid B differs from the latter form in its size, in the relative depth of the dental ramus of its dentary and in the absence of small, functionless additional teeth at the posterior end of its mature lower tooth row. None of these differences is of more than specific significance. As Sphenodontid B agreed exactly, or almost exactly, with Sphenodontid A in the morphology of its lower functional additional teeth, in the known morphology of its dentary, and in its occlusal pattern, it can, in spite of our very incomplete knowledge of its anatomy, be referred to the same genus with a high degree of confidence.

Sphenodontid C also differs from Sphenodontid A in its size and in the relative depth of the dental ramus of its dentary. More importantly, however, it differs from the latter species in that (a) two (and very probably three) of its more anterior lower additional teeth have mesial flanges, and (b) its anterior lower additional teeth do not exhibit a progressive increase in size passing posteriorly. In the light of the relative uniformity of Sphenodontids A and B in the nature of their more anterior lower additional teeth, these differences would appear to exclude Sphenodontid C from the same genus.

Within the Sphenodontidae, the Welsh genera and Glevosaurus appear to constitute a natural group of genera occupying a rather isolated position. Unfortunately, as none of the other fossil sphenodontids ( viz - Homoeosaurus, Meyasaurus, Monjurosuchus, ?Chometokodmon and Opisthias ) have yet been described in detail it is not possible here to present an adequate picture of inter-generic relationships within the family as a whole. It should be emphasised, however, that the differences between the extant genus Sphenodon and the group of genera comprising the Welsh forms and Glevosaurus are of sufficient importance to have taxonomic significance above the generic level. The latter genera should certainly be placed in a different subfamily from the former one.

Class                    REPTILIA  
Sub-class                LEPIDOSAURIA  
Order                    INCERTAE SEDIS  
PLEURODONT FORM

About half a dozen small fragments of the dentition of the pleurodont lepidosaur of the Hirmeriella association are present in the assemblage. The teeth of the form - which is about the same size as Sphenodontid A - vary in their morphology along the jaw; those at the front are slender, relatively elongated, and clearly pleurodont, whilst those at the back are broad-based, low, robust, and nearly acrodont.

As a result, where only a few small fragments of the dentition occur, as in the present case, the initial impression gained is that more than one type of dentition is represented by the material. The osteology of the form - which is about almost certainly not a squamate - is currently being studied by Miss Susan Evans. Its morphology and affinities will now, therefore, be considered here.

Class        REPTILIA

Subclass    ARCHOSAURIA

There are some eighty specimens of isolated archosaurian teeth - including fragments - in the assemblage. The specimens include the largest teeth obtained from Pant 4. A number of different types of teeth occur, and more than one major taxon is represented.

1.    THEROPOD-TYPE TEETH

The majority of archosaur teeth in the assemblage are of this type. All are laterally compressed, conical and sharply pointed, and all bear mesial and distal crests on the crown. The enamel is invariably thin and in many cases it is marked by minute sub-surface cracks which probably formed as a result of posthumous drying. The specimens may be divided into three groups on the basis of their morphology.

Group one : This includes about forty teeth. They exhibit a very considerable size range and they can be divided into two sub-groups on the basis of size. The first sub-group comprises the three largest teeth to have been obtained from the Welsh fissure. None of the three is intact. Figure 21 shows the most complete specimen, T.705. The apex of the crown, the root and the base of the crown have been broken off. The crown is very compressed laterally and has a flat blade-like appearance. In lateral views its shape resembles that of an elongated triangle, the height of the specimen being about twice that of its basal length. The mesial edge of the crown is convex and the distal edge slightly concave. The former is serrated near the crown tip but is otherwise smooth. The latter is serrated all the way along its length. There is an elongated, narrow pulp cavity.

The majority of specimens in the second sub-group are morphologically indistinguishable from those in the first, but they are very substantially smaller; the largest is less than one quarter of the size of T.705. There is a marked gradation in size within the sub-group. Figure 22 shows a large, a medium, and a very small sized specimen. A number of specimens retain all, or a substantial part of the root in addition to the complete crown. Some crowns have both mesial and distal edges serrated all the way along, whilst others have a smooth

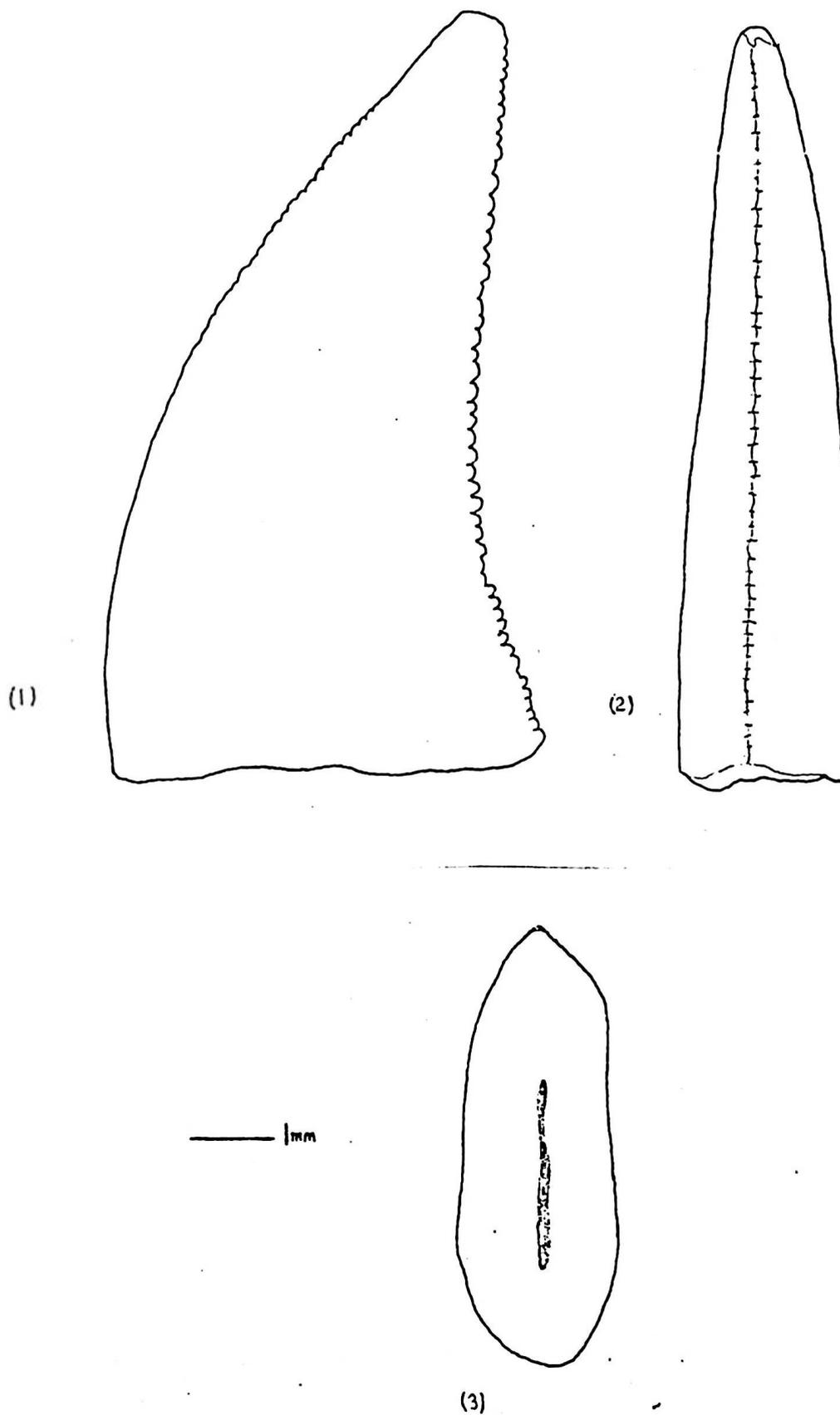


Figure 21. Archosaur tooth. T.705; (1) Lateral and (2) distal views; (3) end view of root.

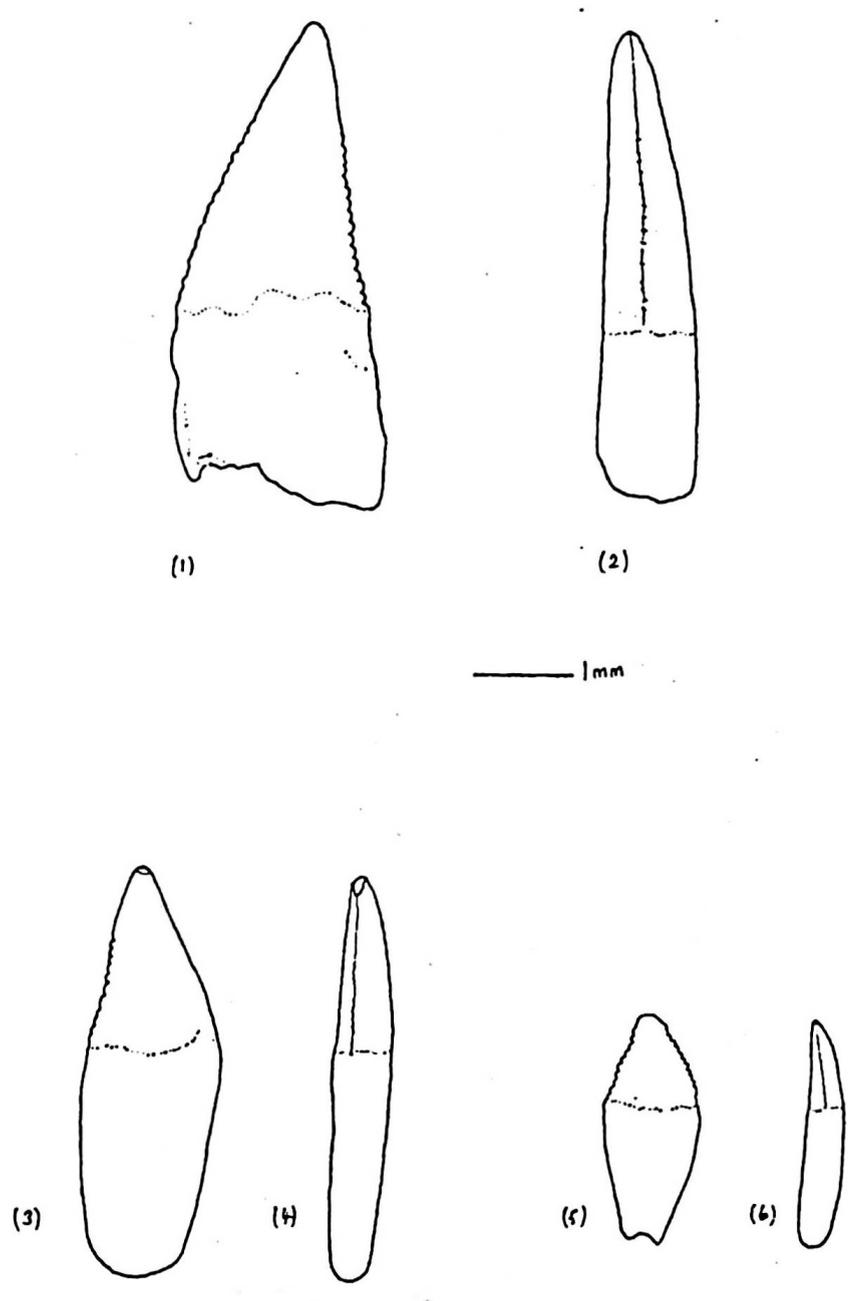


Figure 22. Archosaur teeth. Upper row shows specimen T 708; (1) lateral & (2) distal views. Lower row left shows specimen T. 709; (3) lateral & (4) distal views. Lower row right shows specimen T. 710; (5) lateral & (6) distal views.

mesial edge and an only partially serrated distal edge. This variation is independent of size. The smallest specimens differ from the others and from those in the first sub-group in that in lateral view the apex of the crown is directly over the midline of the root, and the height of the crown is about equal to its basal length. The massive disparity in size between the teeth in the two sub-groups shows clearly that they belong to different forms. This does not necessarily mean that all the teeth in the second sub-group are specifically distinct from those in the first, as the possibility that they belong to juveniles cannot be ruled out. The size range in the teeth in the second sub-group suggests that more than one size of animal is represented by this material. The slight morphological difference between the smallest teeth and the rest is perhaps indicative of a specific difference although this is by no means certain.

Group two : This comprises six teeth of approximately similar size. None are intact. Figure 23a shows a typical specimen. The apex of the crown, the root and the base of the crown are missing. The crown is elongated. It is rather less laterally compressed than in the previous specimens, and it has a tusk-like rather than a blade-like appearance. In lateral view its mesial edge is convex and its distal edge slightly concave. The former is smooth whilst the latter is serrated in its lower half. The pulp cavity is minute. The specimens in this group are reasonably attributed to a different species from those to which the blade-like teeth belong.

Group three : This group includes about half a dozen specimens. They appear to be rather smaller than the specimens in the previous group although none is intact : all lack the root and crown base. Figure 23b shows a relatively well preserved specimen. The crown is more laterally compressed than the crowns of the teeth belonging to group two, but less so than the crowns of those belonging to group one. In lateral view the height of the crown only slightly exceeds its basal length although as the intact size of the crown is uncertain this may be misleading. The mesial edge of the crown is markedly convex and, if the intact crown was only a little longer than the fragment, it would have bulged forward of the root. The distal edge of the crown is concave. The former is smooth and the latter serrated except near the crown apex and base. The pulp

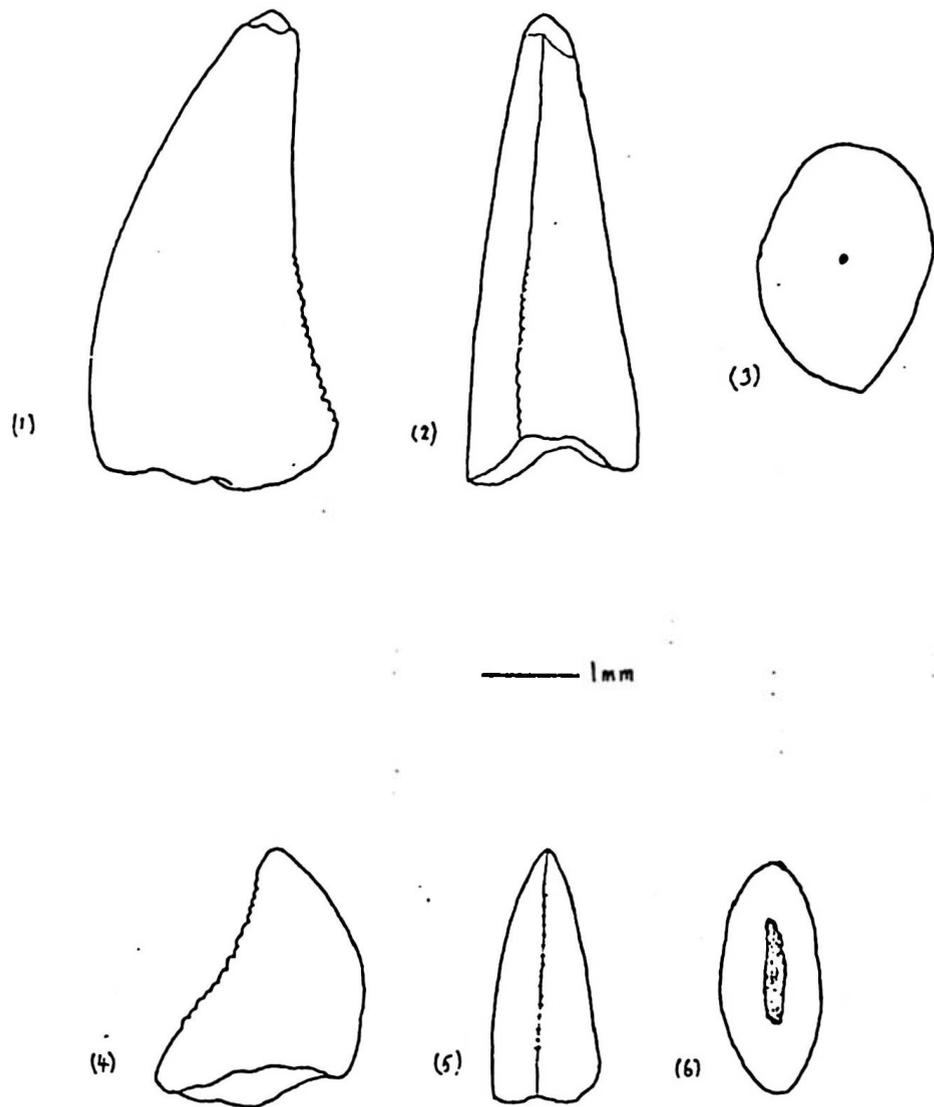


Figure 23 Archosaur teeth. Upper row shows specimen T. 712; (1) lateral and (2) distal views; (3) end view of root. Lower row shows specimen T. 713; (4) lateral and (5) distal views; (6) end view of root.

cavity is relatively large. The specimens in this group are rather too broad to belong to the same dentitions as any of the blade-like teeth. If the relatively squat appearance of the crown is an accurate reflection of its intact appearance, the teeth may well belong to the posterior end of a dentition which also includes more elongated anterior teeth. They may, for example, belong to the same dentition as the tusk-like teeth which have just been described, although there is, of course, no real evidence that they do.

Classification

The classification of isolated theropod-type teeth frequently presents an insuperable problem, and this is the case here. The problem arises quite simply from the fact that few theropod genera possess teeth which are sufficiently morphologically distinctive to be identified with certainty. F. Von Heune first drew attention to this situation in 1926 in his general review of the carnivorous Saurischia of the Jurassic and Cretaceous. With respect to isolated carnosaur teeth, he stated - "In particular cases a species can be identified, but principally to find the differences between the genera will hardly be possible". He also observed - "According to experience it is not even possible to distinguish Carnosauria and Coelosauria by their teeth". None of the groups of Welsh teeth can be narrowed down to a particular infra-order with any confidence. It should be added that the possibility that some of them belong to saurischian-like pseudosuchians cannot even be ruled out. The teeth belong to several species of small, carnivorous, theropod-like archosaurs. Nothing more may be said about them.

2. OTHER TEETH

There is a small number of teeth in the assemblage which, on the basis of their overall shape, appear to belong to one, or several semi-aquatic archosaur species. None of the specimens is completely intact. All are conical and elongated and in each case they broaden progressively and uniformly passing downwards, away from the crown apex. All are slightly laterally compressed - so that they are oval in cross-section - and almost all bear minute but distinct mesial and distal crest on the crown. The enamel covering of the crown of each tooth is thin and, on initial inspection with the naked eye, appears rugose, fine, irregular and interrupted striae running longitudinally down from the crown apex to its base. Upon exam-

ination under adequate magnification however the enamel surface is seen to be smooth, the apparent striae consisting of sub-surface cracks. All the teeth retain a small pulp cavity.

T.715 (figure 24). Almost all of the root of this tooth has been broken away. The specimen has a robust, tusk-like appearance and it is one of the largest teeth to have been obtained from the Welsh fissure. In lateral view it is curved, the concave edge of the crown facing distally, whilst in mesial view it is perfectly straight, so that its lingual and buccal sides cannot be distinguished from one another. There is a mesial crest which extends down from the tip of the tooth for about two thirds of the length of the crown. There is also a distal crest, which extends down the full length of the crown, passing below the lower limit of the enamel. The tip of the crown has been worn into a very blunt shape. The robust form of the tooth and its general state of preservation suggests that the major part of this wear was effected through use. Additional enamel has clearly been posthumously abraded from the border of the functionally worn tip, especially on one side. The lower-most limit of the crown enamel is difficult to discern because the enamel is extremely thin in the region just above the root, as in the case of the other specimens in which the enamel- dentine border is preserved. On one side of the tooth the enamel-dentine border is very irregular indicating some posthumous removal of enamel.

T.716 (figure 25 ). This is a rather smaller and more slender tooth. The apical region of the crown is missing and the root is broken off a short distance below the crown base. In lateral view the tooth is almost perfectly straight although its mesial edge is very incipiently convex. In mesial view the tooth is slightly curved, the concave edge obviously being the lingual one. Mesial and distal crests extend from the broken tip of the tooth almost to the crown base.

T.717 (figure 26 ). This tooth is a little smaller than the previous specimen although it is of similar proportions. The root and the lower part of the crown are missing. In lateral view the shape of the tooth is very similar to that of the previous specimen but in mesial view it contrasts with the latter in being perfectly straight. There is a continuous mesial crest and an interrupted, incipient distal crest. As in the case of T.715 the tip of the crown has been worn.

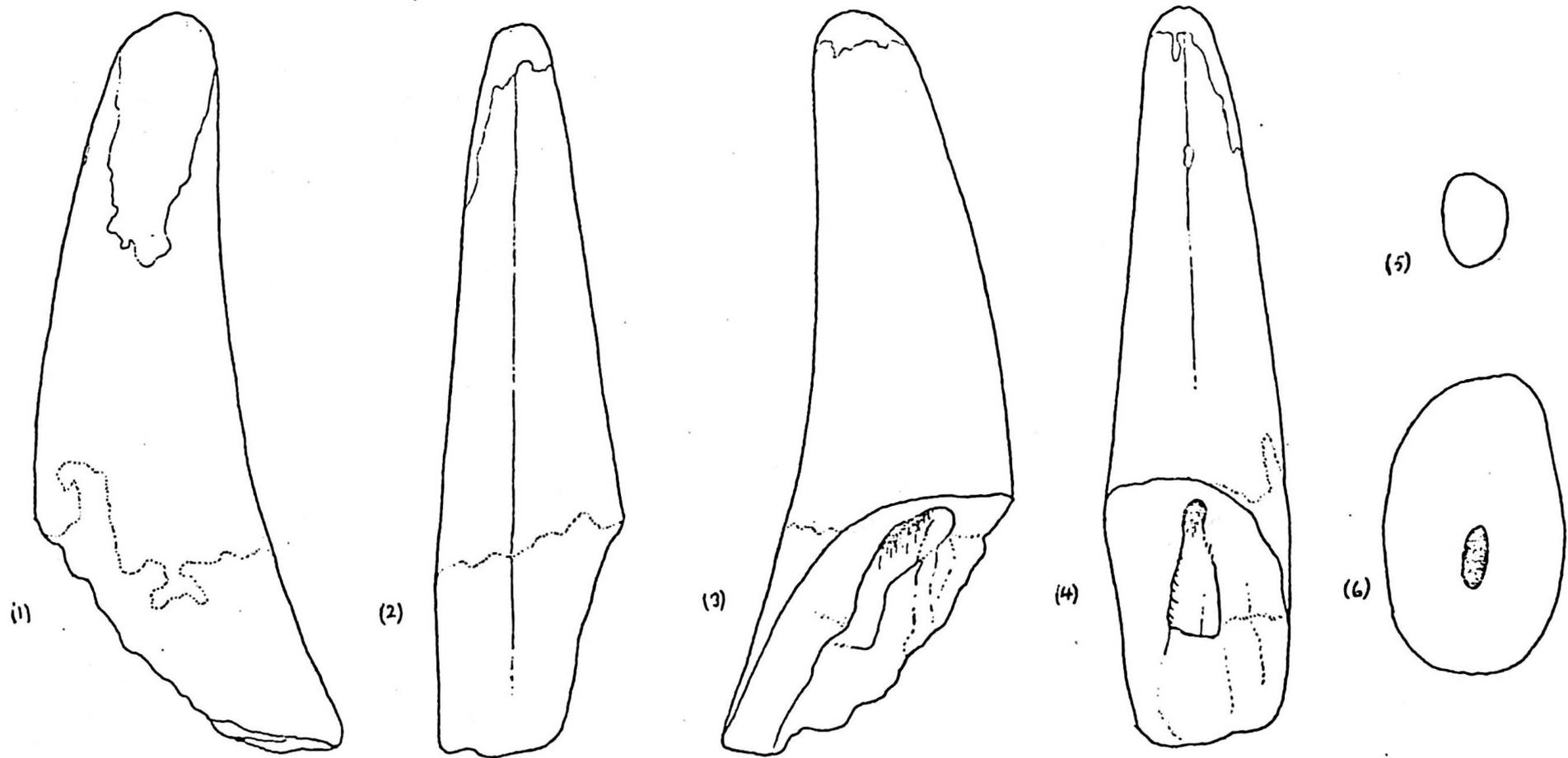


Figure 24 Archosaur tooth, specimen T.715. (1) and (3) lateral views; (2) distal, (4) mesial and (5) apical views; (6) end view of root, slightly simplified. Dotted line indicates enamel dentine boarder, as in all following specimens.

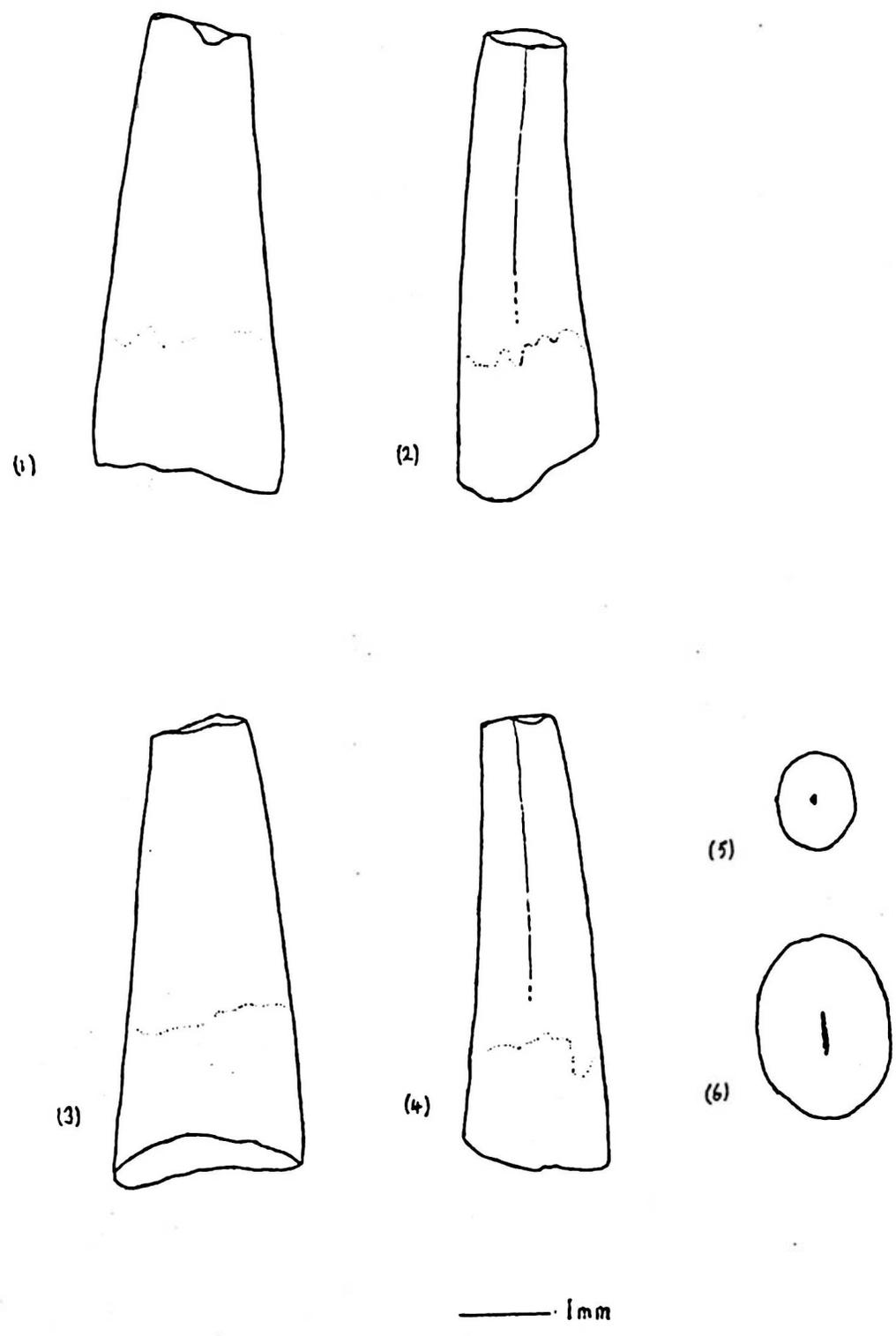


Figure 25 Archosaur tooth, specimen T.716. (1) buccal, (2) distal, (3) lingual, (4) mesial and (5) apical views, (6) End view of root.

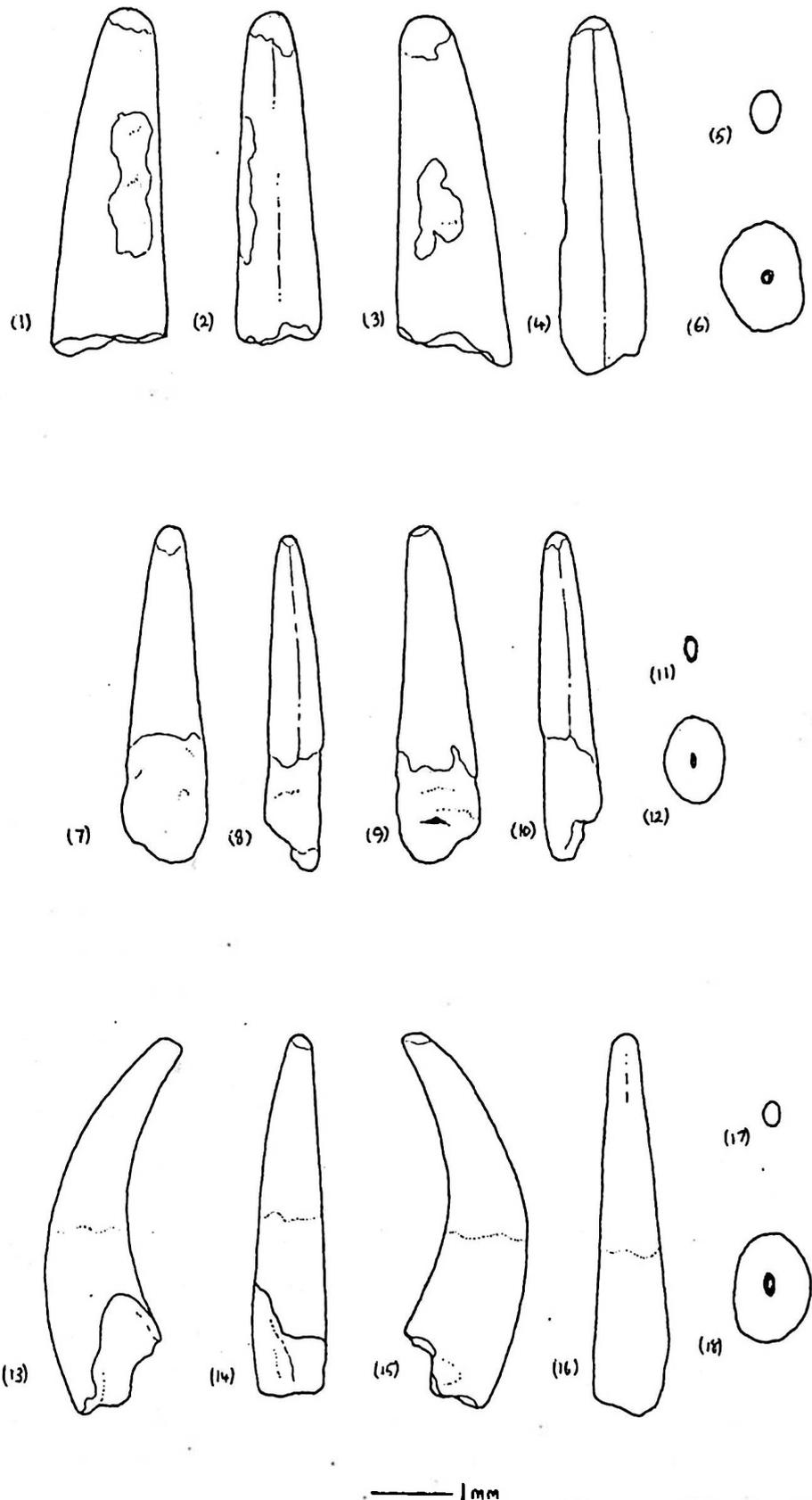


Figure 26 Archosaur teeth. Upper row shows specimen T.717; (1) and (3) lateral views, (2) distal, (4) mesial and (5) apical views; (6) end view of root. Middle row shows specimen T.718; (7) and (9) lateral views; (8) mesial, (10) distal and (11) apical views; (12) end view of root. Bottom row shows specimen T. 719; (13) and (15) lateral views; (14) distal, (16) mesial and (17) apical views; (18) end view of root.

T.718 (figure 26 ). This is a slightly smaller tooth. The crown is extremely slender. The lowermost part of the crown has been heavily abraded and most - or all - of the root is missing. In lateral and mesial views the crown is perfectly straight. Mesial and distal crests are present. The tip of the tooth has been worn, very possibly posthumously.

T.719 (figure 26 ). This is the smallest specimen. The crown is intact, except for the apex - which has been broken off - and a substantial length of the root is preserved. The crown is proportionally about as slender as in the previous specimen. In lateral view the tooth is markedly curved, whilst in mesial view it is straight. There is an incipient mesial crest near the tip of the crown, but there is no distal crest.

In addition to the five teeth just described, the assemblage includes a few small fragments of teeth of similar morphology to T.717 and 719.

Number of Species

None of the teeth described above exactly matches any of the teeth which have been described in the literature dealing with semi-aquatic archosaurs. Since the teeth are isolated, and variable in their size and morphology, it is therefore impossible to be certain about the number of species which they represent. The variation exhibited by the teeth does not, however, appear to preclude the possibility that they all belong to the dentition of a single form. An equivalent level of variation in size and morphology is, for example, encountered within the dentition of the phytosaur Rutiodon (McGregor, 1905; Camp, 1930). On the positive side, the similarities between the teeth in their cross-sectional shape, in the extent of their pulp canal, and in the thickness and smoothness of their enamel, all suggest that they belong to a single form. In view of the very small number of specimens with which we are dealing, I think in these circumstances that it is most probable that no more than one species is involved. Very probably, no more than one animal is represented.

The Dentition

Only a few, very general, comments can be made regarding the dentition. The large, tusk-like, tooth, T.715, quite obviously belonged to the anterior end of the dentition, probably occupying a position similar to that which is occupied by the tusk-like teeth of Rutiodon. The

specimen is almost certainly an upper tooth. The largest of the remaining teeth, T.716, probably occupied a relatively anterior position, although it was not necessarily situated at the anterior end of the dentition; in some phytosaurs (e.g. Rutiodon and Angistorhinus) there are enlarged teeth in the posterior part of the premaxilla. There is no way of determining whether T.716 is an upper or a lower tooth. The relatively small teeth obviously occupied more posterior positions to T.715, and they were quite probably situated behind T.716. The marked distal curvature of T.719 was evidently designed to prevent the anterior escape of prey from the mouth.

The nature of the post tusk-like teeth indicates that the form was predominantly piscivorous - these elongated, relatively slender, slightly laterally compressed teeth would have been quite unsuitable for shearing or crushing purposes. The presence in the dentition of a large tusk-like tooth is not inconsistent with this interpretation since an analogy may be drawn with Rutiodon. Here the rather gavial like shape of the snout and the nature and number of the post tusk-like teeth clearly demonstrate that this phytosaur was mainly a fish eater.

Classification

The affinities of the Welsh piscivor - if, indeed, the teeth described above belong to a single form - are very problematic. On the basis of the general morphology of the teeth, the form would appear to be either a tiny phytosaur or an early crocodile. It is, unfortunately, impossible to establish which, with any certainty, as no-one has ever demonstrated the existence of any consistent macro, or micro structural differences between the teeth of the two groups in question (by this I do not mean to imply that no such differences exist, but merely that the extensive, detailed comparative work, which is necessary to determine whether or not they do, has never been carried out). The form is substantially smaller than all known phytosaurs, and the majority of early crocodiles. Its minute size may be a specific or generic feature, although it is also possible that it is no more than a reflection of juvenility.

Class REPTILIA  
 Order THERAPSIDA  
 Family TRITYLODONTIDAE, Cope, 1884

In terms of numbers of specimens, the Tritylodontidae is the most abundantly represented non-sauropsid tetrapod family in the assemblage. The material consists of over eight hundred isolated teeth, every dental position apparently being represented. There are no identifiable jaw fragments. Tritylodonts are very easily recognised by the morphology of their cheek teeth, which are unique. The upper cheek teeth are quadrate with three parallel rows of from two to four cusps each, and the lower cheek teeth are rectangular with two parallel rows of cusps. The components of each cheek tooth row are very little differentiated.

All the Welsh tritylodontid specimens belong to a single genus.

Genus OLIGOKYPHUS, Hennig, 1922

More than one form of Oligokyphus is represented. Because all the teeth are isolated, it has only been possible to determine the number of these forms, and their identity as a result of a detailed morphological and numerical analysis of the material.

The genus was founded by Hennig (1922) on the basis of two isolated cheek teeth from the Rhaeto-Liassic Bone Beds of Wurtemberg. One is an upper cheek tooth from either Olgahain or Schlosslemuhle (Simpson 1928) and this is the genoholotype: Oligokyphus triserialis. The other is a lower cheek tooth from Olgahain and this constitutes the hypodigm of Oligokyphus biserialis.

In 1956 Kuhne published a monograph on a large assemblage of Oligokyphus remains - disarticulated bones (including dentaries and maxillae with cheek teeth in situ) and isolated teeth - from a Liassic age deposit in a neptunian dyke at Windsor Hill in Somerset. This assemblage consists largely of the remains of two adult forms of different size. Kuhne gave these forms different binomials, for convenience, without believing that they were necessarily different species. The larger form he called Oligokyphus major and the smaller form O. minor. The two forms are distinguished simply on the number of cheek teeth, and the nature of the terminal upper and lower cheek teeth. The Windsor Hill assemblage also includes a few remains of a small unnamed form.

In the following description, the Welsh material will be compared to the dental material from Windsor Hill. Kuhne's assemblage is housed in the British Museum (Natural History) and the specimens which he catalogued carry an 'R' prefix.

Description

Cheek teeth with a full cusp complement

The majority of the cheek teeth in the assemblage exhibit the full complement of cusps which characterise the genus Oligokyphus. In the upper cheek teeth, this comprises three buccal, four medial and four lingual cusps; in the lower cheek teeth, three buccal and three lingual cusps. By analogy with the Oligokyphus dentitions from Windsor Hill, these teeth are ascribable to a pre-ultimate, or functional position, and this is supported by the functional wear seen on many specimens of all sizes. Almost every functional cheek tooth is incomplete. The size ranges of the upper and lower specimens are considerable (cf figures 28 & 29).

The general morphology of Oligokyphus functional cheek teeth has been fully described by Kuhne and need not be repeated. The functional upper and lower cheek teeth are, in each case, effectively morphologically uniform (with a few rare exceptions). There is no variation which enables specimens to be placed in groups which might correspond to different positions along the tooth row or different forms of Oligokyphus. Examination of the functional cheek teeth in the Windsor Hill dentitions similarly reveals no consistent variation along the tooth row (with the exception of the fifth upper cheek tooth in a few maxillae of Oligokyphus minor where the number of cusps is reduced). There is also no variation between the functional cheek teeth belonging to the different forms of Oligokyphus from the Mendip locality.

The functional upper cheek teeth:

There are about three hundred and twenty functional upper cheek teeth in the assemblage. Of these, only one specimen has a perfectly intact crown, and this is illustrated in figure 27. Very few of the specimens have any remains of roots. The majority of these teeth are morphologically indistinguishable from the functional cheek teeth in the Windsor Hill assemblage.

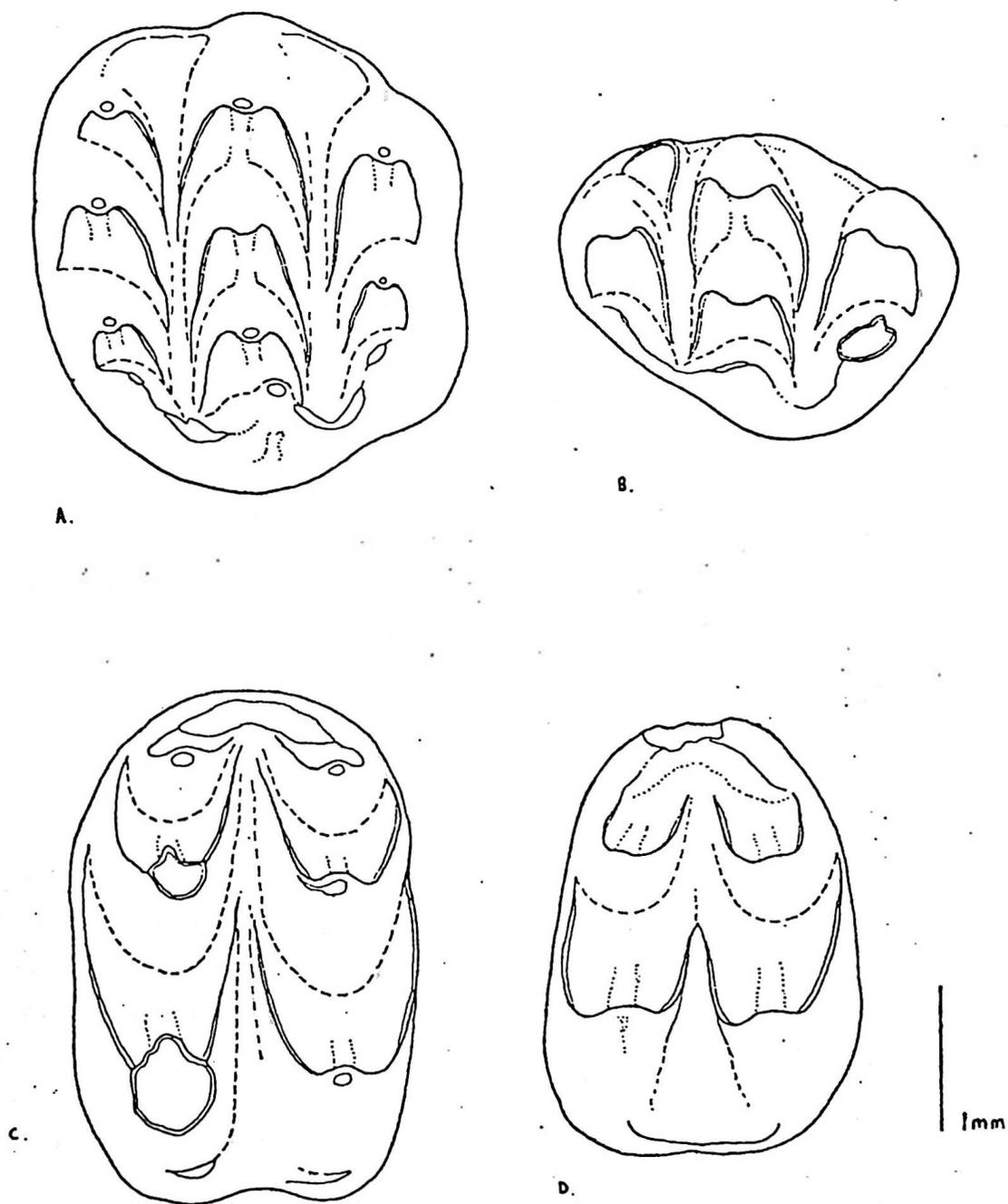


Figure 27 Oligokyphus. Crown views of cheek teeth. All specimens orientated so that mesial end is below.

A, Right functional upper (T.70); B, right ultimate upper (T.78);  
 C, left functional lower (T.95); D, lower from distal end of adult  
 dentition - probably penultimate tooth (T. 96).

In any large collection of teeth, a few variations on the normal morphological pattern may be expected and this is the case here.

Three functional upper cheek teeth exhibit a tiny supernumery cuspule. In two of the specimens the cuspule is situated directly lateral to the buccal edge of the crescent face of the third buccal cusp (B3). This cuspule corresponds exactly in size and position to the cuspule described by Kuhne (p.74) on the crowns of some of the Windsor Hill upper cheek teeth. Five of the maxillae of Oligokyphus minor and one of the maxillae of Oligokyphus major that are figured by Kuhne (text figure 23) possess one upper cheek tooth on which the cuspule is developed. Both of the Welsh teeth are the size of Oligokyphus minor specimens. It is quite possible that the cuspule was originally present on other upper cheek in the Welsh assemblage, and has been obliterated during the course of post-mortem transportation. Its marginal position on the crown would have rendered it particularly susceptible to abrasion.

In the third upper cheek tooth which exhibits a supernumery cuspule (T.77), the cuspule is situated directly mesial to the centre of the crescent face of the B 3. This tooth has no counterpart amongst the functional upper cheek teeth from Windsor Hill.

One functional upper cheek tooth crown from Pant 4 exhibits an extra, fully differentiated cusp. It is the only known upper cheek tooth of Oligokyphus which does so. The crown is damaged, the lingual row of cusps being almost entirely obliterated, although the medial and buccal rows are intact. The extra cusp occurs in front of the normal B2, where there are two fully differentiated cusps. The first of these is ridge-like and normal for a B 1. The second is in some ways intermediate between a normal B 1 and a B 2. It is basically ridge-like, and, like the preceding cusp, without a crescent-shaped anterior face. However, unlike the preceding cusp, its antero-buccal edge resembles that of a normal crescent-faced cusp. The two anterior cusps are both smaller than a normal B 1, being approximately half its size.

No functional upper cheek tooth from Pant 4 corresponds to the reduced fifth upper cheek tooth which is present in some of the maxillae of Oligokyphus minor.

#### Functional Lower cheek teeth:

There are over two hundred and ninety functional lower cheek teeth. Only six specimens have completely intact crowns, and one of these is illustrated in figure 27.

Part of the roots (which are always incomplete) are preserved in about half the specimens. This is a higher proportion than that found in the case of the functional upper teeth, and it reflects the slightly more robust, hence fracture-resistant, nature of the roots of the lower teeth.

As in the case of the functional upper cheek teeth, the functional lowers are morphologically indistinguishable from their Windsor Hill counterparts. Rather surprisingly, there are no variations on the normal crown pattern, and the same is true of the Windsor Hill specimens.

#### Wear of the functional cheek teeth:

The water wear on most of the functional cheek teeth from Pant 4 makes it impossible to assess reliably the exact extent of their functional wear. Unidirectional striae of the type seen in the enamel grooves of some of the Windsor Hill specimens are hardly ever discernible.

Amongst the upper cheek teeth the cusps of the lingual row have been more commonly obliterated by post-mortem abrasion than those in either of the other rows. In the upper cheek teeth from Windsor Hill the lingual row is normally the most worn through use, and the two facts are probably related: in the Welsh specimens, if the lingual row was the most worn and hence had the greatest exposure of dentine prior to fluvial transportation, this row would have been the most susceptible to subsequent abrasive reduction.

The visible wear on the Welsh cheek teeth accords in pattern with that described in Kuhne on the specimens from Windsor Hill. The upper and lower cheek teeth in figure 27 exhibit only a slight degree of ante-mortem wear. On the upper tooth the enamel is intact everywhere except on the apices of the cusps (the M3 excepted) and on the mesial ridges of the crown where these enclose the longitudinal grooves. On the lower tooth enamel has also been worn from the cusp apices and it has been worn from the distal border of the central groove. The small areas of exposed dentine on these teeth merge

smoothly with the surrounding enamel; in other specimens the exposed dentine is at a slightly lower level than the surrounding enamel. There are no functional cheek teeth from Pant 4 that are less worn than the two figured specimens but there are many which exhibit evidence of greater wear. In a few specimens the cusps have been completely worn away leaving enamel tracts - the floors of the longitudinal grooves - as the only crown landmarks. It is impossible to be certain in the case of most of these specimens that this extreme condition is not the result of a post-mortem abrasion. Where the outer edges of the upper cheek teeth have retained their enamel intact, however, this cannot be the case. Very worn cheek teeth occur in mature dentitions of Oligokyphus major and minor in the Windsor Hill assemblage, but not in every instance. Thus, for example, in mature maxilla R/254 the first four teeth are very heavily worn, whilst in mature maxilla R7026, the teeth are relatively little worn (these maxillae are shown in Kuhne's text figure 23). It seems therefore that extreme wear is only produced in non-deciduous teeth after prolonged use. The very heavily worn cheek teeth in the Welsh collection must thus have come from the dentitions of relatively old individuals. These specimens occur, as rarities, amongst cheek teeth of all except the smallest size.

It is clear from Kuhne's account of cheek tooth wear in Oligokyphus, and from a detailed examination of the specimens (particularly those in the Windsor Hill assemblage), that this wear was bimodally produced. The planing down of exposed dentine below the level of the surrounding enamel on the wear facets of some specimens is characteristic of the kind of attrition produced by food on the tooth during mastication (Every and Kuhne, 1971). On the other hand, the unidirectional striae seen in the surfaces of the wear facets on some teeth and the flush junctions of exposed enamel with surrounding dentine at the edges of facets on certain teeth can only have been produced by the action of tooth against tooth; in other words by thegnosis (Every and Kuhne 1971).

#### Measurements and statistical data:

Figures 28 & 29 show the plotted lengths and breadths of functional upper and lower cheek teeth from the Welsh and English localities. The measurements of the Windsor Hill teeth are original and have been made both to obtain larger numerical samples than those given by

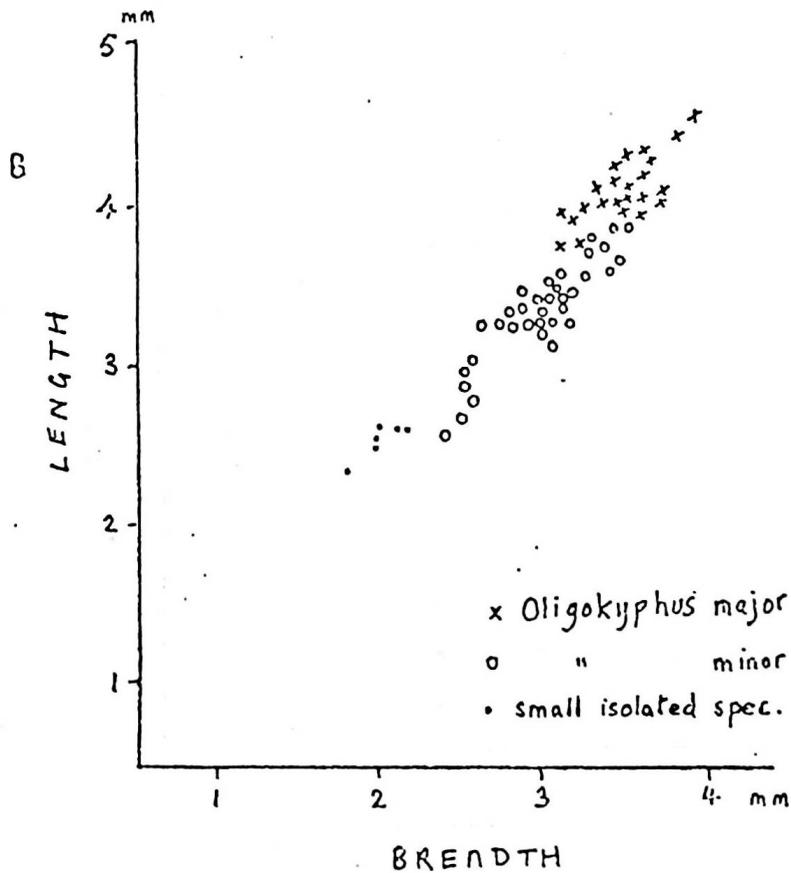
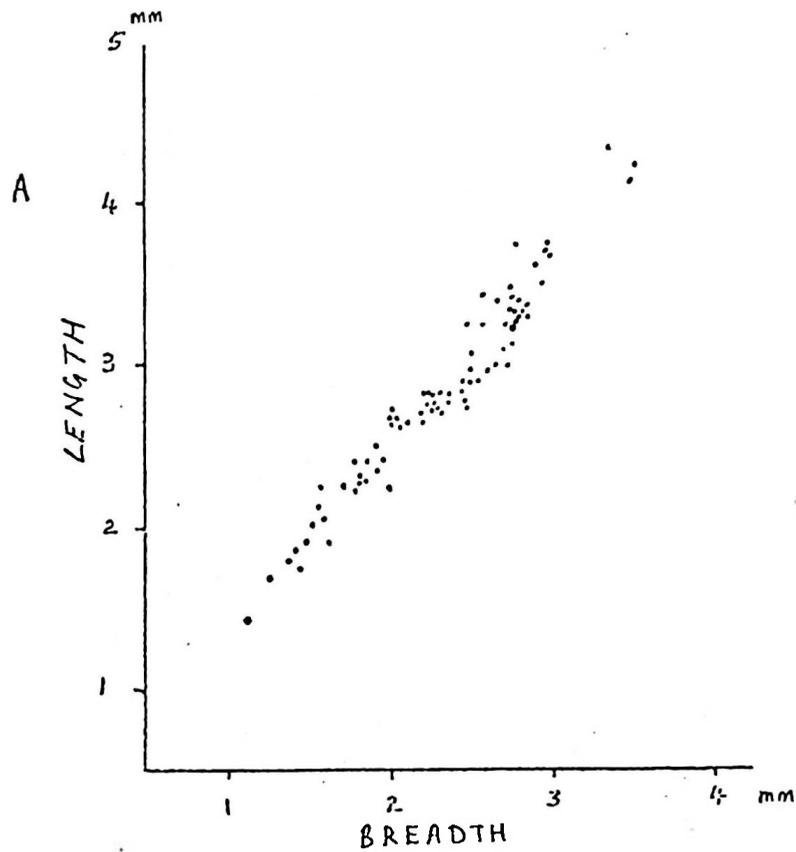


Figure 28 . Oligokyphus.

measurements of length and breadth of upper cheek teeth. Upper diagram :  
Pant 4 specimens, lower diagram : Windsor Hill specimens.

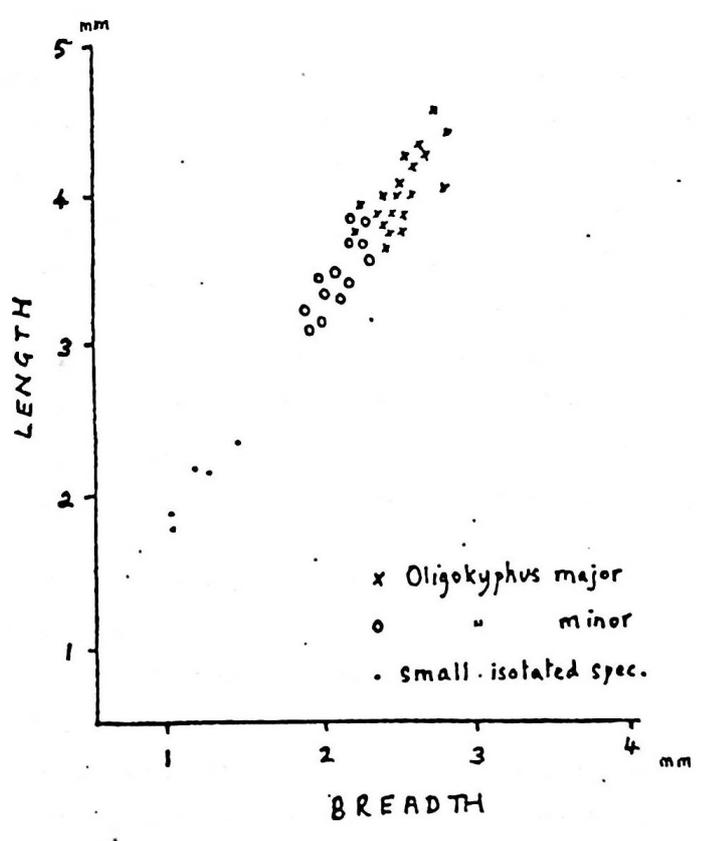
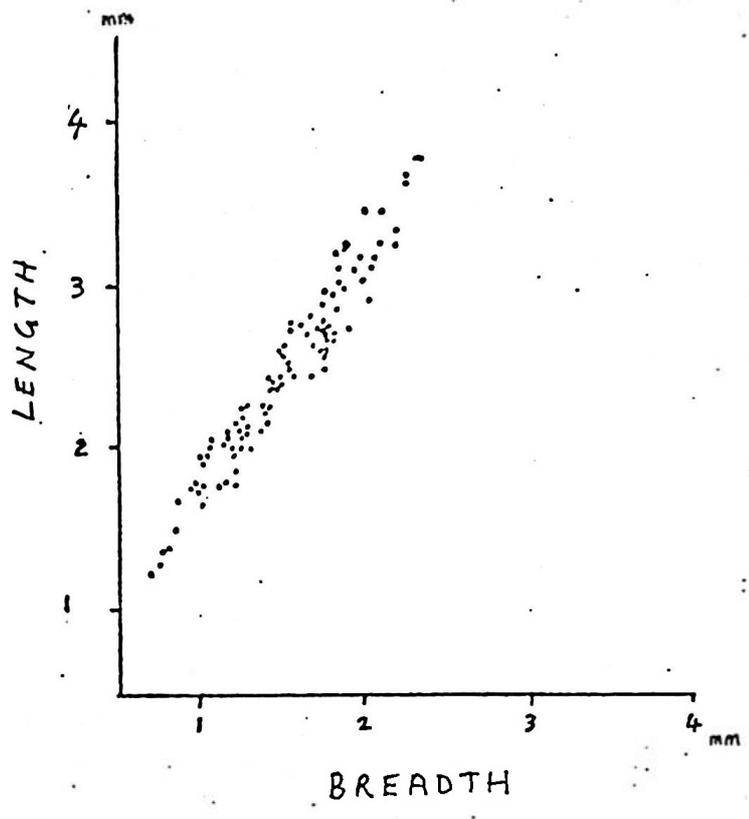


Figure 29 Oligokyphus. Measurements of length and breadth of lower cheek teeth. Upper diagram : Pant 4 specimens. Lower diagram : Windsor Hill specimens.

Kuhne (Kuhne's text figures 39 and 40) and to ensure that the dimensions of the teeth from the two localities which are compared have been defined in exactly the same way. The length of an upper cheek tooth is defined as the distance from the distal edge of the M4 to the mesial edge of the M1. The breadth is the distance between the extremities of the tooth on a line which passes at right angles to the length, immediately mesial to the M3. The length of a lower cheek tooth is defined as the distance from the distal extremity of the crown to the mesial edge of the median trough. The breadth is the distance between the extremities of the crown on a line which passes at right angles to the length directly distally to the mesial cusps of each row.

With the exception of the three largest upper cheek teeth, there is no separation. The size distribution of the measured upper cheek teeth from Pant 4 (figure 28) is distinctly bimodal: the three largest specimens are substantially larger than the rest. The size distribution of the lower cheek teeth from Pant 4 (figure 29) is, by contrast, unimodal. The size distribution of the upper cheek teeth from Windsor Hill (figure 28) is also unimodal: the size ranges of the specimens belonging to Oligokyphus major and minor overlap, and the largest of the group of six small isolated teeth is as long as the smallest O. minor specimen. The size distribution of the lower cheek teeth from Windsor Hill is distinctly bimodal: the size ranges of the O. major and minor specimens overlap, but the five small isolated specimens are substantially smaller than the smallest O. minor tooth. The difference between the size distributions of the upper and lower Windsor Hill teeth is accounted for by the fact that the O. minor upper cheek teeth include specimens from two sub-adult dentitions (R7048 and 7049 - see Kuhne, text figure 23) whilst the O. minor lower cheek teeth are all from mature dentitions.

Comparing the sizes of the teeth from the two localities, we observe that the three largest Welsh upper cheek teeth are the size of moderate O. major specimens. They are larger than functional teeth occurring in the maxillae of O. minor. The fact that these three teeth are well separated in size from the remaining upper cheek teeth minimises the possibility that they belong to dentitions which are also represented by some of the smaller specimens. The larger specimens among the lower cheek teeth and the main group of upper cheek teeth from Pant 4 are of Oligokyphus minor size. In each case

they span the full size range of the Windsor Hill specimens belonging to this form. At least one discreet form of Oligokyphus substantially smaller than an O. minor is represented by the remaining Welsh specimens.

It is notable that the ratios of crown length and breadth are not constant throughout the size ranges of the upper and lower teeth from the two localities. Thus, for example, the larger upper cheek teeth in each case are proportionally longer than the smaller specimens. If the sets of measurements are converted to the logarithmic scale the varieties of the teeth within specific size intervals acquire a high linear correlation as can be seen in figures 30, 31, 32, & 33. In other words, within each specific size interval, multiplication (or division) of crown length and breadth is constant with change of size (on the logarithmic scale, equal spaces on the graph denote equal multiplication). The relationship between the varieties length (x) and breadth (y) can therefore be expressed by the allometric equation first formulated by Huxley (1932):

$$y = bx^a$$

Where coefficient a is the ratio of the multiplications of the varieties with increase in size (and may be called the constant differential multiplication ratio), and coefficient b is the value of y when x = 1 (and may be called the inherent or initial proportionality index). a is thus a pure number, without dimensions, whilst b has dimensions which are dependent upon the value of a, and therefore varies under change of scale. In spite of this both coefficients have a separate and independent biological significance, as a number of workers have clearly demonstrated (see for example White and Gould, 1965). Given the values of a and b and substituting the values of y, the relationship of the varieties may be plotted as a curve. On the logarithmic scale, the linear expression of the relationship becomes:

$$\log y = \log b + a \log x$$

The allometric relationships between length and breadth will be compared for the groups of cheek teeth from the two localities. Coefficients a and b are most conveniently estimated by fitting a trend line to the logarithmic data (coefficient a is the slope of the trend line). The method used in calculating the values of a and b will depend upon the type of trend line that one wishes to fit. If Regression lines are used, one of the varieties must be designated independent, the other dependent. Since in the case of teeth there

is no basis for deciding that length is the factor which directly determines breadth (or vice-versa), Regression lines are inappropriate. The trend line that has in fact been calculated for each group of cheek teeth is the reduced major axis of Kermack and Haldane (1950), which does not minimise the sum of the squares of the deviations of one of the variates. Table 4 shows the estimates of  $\underline{a}$  and  $\underline{b}$  for the various groups of cheek teeth from the two localities, obtained by fitting reduced major axes by means of the short method of Kermack and Haldane (1950). The estimates of  $\underline{b}$  are expressed as logarithms for the purposes of convenience. In each case the standard errors of the coefficient estimates are also given together with the estimates of the coefficients of correlation for the logarithmic distributions. It will be noted that in the case of each group of teeth the linear correlation of the variates is high. The allometric relationships between the lengths and breadths of the upper cheek teeth from the two localities will be considered first.

(1) The Pant 4 specimens:

Figure 30 shows the distribution of the logarithmic data about the reduced major axis for the group comprising all the Welsh specimens. It will be observed that although the smaller specimens are normally distributed about the reduced major axis, those with a log y value of over 0.8 have a slightly skew distribution across it. The data therefore appears to constitute at least two linear groups connected by a point of inflection where log y equals 0.8. The table shows the estimates of  $\underline{a}$  and  $\underline{b}$  obtained by fitting separate reduced major axes to the data above and below this point of inflection. Both the coefficient estimates for the specimens above the point of inflection are significantly different from those for the specimens below it. It is therefore clear that the larger upper cheek teeth from Pant 4 (i.e. those where log y exceeds 0.8) are allometrically distinct from the smaller cheek teeth. This distinction is only biologically significant with regard to the difference in  $\underline{a}$ ; the difference in  $\underline{b}$  has no definite biological meaning because it is inverse to the difference in  $\underline{a}$  and the reduced major axes of the two groups of teeth intersect at a point where log x is greater than unity (see White and Gould, 1965, for discussion). Figure 31 shows that the reduced major axis for each allometrically distinct group of teeth fits all the specimens within that group. There is therefore no need to postulate the presence of more than two allometrically distinct

TABLE 4

<u>Tooth type</u>	<u>Locality</u>	<u>Group</u>	<u>Coefficient a</u>	<u>Log. Coefficient b</u>	<u>Coefficient of Correlation</u>
Upper cheek teeth	Pant 4	All specimens	1.15969±0.0458	-0.3682±0.079	0.9346
		Specimens where log y exceeds 0.8	0.8806±0.048	-0.0449±0.088	0.92518
		Specimens where log y = 0.8 or less	1.0161±0.0457	-0.2661±0.074	0.9669
	Windsor Hill	<u>0.major</u>	0.8664±0.0881	0.0378±0.1730	0.8504
		<u>0.minor</u>	0.9741±0.0771	-0.0818±0.143	0.89041
		6 tiniest specimens	1.63665±0.31	-0.82654±0.526	0.88517
		<u>0.major</u> and <u>minor</u> combined	0.88096±0.0414	0.02395±0.079	0.92768
Lower cheek teeth	Pant 4	All specimens	1.1656±0.029	-0.6463±0.058	0.9688
	Windsor Hill	<u>0.major</u>	1.1309±0.107	-0.6488±0.197	0.8745
		<u>0.minor</u>	1.1838±0.160	-0.7283±0.293	0.9039
		Smallest teeth	1.2137±0.110	-0.7420±0.175	0.9790
		All specimens	1.1827±0.035	-0.7210±0.08	0.9815

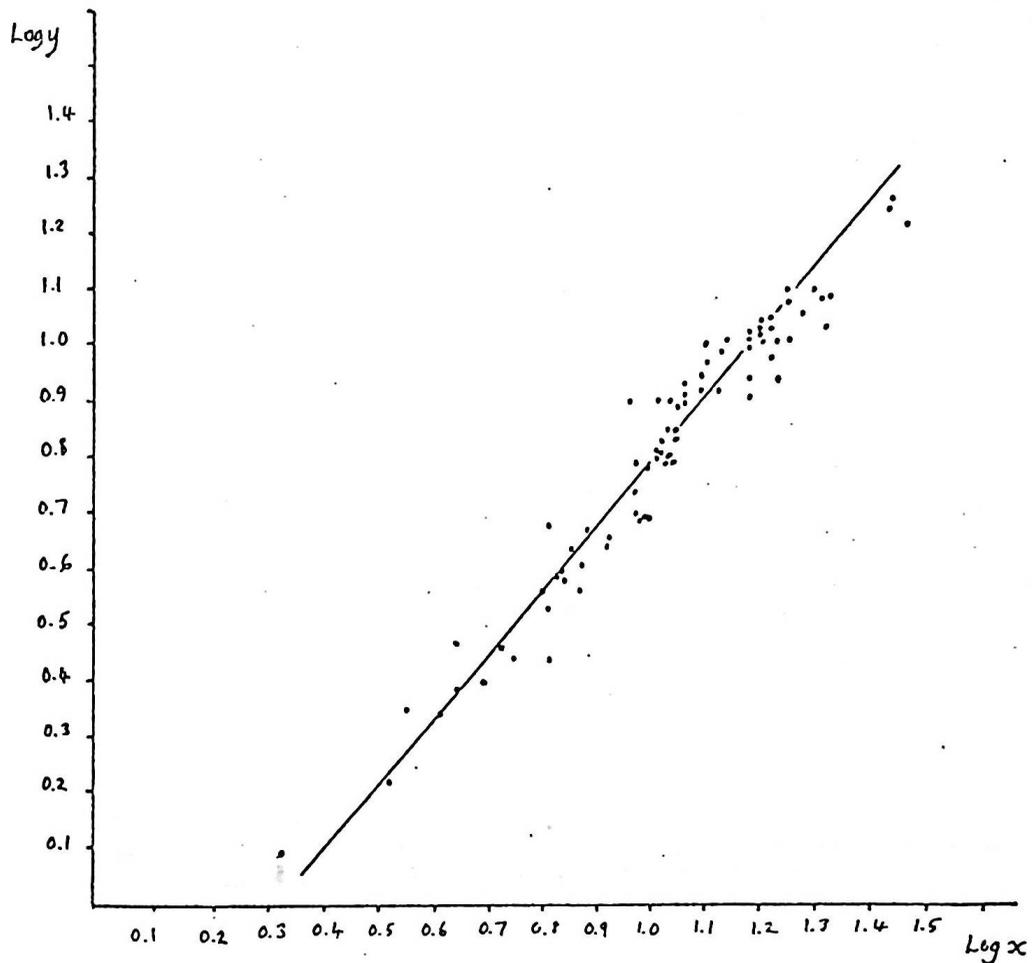


Figure 30. Oligokyphus. The distribution of the logarithmic data pertaining to all of the measured functional upper cheek teeth from Pant 4. A single reduced major axis has been fitted to the data.

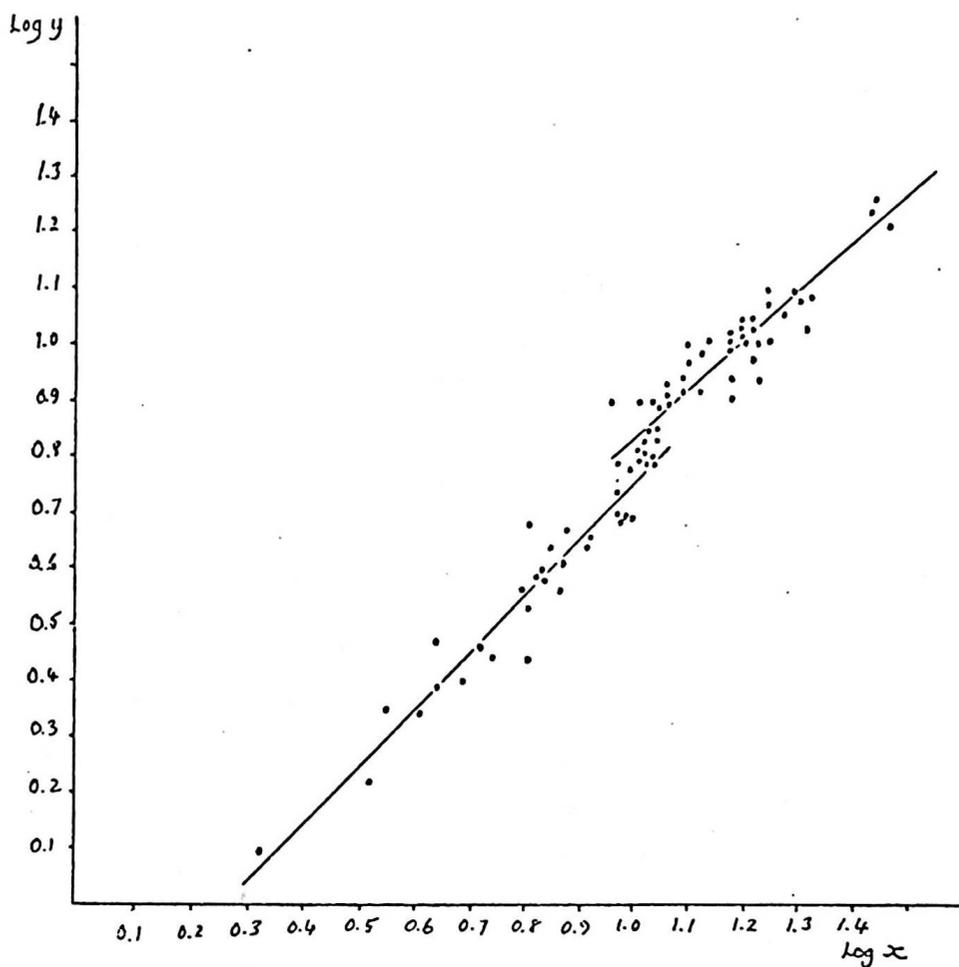


Figure 31. Oligokyphus. The distribution of the logarithmic data pertaining to all of the measured functional upper cheek teeth from Pant 4. Separate reduced major axes have been fitted to the data above and below the point where  $\log y = 0.8$  (see text for explanation).

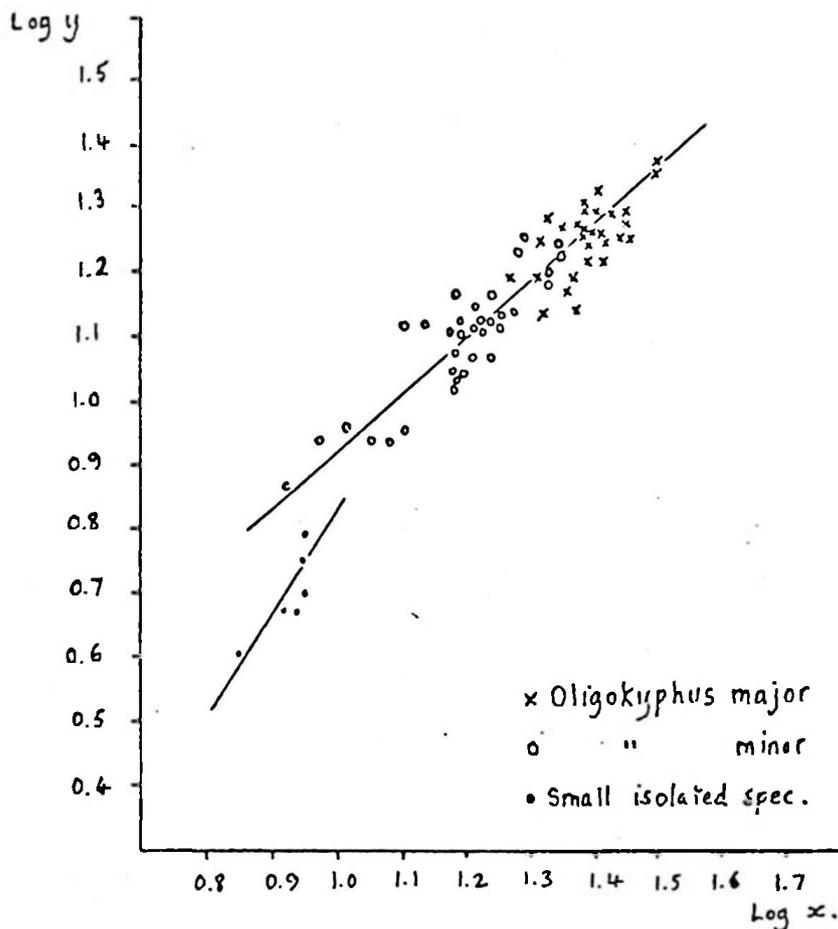


Figure 32. Oligokyphus. The distribution of the logarithmic data pertaining to all of the measured functional upper cheek teeth from Windsor Hill. Separate reduced major axes have been fitted to the data pertaining to (a) the group of six very small specimens, and (b) the group comprising the remaining specimens (i.e. those which belong to O.major and minor).

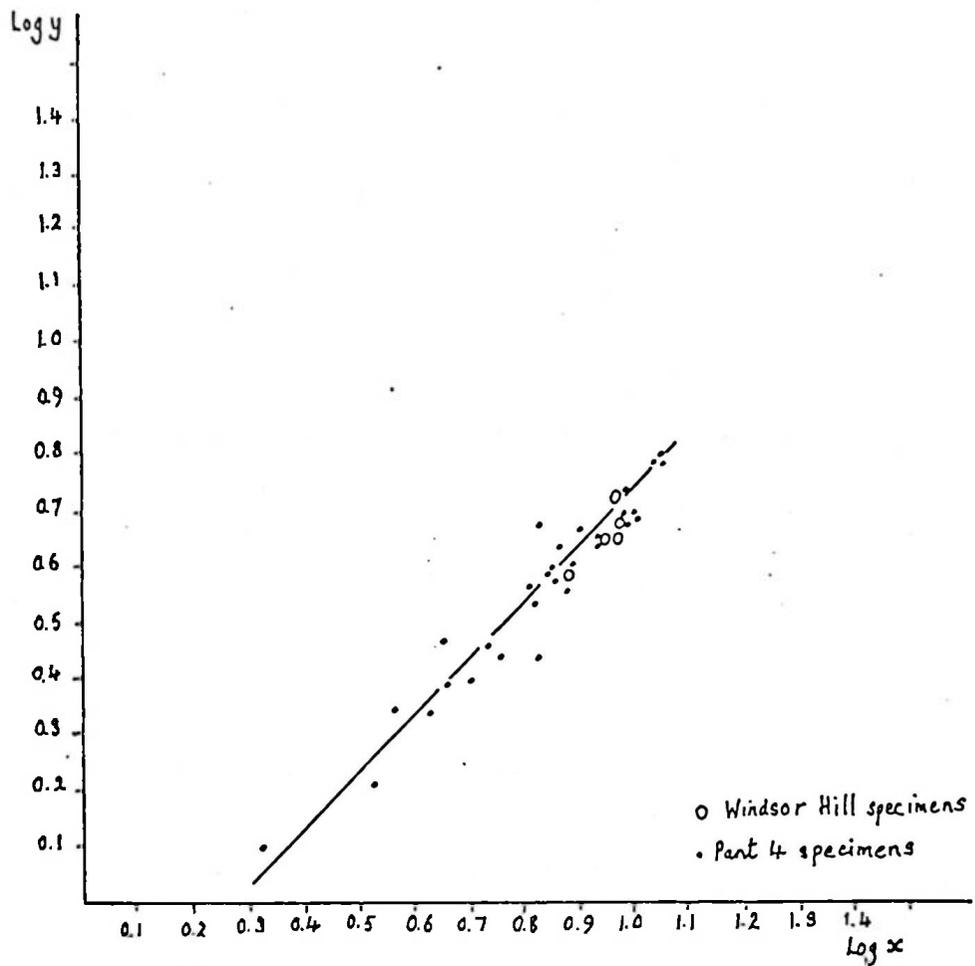


Figure 33. Oligokyphus. The distribution of the logarithmic data pertaining to (a) the smaller Part 4 functional upper cheek teeth, and (b) the five smallest Windsor Hill specimens about the reduced major axis which was fitted to the former set of data in figure 31.

groups of upper cheek teeth within the Pant 4 material.

(2) The Windsor Hill specimens:

Table 4 shows that there is no significant difference between Oligokyphus major and minor in the estimates of a or b. The specimens belonging to these forms have therefore been combined into a single group, and a single reduced major axis has been fitted to the logarithmic data (figure 32). The distribution of the points about this reduced major axis is normal, so that the upper cheek teeth of O. major and minor are allometrically indistinguishable. The estimates of a and b for the six smallest Windsor Hill specimens both differ significantly from those for the major and minor teeth. Figure 32 shows that this is not simply a question of the small sample size of the group of six; the majority of specimens in this group are quite clearly allometrically distinct from the teeth of O. major and minor. As in the case of the two allometrically distinct groups of upper cheek teeth from Pant 4, this distinction is only biologically significant with regard to the difference in a. The reason for this is the same.

(3) Comparison:

Comparing the upper cheek teeth from the two localities it is seen that the point of differentiation between the allometrically distinct groups in each case occurs approximately where log y equals 0.8. The estimates of a and b for the group of larger Welsh specimens do not differ significantly from those for the Windsor Hill group of major and minor specimens. In other words the Oligokyphus major and minor sized specimens from the two localities are allometrically indistinguishable.

There is a significant difference between the group of smaller Welsh specimens and the group of six small Windsor Hill specimens in the estimates of both a and b. This does not necessarily have any biological significance however because the Windsor Hill specimens constitute too small a statistical sample to permit a satisfactory comparison (each tooth exerts a disproportionately large effect upon the coefficient estimates compared to that exerted by an individual Welsh specimen). The distribution of the logarithmic data from the group of six Windsor Hill specimens (figure 32) is such that the largest specimen can be as easily accommodated in the linear series of the Oligokyphus major and minor specimens as it can in that of the

remaining members of the group. If this tooth in fact comes from a sub-adult O. minor dentition - which is possible - then the estimates of a and b for the group of six will be reflecting a relationship which has no biological meaning. An important point is that if the largest of the group of six Windsor Hill specimens is omitted, the remaining specimens are well accommodated by the reduced major axis that has been fitted to the group of small Welsh specimens (figure 33). In these circumstances it is obviously not legitimate to conclude that the five smallest Windsor Hill specimens belong to a different allometric series from the similar sized Welsh specimens.

The lower cheek teeth from the two localities will now be considered.

(1) The Pant 4 specimens:

Figure 34 shows that the logarithmic data from the group comprising all the Welsh specimens has a normal distribution about the reduced major axis. There is therefore no need to postulate the existence of any allometric distinction between the lower cheek teeth of any of the forms of Oligokyphus which are represented in the Welsh assemblage.

(2) The Windsor Hill specimens:

Table 4 shows that there is no significant difference between Oligokyphus major, minor and the group of small specimens, in the estimates of a or b. All the lower cheek teeth from Windsor Hill have therefore been combined into a single group and a single reduced major axis has been fitted to the logarithmic data (figure 35). The distribution of the points about this reduced major axis is normal. The lower cheek teeth of O. major and minor and the smallest specimens are thus allometrically indistinguishable.

(3) Comparison:

There is no significant difference between the lower cheek teeth from Pant 4 and Windsor Hill in the estimates of a and b. The lower cheek teeth from the two localities are thus allometrically indistinguishable.

2. Other Cheek Teeth

In addition to the functional cheek teeth described above, there are a number of upper and lower Oligokyphus cheek teeth in the Welsh assemblage which exhibit a reduction in the number of their crown cusps. Cheek teeth of this kind occur in the mature dentitions of

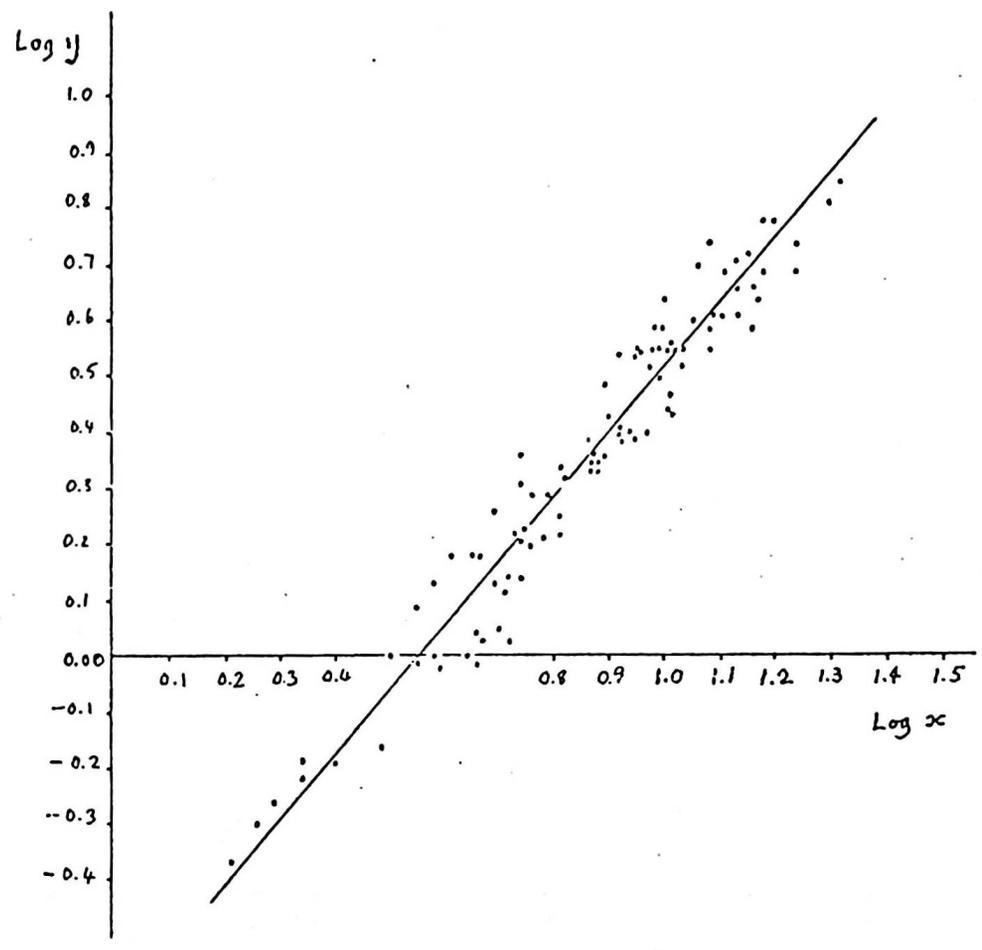


Figure 34. Oligokyanus. The distribution of the logarithmic data pertaining to all of the measured functional lower cheek teeth from Pant 4. A single reduced major axis has been fitted to the data.

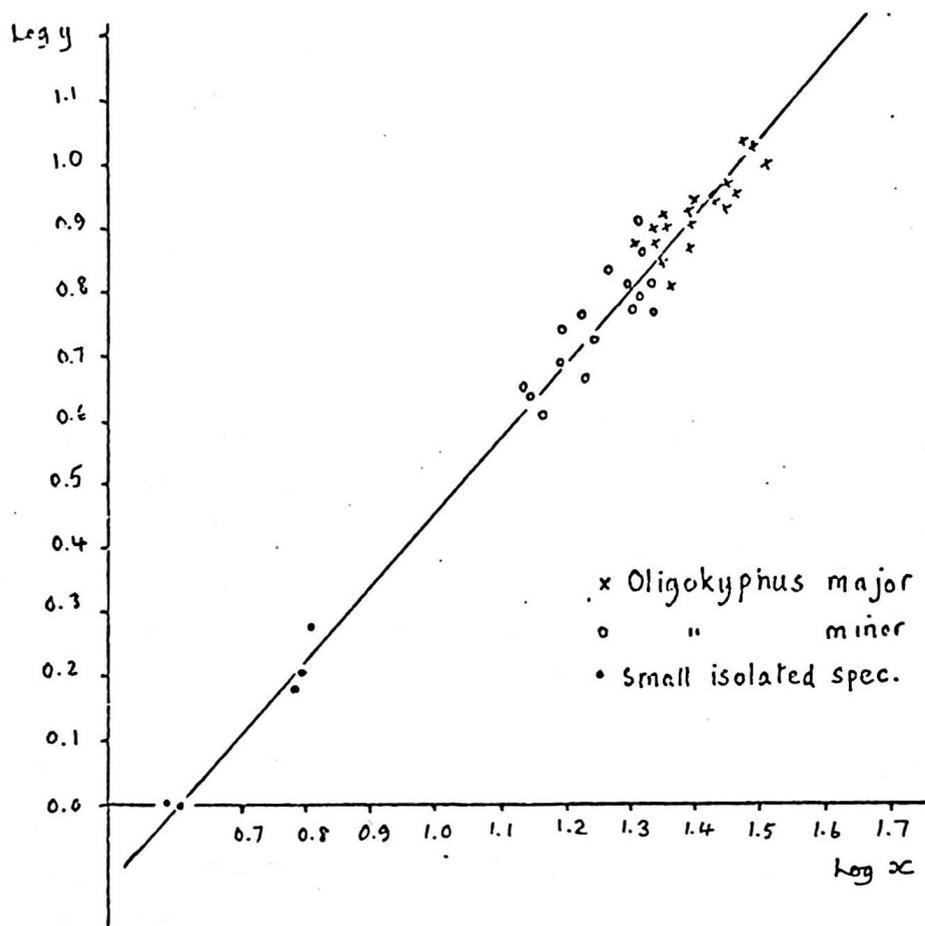


Figure 35. Oligokyphus. The distribution of the logarithmic data pertaining to all of the measured functional lower cheek teeth from Windsor Hill.

Oligokyphus major and minor in the Windsor Hill assemblage, where they occupy terminal positions at the distal end of mature tooth rows. The Pant 4 reduced cheek teeth demonstrate that at least some of the Oligokyphus individuals which are represented in the assemblage are adults. This supports the inference drawn from the study of ante-mortem wear in the functional teeth.

Reduced upper cheek teeth:

Fourteen of the reduced cheek teeth are from upper dentition. Except for one very small specimen, all are of similar size to the ultimate upper cheek teeth in the adult Oligokyphus minor dentitions from Windsor Hill. The O. minor sized specimens will be considered first. Only four of these have unbroken crowns and in only one case is the crown completely devoid of postmortem wear. None of the specimens has any remains of the roots. In the undamaged crown T 78 the buccal row contains only two cusps, the second of these being in the position of a normal third, relative to the ultimate cusp (see figure 27). The medial row comprises three cusps. The first of these does not bear the usual wrinkled mesial face and its position relative to the distal cusp is that of a normal second medial cusp. The lingual row has three cusps, the second of which, by its position and size corresponds to a normal L3. The first cusp is ridge-like and the last is slightly reduced. By homology with a cheek tooth from a more mesial position, T 78 has eliminated the first cusp of each row and reduced the L2 and L3 cusps. The morphology of the crown is almost identical to that of the ultimate upper cheek tooth in Oligokyphus minor maxillae R 7208 (see fig 36). In the case of the three other relatively intact O. minor sized the same cusps are eliminated as in T 78. In addition however these specimens have also lost the L4. These teeth are identical to the ultimate upper cheek tooth in O. minor maxilla R 7354. In the damaged specimens of Oligokyphus minor size, either the lingual or buccal row of cusps has been broken off. Six teeth have lost the lingual row. In each of these specimens the B1 and M1 are eliminated. These teeth are therefore unlike the ultimate upper cheek tooth in Oligokyphus major maxilla R 7031, where the B1 is present. (This maxilla is the only O. major maxilla in the Windsor Hill assemblage where a reduced cheek tooth is preserved. All the other maxillae are broken off behind the last functional tooth, or more mesially). In two of the three reduced upper cheek teeth where the buccal row has been broken off, the L1 and M1 are

CUSP ELIMINATED						
SPECI-MEN	B1	M1	L1	L4	L2	Other
T. 78	X	X	X			
T. 82	X	X	X	X		
T. 79	X	X	X	X		
T. 83	X	X	X	X		
T. 88	?	X	X			
T. 85	?	X	X			
T. 89	?	X				
T. 86	X	X	?	?	?	
T. 93	X	X	?	?	?	
T. 87	X	X	?	?	?	
T. 87	X	X	?	?	?	
T. 90		X	?	?	?	
T. 700	X	X	?	?	?	

CUSP ELIMINATED						
SPECIMEN	B1	M1	L1	L4	L2	Other
R. 7031		X	X			
R. 7205	X	X	X			
isol. spec.	X	X	X			
" "	X	X	X			
" "	X	X	X			
" "	X	X	X			
R. 7254	X	X	X	X		
isol. spec.	X	X	X	X		
" "	X	X	X	X		
" "	X	X	X	X		
" "	X	X	X		X	
" "	X	X	X		X	
" "	X	X	X		X	
" "	X	X	X	X	X	
" "	X	X	X	X	X	
R. 7206	X	X	X	X	X	
R. 7038	X	X	X	X	X	(M2) X

Figure 36 Oligokyphus. Cusp elimination in ultimate upper cheek teeth. Left diagram : Pant 4 specimens. Right diagram : Windsor Hill specimens.

eliminated. The remaining specimen, T 89, is unique in that the medial cusp row is reduced but the lingual is not. There are only three cusps in the medial row, and the first of these does not have the usual wrinkled mesial face. It therefore evidently corresponds to the normal M2. The normal M1 is indicated by a slight mesial prominence.

The smallest reduced upper cheek tooth in the assemblage, T 217, exhibits the greatest level of cusp elimination known in any definitive Oligokyphus upper cheek tooth. The specimen is illustrated in figure 37 in the orientation in which it will be described. The crown bears two intact cusps, one situated medially, the other laterally. Each cusp clearly represents one longitudinal cusp row. To the left of the median cusp there is a damaged area where a lateral cusp has probably been broken away. The right lateral cusp almost certainly represents the buccal cusp row because of the relative width of the groove which separates it from the medial cusp. Mesial to the cusps is a basionid region which is partly enclosed at the front by a small median ridge. The lateral edges of the buccal and lingual cusps extend forward to this ridge and each bears a small cuspule. There is also a cuspule in the middle of the crescent face of the median cusp. These three cuspules and the median ridge may be the vestiges of lost cusps. The two intact cusps clearly correspond to the largest buccal and medial cusps on a normal tooth (the B3 and M3), and they are approximately the same size as their homologues in an Oligokyphus minor ultimate tooth. On these grounds it is probable that T 217 occupied a still more distal position in the maxilla than the reduced upper cheek teeth described above. Its occurrence in the dentition probably represented a minor variant.

All the reduced upper cheek teeth in the collection are, like their Windsor Hill counterparts, completely devoid of functional wear. The absence of wear on the mesial edges of the crowns where the longitudinal grooves are enclosed is particularly impressive; an unworn condition of the enamel here is never found amongst the functional upper cheek teeth. It is clear that the reduced specimens never attained the occlusal level of the teeth which preceded them. The same is true for the ultimate upper cheek teeth from Windsor Hill. The manifest variation in the morphology of the reduced upper cheek teeth from the two localities contrasts markedly with the uniformity of the upper cheek teeth from more mesial positions. Since the

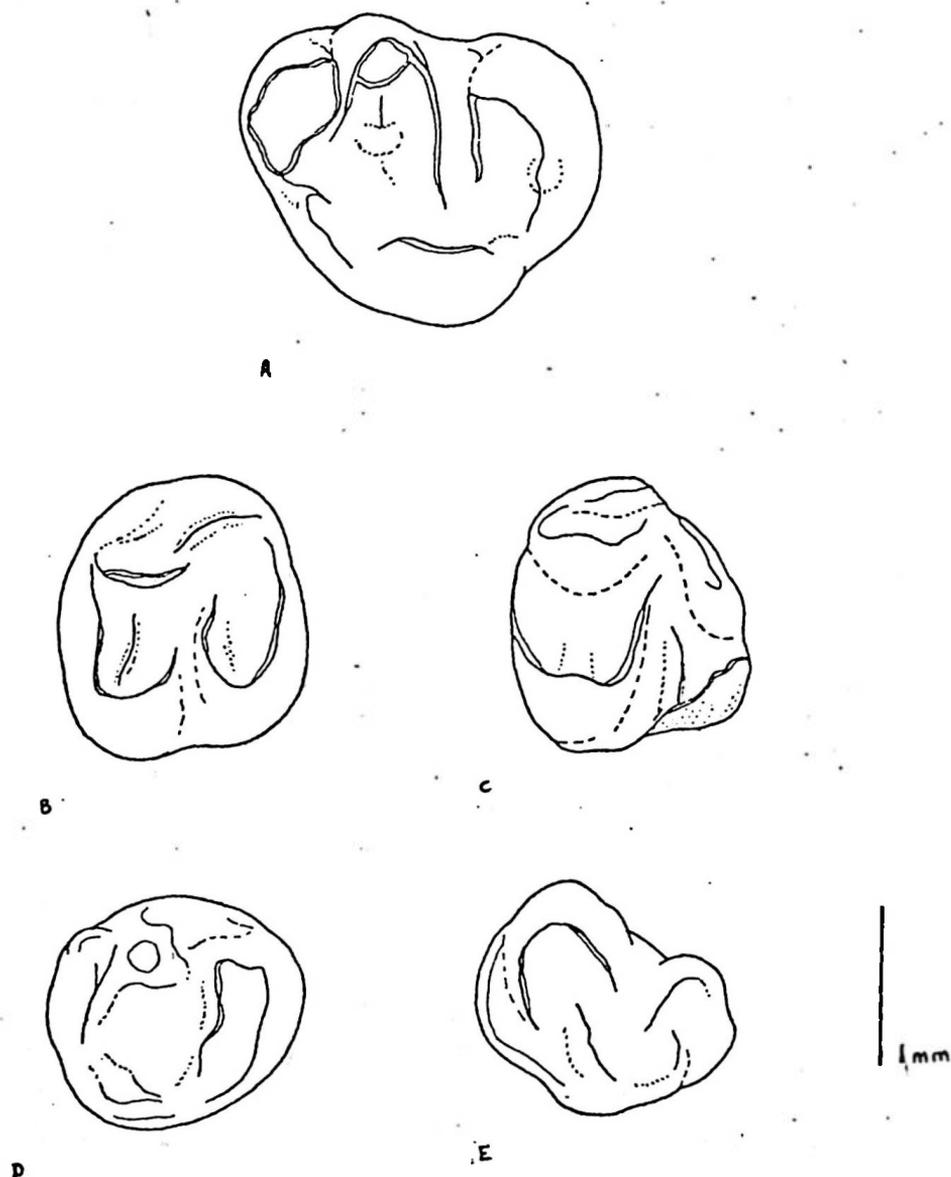


Figure 37 Oligokyphus. Crown views of cheek teeth. Each specimen morphologically unique. First three specimens orientated so that mesial end is below.

A : T 217 ; B : T 184 ; C : T 84 ; D : T 185 ; E : T 181 .

See text for interpretation.

reduced cheek teeth never functioned in occlusion, there was no selective restraint on morphological variation.

Reduced lower cheek teeth:

There are eight lower cheek teeth in which two cusps have been eliminated. Nearly all the crowns of these specimens are substantially intact, although none has any remains of the roots. Their crown morphology is as follows: There are only four differentiated normal cusps, and the cuspules mesial to the first two cusps are not developed. By homology with anterior teeth, it is the third pair of cusps that have been lost, their position being indicated by a slight thickening of the distal rim of the crown. There is no evidence of any functional wear, and this is particularly impressive in the case of the narrow groove between the anterior cusps.

The morphology of these teeth is exactly the same as that of the penultimate upper cheek teeth in the dentaries of Oligokyphus major from Windsor Hill. Examination of the latter reveals that they have normally failed to attain the occlusal level of the preceding cheek teeth. They therefore came into use relatively late in life and in some individuals they may not have come into use at all. The same morphological type of tooth occurs as a penultimate in only one dentary of Oligokyphus minor (R 7173; cf. Kuhne P.81). However the ultimate tooth in at least three O. minor dentaries is of the same morphology (see for example R 7204 in Kuhne's text figure 31). In these dentaries the tooth is unerupted and Kuhne has exposed it by dissection. The size distribution of the measurable Welsh specimens is shown in figure 38 together with that of the morphologically identical teeth from Windsor Hill. It will be noted that the largest Welsh specimen corresponds in size to the specimens which belong to Oligokyphus major. The remainder correspond in size to the specimens which belong to the smaller Mendip form. Of the teeth which are too damaged to be accurately measured, both appear to be of similar size to O. minor specimens.

There are two reduced lower cheek teeth in the assemblage which are very similar to those first described, except that the process of cusp elimination has been carried further. Although both specimens consist of only one side of the crown, it is clear that the intact crown pattern of each was identical to that of the ultimate lower cheek tooth of Oligokyphus major (the same type of tooth is known in

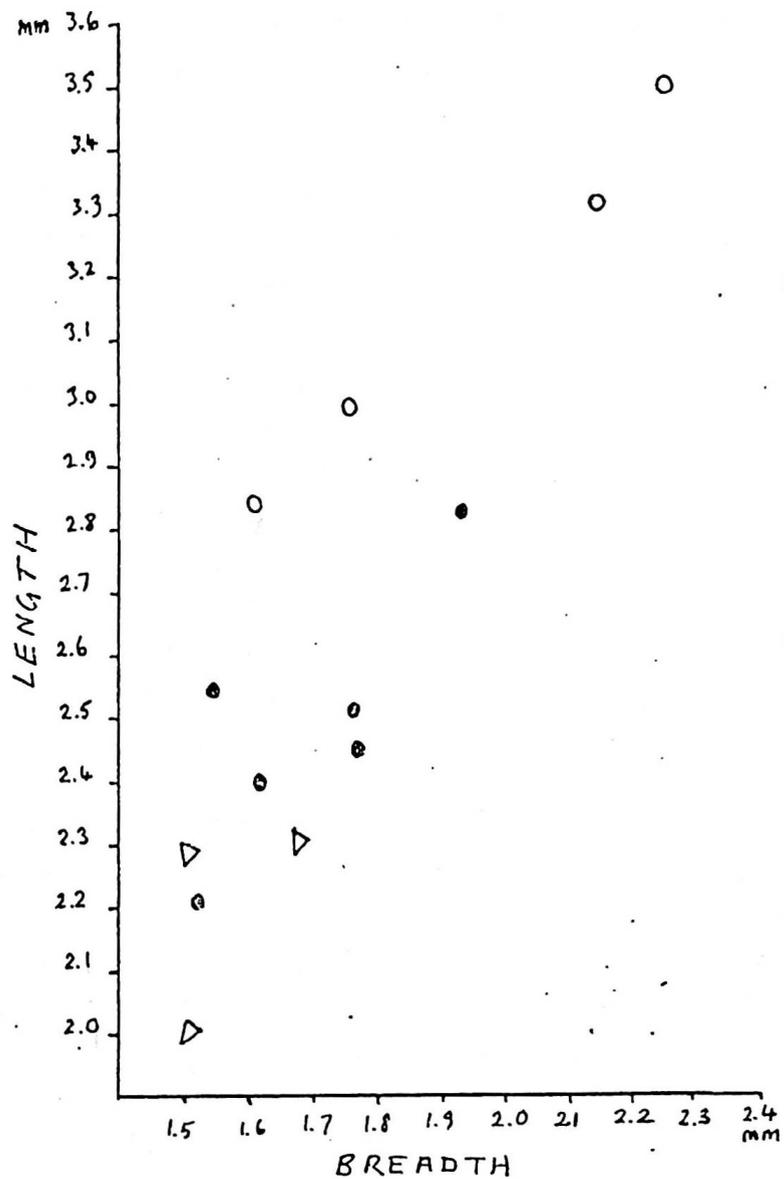


Figure 38 *Oligokyphus*. Crown measurements on lower cheek teeth with only four cusps. Pant 4 specimens = ●. Windsor Hill specimens : O.major = ○; O.minor = ▷

only one of the O. minor dentaries in the Windsor Hill collection - R 7173; c.f. Kuhne 1956:81). In this type of tooth there are two mesial cusps, with the second cusp of each row reduced to a prominence in the terminal ridge of the crown. Both the Welsh specimens are devoid of antemortem wear. One of the specimens has a crown length of 1.84mm the other of 1.25mm.

Two reduced lower cheek teeth from Pant 4 have no counterparts in the Windsor Hill assemblage. The first of them, T 84, is illustrated in figure 37 in the orientation in which it will be described. The crown is asymmetrical, the right side being more reduced than the left. The left side resembles a cusp row in a penultimate tooth of Oligokyphus major in that there are only two cusps followed by a ridge. On the right side there was evidently a mesial cusp which has been broken, and this is followed by a ridge-like distal cusp.

The disparity in width between the left and right cusp rows and the fact that the internal edge of the left mesial cusp blocks the central groove make it clear that the tooth could never have functioned in occlusion. By way of corroboration, the crown is completely unworn.

The second specimen, T 184, is rather smaller. There are only two cusps and these are situated mesially. On the right of the crown (orientating the specimen as in figure 37) the mesial cusp is relatively normal. The crescent face of the left hand cusp however is divided by a prominent median ridge. On the distal edge of the crown there are two transverse, subparallel ridges which may represent the vestiges of lost cusps. There is no evidence of wear and the overlapping nature of the ridges suggests the possibility that the tooth could have functioned in occlusion. In its degree of crown reduction the tooth resembles the ultimate teeth described above, although it is of substantially smaller size.

The sizes of the cusps of T 84 and T 184 suggest that these teeth may be from the distal end of the tooth row of an adult form of substantially smaller size than Oligokyphus minor. Both specimens would fit ultimate alveoli in some of the smallest dentaries from Windsor Hill.

Problematic reduced cheek teeth:

Two cheek teeth remain to be considered. Both are minute and the morphology of the crown is such that neither specimen can be

definitively ascribed to the upper or lower dentition. As the teeth lack any obvious affinity with the other tetrapods that are represented in the Welsh assemblage and, as in each case, some aspect of the crown morphology is suggestive of the normal cheek teeth of Oligokyphus, they are included here, *incertae sedis*. It is likely that both specimens are vestigial teeth which have developed distally to the normal ultimate tooth. Such a tooth occurs in Oligokyphus major dentary R 7121 (Kuhnestext figure 31). The teeth will be described both for the sake of completeness and because of the slight possibility that they have some other significance.

The larger of the two specimens, T 185, has a crown on which there are no differentiated cusps of the normal Oligokyphus type. Instead the crown exhibits several irregular ridges and depressions which give it a superficial resemblance to a murine molar. When the crown is orientated as in figure 37, three ridges are observed running approximately antero-posteriorly. The left pair of ridges are confluent anteriorly and they enclose a basinid area which is suggestive of the normal crescent concave face of a cusp. The right hand ridge is expanded anteriorly and encloses a small depression. At the posterior end of the crown there is a fourth ridge running approximately from left to right. The crown passes imperceptibly into a single root which is broken, and which may well have been open in life. The tooth is completely unworn.

The smaller tooth, T 181, is shown in figure 37 in the orientation in which it will be described. Two well defined cusps occupy a posterior position on the crown. The largest of these has a concave anterior crescent face and resembles a normal cusp. The second, which is offset slightly anteriorly on the right of the first, is almost conical, but possesses a medial anterior ridge which may represent part of a crescent face. A ridge originates on the anterior face of each cusp and passes obliquely forward. These ridges turn towards one another and merge anteriorly to enclose a basinid region. Lateral to the anterior ridge a slight rim passes round the side of the largest cusp enclosing a small crown shelf. This merges into the postero-lateral aspect of the cusp.

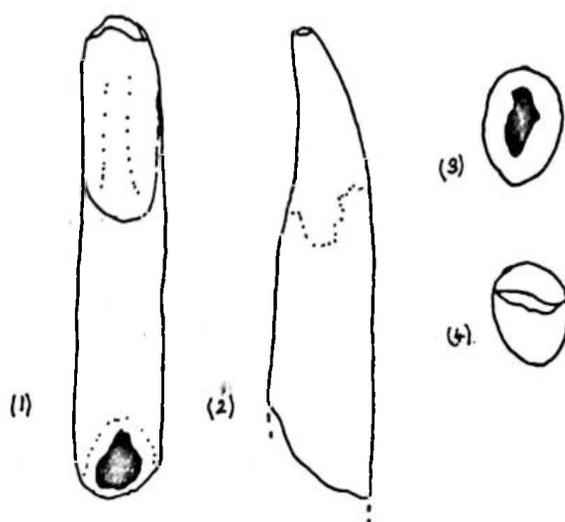
### 3. The Incisors

First lower incisors:

Two distinct morphological types of first lower incisor occur in the

assemblage. The first type is represented by some ninety fragments of teeth, probably corresponding to about forty complete teeth in all. The morphology of these teeth is identical to that of the  $I_1^-$  of Oligokyphus major and minor from Windsor Hill. (figure 39) The enamel covering of the spatulate crown is extremely thin, as in the latter, and the same apical wear facet can be discerned where the tip of the crown is preserved. Kuhne measured and plotted the maximum root widths of the  $I_1^-$  of O. major and minor. The resultant size distribution of the material, which is shown in his text figure 37, is bimodal, each mode consisting exclusively of incisors from either one form or the other. Unfortunately only two root fragments in the Welsh assemblage permit the same measurement to be made for the purposes of comparison. The larger root has a width of 3.4mm, which is in the Oligokyphus major range, and the smaller specimen has a width of 3.0mm, which is in the O. minor range. A much larger number of  $I_1^-$  from Pant 4 can be compared to the Windsor Hill specimens if the maximum widths of the superior crown surfaces are measured in each case (see figure 40). Figure 40 shows that the resultant size distribution of the Windsor Hill specimens is not now bimodal, but in fact there is no overlap between specimens belonging to O. major and minor: those which belong to the former have a maximum crown width of 2mm or more, whilst those belonging to the latter have crown widths which never attain 2mm. The size distribution of the Welsh specimens is distinctly trimodal. Each mode clearly represents a distinct size group of Oligokyphus. The specimens in the right hand group are the size of O. major specimens from Windsor Hill. The majority of those in the middle group correspond in size to Windsor Hill O. minor specimens. The very small specimens have no counterpart in the Windsor Hill collection. These teeth must belong to individuals which are no larger than those represented by the five smallest dentaries from Windsor Hill (see Kuhne, 1956:82).

The second morphological type of  $I_1^-$  in the Welsh assemblage is the same as the small incisor type from Windsor Hill which Kuhne called A. Kuhne suggested that A is the  $I_1^-$  of the form represented by the five very small dentaries in the Windsor Hill assemblage. There can be no doubt concerning the identification of A as an  $I_1^-$ . The crown proportions are only slightly different from the  $I_1^-$  of Oligokyphus major and minor, the enamel covering is similarly very thin and the wear is



— 1mm

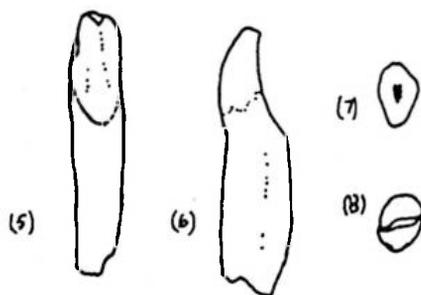


Figure 39. *Oligokyphus*. First lower incisors. upper specimen: T152, a very small major-minor morphological type of  $I_1$ . (1) dorsal and (2) buccal views, (3) end view of root, (4) apical view of crown. Lower specimen T157, a minute A. (5) Dorsal and (6) buccal views; (7) end view of root, (8) apical view of crown.

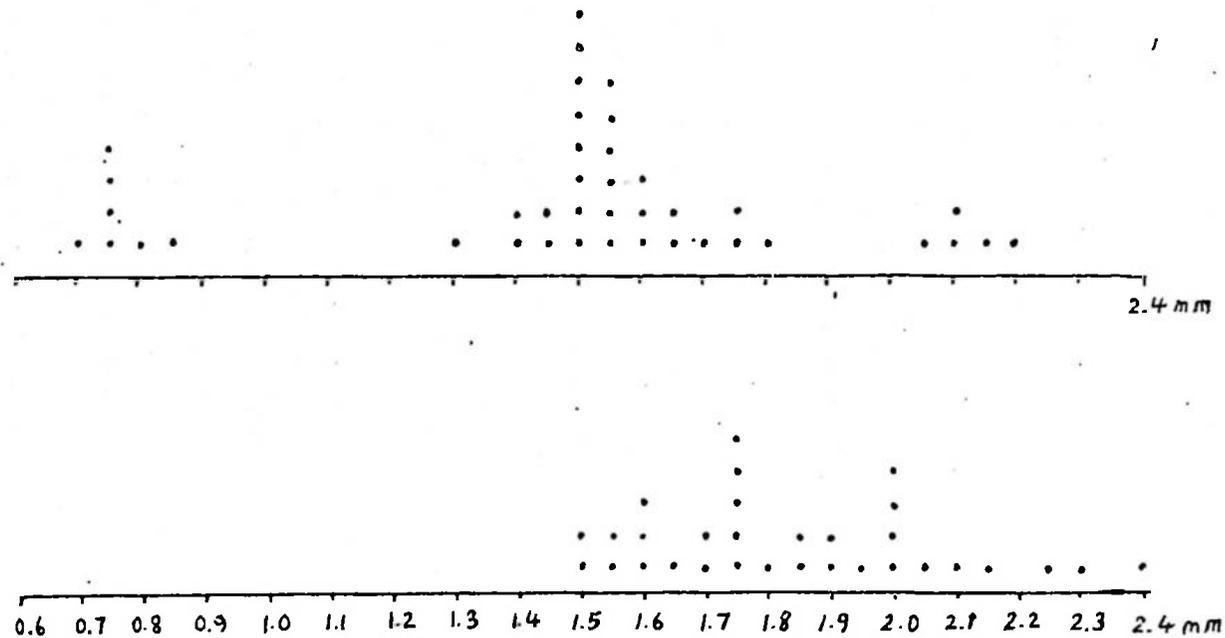


Figure 40 Oligokyphus

Measurements of crown breadth of  $I_1$ . Upper diagram: Pant 4 specimens. Lower diagram:  
Windsor Hill specimens.

identical (of Kuhne p. 91). There are 29 specimens in the Welsh assemblage. The majority are relatively intact although none is completely undamaged.

The A from both localities have been measured across the maximum width of the superior surface of the crown, as in the case of the first morphological type of  $I_1$ . The data from both sets of specimens is shown in figure 41. The Windsor Hill specimens comprise a single size group and are reasonably ascribed to a single small form of Oligokyphus. The Welsh specimens are bimodally distributed and are clearly representative of two forms differing substantially in size. The majority of specimens in the larger group correspond in size to Windsor Hill A. The three tiny A in the Welsh assemblage are by far the smallest incisors of Oligokyphus known. They represent a minute form which is substantially smaller than that which is represented by the smallest major/minor type of first lower incisors.

Other Lower Incisors:

Six of the incisors in the assemblage are suggestive in size and morphology of Oligokyphus lower incisors from a more distal position. Second and third lower incisors are known to exist in Oligokyphus major as one dentary bears proximal root fragments of these teeth (R 7143, of Kuhne p. 90). Alveoli in several Oligokyphus minor dentaries also indicate the existence of these incisors in this form (Kuhne p. 90). The roots of the Welsh specimens are broken and the crowns damaged. In one specimen, T 182, the crown damage is relatively slight and this specimen is illustrated in figure 43. The illustration needs few supplementary remarks. The tooth is compressed and the two crown surfaces which lie in the plane of the compression are separated from one another by a well-defined marginal rim which descends on each side from the crown apex. In apical view, these surfaces are convex. The crown is slightly recurved in the plane of compression, and when viewed at right angles to this plane, the crown apex is strongly inclined to one side. The apex has been posthumously abraded. There is no definitive evidence of functional wear on any of the specimens. The crown passes smoothly and imperceptibly into the root. The oval cross-sectional shape of the root perfectly matches the cross sectional shape of the root fragments which are preserved in R 7143. The widest part of the root is just below its junction with the crown.

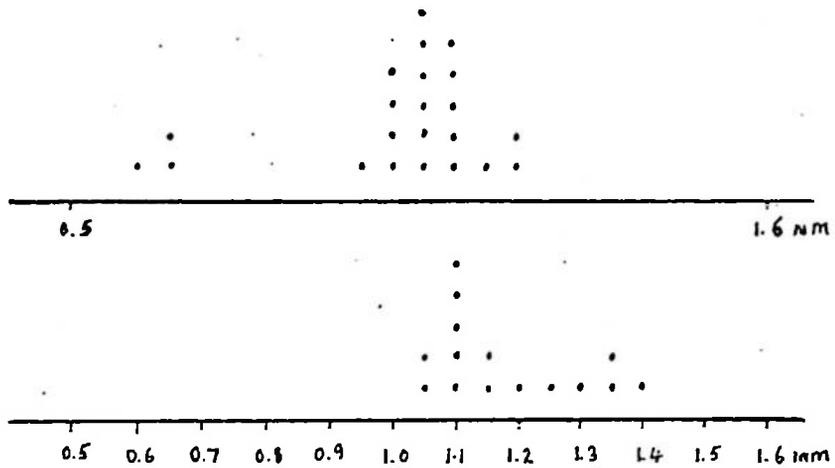


Figure 41 Oligokyphus. Incisor A : crown breadth measurements. Upper diagram : Pant 4 specimens. Lower diagram : Windsor Hill specimens.

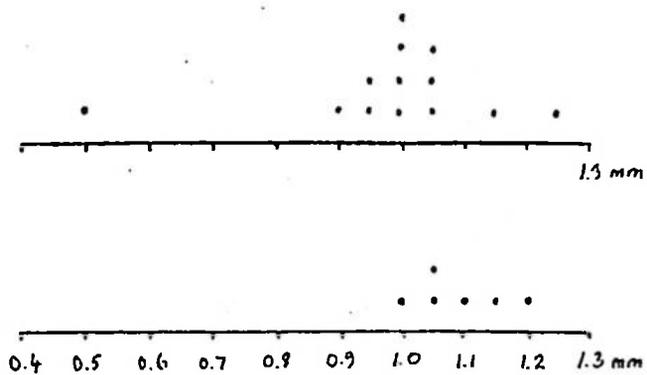


Figure 42 Oligokyphus. Measurements of crown breadth of I<sup>1</sup>. Upper diagram : Pant 4 specimens. Lower diagram : Windsor Hill specimens.

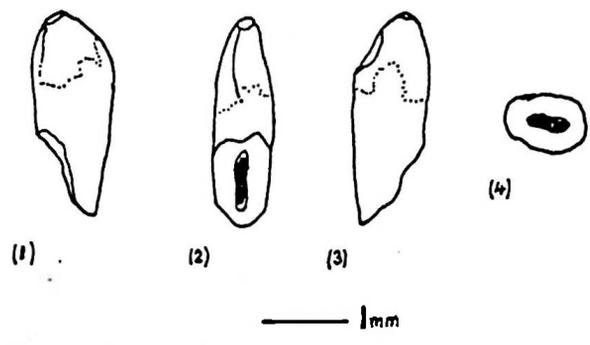


Figure 43. Oligokyphus. Lower incisor of uncertain position, specimen F. 182. (1) dorsal, (2) lateral and (3) ventral views, and (4) end view of root.

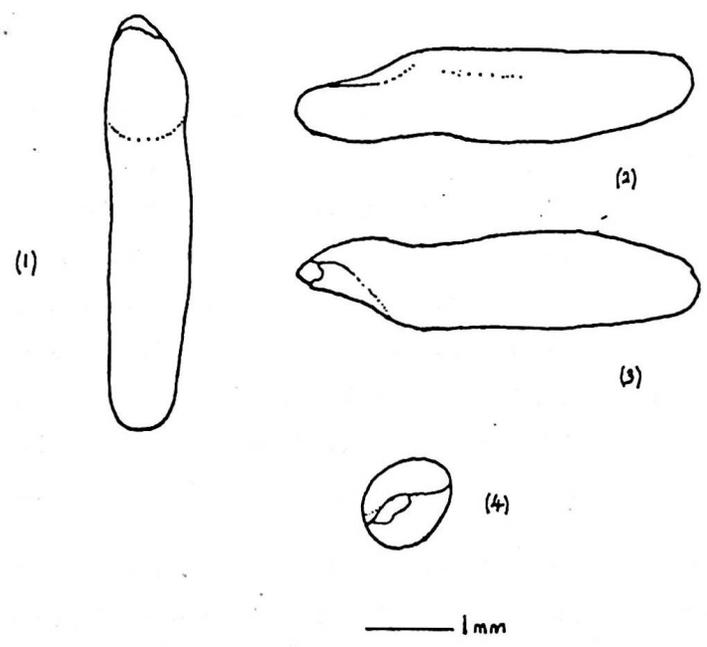


Figure 44. Oligokyphus. Incisor 'C', specimen T. 176. (1) dorsal, (2) Buccal and (3) lingual views, and (4) apical view of crown.

Because of the posthumously worn condition of the teeth, precise length and breadth measurements of the crowns are impossible. The following, however, are reasonable assessments for five of the specimens:

	<u>Maximum crown length</u>	<u>Maximum crown width</u>
(T 182)	0.9mm	0.9mm
	0.8mm	0.9mm
	0.9mm	0.9mm
	0.95mm	0.9mm
	1.6mm	1.4mm

The remaining specimen is too abraded for reasonable estimates of its crown dimensions to be made. It is of the same order of size as the largest specimen that has been measured. To judge from the relative sizes of the root fragments in R 7143, two different sizes of tooth probably reflect two different sizes of Oligokyphus rather than different dental positions. The smaller specimens are of appropriate size to belong to the Oligokyphus minor sized individuals which are represented in the collection.

#### First Upper Incisors:

Sixteen incisors in the Welsh assemblage are morphologically identical to the first upper incisors of Oligokyphus major and minor. Most are strongly worn like their Windsor Hill counterparts but two specimens are perfectly intact and completely devoid of functional wear. These specimens clearly cannot have come into use very long before the deaths of the animals to which they belong. The two incisors differ from the  $I^1$  available to Kuhne (which are all worn) in that the edges of the working surface of the crown are sharply defined and the crown apex is obtusely pointed.

The maximum crown widths of the specimens have been measured, and the resultant size distribution is shown in figure 42. The same measurement has been made on the Windsor Hill specimens. The majority of Welsh  $I^1$  are of about the same size as, or slightly smaller than, the smallest Windsor Hill specimen. They are therefore reasonably attributable to individuals of Oligokyphus minor size. The two largest specimens are of O. major size. The smallest specimen is considerably smaller than any other  $I^1$  (the crown width measurements do not emphasize the disparity sufficiently). This tooth belongs to

an individual of similar size to the individuals which are represented by the very small major/minor type of  $I_1^-$ .

Second Upper Incisors:

Eleven large broken incisors are morphologically identical to the teeth which Kuhne identified as the second upper incisors of Oligokyphus major. Almost all the specimens show considerable functional wear like their Windsor Hill counterparts. The mesio-distal width of the root just below the crown base has been measured on the  $I_2^2$  from both localities, and the size distributions of the two sets of specimens are shown in figure 45. As will be seen from figure , the Welsh specimens are generally rather smaller than those from Windsor Hill, and here the disparity is such that it cannot be reasonably attributed to sampling error. In other words the main group of Welsh specimens cannot belong to the same sized form of Oligokyphus as that represented by the majority of Windsor Hill specimens. The two smallest Welsh specimens are substantially smaller than the rest (as in the case of the first upper incisors, the measurements made do not sufficiently reflect the size disparities between these specimens and the remainder).

Third Upper Incisors:

The most abundantly represented incisor in the Welsh assemblage is morphologically identical to the third incisor of Oligokyphus major and minor. There are more than ninety fragments of this tooth type, and at least eighty teeth must be represented. Every crown has been functionally worn and many are considerably worn. The smaller specimens are on average the best preserved Oligokyphus teeth from Pant 4; a number are completely intact. Most of the crowns are heavily worn. It was found that the only reliable measurement that could be made on a majority of specimens was that of the maximum width of the root just below its junction with the crown, as in the case of the  $I_2^2$ . The measurement has also been made on the Windsor Hill specimens and the size distributions of the two sets of teeth are shown in figure 46. The Windsor Hill specimens are not separated into discrete size groups even though both Oligokyphus major and minor are represented (Kuhne p. 87). The distribution of the Welsh specimens is trimodal, as in the case of the major/minor type of  $I_1^-$ . The three largest Welsh specimens are of appropriate size to belong to Oligokyphus major-sized individuals and those in the middle group

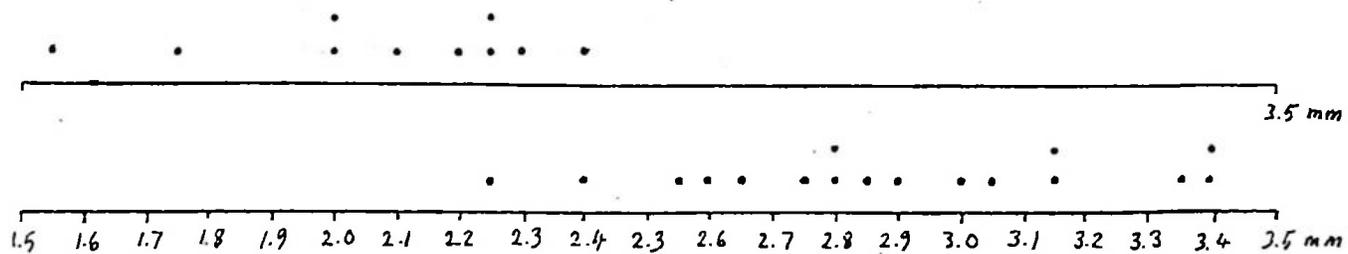


Figure 45. Oligokyphus

Measurements of root breadth above the crown of  $I^2$ . Upper diagram: Pant 4 specimens.

Lower diagram: Windsor Hill specimens.

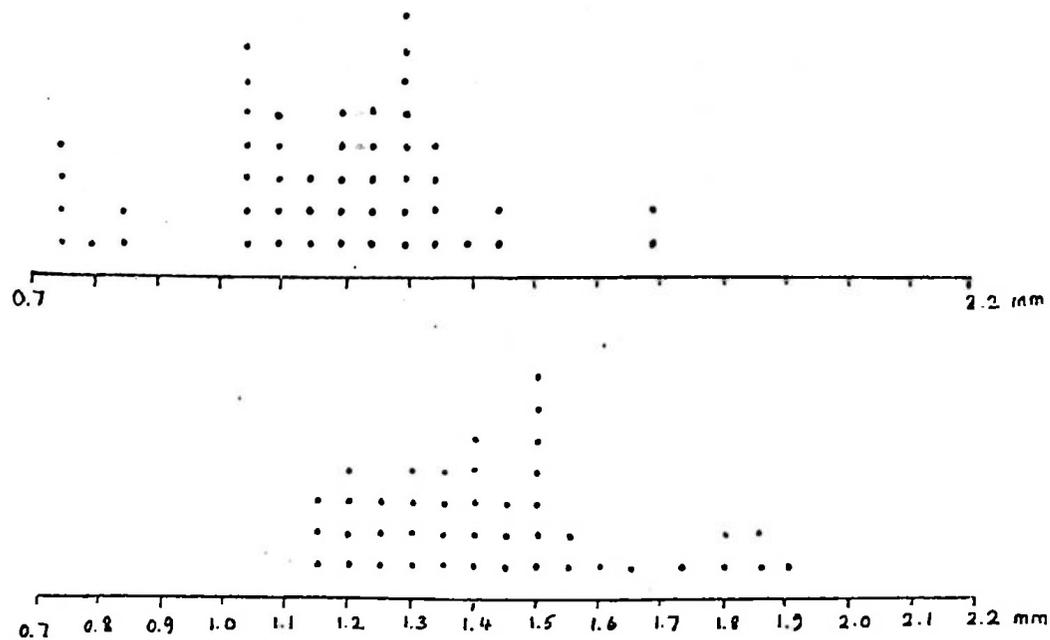


Figure 46. Oligokyphus.

Measurements of root breadth above the crown of 1<sup>3</sup>. Upper diagram :  
 Pant 4 specimens. Lower diagram : Windsor Hill specimen.

of appropriate size to belong to O. minor-sized individuals. (As in the case of the  $I_1^-$ , some of these specimens are smaller than their Windsor Hill counterparts.) The very small specimens would fit the same sized dentitions as the very small major/minor type of  $I_1^-$  and  $I_1^1$  which occur in the collection.

#### Other Incisors:

In addition to the incisors described above, two smaller incisor types occur in the Welsh assemblage. They are of uncertain position in the dentition of Oligokyphus. Both have morphological counterparts in the Windsor Hill collection and Kuhne referred to these by letters. Nine incisors correspond to the Windsor Hill incisors which Kuhne called C. This incisor type resembles A in some respects. However, the greater lingual inclination and recurvature of the crown, together with the shape of the root (see figure 44 and Kuhne's text figure 38) preclude C from being a first lower incisor. The Welsh specimens exhibit a modest size range. The largest specimen has a crown length of 1.4mm, which is the same as the largest C from Windsor Hill. The smallest Welsh specimen is rather larger than the smallest specimen in the English assemblage having a crown length of 1.0mm compared to 0.6mm.

The final incisor type to be described from Pant 4 is the same as the incisors Kuhne called D. The dimensions of the Welsh specimens are as follows:

<u>Crown length</u>	<u>Crown width</u>	<u>Total tooth length</u>
0.9mm	0.75mm	3mm
0.85mm	0.7mm	-
0.70mm	0.6mm	-
0.70mm	0.6mm	-
1.0mm	0.6mm	-

The type of D from Windsor Hill is of similar size to the largest Welsh specimen. (Although three specimens are recorded by Kuhne, one of the three specimens labelled "D type" in the B.M.N.H. collection is in fact an  $I_1^1$ .)

#### Summary of material

In concluding the description, it is worth emphasizing that, with three exceptions, every morphological type of tooth which occurs in

the Windsor Hill assemblage has been obtained from Pant 4. The exceptions are: the Oligokyphus major type of ultimate upper cheek tooth, the reduced penultimate upper cheek tooth which is found in some O. minor maxillae, and the incisor B. The latter tooth very probably is not an incisor of Oligokyphus.

The estimated number of specimens of each tooth type obtained from Pant 4 together with the approximate number of individual animals which they represent is as follows:

<u>Tooth type</u>	<u>Estimated number of Specimens</u>	<u>Approximate number of animals represented</u>
Functional upper cheek teeth	320	22
Functional lower cheek teeth	280	20
I <sub>1</sub>	45	23
I <sup>1</sup>	16	10
I <sup>2</sup>	13	9
I <sup>3</sup>	80	40
A	26	14
C	9	?
D	5	?

A conservative estimate of the total number of animals represented is forty. This number is given by the I<sup>3</sup> material. The number is about the same as that represented in the Windsor Hill assemblage, where the greatest number of individuals is indicated by the dentaries.

The forms of Oligokyphus which are present in the Welsh assemblage

The size distributions of the functional cheek teeth and incisors, and the presence of more than one morphological type of incisor from certain dental positions, shows clearly that several forms of Oligokyphus are present in the assemblage. The maximum number of forms for which there is evidence is five. This number is given by the I<sub>1</sub><sup>-</sup>. It has been shown that nearly every Oligokyphus minor tooth from Windsor Hill is duplicated in the Welsh material. There can thus be no doubt that one of the five Welsh forms is O. minor. The evidence for the presence of this form may be summarised as follows:

- (1) Amongst the major/minor types of I<sub>1</sub><sup>-</sup>, I<sup>1</sup> and I<sup>3</sup> there is in each case a discreet size group containing specimens of definitive O. minor size.

(2) Within the main group of functional upper cheek teeth, all the larger specimens are indistinguishable in size, proportions (and morphology) from the equivalent O. minor teeth from Windsor Hill, and they also span fully the size range of the latter teeth. Amongst the functional lower cheek teeth all the larger specimens are similarly indistinguishable from their O. minor counterparts in the Windsor Hill assemblage. These teeth also span fully the size range of the latter specimens.

(3) Amongst the five relatively intact reduced upper cheek teeth which occur, four specimens are identical in size and morphology to ultimate teeth in O. minor maxillae from Windsor Hill (of the broken specimens which occur - and which are all of O. minor size - almost all are identical, in what is preserved of their morphology, to O. minor ultimate teeth).

(4) Of the eight non-functional lower cheek teeth which possess four cusps, seven specimens are of similar size to their morphological counterparts which occur in some of the O. minor dentaries from Windsor Hill.

We may consider the question of whether there is any evidence of a difference in the genetic compositions of the O. minor populations which are represented in the Welsh and English assemblages. The absence from the Welsh assemblage of the reduced penultimate upper cheek tooth which is present, as a variant, in some of the O. minor maxillae in the Windsor Hill assemblage cannot be interpreted as evidence of such a difference. Only eight Windsor Hill maxillae have a penultimate cheek tooth in situ. There are approximately forty-five O. minor sized functional upper cheek teeth in the Welsh assemblage which are sufficiently intact for their full cusp complement to be determined. This number is equivalent to that which would be obtained from only nine mature maxillae. The sample sizes of the relevant material in the Welsh and English assemblages are thus so small that the absence of reduced penultimate upper cheek teeth in the former may plausibly be attributed to sampling error. The absence, amongst the intact O. minor ultimate upper cheek teeth in the Welsh assemblage, of three of the five morphological variations which occur amongst the equivalent Windsor Hill specimens (see figure 36) may also be adequately accounted for by postulating sampling error. The Welsh sample is far too small to have statistical significance. It is notable that the mean sizes of the O. minor

$I_1^-$ ,  $I_1^1$  and  $I_1^3$  in the Welsh assemblage are slightly smaller than those of their Windsor Hill counterparts. As all three groups of Welsh specimens agree in this respect, the discrepancy is unlikely to be the result of chance. It is, however, more likely to be due to the size selection which operated during the transportation of elements to the Welsh fissure, than to any difference to the mean sizes of the animals in the Welsh and English O. minor populations. There is, in fact, no evidence in the Welsh material of any difference in the genetic composition of the two populations. On the positive side, the occurrence in the Welsh assemblage of (a) two of the morphological varieties of O. minor ultimate upper cheek teeth which are found in the Windsor Hill collection, and (b) two O. minor sized functional upper cheek teeth which bear the same buccal cuspule that is occasionally found in equivalent Windsor Hill specimens, provides impressive evidence of a close similarity in the genetic composition of the populations.

Of the four remaining forms of Oligokyphus which are present in the Welsh assemblage, one has been shown to be identical, in its preserved teeth, to Oligokyphus major. This form is represented by the following specimens:

- (1) The very large specimens amongst the major/minor types of  $I_1^-$ ,  $I_1^1$  and  $I_1^3$ .
- (2) The three largest functional upper cheek teeth.
- (3) The largest specimen amongst the reduced lower cheek teeth which possess four cusps.

Although the dentition of the form is less completely represented than that of Oligokyphus minor, there can, I think, be little doubt that it is O. major, especially in the content of the occurrence of the smaller form.

There is no large Oligokyphus tooth in the Welsh assemblage which cannot be reasonably allocated to either Oligokyphus major or minor.

It is convenient at this point to discuss the allocation of the  $I_1^2$  which occur in both collections. Kuhne's allocation of all the Windsor Hill specimens to Oligokyphus major naturally implied the absence of a similar type of incisor in O. minor. It has been shown, however, that the majority of the Welsh specimens are smaller than their Windsor Hill counterparts, and that they cannot reasonably be

attributed to the same form as the majority of the latter. It is therefore clear that Oligokyphus minor in reality possesses a  $I_2^2$  which is morphologically indistinguishable from that in O. major. Very probably a few of the Mendip specimens also belong to O. minor, there being no sharp size distinction between the largest specimens which belong to the latter form and the smallest which belong to O. major. The two smallest second upper incisors in the Welsh collection are perhaps a little too small to belong to adult O. minor dentitions. As they are certainly too large to belong to any of the dentitions which are represented by the various very small first lower incisors which occur it seems probable that they belong to sub-adult individuals of minor or half grown individuals of major. Unfortunately there is no corroborating evidence regarding the number of generations of incisors which erupt during growth in Oligokyphus.

The considerable disparity in the relative numbers of Oligokyphus major and minor teeth which is apparent in the Welsh assemblage (see table ) contrasts markedly with the situation which pertains in the Windsor Hill collection. In the latter assemblage, the two forms are about equally abundant, as can be seen, for example, from Kuhne's text figures 23, 24, 30, 31 and 37. It might be concluded that the relative dearth of Oligokyphus major teeth in the Welsh assemblage is simply the result of their larger size having prevented the transportation of so many specimens to the fissure. Yet not all the teeth of O. major are larger than all those of O. minor. The  $I_1^1$  of the larger form, for example, are substantially smaller than the  $I_1^1$  of the smaller one. Despite this, the latter teeth are very much more abundant in the Welsh assemblage than the former. It therefore seems that there must have been a genuine disparity in the relative numbers

Table 5

Tooth type	Number of measurable specimens of major size	Number of measurable specimens of minor size
Functional upper cheek teeth	3	approx. 50
Functional lower cheek teeth	0	approx. 35
Non functional upper cheek teeth	0	14
Non functional lower cheek <sub>1</sub> teeth	1	7
$I_1$	5	28
$I_1^1$	2	10
$I_2^2$	0	8
$I_3^3$	2	40

<sup>1</sup> See footnote overleaf.

of individuals of the two forms which were present in the source material of the Welsh taphocoenosis.

Turning now to the three small forms of Oligokyphus which are present in the Welsh assemblage, we may first consider the question of the relationship between the form to which the group of larger A belong and the smallest Mendip form. The latter form is represented in the Windsor Hill collection by seventeen A, five C, two D, the five smallest functional upper cheek teeth, the five smallest functional lowers, and the five smallest dentaries.<sup>2</sup> The form thus differs from Oligokyphus major and minor not only in size but also in the morphology of its known incisors, and in the allometric relationship between the lengths and breadths of its upper cheek teeth (cf. figure 32).

With regard to the Welsh material, it has been shown that the specimens in the group of larger A, and the C and D incisors correspond closely in size to their Windsor Hill counterparts. It has also been shown that the smaller functional upper cheek teeth in the collection are allometrically indistinguishable from the five smallest functional upper cheek teeth from Windsor Hill, and that the smaller functional lower cheek teeth are similarly indistinguishable from the five smallest functional lower cheek teeth from the Mendip locality.

Since the main size group of A comprises by far the majority of small  $I_1$  in the Welsh assemblage, it follows that the majority of the smaller functional cheek teeth in the collection must belong to the same form as these specimens. It is therefore evident that this form is specifically identical to the smallest Mendip form. I propose, for convenience, to call the form in question Oligokyphus A. In both the Welsh and English assemblages, it accounts for more than a quarter of the total number of individuals of Oligokyphus that are represented.

<sup>1</sup> The two reduced lower cheek teeth which possess only two cusps have not been included because their size is not a reliable indication of which of the two forms of Oligokyphus they belong to. On the circumstantial grounds of relative abundance, they very probably belong to Oligokyphus minor.

<sup>2</sup> The allocation of all three elements to a single form is reasonable since the A - which are the only small  $I_1$  in the assemblage - are relatively so abundant; it would be manifestly unreasonable to suppose that one small form could be represented by seventeen  $I_1$  but, for example, by no dentaries, at the same time as another similar sized form is represented by five dentaries but by no  $I_1$ .

In comparison to Oligokyphus A, the two other small forms of Oligokyphus which occur in the Welsh material are rather sparsely represented. The larger of the two forms is that to which the smallest specimens amongst the major/minor types of  $I_1^-$ ,  $I_1^1$  and  $I_1^3$  belong. This form will be called Oligokyphus B. It is only a little smaller than Oligokyphus A but it is substantially smaller than O. minor; the difference in the linear dimensions of the  $I_1^-$  is about one-half. As there are seven very small major/minor type  $I_1^-$  it is reasonable to postulate that a few of the smaller functional cheek teeth in the assemblage belong to Oligokyphus B. This does not necessarily mean that the functional upper cheek teeth of this form are allometrically distinct from those of Oligokyphus major and minor however; figure shows that a few of the small functional upper cheek teeth that have been measured could feasibly belong to the same allometric series as the equivalent O. major and minor specimens. These teeth may well belong to Oligokyphus B.

The final small form of Oligokyphus which occurs in the assemblage - that which is represented by the minute A - comprises by far the smallest tritylodont individuals known. The difference in the linear dimensions of the minute A and the larger A is approximately one half. On the basis of their relative sizes, the two or three smallest upper and lower functional lower cheek teeth in the assemblage probably belong to this form. The form will be designated Oligokyphus C.

Although Oligokyphus B and C are not present in the Windsor Hill assemblage this cannot be regarded as evidence that they were not present in the fauna of the Liassic island upon which the Mendip populations of Oligokyphus lived. Kuhne has shown that the Neptunian Dyke at Windsor Hill collected elements selectively, larger elements being favoured over smaller ones. Oligokyphus B and C are sparsely represented in the Welsh assemblage and a similar paucity of representation amongst the Oligokyphus remains which comprised the source material for the Windsor Hill taphocoenosis would - in the context of their small size - have minimised the chances of the forms being represented amongst the remains collected by the Neptunian Dyke. The possibility that Oligokyphus B and C were present in the fauna of the Liassic island at Windsor Hill has an important bearing on the following discussion.

The specific positions of the forms

Kuhne considered the relationship between the two large, adult forms of Oligokyphus in the Windsor Hill assemblage to be uncertain. Although he gave them different trivial names, for convenience, he emphasised that this was not intended to preclude the possibility that they were male and female of a single species. This is a possibility that naturally arises from the fact that the two forms occur in the same fissure and are morphologically very similar. Kuhne did not give specific rank to the five small Windsor Hill dentaries which belong to the form that I have called Oligokyphus A. He regarded these dentaries as juvenile.

If either Oligokyphus major or minor had not been found in the Welsh fissure this might have been taken as evidence that the two forms are actually different species. However, this is not the case. The Welsh material does, on the other hand, provide definite evidence of the presence of at least one small species of Oligokyphus in addition to major and minor: Oligokyphus A and B are not very dissimilar in size but they are markedly different in the morphology of their incisors. Clearly, at least one of these forms must be specifically distinct from the larger forms. On the basis of the morphology of its incisors, Oligokyphus A is less likely to be a juvenile form of major and/or minor than Oligokyphus B. The fact that the upper cheek teeth of Oligokyphus A are allometrically distinct from those of major and minor also suggests that the form is a different species. Whilst the isolated teeth of Oligokyphus A are suggestive, however, they do not, of themselves, provide sufficient evidence for the unequivocal determination of its specific position. The only other material which is pertinent to this problem is the group of five small Windsor Hill dentaries. The essential question that needs to be answered concerning these dentaries is that of their relative age. If they are very immature then the possibility that Oligokyphus A is a juvenile form of major and/or minor cannot be ruled out. If, on the other hand, they are sub-adult or adult dentaries then Oligokyphus A must, by virtue of its size, be a distinct species.

Unfortunately all five dentaries are incomplete, and what remains in each case is damaged. All have lost the anterior, diastemal, part of the horizontal ramus and much of the area of the coronoid process. With one exception, none of the specimens retains any cheek teeth in

situ. Kuhne gives the following as his reasons for regarding these dentaries as juvenile:

- (1) 'the crypt of their ultimate cheek tooth is always undivided'
- (2) 'the bone is characteristically sculptured, for instance, at the masseteric fossa and at the angular corner.'

Whilst Kuhne is certainly correct in asserting that the crypt of the ultimate tooth is always undivided, this is not, of course, evidence that the dentaries necessarily belong to young juveniles. There are, for example, two dentaries of O. major (R7136 and 7151) in which the crypts of lost posterior teeth are undivided, showing that these posterior teeth had not yet formed roots at the time of the deaths of the animals. It may be added that there is no intrinsic reason why small, fully mature dentaries should not have possessed functionless ultimate teeth - analogous to those in adult major dentaries - in which there was a single, permanently undivided, root.

With regard to the supposed sculpturing of the small Windsor Hill dentaries, re-examination reveals clear evidence of this on only one specimen: R7172. I am not entirely satisfied that the sculpturing on this specimen is not the result of uneven surface exfoliation caused by weathering of the bone prior to its transportation to the fissure. Similar sculpturing may be observed from time to time on various bones in the Windsor Hill assemblage, seemingly irrespective of size or skeletal position. Even if the sculpturing on 7172 is not posthumous in origin its significance is doubtful. It certainly cannot be used as a valid reason for regarding the dentary as juvenile.

Kuhne did not figure any of the five small dentaries or describe them in any detail. Figure 47 shows the only specimen which still retains any remains of the cheek teeth, R7169. The anterior part of the dental ramus, including the diastemal region, is missing, and the back of the bone is broken off shortly behind the point at which the leading edge of the coronoid process joins the dental ramus. The medial side of the latter is damaged dorsally. The buccal side is largely intact. There are two damaged cheek teeth still in situ. When the dentary was complete it would appear to have been approximately two fifths of the size of a typical adult O. major dentary.

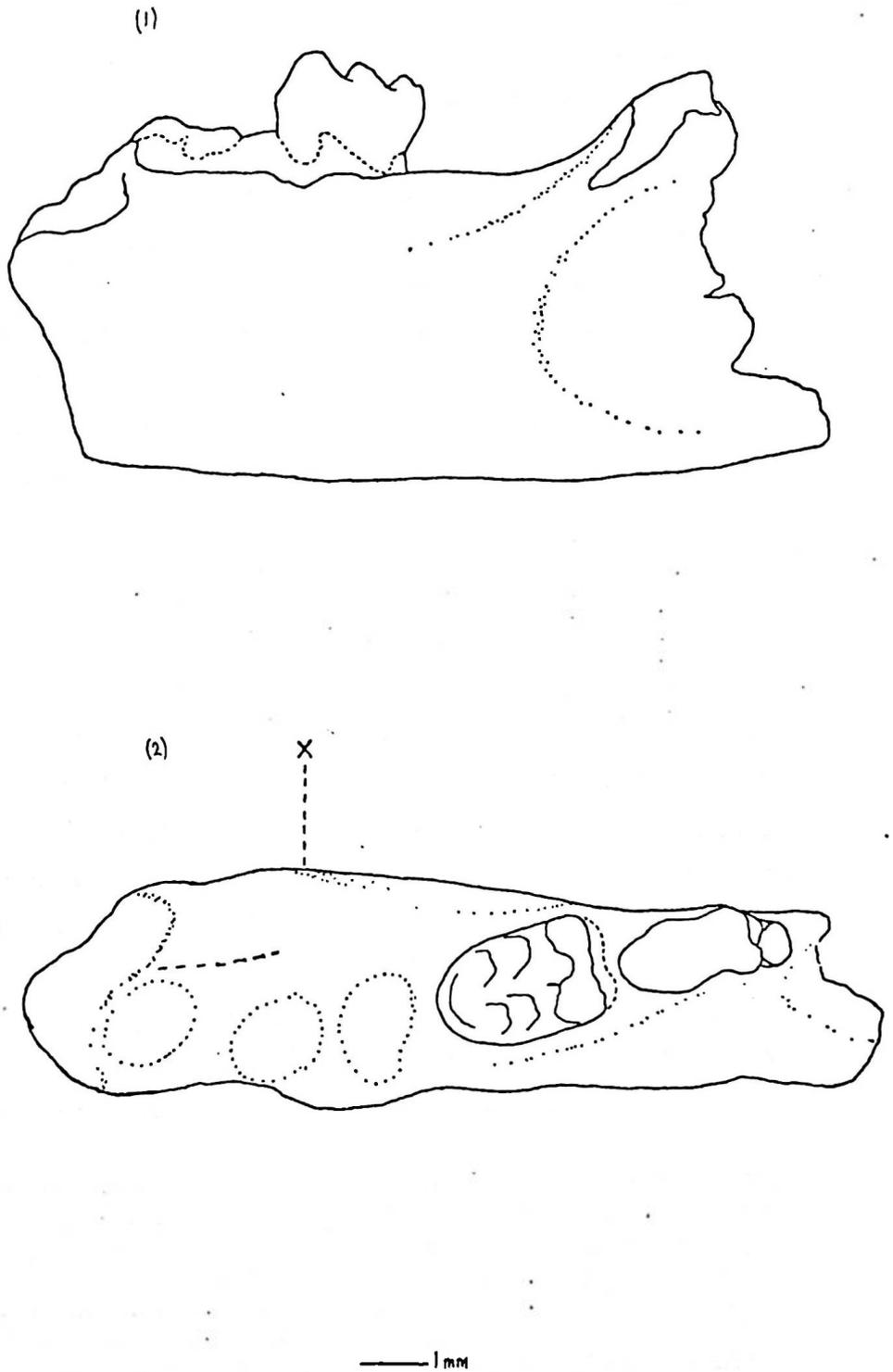


Figure 47. Oligokyphus. Windsor Hill dentary, specimen R 7169 (1) Lateral and (2) dorsal views. X denotes the anterior end of the malleolar fossa.

The first of the damaged teeth is situated at the anterior end of the preserved part of the jaw, and it consists only of the base of the crown. The second, which immediately succeeds it, is intact except for the apices of the mesial cusps. This tooth is followed by the alveoli of a normal functional tooth, which in turn are followed by a single, oval shaped crypt, situated at the posterior end of the specimen. There is thus evidence for the original presence of four cheek teeth. In dorsal view (figure ) it can be seen that the alveolar row is orientated slightly obliquely to the long axis of the jaw, the anterior end of the row being buccal to the posterior end. The arrangement is such that when the jaw was intact the present anterior cheek tooth could not have been preceded by a cheek tooth. In other words the original number of cheek teeth in the jaw was the same as that for which there is evidence.

The first tooth, as shown by the length of the residual fragment, was not smaller than the second. The maximum possible size of the missing third tooth cannot have significantly exceeded that of the second. The subequal size of these three pre-ultimate teeth accords with the situation which pertains in the functional cheek tooth row of mature Oligokyphus dentaries (for example, the ratio of the length of the largest functional cheek tooth to that of the smallest in O. major dentary R7123 (Kuhne; text figure 32 is only 11:9). Significantly, however, it does not accord with the situation which pertained in the deciduous, pre 'zero' cheek tooth row<sup>1</sup> of immature dentaries. This is well illustrated by O. major dentary R7133 (Kuhne; text fig. 31). Here the alveoli of the lost 'zero' tooth are preceded by the alveoli of two deciduous teeth, the more anterior of which must have been

<sup>1</sup> Kuhne termed the last deciduous cheek tooth in the dentition of Oligokyphus major and minor the 'zero' tooth. This tooth has been lost in all the fully mature dentaries belonging to these forms, although its alveoli normally persist. The tooth itself is present in two of the O. major dentaries shown in Kuhne's text figure 31 (R7372 and 7180). In neither dentary has the fifth permanent tooth erupted, but in each case the dentary appears to be fully grown. It is, therefore clear that the 'zero' tooth was lost at a relatively late stage during the course of ontogeny, after the animal had attained its maximum size. The pre 'zero' cheek tooth row is the tooth row which spacially precedes the 'zero' tooth in the immature dentary. In other words, the members of this row comprise the preultimate deciduous teeth. They were lost progressively as the young dentary grew and the diastema extended backward. At the same time permanent teeth erupted posteriorly, the whole process continuing until the adult situation was attained.

substantially smaller than its successor, which in turn was clearly rather smaller than the 'zero' (the latter appears as usual to have been of similar size to the following permanent tooth).

The lost ultimate tooth in R7169 was clearly rather smaller than its predecessors, as in the case of the analogous tooth in adult O. major dentitions. Its crypt is situated internal to the anterior part of the coronoid process, and the tooth would have occupied a similar position to that of the ultimate tooth in the mature minor dentary R7164 (Kuhne's text fig. 31). As Dr. Kermack has pointed out to me, the position of the tooth relative to the coronoid process would effectively have precluded the possibility of any subsequent substantial backward growth of the alveolar border. Still more significantly, the crypt of the tooth is not perfectly in line with the preceding alveoli and teeth, but is displaced slightly buccally. Even if the tooth had erupted, therefore, it is clear that it could never have functioned. The presence of a reduced, non functional, tooth at the back of the tooth row completely rules out any possibility that the cheek teeth of R7169 are part of the deciduous pre 'zero' dentition of Oligokyphus major or minor. No functional teeth could ever have erupted behind them.

Kuhne has suggested that the cheek teeth in R7169 constitute a 'milk dentition' (Kuhne, p.82), by which he appears to mean a dentition which was later replaced by a second generation of teeth - presumably the pre 'zero' teeth. However, the cheek tooth row of tritylodonts functioned as a single masticatory unit and it is difficult to see how there could have been any replacement of the teeth of R7169 whilst the unit continued to be operative. In mammals where the milk molars are replaced, replacement only takes place after the area of primary masticatory action has moved to a more posterior part of the jaw, a procedure which is, of course, inapplicable in the present instance. Any replacement of the cheek teeth in R7169 would certainly have caused a very considerable disruption of the masticatory unit with equivalent loss of effectiveness, and for this reason the possibility that these teeth belong to a 'milk dentition' may, I think, be safely dismissed. R7169 is as manifestly adult, in the nature and arrangement of its cheek teeth, as any of the mature dentaries of O. major and minor. Indeed, it compares closely in the original number and arrangement of its cheek teeth with adult O. minor dentary R7164. The adult nature of the dentition is emphasised if a reconstruction of the

relevant part of the jaw is compared to a very immature dentary of Bienotherium yunnanese (CUP 2218, figure 48). It will be noted that in the latter specimen the cheek teeth increase markedly in size from first to last - as they do in the pre 'zero' dentition of Oligokyphus - and that the cheek teeth are situated well forward of the coronoid process, permitting backward growth of the alveolar border. In both of these features, the jaw contrasts strikingly with R7169, and with all adult tritulodont dentaries. Of the four remaining small Windsor Hill dentaries, three agree with R7169 in that the missing pre-ultimate teeth were of subequal size, and the ultimate rather smaller and situated internal to the coronoid process. These dentaries were thus also quite obviously mature. The fourth dentary, R7172, is rather too badly damaged for the situation regarding the dentition to be clearly seen, but this is relatively unimportant; the nature of the dentition of four out of the five small dentaries demonstrates clearly that Oligokyphus A is an adult form and, hence, is specifically distinct from Oligokyphus major and minor. This has a bearing on the question of the relationship between the two latter forms. As Kuhne has noted, the size disparity between O. major and minor is a considerable one. He estimates the difference in the linear dimensions of the two forms as about one third, and their difference in weight as more than 100%. If the forms are male and female of a single species then, on the basis of such a size disparity, one would naturally expect some evidence of a marked size difference between the males and females of Oligokyphus A. In fact there is none. The estimate of the coefficient of variation for the crown breadths of the  $I_1$  (A) of Oligokyphus A from the two localities is 0.116, an estimate quite compatible with monomorphic material. By contrast, the coefficient estimate for the crown breadths of the combined O. major and minor  $I_1$  from the two localities is 0.268. This estimate is entirely incompatible with monomorphic material. As there are some 43 first lower incisors of Oligokyphus A from Pant 4 and Windsor Hill, the absence of a marked size disparity between the males and females of this species is genuine. This greatly strengthens the likelihood that Oligokyphus major and minor are different species.

The small forms Oligokyphus B and C remain to be accounted for. It seems very probable on grounds of size and incisor morphology, that Oligokyphus B is a young juvenile form of O. minor, and Oligokyphus C a young juvenile of Oligokyphus A. This cannot, of course, be proven

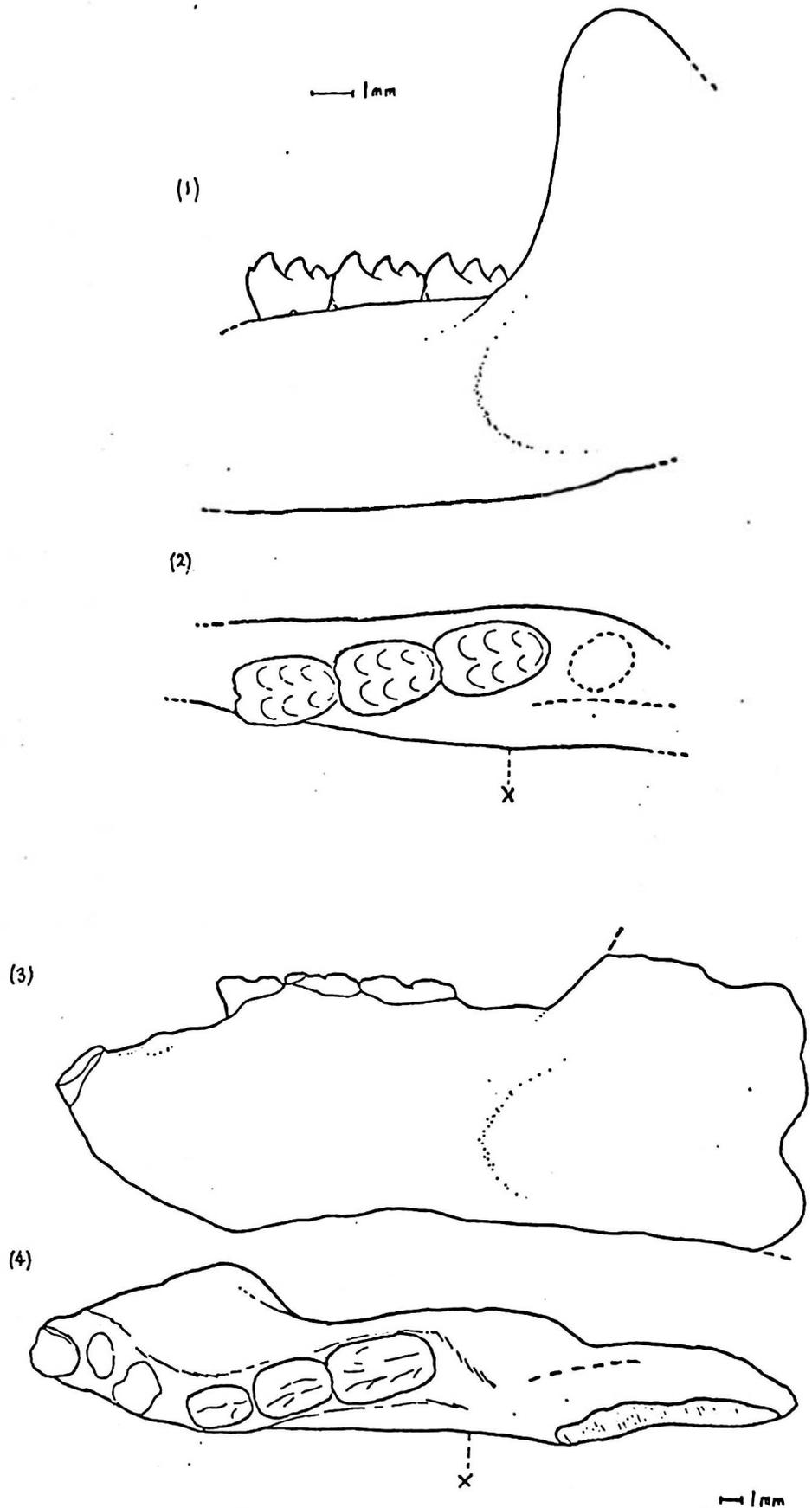


Figure 48. Tritylodont dentaries. Upper specimen, Oligokyphus dentary R 7169, partially restored. (1) Lateral and (2) dorsal views. Dotted oval outline following third cheek tooth indicates the position of a reduced cheek tooth. Lower specimen, young juvenile Bienotherium dentary C U P 2218. (1) lateral and (2) Medial views. X denotes the anterior end of the masseteric fossa.

on the present meagre evidence, but the alternative - that there are three tiny species of Oligokyphus - is less plausible on ecological grounds.

The relationship between the British and German species

Kuhne has discussed very thoroughly the problem of the relationship between the British and German species of Oligokyphus (Kuhne, 1956:97), and I have little to add to what he has said. The two German species may come from different localities and/or even different horizons from one another (Simpson, 1928). Each is represented only by a single tooth which is so water-worn that its detailed morphology cannot be made out. Each of the German species is thus effectively a nomen vanum (sensu Simpson, 1945), and material from another locality cannot be referred to it. As Kuhne has pointed out, the genoholotype is the same size as a functional upper cheek tooth of Oligokyphus major, and the tooth called O. biserialis is the size of a functional lower cheek tooth of O. minor. It simply remains for me to add that there is, therefore, one relationship concerning the German species about which we can be absolutely certain. On grounds of size, neither can be synonymous with the species which I have called Oligokyphus A.

Class	<u>MAMMALIA</u>
Subclass	<u>ATHERIA, Kermack, Mussett &amp; Rigney, 1973</u>
Order	<u>MULTITUBERCULATA, Cope, 1884</u>
Suborder	<u>HARAMIYIODEA, Hahn, 1973</u>
Family	<u>HARAMIYIDAE, Simpson, 1947</u>

A single cheek tooth belonging to this problematic family is present in the assemblage. There are no incisiform or caniform teeth in the assemblage which match any of those previously ascribed to the Haramiyidae (see Simpson 1928; Parrington 1946; Peyer 1956), or which could be included here on any convincing morphological basis.

Typical haramiyid cheek teeth are oval or rectangular in occlusal view. An elongated central basin separates two longitudinal rows of cusps, except at one end of the crown where the bases of the leading cusps are confluent. This is conventionally designated the anterior end of the tooth (Simpson, 1928; Parrington 1946). At the back of the crown a U-shaped ridge curves round from the end of one cusp row to the other, enclosing the basin. One of the cusp rows consistently possesses three cusps and this may conveniently be referred to as the 'row of three' following the practice of Parrington (1946). The number of cusps in the other row is variable, but is commonly at least four. The cusps on either side of the basin do not correspond to one another in size, and the second cusp of the 'row of three' is always substantially larger than the second cusp of the opposite row.

Description

The Welsh specimen is broken, and consists of only a fragment of the crown. The first cusp of each row is incomplete and the posterior end of the crown is missing. The remainder of the crown conforms to the general haramiyid pattern, as can be seen in figure 49. The preserved portions of the two cusp rows are effectively parallel, so that the fragment has a sub-rectangular shape. Internally the cusp bases merge smoothly into the central basin. The enamel covering of the crown is relatively thick, as can be seen from the broken anterior cusp of the 'row of three'. The surface of the enamel is smooth, although it appears to be furrowed when seen with the naked eye, owing to the presence of sub-surface cracks, which have probably been caused by posthumous drying. The first cusp of the left hand row is substantially larger and higher than its successors and it is

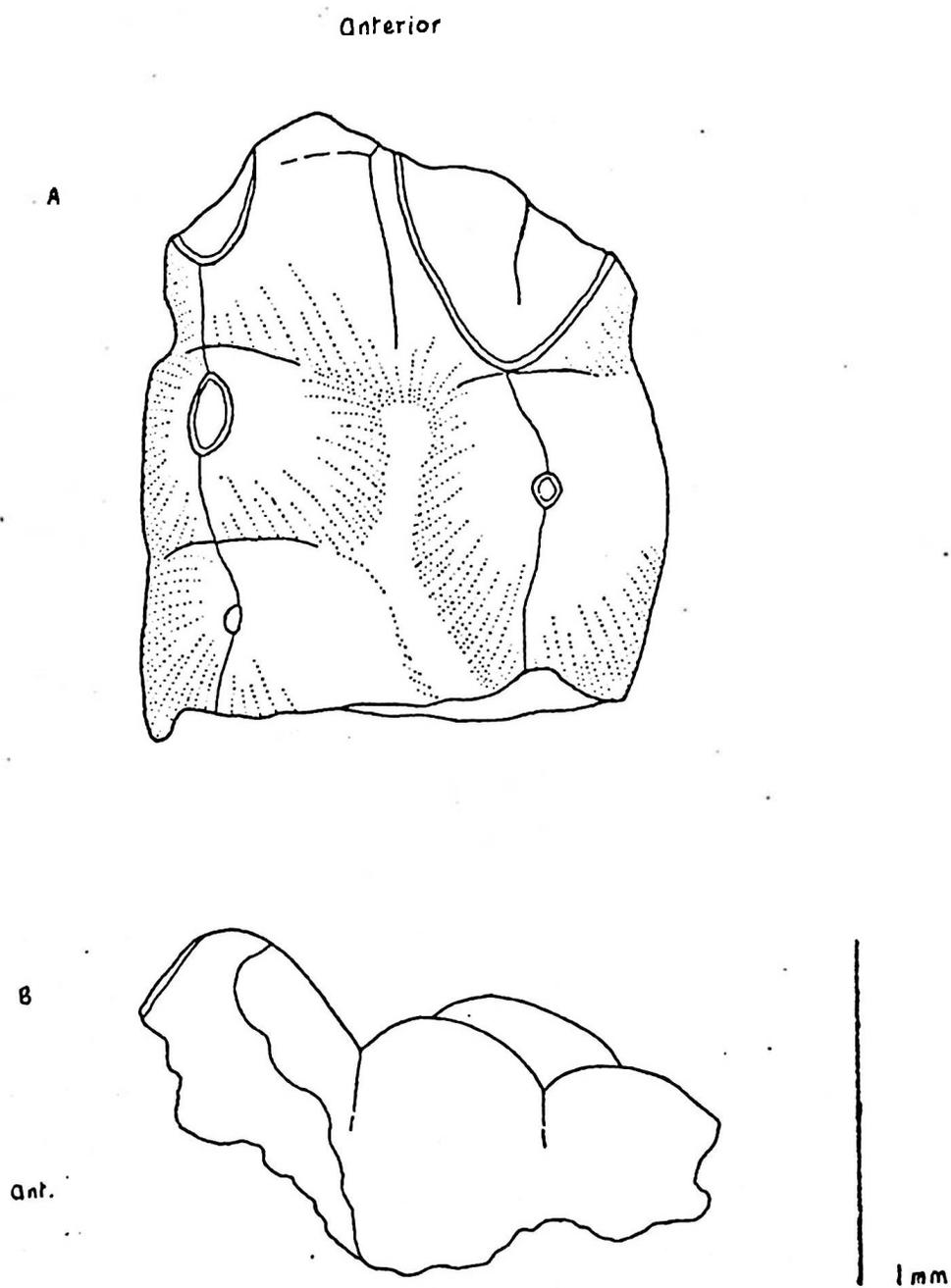


Figure 49. Haramiyid cheek tooth, specimen U658. A. Occlusal view, B side view (left side).

distinctly higher than the second cusp of the 'row of three'. Most of the external border of the cusp has been broken away and the antero-lateral corner is missing almost as far in as the apex. The apex is worn and bluntly rounded, the exposed dentine merging smoothly with the surrounding enamel. The base of the cusp is confluent medially with that of the first cusp of the 'row of three', and the junction between the two is marked with a groove. This groove lies directly in the midline of the crown and its highest point is above the level of the notches between the two anterior cusps and their successors. Posterior to this point, the groove descends backward almost to the level of the basin. Anteriorly it descends slightly for but a short distance to where the anterior end of the crown has been broken away.

The second and third cusps of the left hand row are of about equal prominence. In side view, each has an elongated, low and rounded profile. The second cusp is higher than the third, and the notch which separates the apices of the first and second cusps is higher than the notch which intervenes between the apices of the second and third. Grooves pass down from the notches, both internally and externally, denoting the junctions of the cusp bases. In vertical section, the internal sides of the second and third cusps are markedly convex, and their external sides slightly convex. In horizontal section the sides of the cusps are almost straight externally. Internally, the side of the second cusp is very markedly convex whilst that of the third curves smoothly and progressively to the right, passing posteriorly. Dentine has been exposed on the apices of both cusps (more on the second than on the third), and in each case this merges smoothly with the surrounding enamel.

The first cusp of the 'row of three' is represented only by the posterior part of its base; at its widest this slightly exceeds the width of the base of the succeeding cusp. The exposed dentine at the anterior edge of the preserved part of the base is almost as high as the apex of the succeeding cusp, so that when the first cusp was intact, it must have been at least as high as the latter.

The notch between the first and second cusps of the 'row of three' is almost directly opposite that between the first and second cusps of the left hand row, and it is at about the same level. As in the latter case, the enamel is grooved below the level of the notch, both

internally and externally.

The apex of the second cusp of the 'row of three' is higher than that of the second cusp of the left hand row, and the preserved length of the cusp is almost equal to the combined length of the two cusps opposite. In vertical and horizontal section, the internal and external sides of the cusp are convex. A small area of enamel has been worn from the apex. The broken posterior edge of the cusp is lower than the notch which separates the cusp from its predecessor.

As in other haramiyid cheek teeth, the internal and external surfaces of the cusps meet at fine but well defined enamel crests.

The central basin is narrow and at its anterior end occupies an almost perfectly median position on the crown. Passing directly backwards, the floor of the basin descends gradually to its deepest point opposite the notch which separates the apices of the second and third cusps of the left-hand row. Thereafter the floor of the basin turns slightly to the right as it passes posteriorly. Just in front of the posterior edge of the specimen, the basin lies wholly to the right of the middle of the crown and its floor is at about the same depth as at the anterior end. This gives the impression that on the intact tooth the basin terminated very shortly after this point. Clearly, if there was originally a third cusp in the 'row of three' it was substantially smaller than the second.

The specimen measures 1.6mm in length by 1.5mm in width. The intact tooth probably had a length of a little over 2.0mm.

Wear

In his paper of 1946, Parrington argued that the relatively large number of haramiyid cheek teeth which had then been collected effectively precluded the possibility that only upper or lower teeth were represented, so that the upper and lower cheek teeth of haramiyids must have essentially the same morphology. He described the wear on a number of specimens, and demonstrated that - in some instances, at least - this wear had resulted from the cusp row opposite the 'row of three' having worked in the central basin of the opposing teeth. These occlusal relations probably account for the fact that in the Welsh specimen the large cusp opposite the 'row of three' is the most worn. Unfortunately it is impossible to be certain, in the context

of the general condition of the tooth, that the wear of the cusp apices was not effected posthumously.

Generic and specific position

As only isolated haramiyid teeth are known, the internal systematics of the family are very uncertain. In his Catalogue of the Mesozoic Mammalia in the British Museum, Simpson (1928) divided all the known haramiyid cheek teeth - with the exception of a problematic specimen described by Boyd Dawkins in 1864 - into the genera Microcleptis and Thomasia, each of which consisted of two species. Microcleptis was subsequently amended to Haramiyia because of preoccupation (Simpson, 1947). Boyd Dawkins' tooth had been lost prior to Simpson's review, and, as the latter author has emphasised (Simpson, 1928) the published descriptions and figures of the specimen do not allow a reliable determination of its morphology or affinities.

According to Boyd Dawkins' figures, the tooth was substantially larger than any other haramiyid cheek tooth known, being about the size of an Oligokyphus major lower cheek tooth. If this size is the correct one, there would seem to be a real possibility that the tooth did not belong to a haramiyid. Simpson's expressed purpose in classifying the undoubted haramiyid cheek teeth was simply to provide names for the different morphological types which occur. He recognised the possibility that teeth belonging to different parts of the same dentition might thus have been placed in different species. However, he pointed out that three of his species comprised a number of teeth of different sizes, proportions and number of roots - in other words teeth very probably from different dental positions - so that there was a good chance that these species were natural.

All the haramiyid cheek teeth that have been described and classified since 1928 have been referred to Simpson's genera, and no new species has been formally established (Parrington, 1946; Hahn, 1973).

Although Peyer (1956) has described a number of cheek teeth from Hallau which have not yet been named, Professor Clemens, who has studied these specimens, has informed me that all are referable to Haramiyia and Thomasia. Recently, Hahn (1973) has drawn attention to the considerable similarity which exists between the cheek teeth of Thomasia and some of the cheek teeth of the paulchoffattid multi-tuberculates. He has argued convincingly on the basis of this

similarity, and also on the basis of a similarity in the occlusal relations of the relevant teeth, that the haramiyids are members of the multituberculate stock. If Hahn is correct then the fact that the paulchoffatiid teeth in question resemble the teeth of Thomasia more closely than they do those of Haramiya provides some evidence that Simpson's generic division of the Haramiyidae is founded on a genuine phyletic dichotomy.

Simpson distinguished between Thomasia and Haramiya on the basis of the relative sizes of the cusps in the 'row of three'. In the former genus, the first cusp of this row is the largest and the last the smallest. In the latter genus, the three cusps are subequal, or the first is the smallest. The damage to the Welsh tooth unfortunately means that it is impossible to determine whether or not the first cusp of the 'row of three' was originally larger than its successor. As pointed out earlier, however, it is quite evident that if the row originally possessed a third cusp, this must have been very much smaller than its predecessor. This precludes the possibility that the tooth belongs to Haramiya. The preserved part of the crown agrees so closely with the equivalent region of one of the Thomasia teeth figured by Simpson - the type of T. anglica - that there be little doubt that the specimen belongs to this genus.

The two existing species of Thomasia - antiqua and anglica - were distinguished by Simpson on the nature of the posterior end of the two cusp rows and the anterior face of the crown. Both regions are missing in the Welsh specimen, so that its taxonomic position in relation to these species is problematic. There is, however, one morphological detail in which the tooth clearly differs from the type of T. antiqua, the tooth referred to T. antiqua by Hahn (1973), and at least some of the teeth which Parrington (1946) referred to this species: the notch between the first and second cusps of the 'row of three' is not markedly posterior to the level of that between the first and second cusps of the opposite row. This suggests that the specimen does not belong to T. antiqua. By contrast, there is no discernible morphological detail in which the tooth differs from the type of T. anglica. Whilst, in the light of the incompleteness of the Welsh specimen, this agreement is insufficient to unequivocally establish the conspecificity of the two teeth, it does make the probability of their conspecificity very great.

Class	MAMMALIA
Subclass	ATHERIA, Kermack, Mussett & Rigney, 1973
Order	TRICONODONTA, Osborn, 1888
Suborder	MORGANUCODONTA, Kermack, Mussett & Rigney, 1973

Morganucodonts are, in terms of species and specimens, the most abundantly represented mammals in the assemblage. The material consists both of isolated teeth and fragments of dentaries. There are no teeth in situ, and almost all the specimens are damaged.

Morganucodonts are recognised and defined largely on the morphology of their molariform teeth. The basic morphology of these teeth may be summarised as follows: The upper molariform teeth bear three linearly arranged crown cusps (as opposed to cingulum cusps),<sup>1</sup> and the central cusp is the largest of the three. Buccal and lingual cingulae are present in the upper molariform teeth and the former, and frequently the latter, bears cusps. The lower molariform teeth also bear three linearly arranged crown cusps of which the central is the largest. These teeth invariably bear a lingual cingulum, but there is never more than an incipient lingual cingulum, and normally none. The lingual cingulum usually bears cusps, and a Kuhnecone is normally present.

It will be recognised that the foregoing description does not fit the molariform teeth of Sinoconodon rigneyi (Olson and Patterson, 1961; Mills, 1971), a form which is included within the Morganucodonta by some authorities (e.g. Hopson and Crompton, 1969; Mills, 1971). The taxonomic position of this enigmatic animal is, in my opinion, very problematic. It might be an aberrant morganucodont, but there are good reasons against this view, as will be shown later.

The Welsh morganucodont material consists predominantly of the remains of two species (I will not be concerned for the present with the question of families or genera). One of these species is Morganucodon watsoni; the other is new. There are also three other species, each of which is represented by only one cheek tooth or by only a few teeth. At least two of these species are new. The new species will be referred to by letters. In describing their teeth I will make

<sup>1</sup> The use of the term 'crown cusp' to distinguish a cusp which is not situated on the cingulum from one which is, follows the practice of Crompton (1972). The term is not an ideal one in certain respects, as the cingulum is, of course, also a part of the crown of the tooth. It has, however, the advantages of brevity and convenience.

frequent use of the equivalent teeth of the best known morganucodont - Morganucodon watsoni - as a morphological standard for comparison. The cusp nomenclature of Crompton and Jenkins (1968) will be followed, wherever possible. Parrington 1971 has shown that the terms 'premolar' and 'molar' can be applied correctly to the premolariform and molari-form teeth of Morganucodon watsoni. For convenience I will also use these terms for the cheek teeth of the other morganucodonts in the collection, although in this instance they are not strictly correct.

#### 1. MORGANUCODON WATSONI, Kuhne, 1949

This species is represented by teeth from every dental position. Amongst the fragments of mammalian dentaries from Pant 4 many specimens probably belong to this species. Unfortunately few of these fragments are sufficiently intact to make their allocation unequivocal.

An idea of the relative abundance of the species is afforded by the number of molars: there are more than sixty lowers and forty uppers.

The teeth of Morganucodon watsoni have been described by Mills (1971), and Parrington (1971), and there is no necessity to describe them again here. I will merely emphasise that the present specimens are not morphologically distinguishable from those which have been obtained from other Welsh fissures (Ewenny 2 possibly excepted). Figure 50 gives the size distributions of the measurable upper and lower molars together with the size distributions of random samples of teeth from Pontalun 3. The length of each tooth has been measured along a line which passes through the apices of the crown cusps, and the breadth along a line which passes at right angles to the latter, and through the apex of the principal crown cusp. As can be seen from the figure, the new teeth cannot be distinguished, in their sizes or proportions, from the Pontalun specimens.

#### The synonymy of Morganucodon watsoni

The species was founded by Kuhne (1949), on the basis of a single lower molar from Dutchy quarry. During the ensuing years its hypodigm has expanded enormously and it now far exceeds that of any other Mesozoic mammal (see, for example, Kermack, Kermack and Mussett, 1956, and Kermack, Mussett and Rigney, 1973). In recent years the species has become the subject of a taxonomic controversy. Parrington

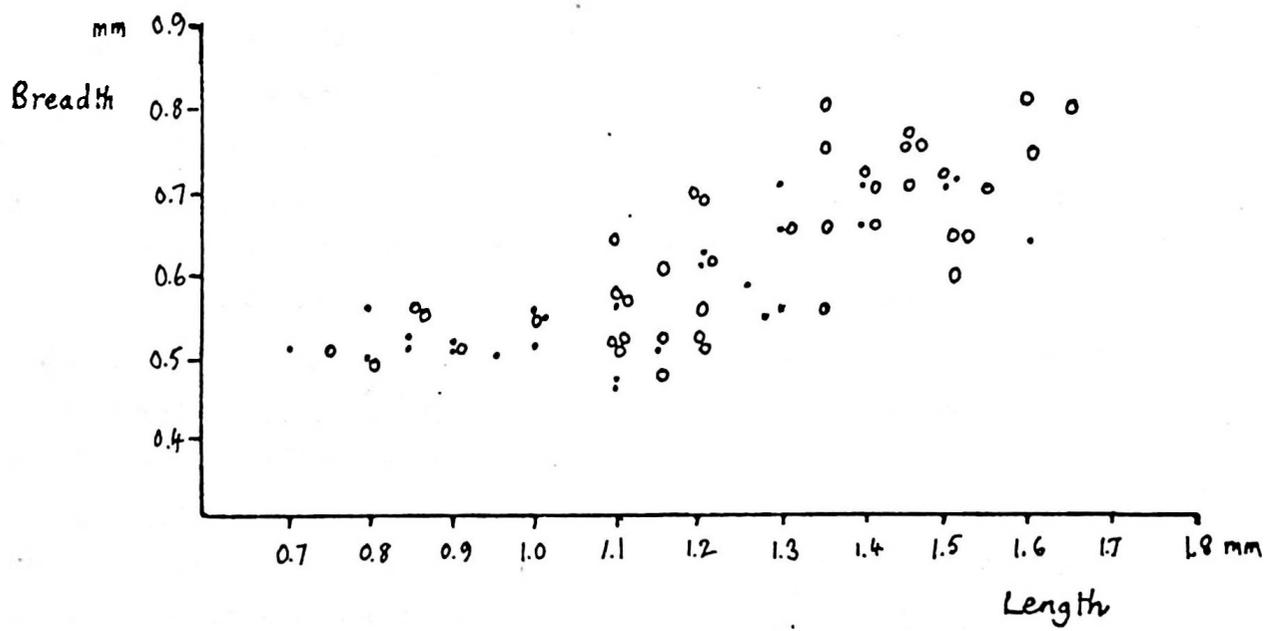
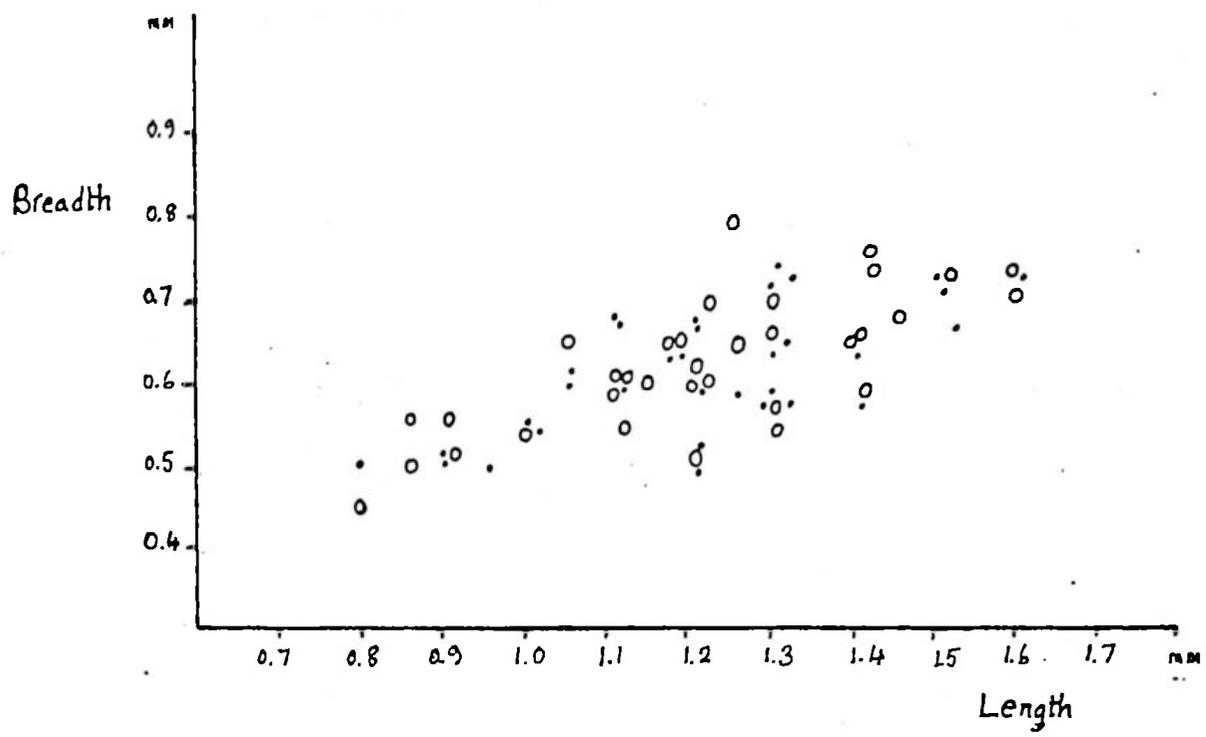


Figure 50. Morganucodon watsoni. Measurements of length and breadth of molars from Pant 4 and Pontalun quarry. · = measurable Pant 4 specimen o = Pontalun specimen (selected at random from the U.C.L. collection). Upper diagram : upper molars; lower diagram : lower molars.

(1967, 1971 and 1972) has stated that both Morganucodon watsoni and Eozostrodon problematicus are synonymous with Eozostrodon parvus. This view has been accepted by Crompton and Jenkins (1968), Hopson and Crompton (1969) and Crompton (1974), but it has been contested by Kermack, Kermack and Mussett (1968), Mills (1971), and Kermack, Mussett and Rigney (1973). Eozostrodon parvus and E. problematicus are the names which Parrington (1941) gave to two mammalian teeth obtained by Kuhne from a Rhaeto-Liassic fissure in Holwell quarry in Somerset (Kuhne, 1946). E. parvus - which was the first named, and is hence the genoholotype of Eozostrodon - is an upper premolar of triconodont form. E. problematicus is a morganucodont right lower molar. The crown of the former specimen appears to be intact, and the tooth bears two completely separated roots, which are broken off a little under half way along their original length (c.f. Parrington, 1941, figure 1). According to Kuhne (1973) the missing parts of the roots were still present at the time of the discovery of the specimen, and they were tapered. Parrington (1971) claims that E. parvus can be matched by the ultimate upper premolar of Morganucodon watsoni. It is important to note that in comparing the Holwell tooth to M. watsoni, Parrington is considering the former specimen only in the state in which it is currently preserved; he makes no mention of the original form of its roots. After carefully examining his drawings and photographs of the specimen, I would agree with him that the crown can be matched by the crown of the ultimate upper premolar of M. watsoni. Kermack et al (1968) also agree but they state that Eozostrodon parvus can be equally matched by one of the premolars of the therian mammal Kuehneotherium precursoris. For this reason they consider that the affinities of the Holwell tooth are indeterminate. The Kuehneotherium premolar in question is a penultimate upper premolar (P. M. Gill, 1973, personal communication). It is certainly true that it bears a close resemblance to Eozostrodon parvus. However, as Hopson and Crompton (1969) and Parrington (1971) have pointed out, there is one notable difference. The Kuehneotherium tooth has a marked constriction at the base of the crown - a feature which is absent in Eozostrodon parvus, and in the ultimate upper premolar of Morganucodon watsoni. As the feature appears to be characteristic of all the penultimate upper premolars of Kuehneotherium, it would not be correct to state that Eozostrodon parvus cannot be distinguished from a Kuehneotherium tooth; in this respect, at least, the affinities of the Holwell premolar are not indeterminate.

Parrington (1971) appears to believe that this means that E. parvus must therefore be synonymous with Morganucodon watsoni. However, Kuhne's recent description of the original shape of the roots of the Holwell tooth, effectively precludes the possibility of synonymy. In contrast to the situation which the latter author has stated pertained in E. parvus, the roots in ultimate upper premolars of Morganucodon watsoni are never tapered. When they are mature, they exhibit the marked taurodontism which characterises the mature molar roots in this species. When they are immature, they have straight, nearly parallel sides. Interestingly enough, the original form of the roots in E. parvus would appear to have been very similar to that of the molar roots in Megazostrodon rudnerae (c.f. Crompton, 1974, p.413).

We may now consider the claim that Eozostrodon parvus and E. problematicus are synonyms. Since the crown of the former specimen resembles that of the ultimate upper premolar of Morganucodon watsoni, it is pertinent to note that there are very few differences between the ultimate upper premolars of triconodonts as diverse as M. watsoni and Trioracodon ferox. Indeed, it is fair to say that there is no way in which an isolated morganucodont ultimate upper premolar can be reliably distinguished from a triconodont tooth, solely on the basis of its morphology. In these circumstances, the relationship between Eozostrodon parvus and E. problematicus must be regarded as indeterminate. It cannot be shown that the former specimen belongs to the same suborder - let alone to the same species - as the latter one. Strictly speaking, the generic name of the morganucodont molar from Holwell should be changed in recognition of this fact. If the name is retained for convenience - as it will be here - it should be used in parenthesis. This situation would change if good samples of E. parvus premolars and 'E' problematicus molars were obtained from Holwell - without, of course, any triconodont cheek teeth which might belong to other species (and which would thus complicate the issue). If this happened, the 'E' problematicus teeth could be reasonably referred to the same species as the E. parvus specimens on the basis of numerical probability. This would make E. parvus an undoubted morganucodont, and its relationship with Morganucodon watsoni could then be discussed in a meaningful way. As things stand at present, however, the names Eozostrodon parvus must be regarded as nomen vana, and it must be recognised that the tooth which bears them does not necessarily belong to a morganucodont.

There is next the question of whether 'Eozostrodon' problematicus and Morganucodon watsoni are conspecific. 'E' problematicus is, unfortunately, a rather poorly preserved tooth. The part of the crown mesial to cusp  $\bar{a}$  is missing, as is the mesial root. The apex of cusp  $\bar{a}$  has been broken off, and the talonid is damaged posteriorly, in the position where one would expect cusp  $\bar{d}$  (cf. Parrington, 1941, figure 2). In spite of the poor condition of the tooth, it is clear that 'E' problematicus differs from a lower molar of Morganucodon watsoni in several morphological details. One of the most conspicuous and important concerns the extent of the division between cusps  $\bar{a}$  and  $\bar{c}$ . In Morganucodon watsoni the two cusps are divided to a low level so that they appear to have arisen independently from the crown base. In 'Eozostrodon' problematicus they are much less completely separated, cusp  $\bar{c}$  giving the impression that it has arisen by splitting off from cusp  $\bar{a}$ . Mills (1971) and Kermack, et al (1973) have already drawn attention to this difference, and the latter authors have shown statistically that on this basis alone 'E' problematicus cannot have been drawn from a population of Morganucodon watsoni. In fact, the very low level of the division between cusps  $\bar{a}$  and  $\bar{c}$  in both of the known species of Morganucodon (i.e. watsoni and oehleri) clearly distinguishes these species from all other morganucodont species described in the literature.<sup>1</sup> It is thus a highly significant diagnostic feature of the genus. Parrington (1972), appears to have accepted that the division between cusps  $\bar{a}$  and  $\bar{c}$  is less complete in 'Eozostrodon' problematicus than it is in Morganucodon watsoni, (ibid, page 88) yet, curiously, he does not appear to have recognised the taxonomic implications of this. Another difference between 'Eozostrodon' problematicus and Morganucodon watsoni lies in the shape and orientation of cusp  $\bar{c}$ . In the latter species, the mesial and distal edges of the cusp are clearly convex whilst in the Holwell tooth are straight. For this reason the apical half of the cusp is more slender in 'Eozostrodon' problematicus, than it is in Morganucodon watsoni. Cusp  $\bar{c}$  leans quite markedly distally in 'E' problematicus. In M. watsoni it normally leans distally, but, whilst the extent of this tilting is variable, it never equals that in the Holwell tooth.

<sup>1</sup> Including Erythrotherium parringtoni (c.f. Crompton, 1974), which is wrongly assigned to the genus Morganucodon by Kermack, et al (1973).

The relative size of the Kuhnecone differs in 'Eozostrodon' problematicus and Morganucodon watsoni. In the latter species the cusp is very prominent, rivalling or even exceeding cusp  $\bar{b}$  in size. In the Holwell molar it is clearly much smaller. It is barely discernible in Parrington's drawings and photographs of the tooth, and its size in no way compares with that in a similar sized Morganucodon tooth (this is well illustrated in figure 1 in Parrington's paper of 1971).

Mills (1971) and Kermack, et al (1973) have pointed out that the shape of the distal root, in 'Eozostrodon' problematicus is significantly different from the shape of any molar root in Morganucodon watsoni. In the former specimen, the root is tapering and curved. In mature M. watsoni molars, the roots are straight and markedly taurodont. Parrington (1971, 1972) has claimed that the absence of a club foot in the root of 'E'. problematicus is simply a reflection of immaturity. He is quite correct in stating that immature, growing, roots of M. watsoni molars are not taurodont. However, as Kermack et al (1973) have emphasised, the important point is that these roots are never tapering or curved; they have straight, nearly parallel sides and in no way match the distal root in 'E' problematicus. The fundamental difference between the root in 'E' problematicus and the molar roots in Morganucodon watsoni entirely corroborates the evidence of the genuine specific disparity between the English and Welsh morganucodonts which is afforded by the study of comparative crown morphology. It may be added that the lack of curvature of the roots of immature M. watsoni molars is not surprising in view of the fact that these roots were destined to develop club feet. Root curvature, and taurodontism are quite different, but equally effective, adaptations to the same functional end - that of anchoring teeth firmly in the jaw. There would therefore be no necessity for a tooth which possesses one of them to develop the other one; in adaptive terms, they are mutually exclusive. This has interesting consequences. It means that 'Eozostrodon' problematicus cannot have given rise to Morganucodon watsoni or vice versa. Each species must have evolved independently from a common ancestral species in which the molar roots were neither curved nor taurodont. The closest possible relationship between the two species is thus one in which they share the same immediate ancestor. In view of the sum of the known differences between the species, elucidated above, I doubt whether the relationship between them is actually as close as this. Since 'E' problem-

aticus does not possess two of the most salient diagnostic features of the known species of Morganucodon - the very low division between cusps  $\bar{a}$  and  $\bar{c}$ , and taurodont roots - there can be no doubt that it is not congeneric with the latter forms.

2. MORGANUCODONT A

This is the most abundantly represented mammalian species in the assemblage. The molars are more than twice as common as those of Morganucodon watsoni. The majority of dental positions appear to be represented and there are also some fragments of dentaries. It should be pointed out, however, that the non-molar elements are only ascribed to the species on the basis of numerical probability, as the form is essentially recognised only by its molars. There is no indication of dimorphism in Morganucodont A, and there do not appear to be any milk molars amongst the material. The molars are not greatly dissimilar from those of Morganucodon watsoni but those differences which there are, are sufficiently marked for the two sets of teeth to be readily distinguishable. There is no evidence that the molars of Morganucodont A intergrade, morphologically, with the premolars.

Description

The molars

There are more than one hundred and sixty lower and eighty upper molars. In each case they exhibit a considerable size range - the largest specimens are twice the size of the smallest. In neither case, however, can they be separated into discrete size groups which might correspond to different dental positions (see figure 51 ).

(a) The crown morphology of the lower molars

The crowns of the lower molars exhibit a slightly greater range of morphological variation than is encountered in the lower molars of Morganucodon watsoni, although this is not as extensive as that shown by the lower molars of Megazostrodon rudnerae. The variation is predominantly correlated with size so that normally the particular morphology of a tooth would appear to reflect its original position in the dentary. Four main morphological categories of specimens are recognised. The size ranges of the specimens within each overlap, slightly, with those of the specimens in the morphologically proximal one(s).

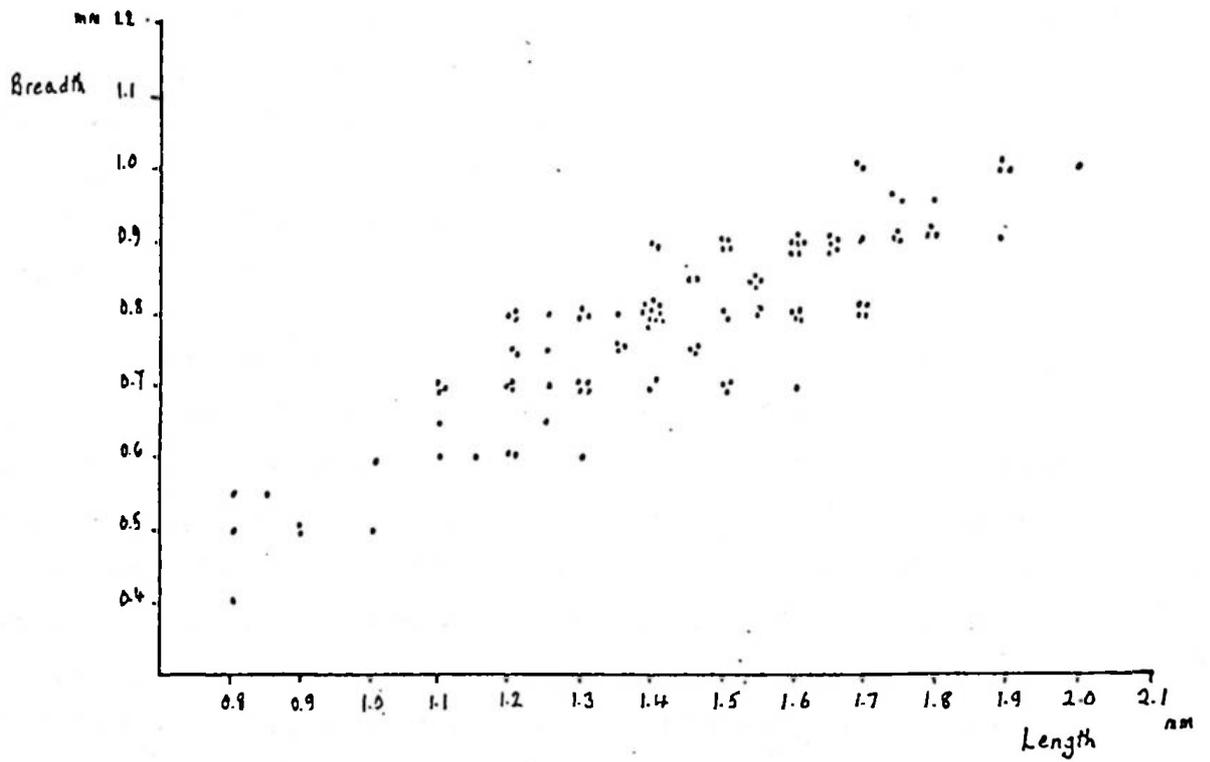
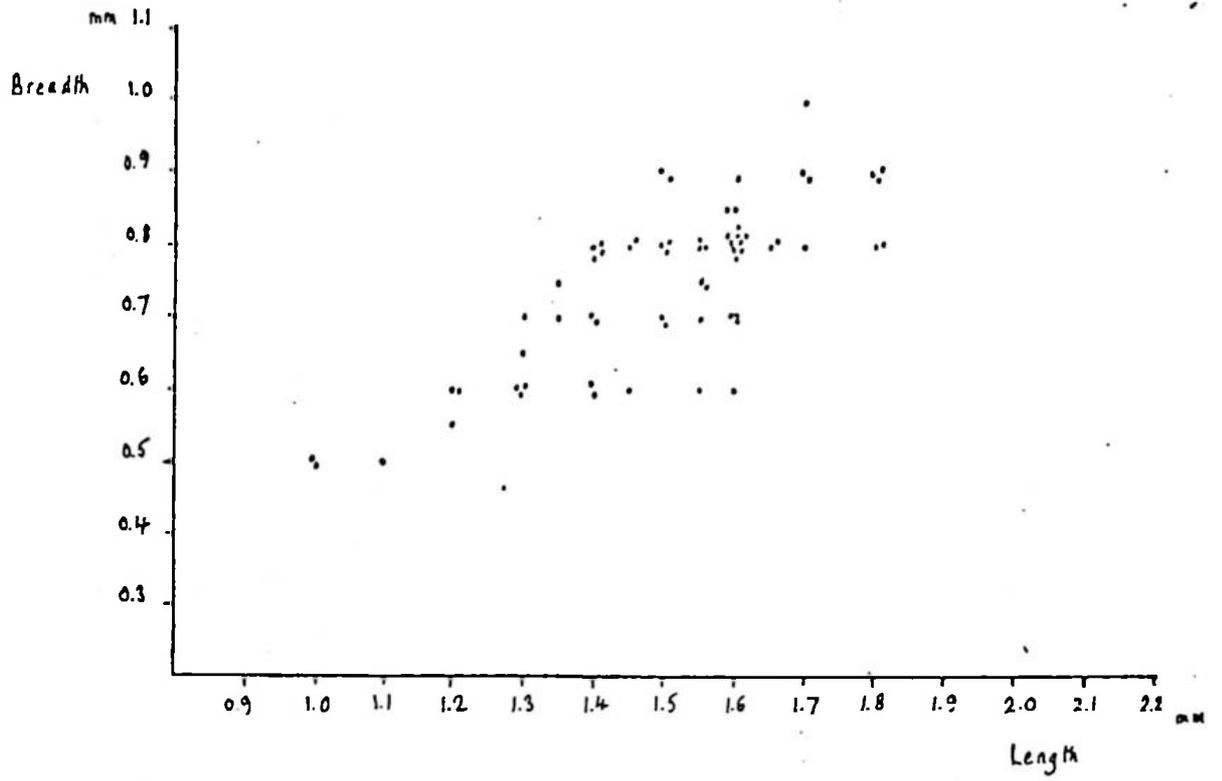


Figure 51. Morganucodont A. Measurements of length and breadth of molars. Upper diagram : upper molars; lower diagram : lower molars.

## Category one:

This morphological category comprises all the largest lower molars. Figure 52 shows the best preserved crown (U644). The specimen is almost perfectly intact, and it is morphologically typical, in most respects. It is a right lower molar crown, from which the roots have been entirely broken away. The length of the crown is about 20% greater than that of a second lower molar of Morganucodon watsoni. The crown is completely devoid of functionally produced wear and there are no pressure marks caused by neighbouring teeth. From this it is apparent that the specimen must have been incompletely, or only recently erupted prior to the death of the animal to which it belongs. The crown is proportionally a little broader than that of a more anterior lower molar of M. watsoni, and the cingulum cusps are fewer and relatively larger. The tooth therefore has a slightly more robust appearance than an M. watsoni molar.

Cusp  $\bar{a}$  is about as prominent as in a second lower molar of M. watsoni although it is a little more bulbous. The apex of the cusp is situated slightly buccal to the midline of the cusp base and slightly mesial to the midpoint of the crown. In lateral view the mesial edge of the cusp is slightly convex whilst the distal edge is virtually straight. In mesial and distal views the sides of the cusp are both slightly convex, and the crests which divide the cusp into buccal and lingual sides are vertical.

Cusp  $\bar{b}$  is slightly more prominent than in an anterior lower molar of Morganucodon watsoni. The size disparity between this cusp and the other crown cusps is never greater than in the present tooth, so that the cusp never appears to be a small cingulum cusp, as it may in some of the anterior molars of M. watsoni. The apex of cusp  $\bar{b}$ , which is broken off, would have been mesial to the midpoint of the cusp base, and the cusp has the appearance of leaning away from cusp  $\bar{a}$ . In occlusal view the mesial edge of cusp  $\bar{b}$  is nearly straight, whilst in lateral view it is slightly convex. The mesial face of the cusp is delimited by buccal and lingual crests which descend from the cusp apex. The lingual crest is continuous with the crest on the edge of the cingulum. The division between cusp  $\bar{b}$  and cusp  $\bar{a}$  is about as complete as in M. watsoni; its lowest point is fractionally above the level of that between cusp  $\bar{c}$  and the distal cingulum cusp. In this respect, however, U644 is atypical: in the majority of the largest

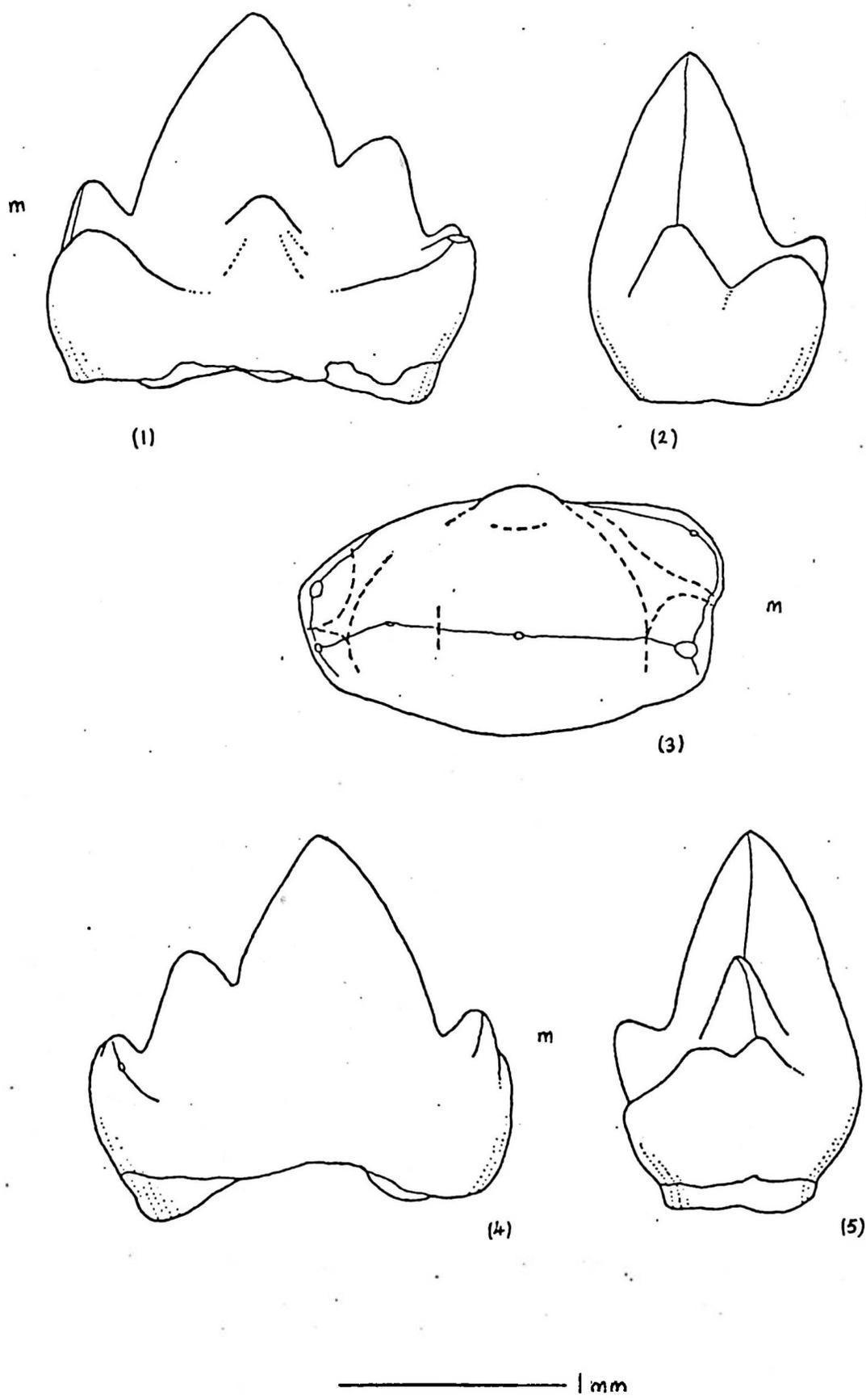


Figure 52. Morganucodont A. Specimen U644. Right lower molar belonging to morphological category one.  
(1) Lingual, (2) mesial, (3) occlusal, (4) buccal, (5) distal views.  
'm' denotes the mesial end of the tooth as in all the succeeding figures.

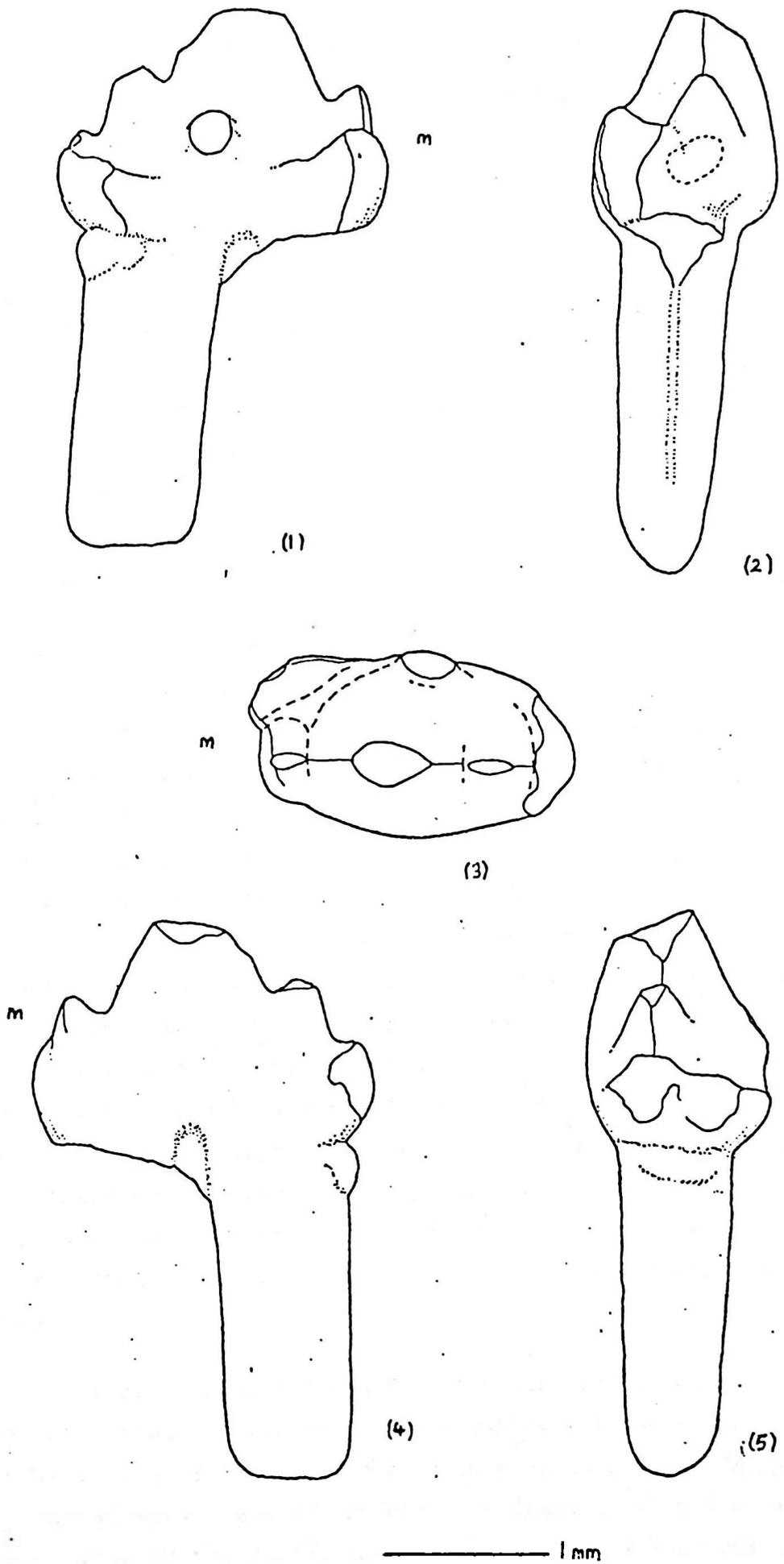


Figure 53 Morganucodont A. Specimen U645. A left lower molar belonging to morphological category one. (1) Lingual, (2) mesial, (3) occlusal, (4) buccal, (5) distal views. Note the pressure mark on the mesial surface of the tooth.

lower molars of Morganucodont A the divisions between cusps  $\bar{b}$  and  $\bar{a}$  is at a higher level. This can be seen, for example, in the damaged specimen (U645) illustrated in figure 53 .

Cusp  $\bar{c}$  is about as prominent as in one of the more anterior lower molars of M. watsoni, but it is much less completely divided from cusp  $\bar{a}$ . In lateral view the mesial edge of the cusp is only half the length of its distal edge so that the cusp has a markedly assymmetric profile, and appears to have split off from cusp  $\bar{a}$ . The lowest point of the division between cusp  $\bar{c}$  and cusp  $\bar{a}$  is above the level of that between cusp  $\bar{b}$  and the latter. In distal view the crest which divides the buccal and lingual sides of the cusp can be seen to be slightly obliquely orientated, its ventral extremity being buccal to the cusp apex.

The lingual cingulum is well developed except opposite the widest part of cusp  $\bar{a}$  where it is obsolete. Directly lingual to cusp  $\bar{b}$  there is a prominent cingulum cusp  $\bar{e}$ . This is larger and more elongated than the equivalent cusp in M. watsoni. The mesial part of the cusp projects further forward than cusp  $\bar{b}$ , although this feature is not as marked in U644 as it is in the majority of specimens (see, for example, those shown in figures 53 & 54). Cusps  $\bar{b}$  and  $\bar{e}$  are separated mesially by a narrow trough which passes backward, disto-lingually to open into a small basinid area between the bases of cusps  $\bar{a}$ ,  $\bar{b}$  and  $\bar{e}$ . This basinid area is continuous distally with the shelf of the cingulum behind cusp  $\bar{e}$ . The cingulum passes back for but a short distance behind cusp  $\bar{e}$  before it is interrupted by the widest part of cusp  $\bar{a}$ . There are no cingulum cusps on the mesial section of the cingulum behind cusp  $\bar{e}$ , and this is generally the case in all the lower molars of Morganucodont A. In a few instances however, a small cuspule is present here (see for example the tooth illustrated in figure 54 ).

The cingulum reappears just forward of the junction of cusps  $\bar{a}$  and  $\bar{c}$ . Although the distal section of the cingulum is well developed, it is not proportionally as broad, alongside cusp  $\bar{c}$ , as it is in M. watsoni, and in occlusal view the tooth is narrower distally than mesially. There is no cusp on the distal section of the cingulum in the position which is occupied by the Kuhnecone in M. watsoni. However, there is a prominent Kuhnecone-like cusp which projects bucco-lingually out of the side of cusp  $\bar{a}$ , above the region where the cingulum is interrupted.

This cusp is one of the most distinctive features of the crown. It is slightly more prominent than the Kuhnecone of M. watsoni. In lateral view it is as large as cusp  $\bar{b}$  and its apex, which is directly below that of cusp  $\bar{a}$ , is distinctly higher than the apex of cusp  $\bar{e}$ . The base of the cusp is wholly confluent with the side of cusp  $\bar{a}$ , so that the cusp has no connection with the cingulum; in fact the lowest part of its base is slightly above the level of the cingulum immediately mesial and distal to it. Although the cusp is wholly a crown cusp and is not therefore strictly a Kuhnecone as defined by Parrington (1967) its position is significantly different in some of the small lower molars of Morganucodont A - as will be seen in due course. In these specimens, the position of the cusp is such that it is most reasonably termed a Kuhnecone, and the cusp will therefore be given this name in all the lower molars for simplicity. The question of whether or not the cusp is homologous to the 'true' Kuhnecone of M. watsoni will be considered later. In mesial and distal views, the apex of the Kuhnecone of U644 is slightly lingual to the widest part of the base of cusp  $\bar{a}$ , so that the lingual edge of the cusp passes downwards and slightly buccally to join the latter. The buccal edge of the Kuhnecone, which is rather shorter than its lingual edge, passes nearly horizontally into the side of cusp  $\bar{a}$ . The cusp therefore appears to project out of the side of the latter cusp at an angle of about  $35^\circ$  to the vertical axis of the tooth (in some specimens, the angle may be as much as  $40^\circ$ ). In contrast to the other cusps on the tooth, the Kuhnecone is entirely bereft of clearly defined crests.

The distal section of the cingulum continues round the disto-lingual corner of the crown to form a posterior heel or talonid behind cusp  $\bar{c}$ . The talonid ends buccally in a cingulum cusp  $\bar{d}$ . A mesial crest unites the apex of this cusp with the distal crest on cusp  $\bar{c}$ , as Morganucodon watsoni. Lingual to cusp  $\bar{d}$  is a prominent cingulum cusp which I shall designate  $\bar{i}$ . This cusp is larger than cusp  $\bar{d}$  (its apex has been damaged) and it projects slightly but distinctly further distally.

Cusp  $\bar{d}$  is slightly smaller than its homologue in Morganucodon watsoni. Although in U644 the apex of the cusp is slightly buccal to the line of the apices of the crown cusps, this feature is not consistently shown amongst the lower molars; the cusp is normally in line. A crest descends the buccal side of cusp  $\bar{d}$  from the cusp apex turning slightly mesially for a short distance. There is no other semblance

of any buccal cingulum on the tooth.

Category two:

U647 (figure 54) is an almost perfectly intact left lower molar crown which, in essentials, is morphologically typical of the lower molars in this category. The crown is about the length of the crown of a second lower molar of Morganucodon watsoni. As in the case of U644, there are no remains of roots, and the tooth is completely unworn. The tooth differs from those in the first morphological category in the following ways:

- (a) The size disparity between the accessory crown cusps is much less, cusp  $\bar{b}$  being only slightly smaller than cusp  $\bar{c}$ .
- (b) The divisions between the accessory crown cusps and cusp  $\bar{a}$  are almost on the same level, the two former cusps appearing to have split off from the latter one to an equal extent.
- (c) The Kuhnecone is slightly lower down on the side of cusp  $\bar{a}$ , its apex now being only fractionally above that of cusp  $\bar{e}$ . The lowest part of the base of the Kuhnecone - which is still entirely confluent with the side of cusp  $\bar{a}$  - is on the same level as the cingulum immediately mesial and distal to it. The cusp still has no connection with the cingulum however, and is thus entirely a crown cusp.

U647 is unusual in that cusp  $\bar{e}$  is followed on the mesial part of the cingulum by a small cuspsule, and there are also two very small cuspsules in front of cusp  $\bar{i}$ .

Category three:

Unfortunately there is no crown in this category which is as completely preserved as the two specimens which have been described in detail above. Figure 55 shows the most complete specimen (U657). The tooth is a left molar of about the same length as a third lower molar of Morganucodon watsoni. It retains part of both of its roots intact. The mesial part of cusp  $\bar{e}$  and the buccal side of the apex of cusp  $\bar{a}$  is damaged, and the apex of the distal cingulum cusp is missing. Cusps  $\bar{b}$  and  $\bar{c}$  have both been substantially worn, and it is unfortunately the case that no tooth in the present category possesses both of these cusps intact. It is apparent from what remains of them in U657 (and in a few of the other specimens), however, that when they were intact they were of nearly equal size, as in the molars belonging to

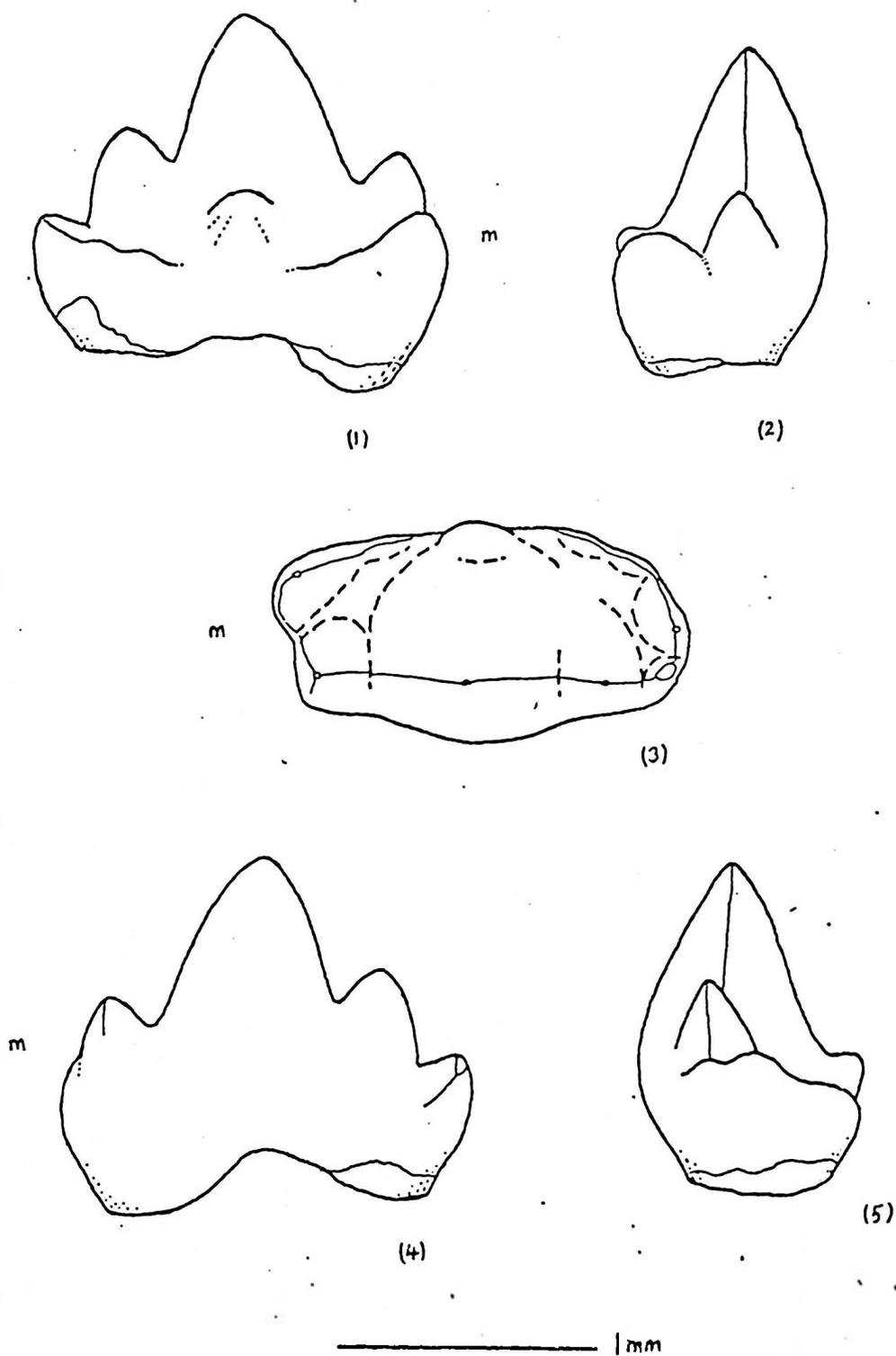


Figure 54 Morganucodont. A. Specimen U647. A right molar belonging to morphological category two.

(1) Lingual, (2) mesial, (3) occlusal, (4) buccal and (5) distal views.

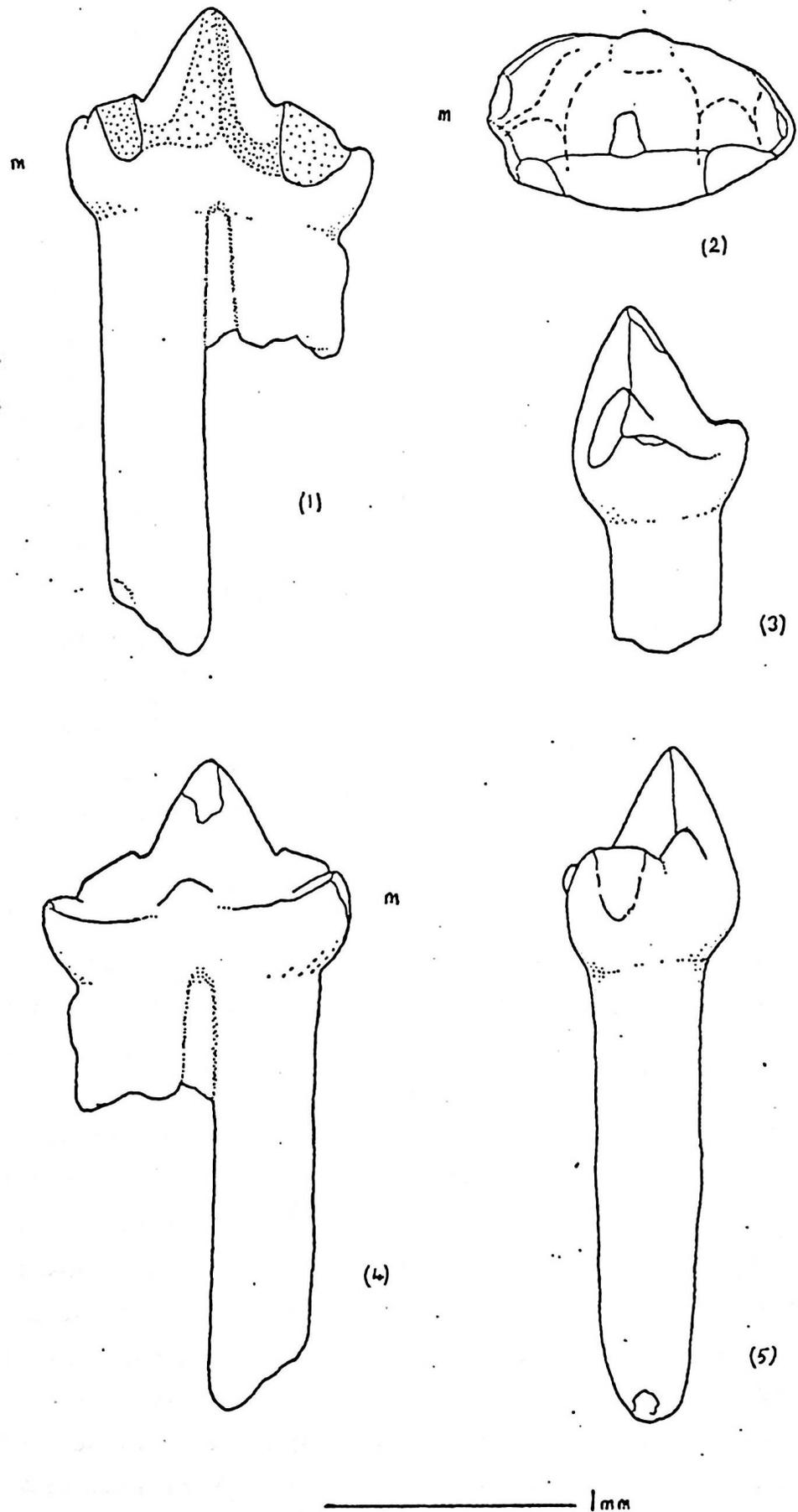


Figure 55. Morganucodont A. Specimen U657. A left lower molar belonging to morphological category three.

(1) Buccal, (2) occlusal, (3) distal, (4) lingual, (5) mesial views. Note the wear on the buccal side of the crown (stippled areas) and also the form of the mesial root.

the previous morphological category. The lowest part of the division between cusp  $\bar{a}$  and each of the accessory crown cusps is on the same level. Cusp  $\bar{a}$  is proportionally smaller than in the teeth described above, and the cingulum is rather wider and no longer interrupted by the widest part of cusp  $\bar{a}$ . The Kuhnecone is slightly smaller in U657, than is usually the case in specimens belonging to the present morphological category, but its position on the tooth is typical. The cusp is situated more ventrally than in the previously described crowns. The lowest part of its base is lingual to the base of cusp  $\bar{a}$ , and it is confluent, mesially and distally, with the dorsal surface of the cingulum. Consequently in distal view, the cusp projects partly out of the side of cusp  $\bar{a}$  and partly up from the cingulum, and it is no longer wholly a crown cusp in position. The greater part of the base of the cusp is still confluent with cusp  $\bar{a}$ , however, and the Kuhnecone does not possess crests which are continuous with those on the edge of the cingulum. The latter are interrupted by the base of the cusp. The talonid bears only one cusp. This is in the position of cusp  $\bar{i}$  in the larger molars, so that, in occlusal view, the talonid tapers backwards almost to a point, its distal extremity lying lingual to middle of cusp  $\bar{c}$ . It would appear, therefore, that it is cusp  $\bar{d}$  which has been eliminated from the talonid.

#### Category four:

Figure 56 shows three well preserved crowns of specimens belonging to this morphological category. All three are about the size of the crown of a fourth lower molar of Morganucodon watsoni. Cusp  $\bar{a}$  is not much larger than the accessory crown cusps, which are of equal size. The divisions between the three cusps are on the same level. Cusp  $\bar{i}$  is the only talonid cusp, as in the specimens belonging to the previous category. Here, however, the cusp is as prominent as cusp  $\bar{e}$  so that, in lingual view, the teeth have a rather symmetrical appearance. The cingulum is slightly broader than in the teeth which belong to category three. The situation regarding the Kuhnecone is variable in the three figured specimens, as it is in all the molars in this category. The cusp is never as prominent as in the larger molars.

In U761, the Kuhnecone is a very low cusp, and it is situated still more ventrally on the side of the tooth than in the molars belonging to the previous category. Consequently the largest part of the base of the cusp is lingual to cusp  $\bar{a}$  and is confluent with the cingulum. The Kuhnecone still retains some contact with cusp  $\bar{a}$  however, as can

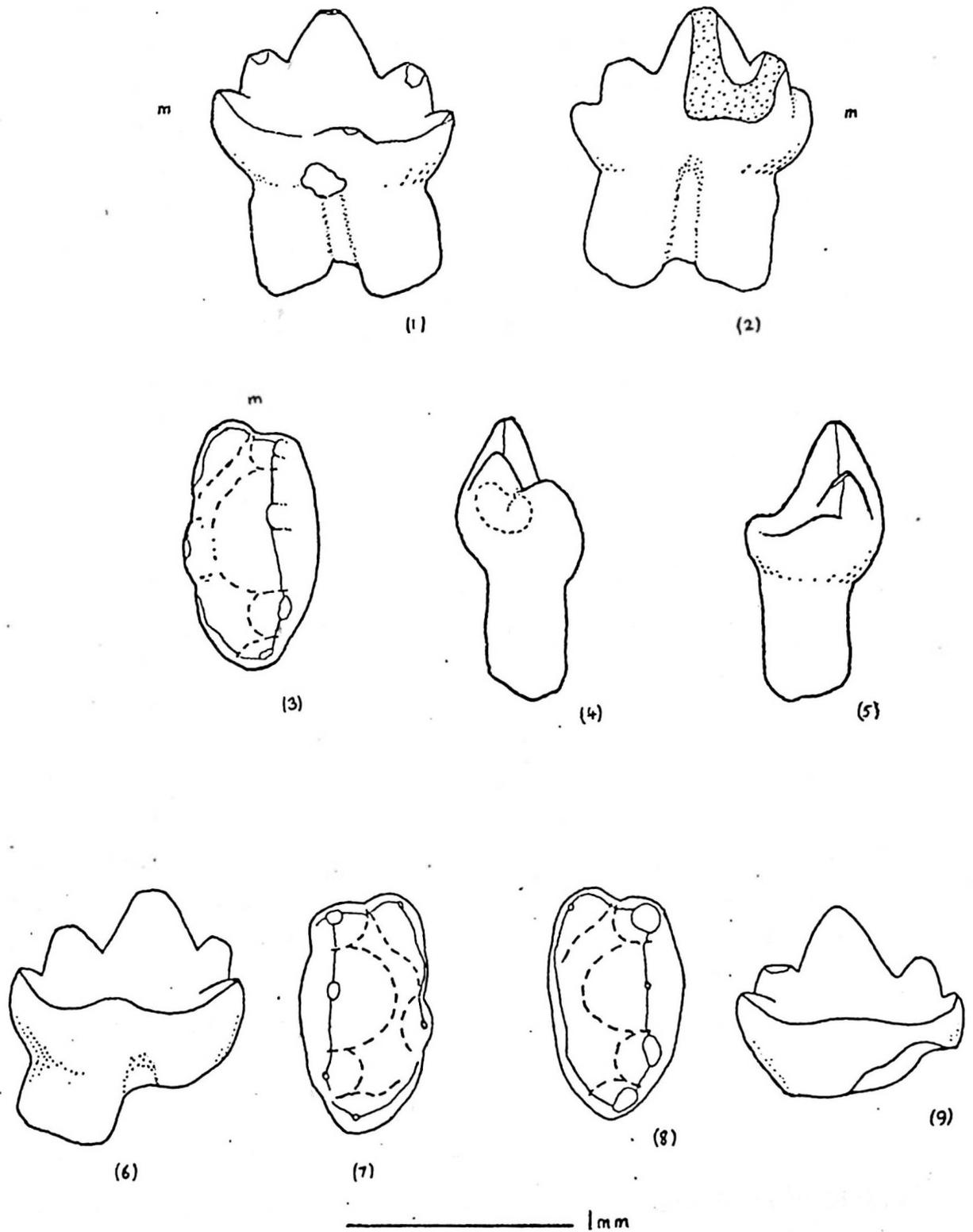


Figure 56 , Morganucodont A. Lower molars belonging to morphological category four.

(1) to (5) lingual, buccal, occlusal, mesial and distal views of right lower molar U761. (6) Lingual and (7) occlusal views of left lower molar U 651<sup>?</sup>. (8) Occlusal and (9) lingual views of lower molar U653.

be seen in figure 565. The cingulum merges into the Kuhnecone, mesially and distally, only a short distance below the level of the cusp apex. The latter is slightly lingual to the cingulum and the lingual surface of the cusp passes down below the level of the dorsal surface of the cingulum, so that it interrupts the edge of the cingulum. The Kuhnecone is still devoid of clearly discernible crests. In U653, the Kuhnecone is absent, the cingulum continuing without interruption or cuspules from cusp  $\bar{e}$  to cusp  $\bar{i}$ . In U651 the Kuhnecone is very low and is situated on the edge of the cingulum entirely lingual to cusp  $\bar{a}$ , having no connection with it. The apex of the Kuhnecone is connected by crests to the mesial and distal cingulum crests; this is the only specimen in which this is the case. Within the morphological range of lower molars belonging to Morganucodont A, therefore, the Kuhnecone progresses from being, in the large specimens, wholly a crown cusp, to being in the smallest specimens largely (and in one case wholly) a cingulum cusp. In this connection it is interesting to note that although the Kuhnecone in Megazostrodon rudnerae is a cingulum cusp in the first, second and fourth lower molars, in the third lower molar it is a crown cusp (Crompton 1974).

There is no tooth amongst the lower molars of Morganucodont A which corresponds to the very reduced fifth lower molar which is present in some dentitions of M. watsoni. The absence of such a tooth does not necessarily mean, however, that a very reduced ultimate tooth was never present in the dentition of Morganucodont A. It may well have been present in a small proportion of instances, in which case its absence from the present collection would be attributable to sampling error.

(b) The crown morphology of the upper molars

In contrast to the situation in the lower molars there is very little morphological difference between upper molars of different sizes.

Figure 57 shows one of the most completely preserved upper molar crowns. The specimen is a right molar and it is about the length of a second upper molar of Morganucodon watsoni. It is completely devoid of functionally produced wear. A well developed cingulum passes all the way round the outside of the crown, and the outline of the tooth is irregularly oval.

Cusp A is about as prominent as in M. watsoni. The apex of the cusp is situated slightly distal to the midpoint of the crown. The crests which ascend from the apex of cusp A divide the cusp into equal lingual and buccal sides. The buccal and distal edges of the cusps are both slightly convex. In lateral view the mesial and distal edges of the cusp are also slightly convex. The mesial edge is only fractionally longer than the distal one, and the two edges meet the accessory crown cusps on about the same level. In both of these features the tooth contrasts with an upper molar of Morganucodon watsoni. The accessory crown cusps are of about equal size so that the crown has a relatively symmetrical appearance in lateral view. As a result it is more difficult, initially, to distinguish the mesial end from the distal end than is the case with M. watsoni upper molars.

Cusp B is preceded by a cingulum cusp, the apex of which is slightly lingual to the line of the apices of the crown cusps. A distal crest descends from the cusp apex and joins the leading crest on cusp B, so that the cusp would appear to be the homologue of the more lingually situated cusp E of M. watsoni. (In the second upper molar of Erythrotherium parringtoni, cusp E occupies a similarly mesial position to that in Morganucodont A as can be seen from figure 2 in Cromptons paper of 1972.) In lateral view the edge of the lingual cingulum is markedly concave above cusp B. Thereafter it is irregularly convex. The lingual cingulum is devoid of cusps except above the leading crest on cusp A, where a small, rather elongated cusp is developed. In some specimens there may be two cusps at this point (see for example U660, figure 58). Behind cusp C there is no distal cingulum cusp D as there is in M. watsoni, although in a few specimens there may be a rather rudimentary cusp. The distal crest on cusp c never extends onto the cingulum, even when such a cusp is present. The edge of the buccal cingulum is slightly concave in lateral view. It bears a few rather low elongated cusps, except at its mesial end where a more prominent cusp F occurs. This is more elongated than cusp E.

Figure 59 shows a left upper molar of rather smaller size. Unfortunately this is rather damaged as in the case of all of the small specimens. The crown differs from that described above in that cusp A is proportionally somewhat smaller, and the buccal cingulum is slightly wider. As in the case of the lower molars there are no very reduced

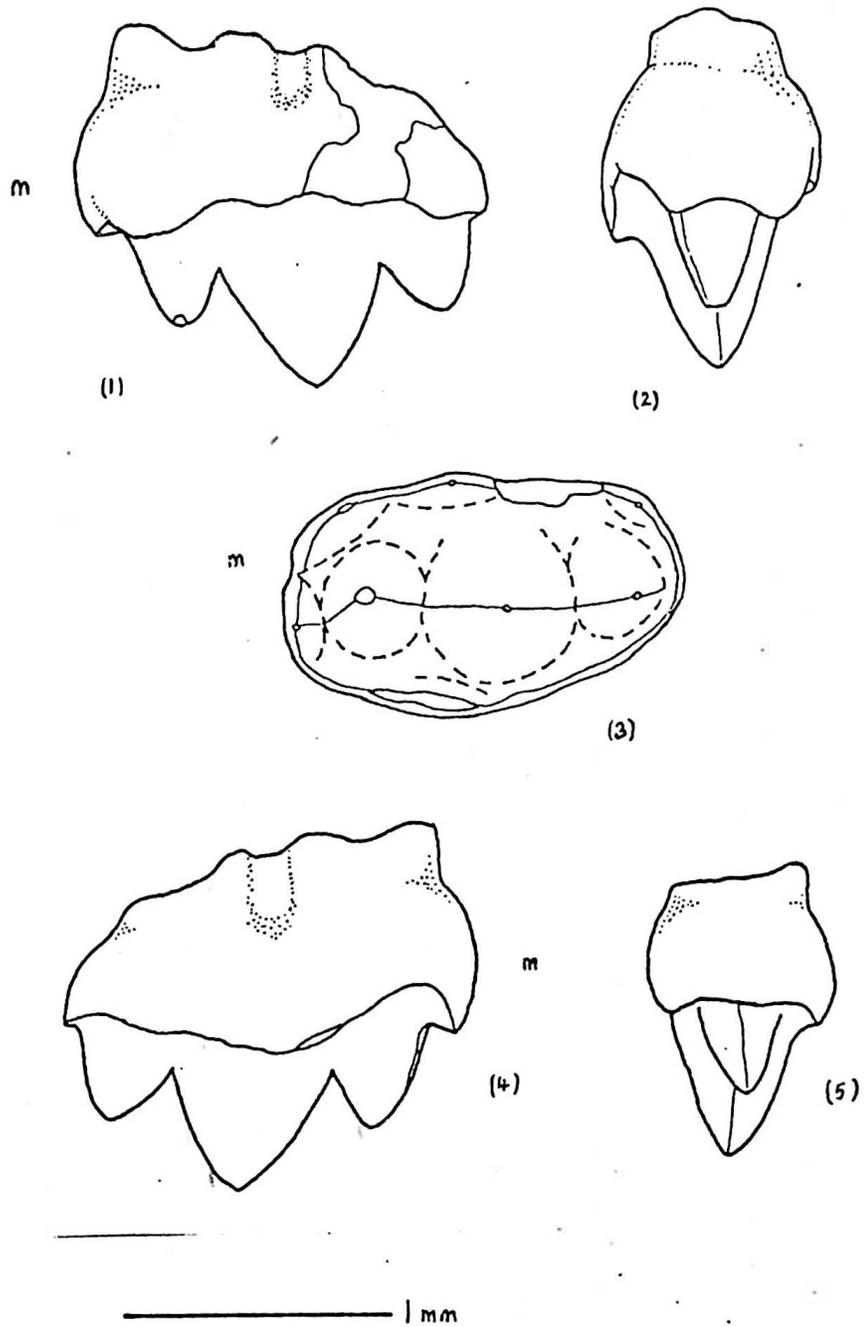


Figure 57. Morganucodont A. Specimen U661. Left upper molar. (1) Buccal, (2) mesial, (3) occlusal, (4) lingual and (5) distal views.

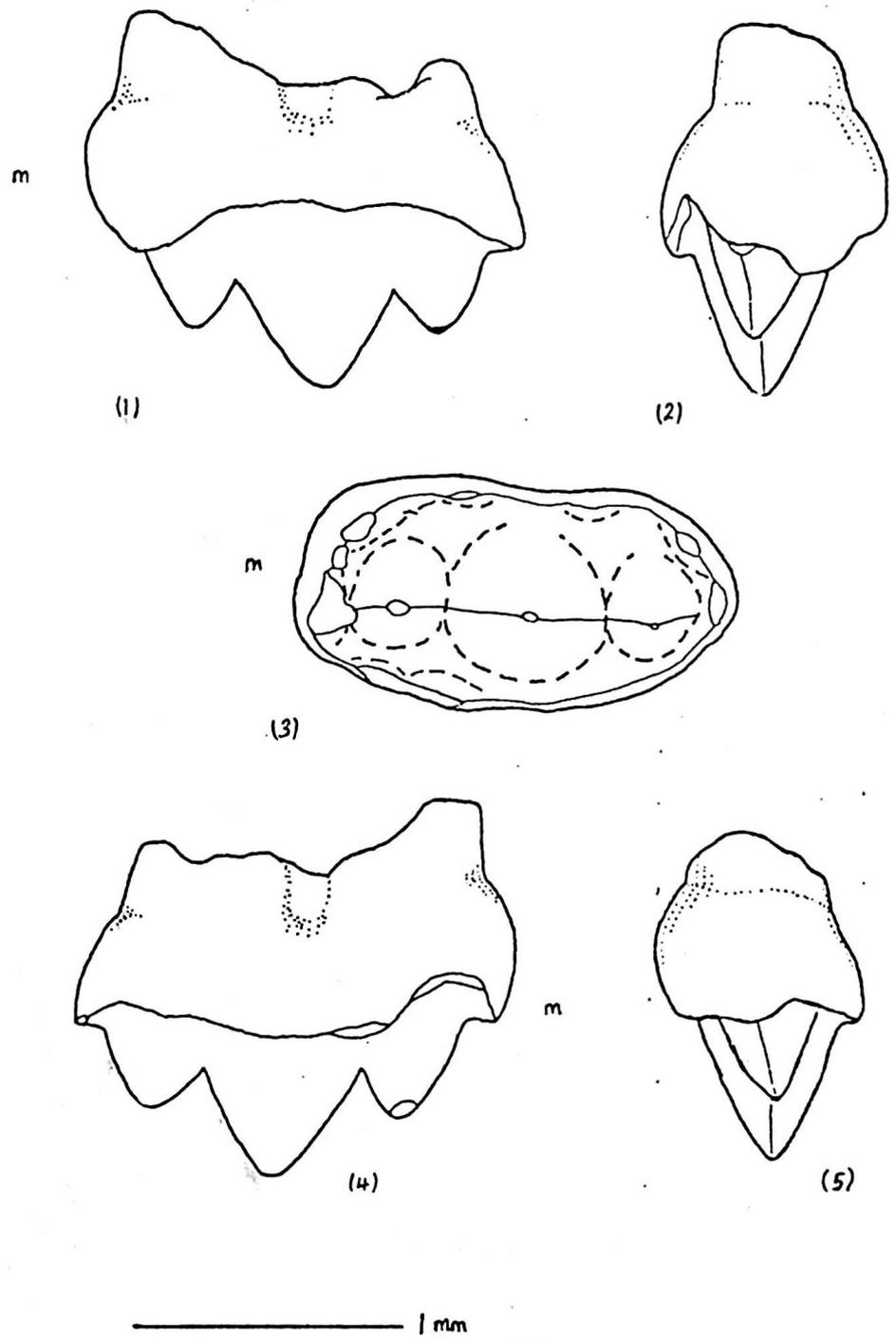


Figure 58. Morganucodont A. Specimen U660. Left upper molar.  
 (1) Buccal, (2) mesial, (3) occlusal, (4) lingual and (5) distal views.

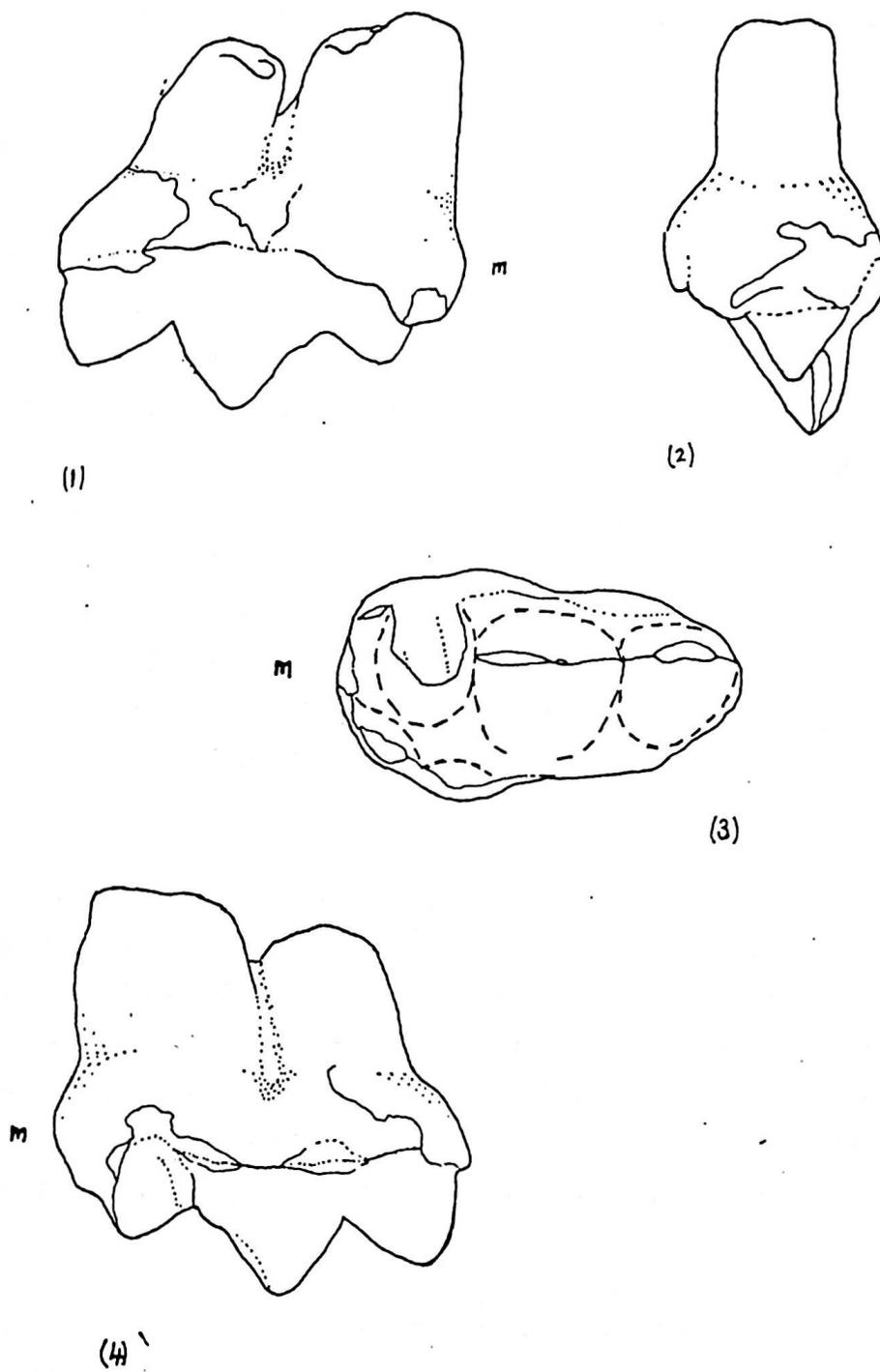


Figure 59. *Morganucodont A.* Specimen U662. Right upper molar. (1) Buccal, (2) mesial, (3) occlusal, (4) lingual and (5) distal views.

specimens which correspond to the fifth molar which appears to be present in a proportion of M. watsoni maxillae (Mills, 1971). Once again, however, the absence of such a tooth may simply be due to sampling error.

(c) Atypical molar crowns

A small number of variations on the usual morphological patterns of the molars occur. Several noteworthy specimens are illustrated in figure 60. U654 is a right lower molar crown in which the Kuhnecone is partly divided into two cusps. U672 is a fragment of left lower molar in which the Kuhnecone has a rather distal position on the side of cusp a so that it partly overlaps onto the base of cusp  $\bar{c}$ . The relative mesio-distal position of the Kuhnecone is thus similar to that of the Kuhnecone in many lower molars of Morganucodon watsoni. U650 is a damaged right lower molar belonging to morphological category three. The Kuhnecone in this specimen is considerably reduced in size. One or two larger molars also possess relatively tiny Kuhnecones.

In upper molar U664 cusp F is very large and its long axis is orientated at a greater angle to the long axis of the tooth than is usually the case. In addition the buccal cingulum of the tooth is partly duplicated mesially; there is a narrow protuberance external to the bucco-mesial corner of the cingulum. Further back a narrow external cingulum appears and continues distally and ventrally to join the normal buccal cingulum opposite the junction of cusps A and C.

Two upper molars - U665 and 686 - each exhibit the same abnormality. In each case the lingual cingulum does not continue past the widest part of cusp A. In each case also the apex of cusp C is slightly buccal to the line of the apices of the preceding crown cusps. Both teeth are right lower molars and are about the same size, so that they must belong to different individuals. It therefore seems that the condition of these teeth is the result of a genetic variation within the sampled population of Morganucodont A rather than simply of a developmental abnormality. These teeth are of interest with regard to some unusual triconodont cheek teeth which are described later.

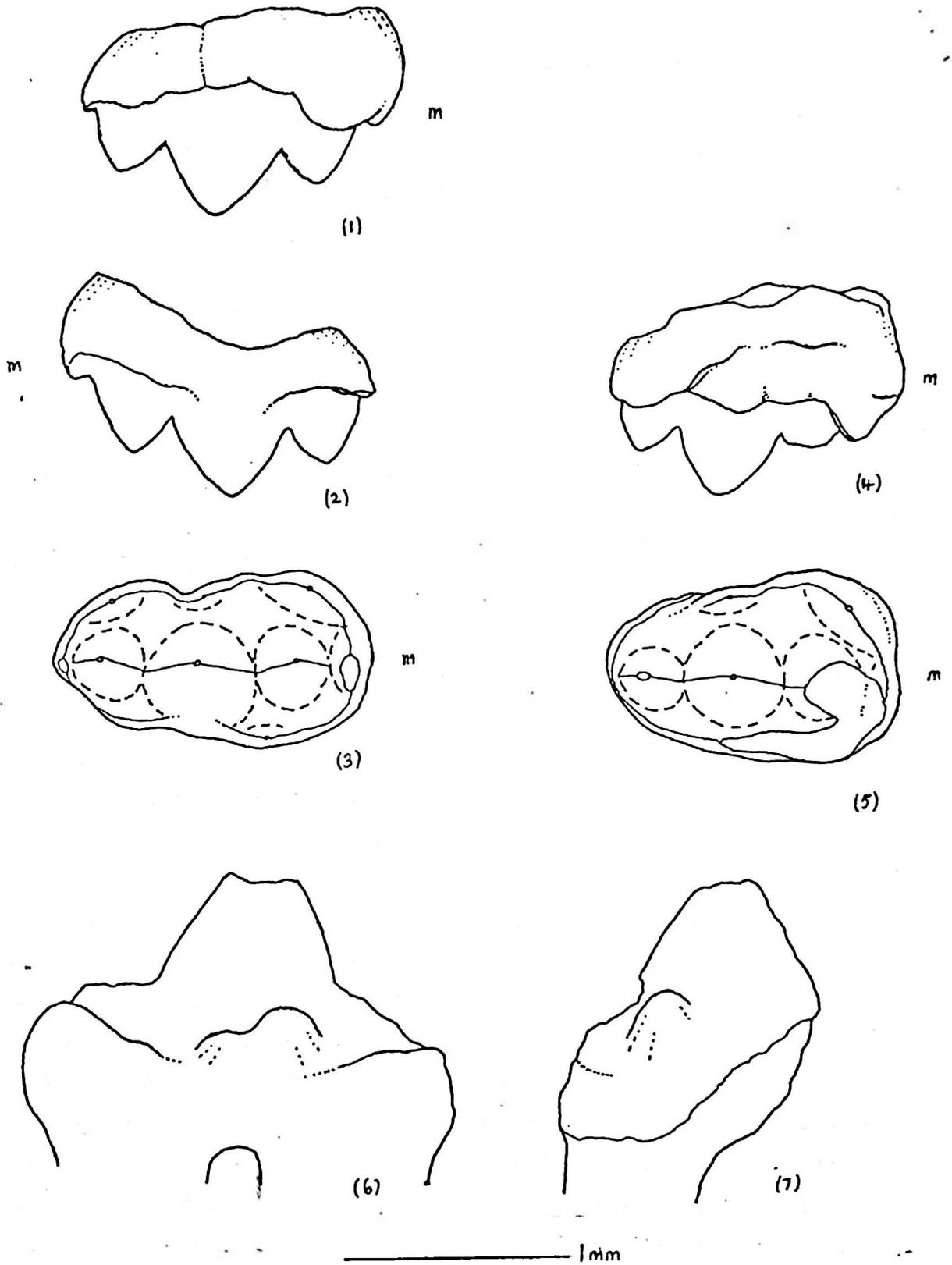


Figure 60. Morganucodont A. Atypical molar crowns. (1) buccal, (2) lingual and (3) occlusal views of right upper molar U665. Note the interruption of the lingual cingulum. (4) Buccal and (5) occlusal views of right upper molar U664. Note the partial duplication of the buccal cingulum. (6) Lingual view of right lower molar U654. Note the form of the Kuhnecone. (7) Lower molar U672. Note the position of the 'Kuhnecone'.

(d) The roots of the molars

Very few molars have substantially preserved roots, a situation which is hardly surprising in view of the fact that these teeth must have been forcibly removed from the jaw bones. Amongst the lower molars, there is no specimen which has both roots intact. In U657 (figure 62) most of the distal root is missing, but the mesial root is the most complete root to be found in any lower molar. Its apex has, unfortunately been damaged mesially so that the distal side of the root is slightly longer than the mesial side. There is no evidence of any damage to the distal side and, as this curves sharply, but smoothly mesially at its extremity, it seems probable that the intact length of the root corresponds to its ante-mortem length. The root is extremely long -proportionally as long as, or longer than mature Morganucodon watsoni lower molar roots, as can be seen if it is compared to the roots of the two M. watsoni molars that are also shown in figure 62. In common with all other Morganucodont A lower molar roots it is straight, has parallel mesial and distal sides, and is slightly compressed laterally, so that in cross-section its outline is elliptical. The root contrasts markedly with a mature M. watsoni molar root in that it does not terminate in a club foot. The crown of the tooth is quite worn, so that the specimen is clearly mature. It might be argued that the root originally possessed a club foot which has been broken off. Against this view, however, there is the fact that its distal side appears to be complete. It must also be borne in mind that to postulate the original presence of a club foot would mean postulating an ante-mortem length for the root which significantly exceeded its already considerable length. In a mature M. watsoni molar the expanded apical part of each root normally accounts for at least a quarter of the total length of the root. If the present root originally possessed a similar club foot, the total length of the root would have been quite remarkable. It would, in proportional terms, have far exceeded the length of any root belonging to M. watsoni. I think, in these circumstances, that it is more reasonable to conclude that the root never possessed a club foot. There is no evidence of taurodontism in any lower molar root belonging to Morganucodont A. In this context it is pertinent to note that amongst the fragments of dentaries in the Welsh collection which probably belong to this species, two (U889 and 890) have a few fully exposed molar root sockets. These sockets occupied almost all of the cancellous part of the bone and it is clear that the roots which

once occupied them must have been fully grown. From the shape of the sockets it is evident that the missing roots did not possess club feet. The roots belonging to U657 do not diverge and this is the case with regard to the majority of lower molars. In a few specimens, the roots diverge slightly.

Turning now to the upper molars, figure 61 shows the only specimen in which both roots are substantially preserved (U670). As the roots are the same length, and as they exhibit little apical damage it is reasonable to conclude that both exhibit their full ante-mortem length. They are proportionally at least as long as the equivalent roots in M. watsoni. As in the case of all other upper molar roots they are straight and non-tapering, and, as in the majority of cases, they do not diverge. A notable feature is that the mesial root is laterally compressed whilst the distal one is mesio-distally compressed. This is invariably the case, and it also appears to be the case with regard to the majority of M. watsoni upper molar roots. The functional significance of this feature is not apparent. As with all other Morganucodont A upper molar roots which are substantially preserved, those belonging to U670 do not end in club feet. The roots of this tooth, however, are very probably immature, as they both possess very large pulp cavity foramina, and the crown of the tooth is little worn. There is only one upper molar root which is both intact and undoubtedly mature, and this is shown in figure 61. The specimen is a mesial root and it belongs to a rather damaged tooth - U671 - from which the distal end of the crown, and hence the distal root, have been broken away. The maturity of the root is demonstrated by the fact that the pulp canal foramen has been reduced to microscopic size, and lies at the bottom of a shallow depression. As in the case of the mesial root belonging to U657, the root is proportionally longer than in the equivalent molars of M. watsoni. Here, however, the difference is more marked, as can be seen in figure 63. It is apparent that the maxilla of Morganucodont A must have been relatively deeper than that of M. watsoni, in order for it to have been able to accommodate upper molars with such long roots. The root under discussion is fractionally broader near its apex than it is near the crown of the tooth, but this situation in no way matches the taurodontism of a mature M. watsoni molar root. The evidence of this root, together with that of the mesial root belonging to U657, and the evidence of the two dentary

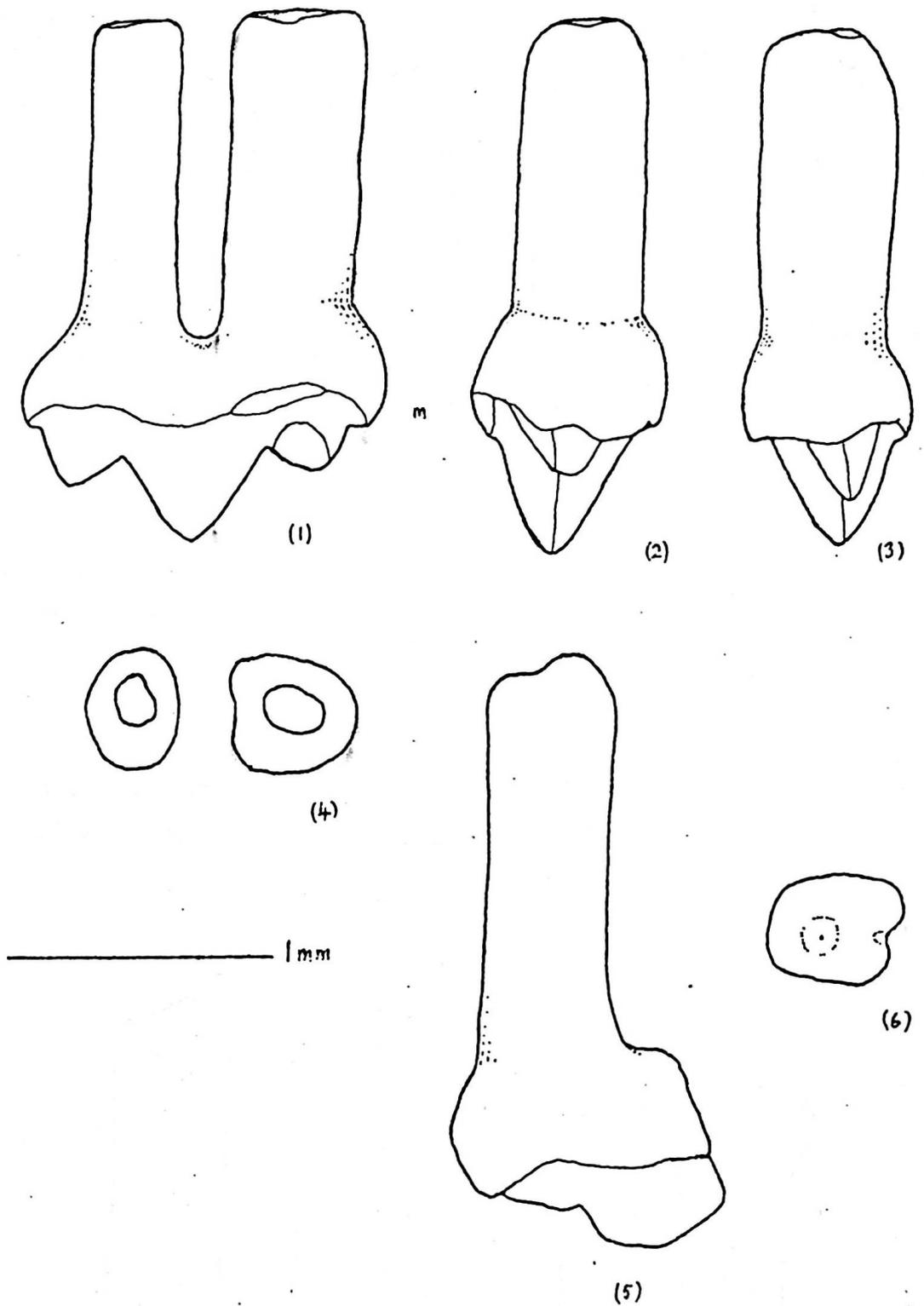


Figure 61. Morganucodont A. Upper molars illustrating the form of the roots.

(1) Lingual, (2) mesial and (3) distal views of left upper molar U670; (4) apical view of the roots belonging to, this specimen. (5) Buccal view of left upper molar fragment U671; (6) apical view of the mesial root belonging to this specimen.

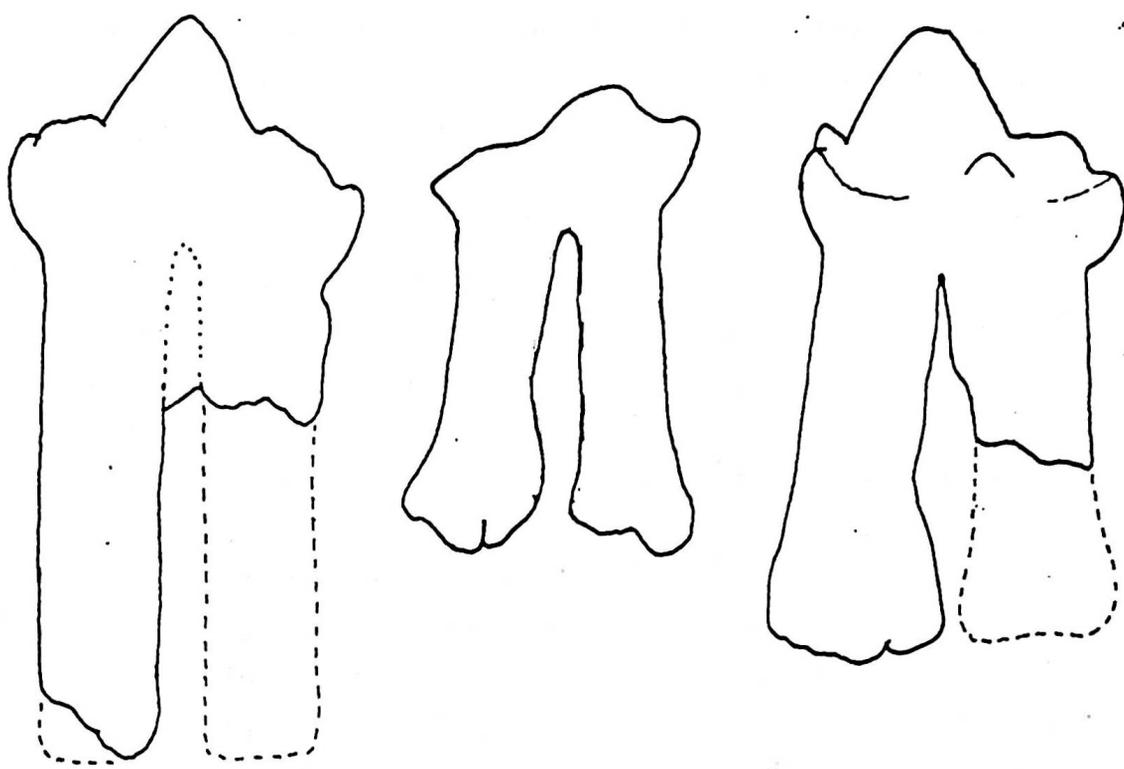


Figure 62. Lower molar roots. (1) Morganucodont A molar (U657); (2) and (3) Morganucodon watsoni molars.

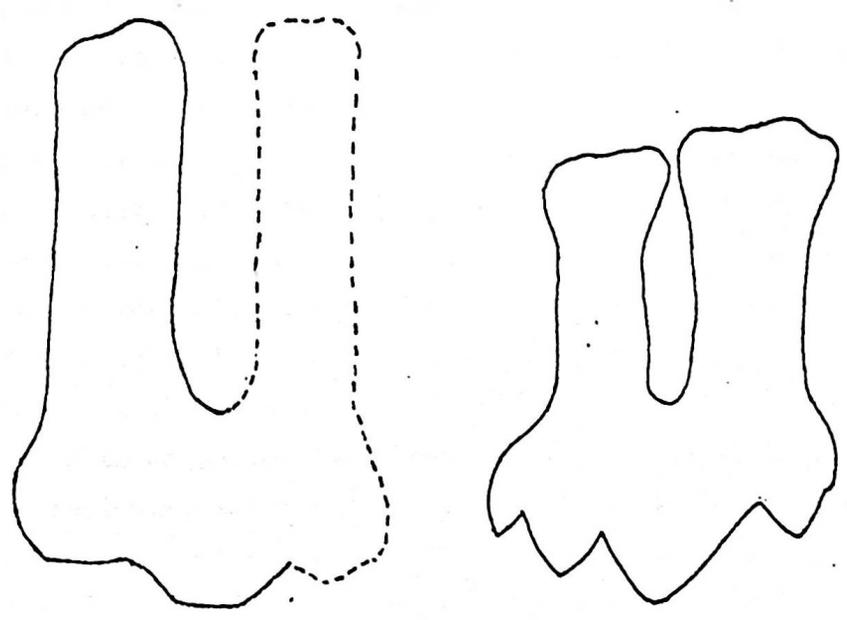


Figure 63. Upper molar roots. (1) Morganucodont A molar (U670); (2) Morganucodon watsoni molar.

fragments mentioned earlier, leaves no doubt that taurodontism was never developed in the molar roots of Morganucodont A. The absence of this feature constitutes a clear distinction between the new species and M. watsoni.

(e) Molar size

Figure 51 shows the size distribution of the measurable upper and lower molars of Morganucodont A.<sup>1</sup> The dimensions of length and breadth have been defined in the same way as for the Morganucodon watsoni molars whose measurements were given earlier (fig. 50 ; p. ). The size ranges of the upper and lower molars of Morganucodont A in each case exceed those of the equivalent M. watsoni teeth. They do not, however equal the size ranges of the equivalent teeth of Morganucodon oehleri (cf Mills 1971:34). The largest specimens are about 20% larger than the largest molars of M. watsoni, but they are rather smaller than the largest molars of M. oehleri. They are of similar size to the large molars of Megazostrodon rudnerae.

(f) The mode of contact between neighbouring molars

The lower molars: The way in which the lower molars of Morganucodont A contacted their neighbours may be deduced from the shape of the teeth and from the positions of the pressure marks which are preserved on a few specimens (e.g. U645 and 649, figures 53+64). The mode of contact is shown diagrammatically in figure 64. The back of the relatively narrow talonid of the more anterior molar fitted buccally to the most mesial part of cusp  $\bar{e}$  on the following molar. In those lower molars where cusp  $\bar{d}$  is present (i.e. those belonging to morphological categories one and two), this cusp was in line with cusp  $\bar{b}$  on the following molar, as in M. watsoni. In marked contrast to the situation in this species, however, the area on the more anterior molar which actually contacted the following tooth was mainly confined to cusp  $\bar{i}$  (this is because cusp  $\bar{i}$  is larger than cusp  $\bar{d}$  and projects further distally). In the case of those lower molars which belong to morphological categories three and four, contact with the following molar was, of course, made exclusively by cusp  $\bar{i}$ .

<sup>1</sup>The reduced fifth molar which occurs in some M. watsoni dentitions is not taken into consideration in this comparison as no equivalent tooth occurs amongst the Morganucodont A material.

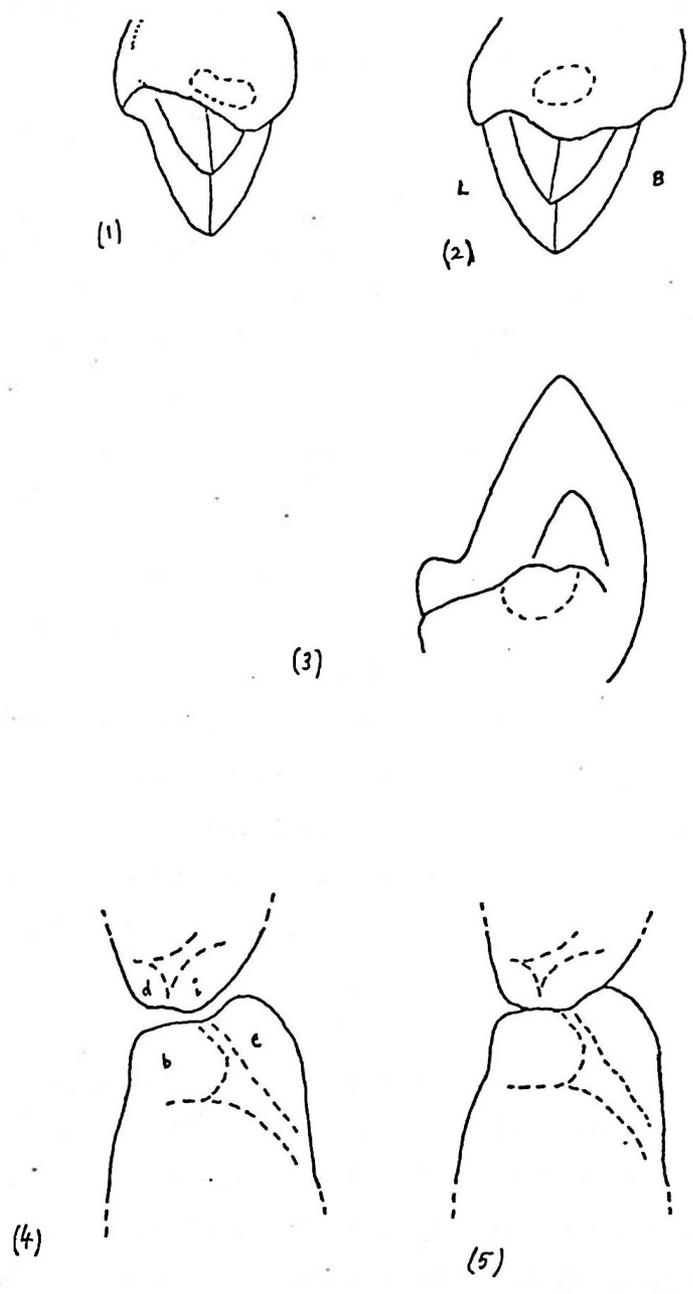


Figure 64. Morganucodont A. Molars illustrating the position of pressure marks. (1) mesial view of upper molar U 726; (2) distal view of upper molar U718 ; (3) distal view of lower molar U 647. For the position of the mesial pressure mark on the lower molars see U 645 (figure 53). (4) and (5) are diagrams illustrating the interlocking mechanism of the lower molars occlusal view. In (4) the molars have been slightly separated to show clearly the relationship of the back of the talonid of the first molar to the front of the following molar. In (5) the teeth are interlocking, the front of the second molar slightly overlapping the back of the talonid of its predecessor and so partly obscuring it from view.

When the molars were in situ, the talonid of the more anterior one was invariably overlapped dorsally by the front of the following specimen. This served to protect the peridental membrane which would otherwise have been liable to have been damaged by food being driven down vertically between the teeth (Kermack, Lees and Mussett 1965).

The lingual bordering of the back of each molar by cusp  $\bar{e}$  on the following molar served a different purpose. This was related to the pressures which the opposing upper molars exerted upon the lower molars during occlusion. As a full appreciation of the functional significance of the feature is thus dependent upon a knowledge of the details of molar occlusion, I will not attempt to elucidate it here. Molar wear and occlusion will be dealt with after the remaining material of Morganucodont A has been described.

The upper molars: In contrast to the situation which appertained to the lower molars, there was no distinct interlocking mechanism between adjacent upper molars. Each tooth simply abutted against its predecessor, the distal surface of the latter tooth slightly overlapping the mesial surface of the former one, as shown by the relative positions of the pressure marks on the teeth illustrated in figure 64. The reason for this overlapping was the same as that given for the overlapping of the adjacent lower molars.

The premolars

Amongst the premolars in the assemblage, there are about thirty specimens which are very similar to the preultimate lower premolars of Morganucodon watsoni, but which differ slightly from them in certain respects. These teeth are present in sufficient numbers and are of appropriate size to be reasonably allocated to Morganucodont A.

The specimens vary in size but they do not divide into discrete size groups. Examples of the largest and smallest specimens are shown in figure 65. In no case are the roots substantially preserved. As in the preultimate lower premolars of Morganucodon watsoni, cusp  $\bar{a}$  completely dominates the crown and is slightly recurved distally. A very small cusp  $\bar{c}$  is present. A weak lingual cingulum is present mesially and distally, but this does not continue past the widest part of cusp  $\bar{a}$ . The teeth differ from the Morganucodon watsoni premolars in that the mesial edge of cusp  $\bar{a}$  does not bulge forward of the leading root, and the cingulum passes round the front of the tooth (a mesial cusp is not developed). The largest specimens are

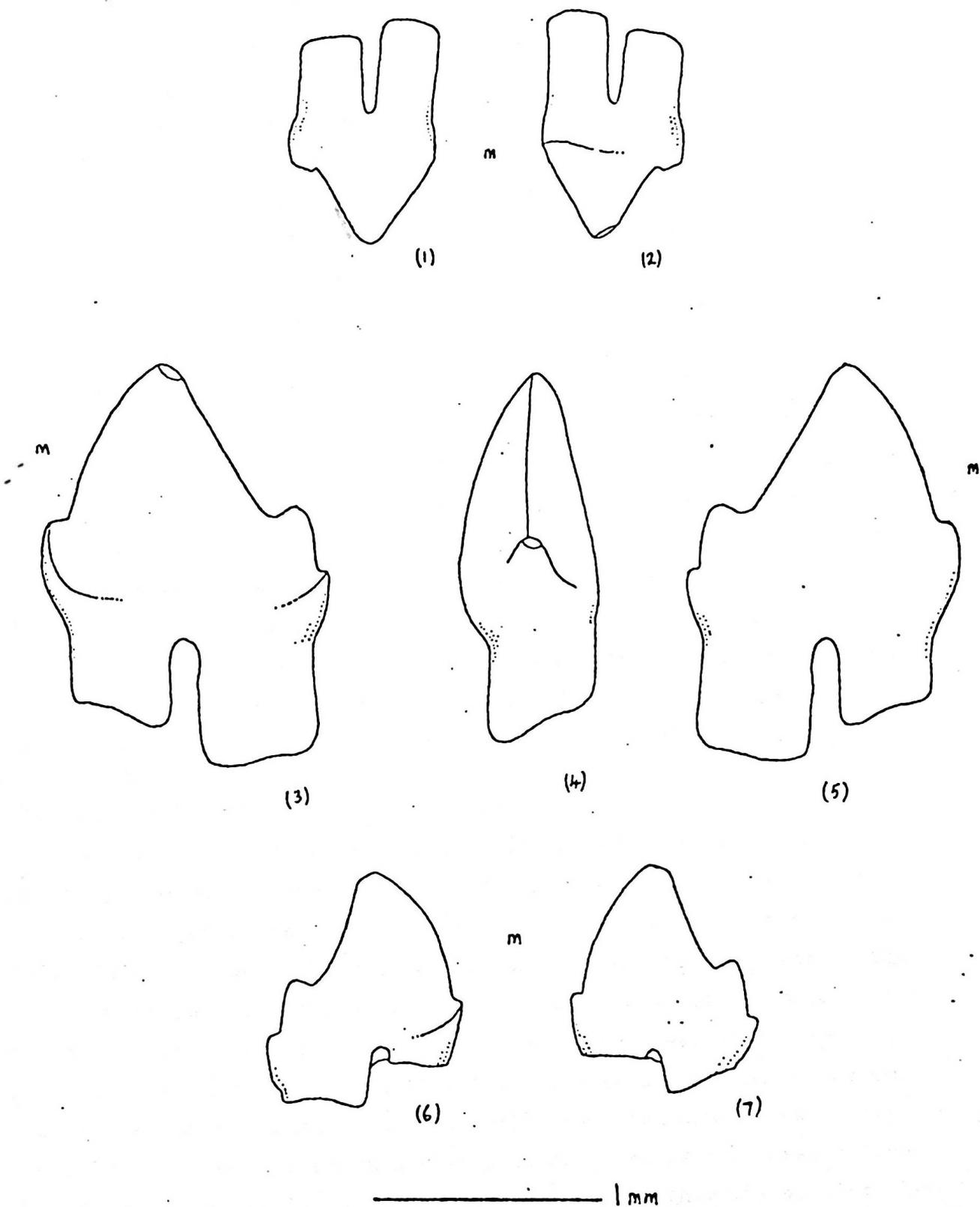


Figure 65. Morganucodont A penultimate premolars. (1) Buccal, (2) lingual views of a right upper premolar. (3) Lingual, (4) mesial and (5) buccal views of a right lower premolar. (6) Lingual and (7) buccal views of a left lower premolar.

the size of the penultimate premolars of Morganucodon watsoni. Because of this and because they are morphologically identical to the smaller specimens these teeth are unlikely to be the ultimate lower premolars of Morganucodont A. (In both Morganucodon watsoni and Megazostrodon rudnerae the ultimate premolar is morphologically distinct from its predecessors.) None of the Morganucodont A lower premolars are worn. It therefore seems that, as in the case of Morganucodon watsoni, the more anterior lower premolars at least did not occlude with the equivalent upper premolars. Amongst the upper premolars in the collection there are some half dozen specimens which are morphologically like the preultimate premolars of Morganucodon watsoni, but which are of slightly larger size. On the basis of their size these teeth are ascribed to Morganucodont A. Figure 65 shows a well preserved specimen.

Figure 66 illustrates a much larger premolar of rather different form (U901). The specimen is unique. The crown is rather damaged and the mesial root is broken off just below the crown base. The distal root is mature as the pulp canal foramen is microscopic and lies in a shallow pit. As preserved the crown measures 1.1 by 0.65mm, and the vertical distance from the broken tip of the principal cusp to the apex of the distal root is 2.9mm. The specimen is tentatively ascribed to Morganucodont A on the basis of its size and proportions, and also on the basis of the form of its distal root. This nearly perfectly matches the form of the foot in upper molar U671.

The principal cusp dominates the crown. One edge of this cusp (the edge above the broken root) was clearly longer than the other, denoting the mesial end of the tooth. At the base of this edge the cusp is damaged where a mesial cusp has almost certainly been broken off. This cusp would have been very small. At the other end of the crown there is a damaged distal cusp. On one side of the base of the crown a tract of exposed abraded dentine passes mesio-distally. Just above this mesially and distally there is a very weak cingulum. When the crown was intact this may well have been continuous. On the other side of the crown a vestigial cingulum passes forward from the distal cusp, rising and becoming obsolete against the side of the principal cusp, above the leading root. The presence of a cingulum on both sides of the crown suggests that the tooth is an upper premolar, the more prominent cingulum being on the lingual side of the crown. If this interpretation is correct then the tooth is presumably

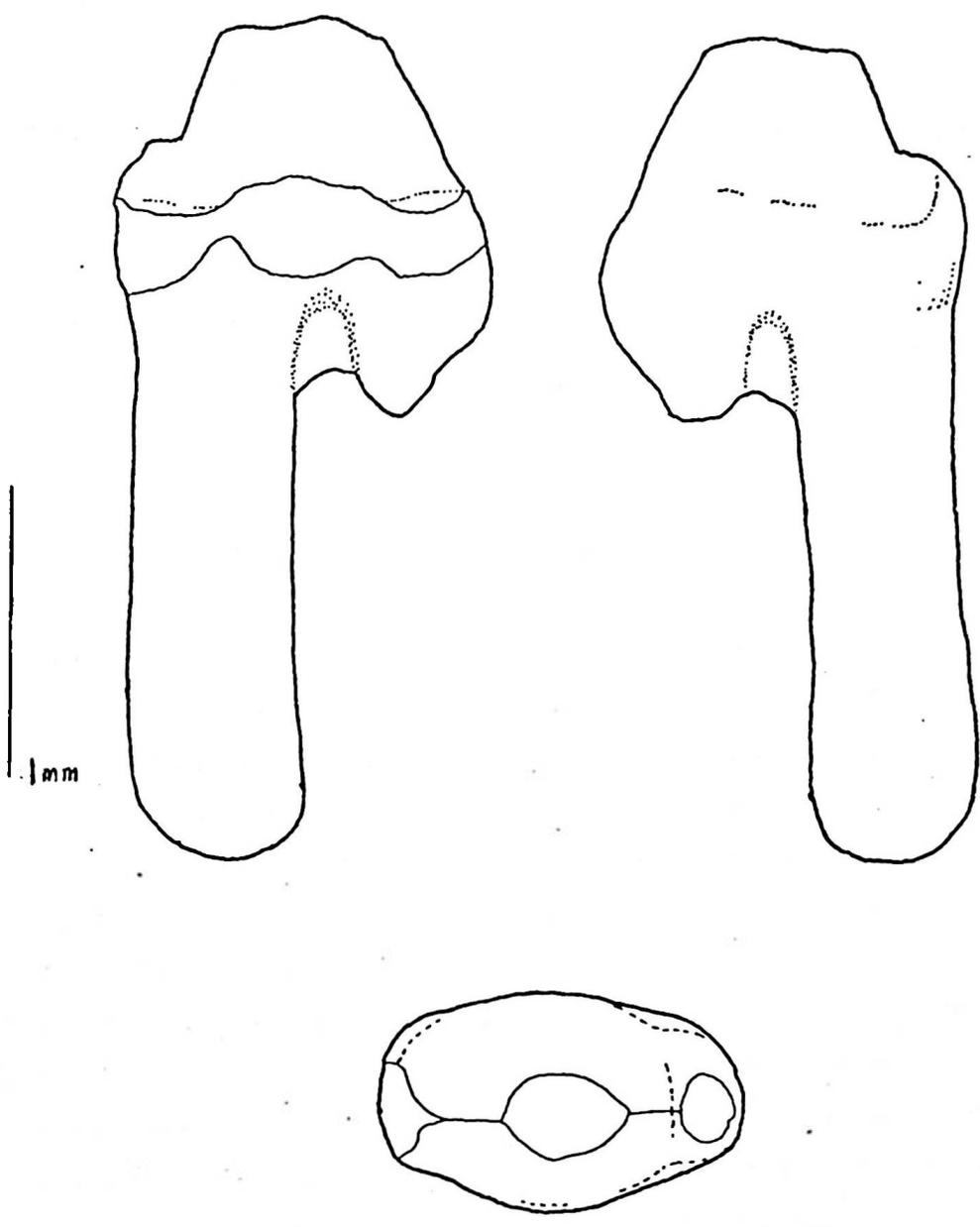


Figure 66. Morganucodont A. Large premolar U901.

the ultimate upper premolar. The preserved parts of the edges of the principal cusp are nearly straight in lateral view. To judge from the angle which they make with one another the apex of the cusp would have been about over the midpoint of the crown base. By analogy with the morphology of the smaller upper and lower premolars described above this feature further suggests that the tooth is an ultimate upper premolar.

There is no specimen in the collection which can be clearly identified as an ultimate lower premolar of Morganucodont A.

Canines and Incisors

The identification of these teeth has posed, and continues to pose, certain difficulties. In view of the fact that the largest molars of Morganucodont A are 20% larger than those of Morganucodon watsoni one would naturally expect to find that the canines and incisors belonging to this species are also larger than those belonging to the latter one. However, all the possible morganucodont canines and incisors in the collection (with the exception of a few specimens which are palpably too large to belong to Morganucodont A) are the size - and form - of Morganucodon watsoni specimens. There are two possible explanations to account for this fact: either the canines and incisors of Morganucodont A are not present in the collection, or they are indistinguishable from those of M. watsoni. As it is manifestly improbable that Morganucodont A would be represented by abundant cheek teeth but not at all by canines or incisors, the second of these explanations would - rather surprisingly - seem to be the one which applies.

Dentaries

Amongst the mammalian dentary material in the assemblage there are a number of fragments which are of dentaries a little larger than any belonging to Morganucodon watsoni. On circumstantial grounds most of these specimens probably belong to adult individuals of Morganucodont A. Unfortunately they are too fragmentary and too water worn to yield much useful information. As mentioned earlier, two specimens (U889 and 890) have a few fully exposed molar root sockets.<sup>1</sup> These

<sup>1</sup> The sockets are adjudged to be those of molar roots because the dentary fragments in each case quite clearly belong to the distal or middle part of the dental ramus of the intact dentary.

occupy almost all of the cancellous part of the bone, as one would expect from what is known of the lengths of the roots. They also show that the fully grown roots were not taurodont.

Dental formula

Because of the isolated nature of the teeth and the absence of adequate dentary material the exact dental formula cannot be determined at present. It is hoped that future discoveries of better preserved material will rectify this situation. The four morphological categories of lower molars described earlier indicate that there are probably at least four molar positions, the specimens belonging to the first morphological category being from a relatively mesial position, and those belonging to the fourth from a distal one. A number of the specimens belonging to the latter category bear mesial pressure marks (e.g. U761, figure ), but none bears a distal pressure mark. It is therefore unlikely that the teeth belonging to this category had any still more distal neighbour, unless such a tooth was only present in a minority of dentitions, as in the case of the fifth molar of M. watsoni.

If the molars in the dentition of Morganucodont A simply decreased in size from first to last, then, on the basis of the relative sizes of the teeth belonging to each of the morphological categories of lower molars, there is no need to postulate the presence of more than four molars in each toothrow. If, on the other hand, the largest molar was the second, as in Morganucodon watsoni, there must be at least five molars in each tooth row (this is without taking into account the possible presence in some dentitions of a very reduced ultimate molar analogous to that found in a proportion of M. watsoni dentitions).

Molar wear and occlusion

Functional wear is discernible on a little over half of the molars of Morganucodont A. As in other morganucodonts matching shearing surfaces are not present on unworn upper and lower molars; all such surfaces are the result of wear having remodelled, to some extent, the original topography of the crowns. In order for these surfaces to have been worn on the opposing molars it was obviously essential for the teeth to have maintained extremely precise antero-posterior positions relative to one another, as in the case of the opposing teeth of Sphenodontid A. In the latter instance the possibility of

longitudinal drift was precluded by the fact that the teeth were ankylosed to the jaw bones. In the case of Morganucodont A the possibility was precluded by the molars of each tooth row being held under inter-dental pressure, as evidenced by the pressure marks on some of the specimens (see for example figure 56). Unfortunately, owing to the effects of water-wear and impact damage, very few of the worn molars of Morganucodont A show clearly the full extent of the functional wear to which they have been subjected. As a result of a detailed study of all the specimens it is nevertheless clear that there is no significant variation in the respective wear patterns on upper and lower molars which have been subjected to equivalent levels of wear. The antero-posterior positions of the upper and lower molars relative to one another must therefore have been the same in all the individuals which are represented, and hence in all the 'normal' individuals of the species, as in the case of Morganucodon watsoni (Crompton & Jenkins, 1968; Mills, 1971).

Figure 67 shows examples of well preserved, extensively worn upper and lower molars. The wear is confined to the lingual side of the upper tooth (U667) and the buccal side of the lower one (U657). In the end views of the teeth it can be seen that the wear on the upper molar is distinctly more transversely orientated than that on the lower molar. In the case of the latter tooth the angle which the shearing surfaces make with the horizontal axis of the crown is very nearly the same as that which was made by the unworn crown surface. During occlusion therefore the jaw on the active side must have moved slightly medially as well as upwards. The more transverse orientation of the shearing surfaces on the upper molar shows that this tooth leaned lingually in the maxilla. The same was true of the upper molars of Morganucodon watsoni (Mills, 1971). In Morganucodont A the shearing surfaces on the upper molars are not quite so steep relative to the horizontal, as those on the upper molars of M. watsoni. This is probably due to the fact that the lower molars of the new species are more bulbous than the equivalent teeth of M. watsoni.

All three main cusps of the two Morganucodont A molars illustrated in figure 67 have been worn and the apical regions of the accessory crown cusps have, in each instance, been obliterated through use. The lingual cingulum of the upper molar has also been obliterated, but it should be noted that below this level the wear on each of the crown cusps is medially centred and there is no wear in the depressions

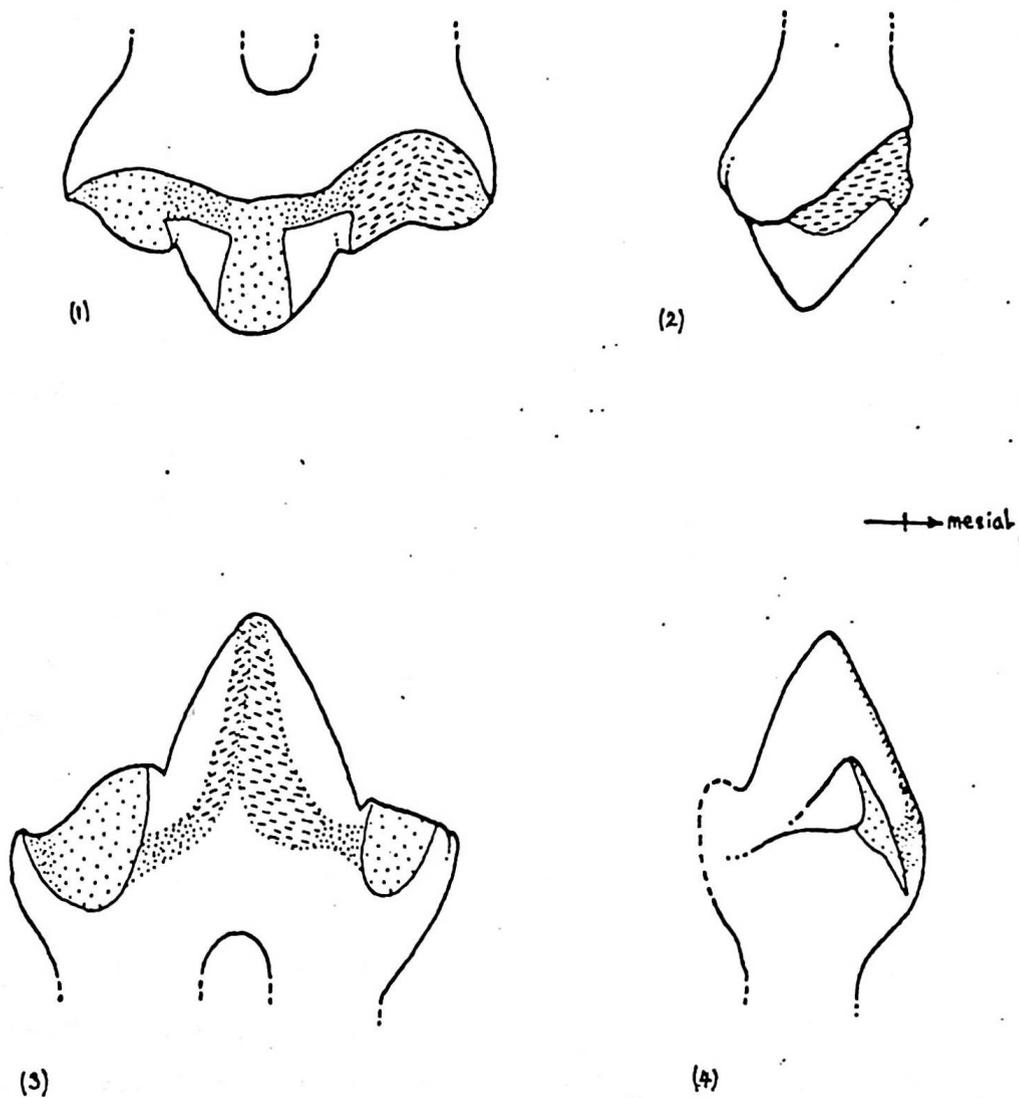


Figure 67. Morganucodont A. Examples of relatively well preserved, extensively worn molars. (1) lingual and (2) mesial views of right upper molar U667. (3) buccal and (4) distal views of right lower molar U656.

which mark the junctions of the cusp bases. In the case of the lower molar the situation is similar. The crown is worn along almost the whole length of the bucco-lingually widest part of its base, but above this level the wear is medially centred on the crown cusps, the wear on each being well separated from that on the adjacent cusp (or cusps). It is therefore clear that there was no alternation of the crown cusps of the opposing molars of *Morganucodont A* during occlusion. Each cusp initially contacted an opposing cusp apex to apex. The most prominent wear on the upper molars is invariably located on cusp B whilst that on the lower molars is located on cusp  $\bar{C}$ . Since this wear must, in each case, have been produced by the principal cusp of the opposing molar it is possible to determine the relative antero-posterior positions of the opposing molars during occlusion. They are shown in figure 68 (the opposing teeth have been separated for clarity). When the jaws were closed cusp  $\bar{a}$  of the lower molar stood opposite cusp B of the corresponding upper molar whilst cusp A of the latter tooth stood opposite cusp  $\bar{c}$  of the former one. Cusp  $\bar{b}$  of the lower molar stood opposite cusp C of the upper molar situated one position further forward. Occlusion in *Morganucodont A* thus differed significantly from that in *Morganucodon watsoni*, where cusp  $\bar{a}$  of each lower molar sheared between cusps B and A of the corresponding upper molar and cusp A of this tooth sheared between cusps  $\bar{a}$  and  $\bar{c}$  of the lower tooth (Crompton & Jenkins, 1968; Mills, 1971).

Because matching shearing surfaces were only produced on the opposing molars of *Morganucodont A* as a result of wear, the extent of the occlusal contact between these teeth was not constant throughout the course of their functional lives. It progressively increased as the teeth wore one another into more accommodating shapes. Figure 69 illustrates three reconstructed stages in the development of the shearing surfaces of opposing molars (the reconstructions are based on a study of all of the worn molars in the collection). Corresponding wear facets on the upper and lower teeth have been given the same numerals for simplicity. Figure 69 shows the molars at an early stage of wear. The apical region of cusp B of the upper molar has been worn through contact with cusp  $\bar{a}$  of the corresponding lower molar. This worn area is incipiently divided into adjoining mesial and distal facets (facets Ia and Ib respectively) the two sloping towards one another in horizontal section to form a groove into which the lower cusp  $\bar{a}$  sheared. The latter cusp has also worn a groove in the lingual cingulum above cusp B. The two grooves worn by cusp  $\bar{a}$

are separated from one another by a large area of unworn enamel. The corresponding facets Ia and Ib on the median part of cusp  $\bar{a}$  pass down from the apex of the cusp to the level of the most bulbous part of the buccal surface of the crown. The two facets slope away from one another in horizontal section, closely following the original shape of the cusp surface. The only other area of wear on the lower molar is a facet II which descends the median part of cusp  $\bar{c}$  from the cusp apex. This facet formed through the contact of the cusp with cusp A of the upper molar, and a corresponding facet is present in the apical region of the latter cusp. It should be noted that at this stage of wear neither the upper nor the lower molar contacted more than one opposing tooth during occlusion.

Figure 69<sup>b</sup> shows the molars at a slightly later stage. Facets Ia and Ib on cusp B of the upper molar are now continuous with those at the level of the cingulum, so that cusp  $\bar{a}$  of the lower molar sheared into a single, well defined groove. Facet II on cusp A of the upper molar has enlarged, and cusp  $\bar{c}$  of the lower tooth also sheared against the cingulum above cusp A with the result that a second facet II is situated here. The two facets II on the upper molar are clearly separated from one another. The upper molar also bears two new facets, facets III, which were formed by cusp  $\bar{b}$  of the lower molar which succeeded its main antagonist. One of the facets is situated on the apical region of cusp c and the other in the cingulum above this cusp. The lingual cingulum of the upper molar between facets Ib, II and III has been worn through contact with the most bulbous parts of the crown bases of the two opposing lower molars. Corresponding shearing surfaces on the lower molars pass between the ventral extremities of the facets on the crown cusps.

Figure 69<sup>c</sup> shows the molars at an advanced stage of wear. The illustrations are based on the most worn molars in the collection. Much of cusp B of the upper molar has been obliterated, and the groove formed by facets Ia and Ib is deep and very prominent. Distal to the groove, the cingulum has been entirely worn away and the facets on cusps A and C extend upwards to its former level. It should be noted, however, that facet II is still confined to the median part of cusp A, so that it is well separated from the facets on the other cusps. With regard to the lower molar, the only significant changes from the situation which pertained at the previous stage are that the wear is proportionally heavier, and the facets slightly more

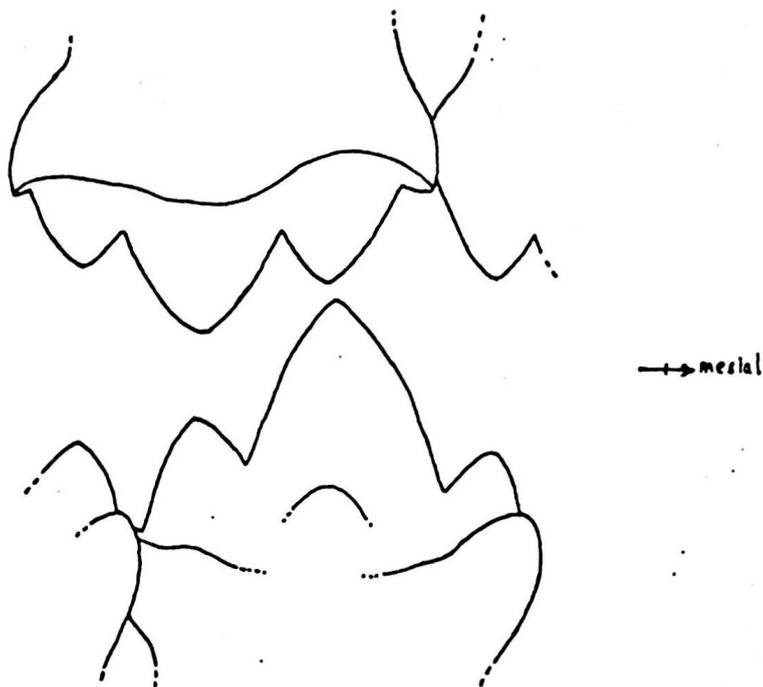


Figure 68. Morganucodont A. The relative antero-posterior positions of the occluding molars. The opposing teeth have been separated for clarity. Lingual views of both upper and lower teeth..

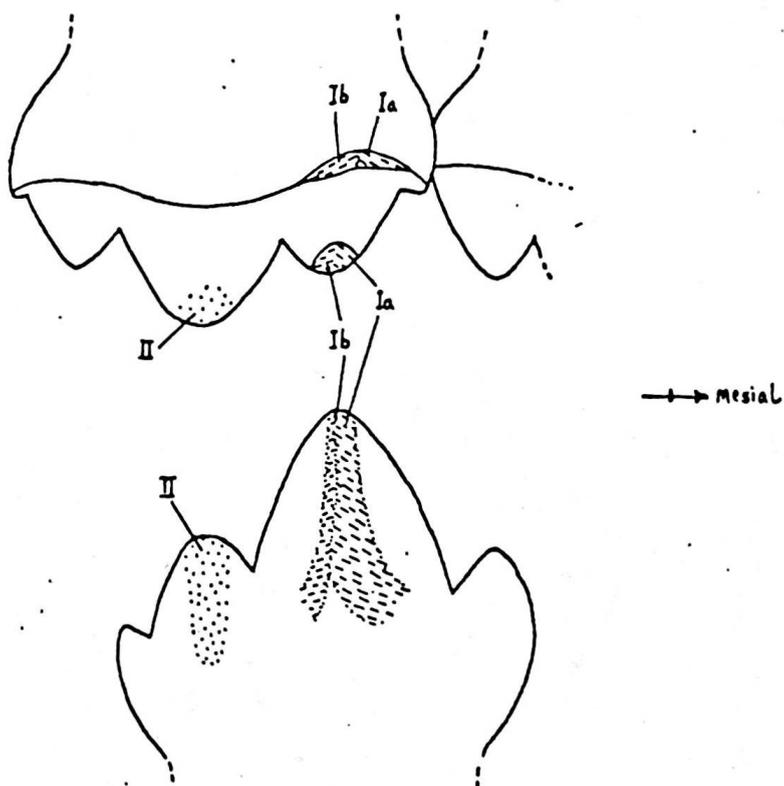
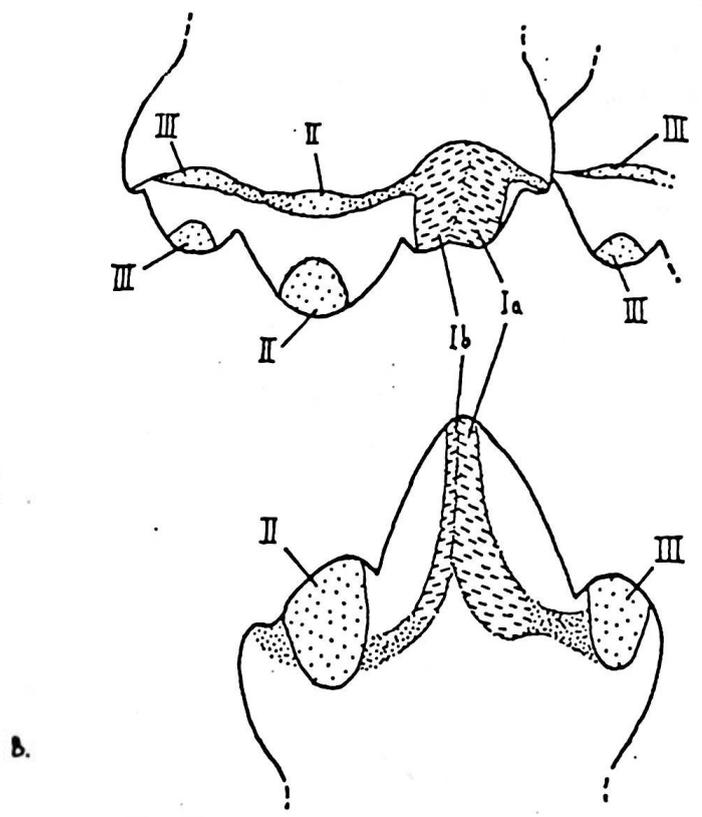
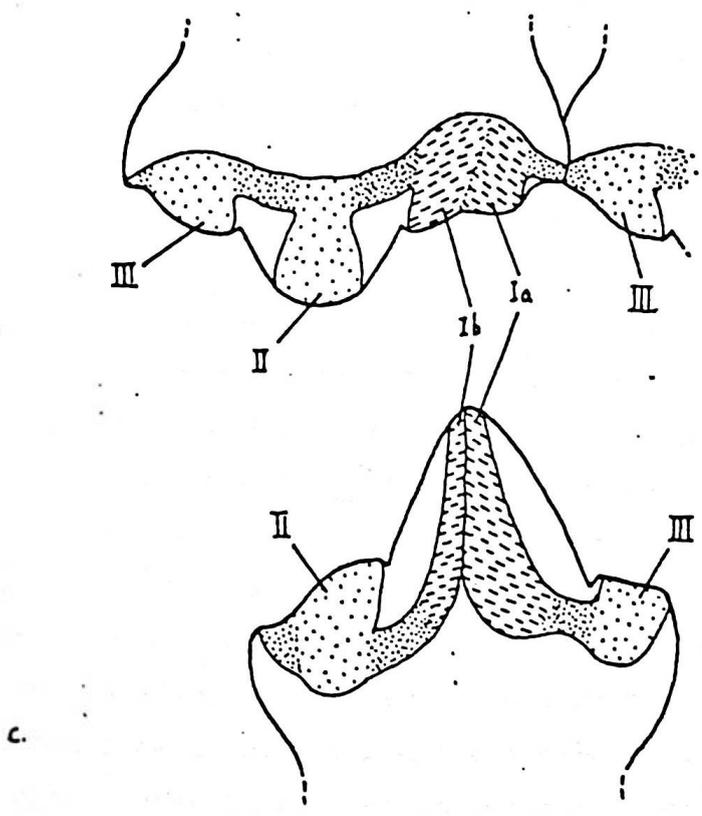


Figure 69. Morganucodont A. Reconstructed stages of molar wear (reconstructions are based on a study of all available worn specimens). I, II and III = wear facets (see text). (A) -Early stage -Continued overleaf..



b.



c.

Figure 69 -continued. (B) -Intermediate stage  
(C) -Advanced stage

extensive. There are no upper or lower molars in the collection in which the whole of the opposing surfaces of the crowns have been worn to produce a series of shearing planes, as in the most worn molars of Morganucodon watsoni (c.f. Mills, 1971, figure 1C and Crompton & Jenkins, 1968, figure 5A).

From the foregoing account it will be appreciated that during the earlier stages of wear in Morganucodont A, the lingual cingulum of the upper molar held much of the main part of the lingual surface of the tooth out of occlusal contact with the opposing lower molar, as in Morganucodon watsoni. Mills (1971) has suggested that the functional reason for this feature in M. watsoni was to prevent the surface of the upper molar from becoming highly polished, thereby improving the 'efficiency of the shearing and grinding action between the two opposed surfaces'. However, I cannot accept that the efficiency of the shearing action would have been improved in this way. In order to cut optimally the blade of a knife not only requires a sharp edge: its sides must be smooth to minimise friction with the cut material which passes over it as it penetrates. When the sides of the blade become scored they need to be repolished. In the same way, if the lingual surface of the upper molars were highly polished, this could only have enhanced the shearing action by reducing friction with the food. Whilst it is possible that the lingual cingulum on the upper molars, in holding apart the opposing crown surfaces, may have helped facilitate some kind of grinding action between them, I think that this is very unlikely. Kermack, Mussett & Rigney (1973) have suggested that shearing was the only element involved in occlusion in Morganucodon, and the same was probably true of all morganucodonts. Consideration of the effect of the holding apart of the approximated molar surfaces by the lingual cingulum of the upper molar suggests that the real function of the feature was to extend the useful lives of the teeth. During the early stages of wear, as a lower molar cusp contacted the lingual cingulum of the upper molar, the shearing surface on the cusp would have passed over a shearing surface on the cingulum which was substantially shorter, dorso-ventrally, than itself. At any one point during occlusion therefore much of the shearing surface on the lower molar cusp would not have been in contact with the upper molar cingulum. The rate of wear of the cusp would thus have been significantly less rapid than when it later came into contact with the more extensive surface of the upper molar crown. In the case of

the upper molars, the functional life of the tooth would have been prolonged simply by the fact that much of the lingual surface of the crown was held out of occlusal contact by the cingulum, and was therefore preserved for later use. A lingual cingulum is present in the upper molars of the upper Jurassic Triconodontidae where it probably served the same purpose.<sup>1</sup>

The absence of any upper or lower molars of Morganucodont A in which all of the opposing lateral surfaces of the crowns have been worn into shearing planes, as in the more worn molars of Morganucodon watsoni, is striking. It cannot be regarded as evidence that no well worn dentitions of Morganucodont A are represented, because the wear on some of the molars in the collection (e.g. U667, figure 67) is quite as heavy as that on the most worn molars of M. watsoni. Rather, it is a reflection of the particular occlusal pattern of the new species. In M. watsoni because cusp sheared between cusp the shape of the opposing surfaces of unworn upper and lower molars - the lingual cingulum of the upper molars excepted - in some measure anticipates the shape of these surfaces in worn teeth. Extensive wear facets could therefore be produced on the teeth without substantial parts of the crown cusps having to be obliterated (see Mills 1971, figure B, and Crompton and Jenkins Plate I C). In Morganucodont A, however, because cusp sheared against cusp the shape of the opposing surfaces of unworn upper and lower molars anticipates the shape of these surfaces in worn molars in almost no respect. Convex surface initially contacted convex surface and the wear on the cusps was thus concentrated on the median part of the opposing surface of each, the resultant facets being narrow and widely separated from those on the adjacent cusps. A facet only became extensive when much of the original cusp had been obliterated, as can be seen in the case of cusp B in U667 (figure 67). The major facets on a tooth could only have been confluent therefore if a very substantial part of all three crown cusps had been worn away.

<sup>1</sup> Mills (1971) has stated that the function of the lingual cingulum in the upper molars of Kuehneotherium was to act as a 'stop' against which the lower molars occluded. However, Parrington (1972) has shown that the cingulum in this species was sometimes extremely worn, or even obliterated - as in the more worn upper molars of Morganucodont A and Morganucodon watsoni. It therefore seems probable that cingulum in Kuehneotherium served - in part at least - the same purpose as in the two latter forms.

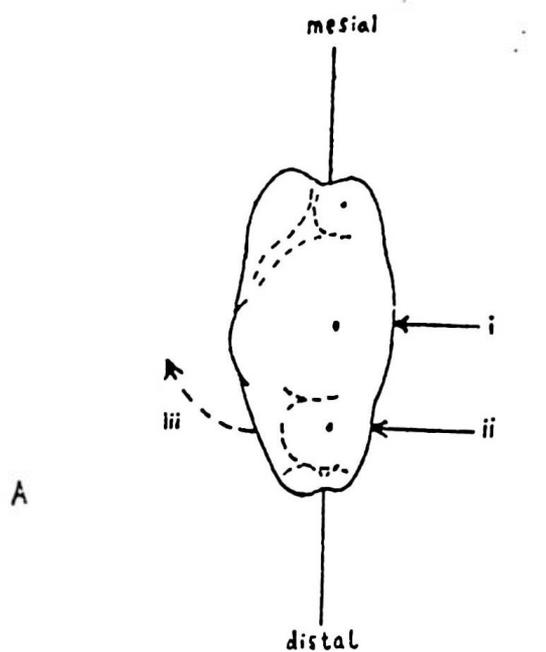
(This is well exemplified by the nature of the wear on U667. Here cusps B and C have been considerably reduced, but, because cusp A has not, unworn areas of enamel still intervene between facet II and facets Ib and III). However, the amount of functional attrition to which a molar would have to have been subjected before the wear on its principal cusp came to occupy the whole of the relevant lateral surface of the cusp would have been extremely great. Infact, both of the accessory cusps would have been completely obliterated before this stage could have been reached. It is thus extremely unlikely that the molars of Morganucodont A could ever have attained a level of wear at which the whole of their opposing surfaces were formed into shearing planes.

A final point may be made concerning wear and occlusion in Morganucodont A. If the upper molar shown in figure 67 is studied in lingual view it will be observed that the deepest part of the groove formed by facets Ia and Ib is slightly obliquely orientated; its dorsal end is slightly mesial of its ventral end. This indicates that during occlusion the movement of the lower jaw included a small anterior component. Mills (1971) and Crompton & Hiemae (1970) believe that an anterior component was present in the primitive jaw movement of the theria. The form of the molar wear in Morganucodon watsoni indicates that there was no anterior component to the power-stroke of the mandible in this species. This is probably correlated with the fact that cusp a of each lower molar sheared between cusps A and B of its opponent, so that there would have been little possibility of such movement.

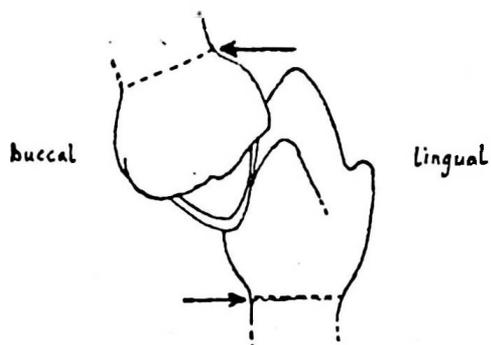
We may now return to the question of the function of the interlocking mechanism between the adjacent in situ lower molars of Morganucodont A which was referred to earlier. As the opposing molars came into occlusal contact and moved past one another the lower molars were pressed tightly against the uppers in order to facilitate the double shearing action which was the principal element in occlusion. The upper molars therefore exerted a transversely directed pressure on the lower molars which tended to displace each from its position in the dentary. We may refer to this pressure as the occlusal displacement (O.D.) pressure. Where the occluding molars were well worn (as in the case of those shown in figure 69c) all three of the main cusps of each of the lower ones were contacted during the later stages of occlusion. The O.D. pressure exerted upon the tooth was therefore

distributed along its mesio-distal length and was resisted about equally by each of the stout roots. There would thus have been little danger of cervical damage to the tooth. During the early stages of occlusion of well worn molars, however, and during the occlusion of molars which were relatively little worn (as in the case of those shown in figure 69a) only cusps  $\bar{a}$  and  $\bar{c}$  of each lower tooth were contacted. As a result, the O.D. pressure was concentrated on the distal half of the tooth and tended to turn it about the axis of the mesial root (see figure 70A). The purpose of the lingual bordering of the back of each lower molar by cusp  $\bar{e}$  on the following molar was to buttress the back end of the tooth against this distally concentrated pressure.

At the same time as the distally concentrated O.D. pressure was applied to the lower molars an equal and opposite mesially concentrated pressure was, of course, applied to the upper molars. This tended to turn the teeth about the axis of the distal root. The absence of a buttressing arrangement for the front of each upper molar analogous to that for the back of the lower molars was, therefore, at first found rather puzzling. Upon reflection, however, I think that it is correlated with the fact that the in situ upper molars leaned lingually in the maxilla. Such an orientation would have meant that the O.D. pressure exerted on these teeth would, when considered in bucco-lingual cross-section, have acted at a more acute angle to the long axes of the teeth than was the case with regard to the O.D. pressure exerted on the lower molars. In other words, the pressure would have been resisted by a relatively greater thickness of the roots, as can be seen from the diagrammatic representation of the situation shown in figure 70. In these circumstances there would have been less potential weakness in the capacity of the mesial roots of the upper molars to resist the mesially concentrated O.D. pressure than there was in the capacity of the lower molars to resist the simultaneously exerted, distally concentrated O.D. pressure.



A



B

Figure 70. Morganucodont A. (A) Diagram indicating the transversely directed occlusal displacement pressure which is exerted on a lower molar when only cusps a and c are involved in occlusion. The pressure is exerted at points i and ii and tends to turn the tooth (shown in occlusal view) in the direction indicated by iii, about the axis of the mesial root. (B) Diagram indicating -very approximately- the relative angles made by the long axes of occluding molars with the lines of action of the forces which the teeth exert upon one another. The lines of action of the forces are shown by the arrows, and dotted lines mark the cervices of the occluding molars.

3. MORGANUCODONT B

This form is represented by a single right lower molar, U567 (figure 71). The roots are broken off a short distance below the crown base, and the crown cusps are damaged; the apex of cusp  $\bar{a}$  is missing, and nothing is preserved of either of the accessory crown cusps above the levels of their junctions with cusp  $\bar{a}$ . The lingual cingulum is also damaged in several places. The crown measures 3.4 by 1.6mm. These dimensions are slightly more than twice those of the crown of a second lower molar of Morganucodon watsoni, and the size of Morganucodont B clearly distinguishes the species from any undoubted morganucodont which has previously been described. The length of the crown of U567 is similar to that of the first lower molar in two of the Trioracodon ferox dentaries in the British Museum (Natural History) collection (47775 and 47782). It seems unlikely on the basis of size, that Morganucodont B was a strictly insectivorous mammal.

Morphology:

When intact, cusp  $\bar{a}$  would appear to have been about as prominent as the equivalent cusp in the more anterior lower molars of M. watsoni, although its basal width is proportionally slightly greater. The mid-point of the cusp is situated slightly buccal to the mid-point of the crown. In lateral view the intact parts of the mesial and distal edges of the cusp are straight. In mesial and distal view the remaining parts of the crests which divide the buccal and lingual sides of the cusp are vertical, and the mesial crest is situated distinctly more buccally than the distal one. The buccal and lingual surfaces of the remaining part of the cusp are both slightly convex when seen in these views.

The buccal side of cusp  $\bar{b}$  has been severely abraded, and its mesio-buccal corner entirely obliterated. The damaged area extends down almost to the base of the crown. From what remains of the cusp it is apparent that it was originally more prominent than in any of the first three lower molars of M. watsoni, although it was clearly still smaller than cusp  $\bar{c}$ . The division between the cusp and cusp  $\bar{a}$  is less complete than in M. watsoni, as in the case of the majority of lower molars of Morganucodont A. An interesting feature of the tooth is that cusp  $\bar{b}$  is not in line with the succeeding crown cusps, but is

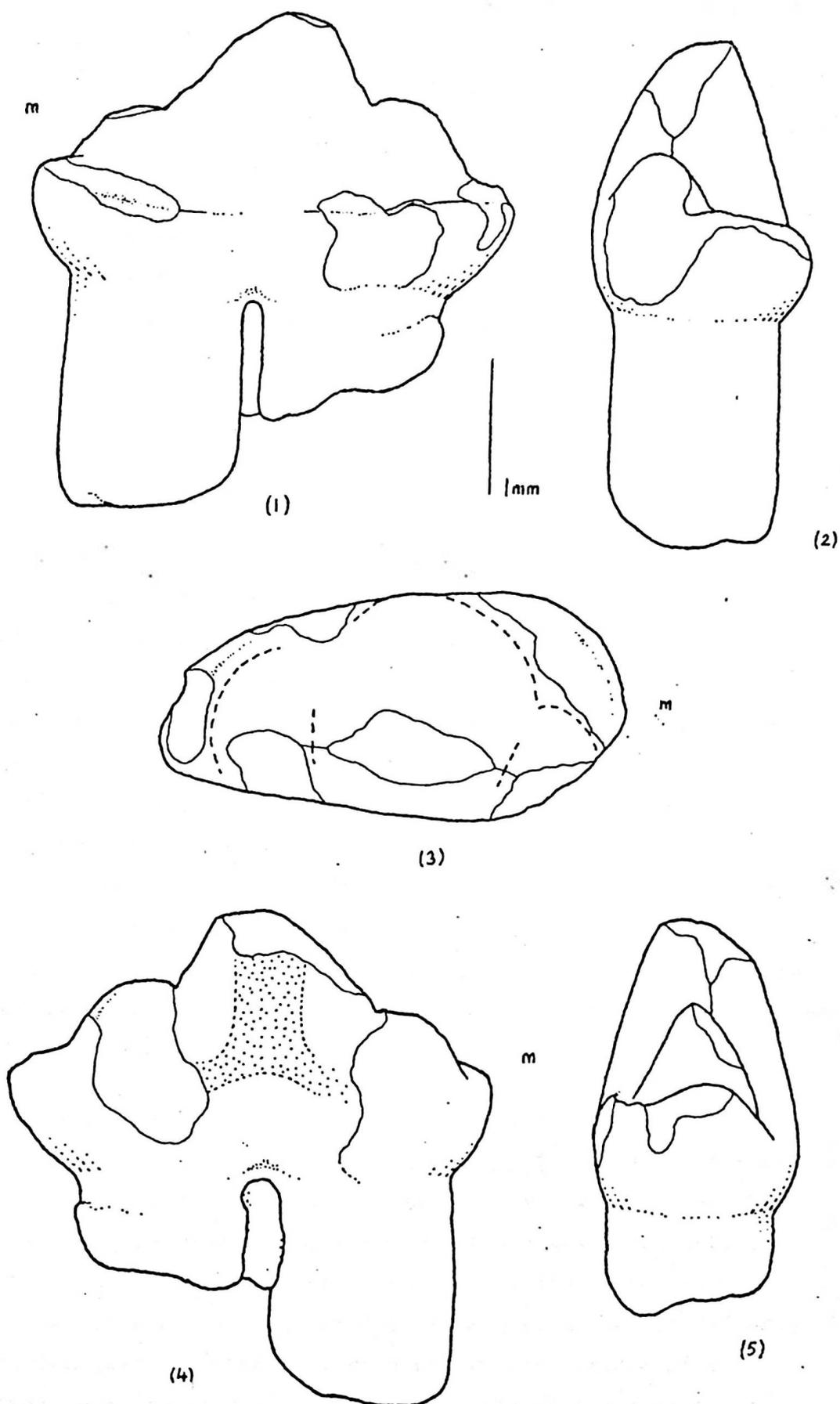


Figure 71 . Morganucodont B: right lower molar, U567. (1) Lingual, (2) mesial, (3) occlusal, (4) buccal and (5) distal views. Note the wear on the buccal side of cusp  $\bar{a}$  (stippled area).

situated so that when intact, its apex would have been buccal to the apices of the latter cusps. The acute angle which its apex would have made with those of the latter cusps would appear to have been about 30 degrees. Cusp  $\bar{c}$  would appear to have been about as prominent, relative to cusp  $\bar{a}$  as it is in one of the more anterior lower molars of *M. watsoni*. A large area of dentine has been exposed on the buccal side of cusp  $\bar{c}$ , extending down almost to the base of the crown. The cusp is relatively incompletely divided from cusp  $\bar{a}$  so that it gives the impression of having split off from the latter. The highest point of the junction between cusp  $\bar{c}$  and cusp  $\bar{a}$  is above the level of that between cusp  $\bar{b}$  and the latter cusp. Although there is a mesial crest on cusp  $\bar{c}$ , as in all other morganucodonts, the intact part of the distal surface of the cusp is bereft of a crest.

There is no trace of any buccal cingulum. The lingual cingulum is well developed, but it is not continuous as it is interrupted by the widest part of cusp  $\bar{a}$ . Forward of this interruption the cingulum widens rapidly to form a broad shelf lingual to cusp  $\bar{b}$ . The edge and surface of this shelf is damaged, and devoid of enamel except for a narrow tract bordering the bases of cusps  $\bar{b}$  and  $\bar{a}$ . Almost certainly this damaged area encompasses the position of a cingulum cusp  $\bar{e}$  which has been broken off. Opposite cusp  $\bar{b}$  the lingual edge of the cingulum shelf projects further lingually than the widest part of cusp  $\bar{a}$ . The mesial edge of the shelf projects well forward of cusp  $\bar{b}$ . Because cusp  $\bar{b}$  is situated relatively buccally, the mesial part of the cingulum extends further buccally than in any of the other morganucodont lower molars that have been described.

Behind the widest part of cusp  $\bar{a}$ , the distal section of the cingulum is conspicuously narrower than in *Morganucodon watsoni*, so that - in occlusal view - the distal part of the tooth is rather narrower than the mesial part. Opposite the junction between cusps  $\bar{a}$  and  $\bar{c}$  - in the position where the Kuhnecone is situated in *M. watsoni* - the cingulum is damaged; an area of exposed dentine extends from the abraded edge of the cingulum just onto the base of cusp  $\bar{a}$ . The surface of this dentine stands out fractionally from that of the surrounding enamel (a feature only seen under high magnification). This suggests that a modest Kuhnecone may have been present on the cingulum at this point. Directly lingual to cusp  $\bar{c}$  the cingulum is slightly crenulated but no cusp is developed.

The cingulum passes round behind cusp  $\bar{c}$  to form a narrow talonid, which is damaged in the position where cusps  $\bar{i}$  and  $\bar{d}$  are situated in Morganucodont A. Homologous cusps were very probably originally present here. The talonid overhangs the distal root rather more markedly than in Morganucodon watsoni.

The preserved parts of the roots are remarkable for two reasons. The first is their extreme stoutness - they are much stouter than the equivalent roots in M. watsoni. The second is their extreme proximity to one another; they are completely separated, but the space between them is miniscule. Both of the roots are round in cross-section, in contrast to the situation appertaining in M. watsoni. More is preserved of the mesial root than the distal one. The sides of the mesial root are straight and parallel. The sides of the other root are also straight except distally where there has been some irregular addition of dentine. The roots show no tendency to diverge.

From the shape of the crown it is clear that contact between adjacent lower molars of Morganucodont B must be such that the back of the rather narrow talonid of the more anterior molar fitted buccally to the most mesial part of the cingulum on the following molar. The mode of contact is therefore rather similar to that in Morganucodont A.

#### Wear and occlusal relations:

From the fact that cusp  $\bar{c}$  is less completely divided from cusp  $\bar{a}$  than in Morganucodon watsoni (so that cusp  $\bar{a}$  of the opposing upper molar could not have been as effectively accommodated between these cusps) one would expect the occlusal pattern in Morganucodont B to have been different from that in the former species. This inference is borne out by the position of the functional wear on U567.

Functional wear is most clearly discernible on the buccal side of cusp  $\bar{a}$ . Here an unmistakable, if poorly defined, elongate area of wear extends directly downward in the enamel from the broken tip of the cusp. This worn area is incipiently divided into adjoining mesial and distal facets, the two sloping away from one another in horizontal section, following the original shape of the cusp surface. Ventrally the two facets diverge sharply, the mesial one passing mesially and the distal one distally. It will be recognised that the form of the wear on cusp  $\bar{a}$  is thus identical to that which occurs on cusp  $\bar{a}$  of moderately worn Morganucodont A lower molars.

Although the buccal side of cusp  $\bar{c}$  has been abraded, careful examination reveals that this post-mortem wear has been imposed over a prominent wear facet. There is no direct evidence regarding the original presence of a facet on the buccal side of cusp  $\bar{b}$ , owing to level of abrasion which has occurred here. However, from the type of wear on the more distal part of the crown there can be no doubt that such a facet was originally present. Molar occlusion in Morganucodont B was thus identical to that in Morganucodont A, with the possible exception of one small but important detail. This arises from the fact that cusp  $\bar{b}$  of U567 is slightly buccal to the line of the succeeding crown cusps. It may be that this feature is atypical and that in the majority of lower molars of Morganucodont B the three cusps were perfectly in line, as in other morganucodonts; (in this connection it may be noted that Parrington (1971) has figured at least one atypical lower molar of Morganucodon watsoni in which the crown cusps are not in line.) However, the probability that the only known tooth of a species is morphologically atypical is not great. If the arrangement of the three crown cusps of U567 is typical, then unless the upper molar cusp which opposed cusp  $\bar{b}$  was similarly buccally displaced, the latter would have been much more rapidly worn during the course of occlusion than was the case in Morganucodont A. It would also have been worn much more rapidly than the other crown cusps. The fact that the mesio-buccal corner of the cusp is missing in the present specimen may well be largely the result of functional wear. It is rather difficult to perceive how any functional advantage could be gained by the rapid wearing of cusp  $\bar{b}$ .

#### 4. MORGANUCODONT C

This species is represented by a single right lower molar, U687 (figure 72). Both roots are broken off just below the base of the crown, but the latter is largely intact. The crown measures 1.9mm by 1.0mm, so that it is about the size of a large Morganucodont A lower molar crown. The morphology of the specimen is strikingly different from that of any of the lower molars described so far.

#### Morphology:

Cusp  $\bar{a}$  is proportionally very much lower than in any of the more anterior lower molars of Morganucodon watsoni, and its base is relatively rather broader. The apex of the cusp is situated slightly

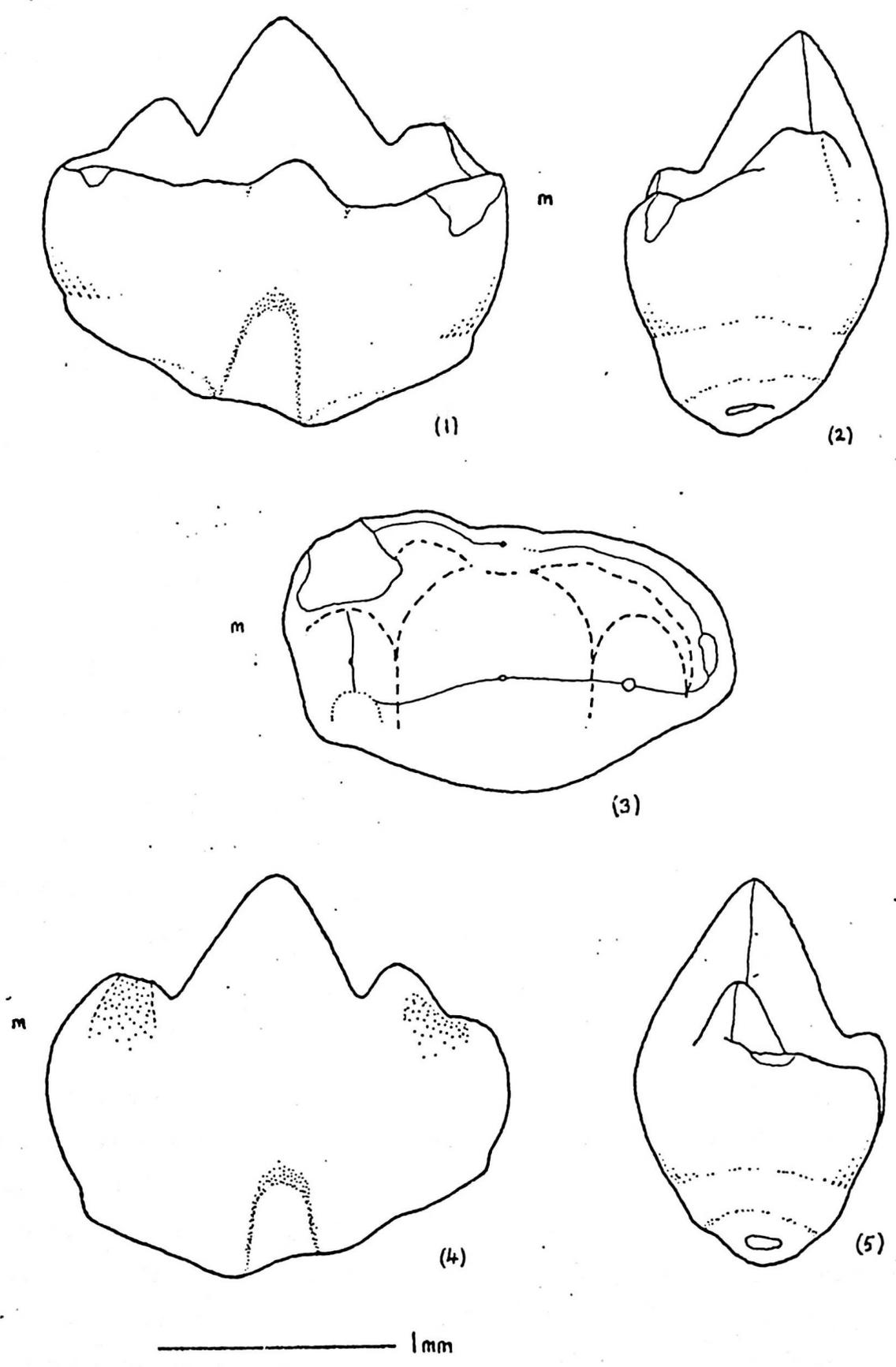


Figure 72 Morganucodont C: left lower molar, U687.  
(1) Lingual, (2) mesial, (3) occlusal, (4) buccal and (5) distal views.  
Note the wear on the buccal sides of cusps  $\bar{b}$  and  $\bar{c}$  (stippled areas).

mesial to the midpoint of the crown and buccal to the midline of the cusp base. In lateral view the cusp is shaped rather like an isosceles triangle; its sides are straight and of nearly equal length, and it separates from both of the accessory crown cusps on about the same level. In mesial and distal views the sides of the cusp are also nearly straight, and they meet at an angle of about  $60^{\circ}$ . The crests which divide the buccal and lingual sides of the cusp are vertical in these views.

The accessory crown cusps are divided off from cusp  $\bar{a}$  as completely as in Morganucodon watsoni. The form of cusp  $\bar{b}$  is very unusual. It is equal in height, and basal length, to cusp  $\bar{c}$ , but its basal breadth slightly exceeds that of the aforementioned cusp. The highest part of cusp  $\bar{b}$  does not take the form of a single point or apex, but comprises a short bucco-lingual crest, which is slightly raised at each end. Consequently in mesial view the cusp gives the impression of being very incipiently divided into two, although there is no indication of any division in the surface of the cusp below the dorsal crest. The buccal end of the crest (which has been worn) is in line with the apices of the succeeding crown cusps. From the lingual end of the dorsal crest a crest descends laterally to the cingulum. The main part of cusp  $\bar{b}$  is, in this way divided into nearly equal mesial and distal parts. Cusp  $\bar{c}$  is proportionally rather lower than in the more anterior lower molars of Morganucodon watsoni. In occlusal view the buccal side of the cusp is much narrower distally, than mesially. The apex of the cusp has been slightly abraded.

There is no trace of any buccal cingulum. The form of the lingual cingulum is distinctive. It continues past the widest part of cusp  $\bar{a}$  and its mesial and distal sections are very broad. Directly opposite cusp  $\bar{b}$ , on the mesio-lingual corner of the cingulum, there is an area of damage. This is separated from cusp  $\bar{b}$  by a very narrow tract of intact enamel. The damaged area probably marks the position of a cingulum cusp  $\bar{e}$  which has been broken off. The mesial edge of the cingulum, which is intact, projects fractionally forward of cusp  $\bar{b}$ . Behind the damaged area the lingual part of the cingulum continues backward as a prominent bulbous ridge, the highest part of which bears a crest. In occlusal view there is some suggestion that the ridge forms a cusp directly behind the damaged area, but this is not discernible in lingual view. The ridge forms the lingual border of a well defined mesial cingulum basin. This basin is enclosed

anteriorly by the damaged part of the cingulum, the exposed dentine surface of which is on the same level as the crest of the cingulum ridge (thereby supporting the view that a cusp  $\bar{e}$  was originally situated here). The basin is enclosed posteriorly by the junction of the buccal side of the base of the cingulum ridge with cusp  $\bar{a}$ . Immediately distal to this point there is a prominent Kuhnecone, which is continuous with the cingulum, rising smoothly and without interruption, above its dorsal edge. The base of the Kuhnecone is rather elongated mesio-distally, and its apex is directly lingual to the apex of cusp  $\bar{a}$ . The Kuhnecone is confluent buccally with the side of cusp  $\bar{a}$ , above the level of the cingulum. In mesial and distal views the lingual side of the Kuhnecone descends almost vertically from the cusp apex to the level of the cingulum, whilst its buccal side passes nearly horizontally into the side of cusp  $\bar{a}$ . The Kuhnecone therefore appears to project partly out of the side of cusp  $\bar{a}$  and partly up from the cingulum, and it makes an angle of about 30 degrees with the vertical axis of the crown. The cusp is thus neither wholly a crown cusp nor a cingulum cusp, and it is very reminiscent of the Kuhnecone in a Morganucodont A lower molar like U657 (figure 55), in its relative mesio-distal position and relationship to the cingulum and to cusp  $\bar{a}$ . It differs from the Kuhnecone in a molar like U657, however, in that it bears well defined mesial and distal crests. These are continuous with the crests on the cingulum. Behind the Kuhnecone, the edge of the cingulum continues backward as a prominent, featureless ridge of similar form to the ridge which precedes the cusp. This ridge borders a distal cingulum basin. The widest part of this basin is opposite the junction between cusps  $\bar{a}$  and  $\bar{c}$ . The basin becomes increasingly narrow as the cingulum turns round the disto-lingual corner of the crown. It is finally obliterated behind the distal crest on cusp  $\bar{c}$  as the cingulum ridge turns mesially to merge into the base of the buccal side of this cusp. The talonid is thus formed almost exclusively by the posterior part of the distal cingulum ridge, and it bears no differentiated cusp. The most distal part of the talonid is lingual to the midline of cusp  $\bar{c}$ . The crest on the cingulum ridge is continuous with the distal crest on the cusp.

The stumps of the roots are stout, and, as in the case of the lower molar of Morganucodont B, they are round in cross-section. They are completely separated, although a thin web of dentine passes between them. They diverge slightly. No pressure marks are discernible on

U687. From the shape of the crown, it is clear that when the tooth was in situ in the dentary, it did not interlock with its anterior neighbour; the distal end of the tooth in front must simply have abutted against its mesial face. There was presumably no distal interlocking mechanism either.

Wear and occlusal relations:

There is only one well defined facet on the tooth. This extends vertically down the buccal side of cusp  $\bar{b}$  from the tip of the cusp. There is a rather poorly defined facet on the buccal side of cusp  $\bar{c}$  just below the distal crest of the cusp. This overlaps distally onto the side of the talonid. The full extent or shape of the facet cannot be determined because the tooth has been water-worn in this region. Cusp  $\bar{a}$  is completely devoid of functional wear.

Quite clearly the mesial facet was produced by cusp  $\bar{c}$  of an opposing upper molar occluding directly with cusp  $\bar{b}$ , as in Morganucodont A. The tip of the principal cusp of the more posterior opposing upper molar would appear to have contacted U687 just distal to the tip of cusp  $\bar{c}$ , but it is difficult to be certain of this because of the uncertain extent of the wear on the latter cusp.

#### 5. MORGANUCODONT D

This form is represented by a single right lower molar, U675 (figure 73). The mesial root is intact, but only the proximal third of the distal root is preserved. The crown is damaged, and the distal part of its lingual side is covered with a thin layer of hard grey matrix. This also covers the lingual side of the distal root and part of the mesial root. No attempt has been made to remove the matrix for fear of further damaging the specimen. The crown is slightly smaller than that of a second lower molar of Morganucodon watsoni, and it is also proportionally slightly narrower. As preserved, the crown measures 1.3 by 1.5mm. The distance from the broken tip of cusp  $\bar{a}$  to the end of the root is 2.7mm.

Morphology:

Cusp  $\bar{a}$  is about as prominent as in one of the more anterior lower molars of M. watsoni. The apex of the cusp is broken off and its distal edge is damaged. In lateral view the mesial edge of the cusp is slightly convex. When the cusp was intact, its apex would have

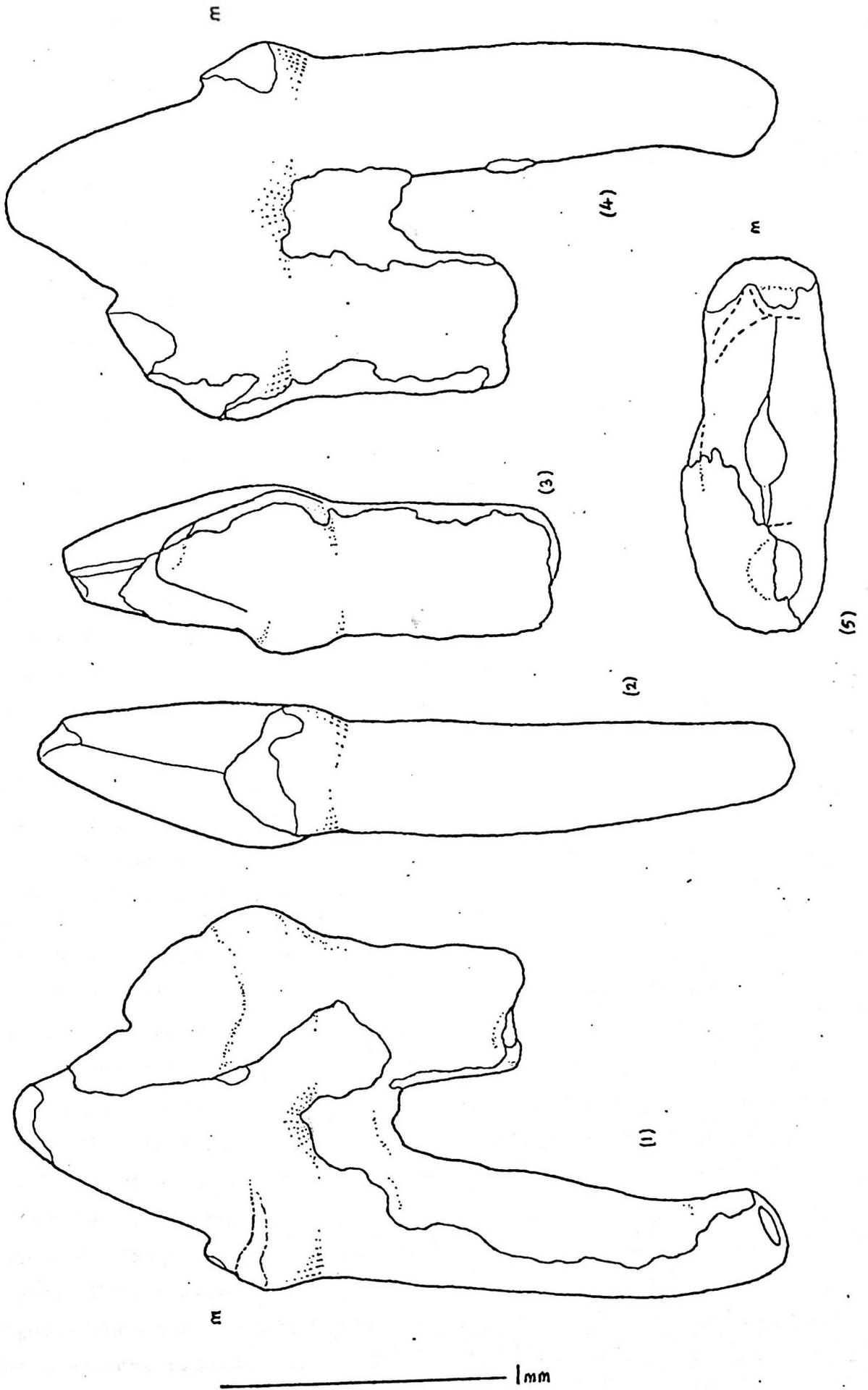


Figure 73 Morganucodont D: right lower molar, U675.  
 (1) Lingual, (2) mesial, (3) distal, (4) buccal and (5) occlusal views.  
 Note the possible wear facet on the buccal side of cusp  $\tau$ .

been situated mesial to the midpoint of the crown. In mesial view the buccal surface of the cusp is slightly convex, whilst the lingual one is almost straight. The cusp can be seen to be leaning slightly lingually, in this view, relative to the vertical axis of the root.

The summit and the mesial part of cusp  $\bar{b}$  is missing, along with the adjacent part of the dorsal surface of the cingulum. Below this damaged area the mesial surface of the crown descends intact to the level of the root. The relative position and shape of this intact surface shows clearly that cusp  $\bar{b}$  was rather smaller than cusp  $\bar{c}$  and it may well have been as small as the equivalent cusp in an anterior molar of M. watsoni. Cusp  $\bar{b}$  is divided from cusp  $\bar{a}$  at a low level, as in M. watsoni. Cusp  $\bar{c}$  is broken off above a line which runs from just above the junction of the cusp with cusp  $\bar{a}$  to just above its junction with the posterior part of the tooth. This line is oblique in lateral view as the division between cusps  $\bar{c}$  and  $\bar{a}$  is much less complete than that between cusps  $\bar{a}$  and  $\bar{b}$ . Accordingly, cusp  $\bar{c}$  gives the impression that it has arisen by splitting off from the side of cusp  $\bar{a}$ . When cusp  $\bar{c}$  was intact it would clearly have had a very asymmetrical lateral profile, the mesial edge of the cusp being much shorter than the distal one. The basal length of the cusp is similar to that of cusp  $\bar{c}$  in an anterior lower molar of M. watsoni. The upper part of the buccal side of the cusp comprises a surface of exposed dentine, which is almost flat, and which faces slightly dorsally and distally as well as buccally.

There is no semblance of a buccal cingulum on the crown. The lingual cingulum is well developed directly opposite the remaining part of cusp  $\bar{b}$ , and it bears the distal part of a cusp  $\bar{e}$ . The cingulum is obsolete opposite the widest part of cusp  $\bar{a}$ . Distal to this point it reappears, although its detailed form is obscured by the overlying matrix. This section of the cingulum is evidently well developed and in occlusal view the distal end of tooth is as broad, or slightly broader than the mesial end. Only a very small part of the distal section of the cingulum projects forward of the matrix, and this is damaged. Very possibly the succeeding edge of the cingulum is also damaged. When the tooth is viewed distally it is apparent that there is no Kuhnecone beneath the matrix. This does not, of course, preclude the possibility that such a cusp was originally present in the tooth; it could easily have been broken off during the posthumous journey of the tooth to the fissure. The cingulum passes behind

cusps  $\bar{c}$  to form a talonid. This is clearly broken off a short distance behind cusp  $\bar{c}$ , and there is, consequently, no evidence of the original presence of a cusp  $\bar{d}$ .

The roots diverge slightly. There is no evidence of any damage to the mesial root so that it would appear to be intact. This root is about as long as a fully grown root in one of the more anterior lower molars of Morganucodon watsoni. It differs from a mature M. watsoni molar root, however, in that it tapers slightly throughout its length, and its lower half is curved posteriorly. The root also differs strikingly from a mature M. watsoni root in lacking any semblance of apical thickening. The root may not be fully mature, as its pulp canal foramen is still large. We may be fairly certain that it was never destined to develop a club foot, however, because of the fact that it is curved. As I have argued earlier, with regard to the tooth called 'Eozostrodon' problematicus, curved roots would have served to anchor a tooth firmly in the jaw - this was the functional reason for the curvature. There would therefore have been no functional necessity for the subsequent development of a club foot in the case of the mesial root of U675.

Wear:

Unambiguous evidence of wear on the tooth is lacking. However, the exposed dentine surface on the dorsal part of the buccal side of cusp  $\bar{c}$ , whilst it has clearly been abraded, is rather reminiscent of the wear facet which is found on the equivalent cusp in worn lower molars of Morganucodont A. It is possible that this resemblance is a misleading one, because there is no evidence of wear on the buccal surface of cusp  $\bar{a}$ . If, however, the exposed dentine surface on the cusp is not entirely the result of posthumous attrition, occlusal relations in Morganucodont D would appear to have been like those in Morganucodont A, rather than like those in Morganucodon watsoni.

The intra-subordinal positions of the Welsh morganucodonts

1. Generic positions

It is desirable to deal with the generic positions of the Welsh morganucodonts before their familial positions are discussed, because the former are more straight forward and less open to controversy than the latter. Their clarification also facilitates a less cumbersome discussion of familial positions. The question of the taxonomic validity of the name Morganucodon - the subject of much recent debate (cf. Kermack, Mussett and Rigney, 1973) - has already been discussed; it has been shown that the genus is well founded. We may now consider the generic positions of the other morganucodonts from Pant 4.

(i) Morganucodont A

It has been shown earlier that this species differs from Morganucodon watsoni in a number of important morphological features and also in its occlusal relations. These differences are such that there can be no doubt that the two species belong to different genera. The lower molars of Morganucodont A are more like those of the southern African species Megazostrodon rudnerae than they are like any other morganucodont lower molars which have been described in the literature (including those from Hallau). They particularly resemble Megazostrodon rudnerae lower molars in the following respects:

- (1) The transverse bulbousness of the crown (although this feature is not quite as marked as it is in the latter teeth).
- (2) The relative prominence of the Kuhnecone and cusps  $\bar{e}$  and  $\bar{i}$ .
- (3) The fact that cusp  $\bar{e}$  projects forward of cusp  $\bar{b}$ .
- (4) The extent of the division between cusps  $\bar{a}$  and  $\bar{c}$  (in this respect they also resemble the lower molars of Erythrotherium parringtoni, Sinoconodon rigneyi, and the tooth called 'Eozostrodon' problematicus).
- (5) The fact that the distal part of the crown is narrower, bucco-lingually, than the remaining part.

Typical lower molars of Morganucodont A differ from the lower molars of Megazostrodon rudnerae, however, in the following details:

- (1) The position of the Kuhnecone (in Megazostrodon rudnerae this cusp is situated in the same position as it is in Morganucodon.<sup>1</sup>)
- (2) The extent of the division between cusps  $\bar{b}$  and  $\bar{a}$  (in the southern African form, these cusps are as completely divided as they are in Morganucodon).
- (3) The shape of the molar roots (in Megazostrodon rudnerae these are tapered - at least in the case of the upper molars; cf. Crompton, 1974, p. 413).

Morganucodont A also differs from Megazostrodon rudnerae in the degree of morphological difference which exists between adjacent molars in the the upper and lower jaws. In the Welsh species this is clearly much less than in the Southern African form. The upper molars of Morganucodont A are rather less like the equivalent M rudnerae teeth than is the case with the lower molars. In particular these teeth lack the characteristic bean shape of the upper molars of the South African species, the buccal cingulum being uninterrupted, and they lack a well developed cingulum cusp D. Finally, Morganucodont A also differs from M. rudnare in its occlusal pattern. In M. rudnare cusp  $\bar{a}$  of each lower molar sheared slightly in front of cusp B of the corresponding upper molar whilst cusp A of the latter tooth sheared behind cusp  $\bar{c}$  of the former tooth and against its talonid (Crompton & Jenkins, 1968; Crompton 1974). In Morganucodont A, as we have seen, cusp  $\bar{a}$  of the lower molar sheared against cusp B of the upper, and cusp A of the latter sheared against cusp  $\bar{c}$  of the former. The differences between the species are such that Morganucodont A cannot reasonably be referred to the genus Megazostrodon. A new genus is clearly required for the reception of the form.

(ii) Morganucodont B

The lower molar which represents this species - U567 - is more like a large lower molar of Morganucodont A, than it is like any other morganucodont lower molar. Occlusion in Morganucodont B was evidently very like that in Morganucodont A, although, as we have noted, it may

<sup>1</sup> As Crompton (1974) has shown, the Kuhnecone is the third lower molar of Megazostrodon rudnerae and is, in contrast to that in the other lower molars, a crown cusp. Its position relative to cusps  $\bar{a}$  and  $\bar{c}$  however appears to be identical to that in the other lower molars.

not have been identical. A number of features distinguish U567 from any lower molar of Morganucodont A. The most conspicuous are as follows:

- (1) The relatively very large size of the tooth.
- (2) The absence of the type of Kuhnecone which occurs in the latter species. (As I have implied earlier, if the tooth originally possessed a kuhnecone, this cusp must have been situated in the same position as it is in Morganucodon.)
- (3) The relatively buccal position of cusp  $\bar{b}$ .
- (4) The extreme stoutness and proximity of the roots.
- (5) The marked distal 'overhang' of the talonid.

(1), (4) and (5) might be regarded as no more than specific differences; (2) and (3) however are more significant, and they warrant the generic separation of Morganucodont B and Morganucodont A. There can be no doubt that the two genera are very closely related.

(iii) Morganucodont C

The Kuhnecone in the lower molar belonging to this species - U687 - is very similar in form and position to that in a 'morphological category three' lower molar of Morganucodont A (e.g. U657, figure 55). The tooth differs from all lower molars belonging to the latter species in the relatively low level of the division between each of the accessory crown cusps and cusp  $\bar{a}$ ; it differs from all known morganucodont lower molars in the relatively broad, low form of cusp  $\bar{a}$  and in the remarkable, and unique form of both the lingual cingulum and cusp  $\bar{b}$ .

Clearly Morganucodont C should be placed in a new genus. I have not emphasised the equal height of the accessory crown cusps in U687 in considering the generic position of the species, and this has not been an oversight. In discussing the relationships of morganucodont species known only on single molars, it is essential to bear in mind the fact that morganucodont molars vary in their morphology along the tooth row. This variation may be very marked, as in the case of Megazostrodon rudnerae. In both Morganucodon watsoni and Morganucodont A the accessory crown cusps become more equal in size as one passes distally from first molar to last, and the same may have been true in Morganucodont C. In other words the equal height of cusps  $\bar{b}$  and  $\bar{c}$  in U687 may be a feature which reflects the original position

of the tooth in the jaw rather than one which was manifest in all the lower molars of the species.

(iv) Morganucodont D

The lower molar which represents this species - U675 - is strikingly reminiscent of the Morganucodont molar from Holwell which Parrington (1941) called Eozostrodon problematicus. As stated earlier, the latter tooth is unfortunately broken, as is the Welsh specimen. U675 matches 'E' problematicus in the following morphological features:

- (1) The shape and relative proportions of cusp  $\bar{a}$ .
- (2) The level of the division between cusps  $\bar{a}$  and  $\bar{c}$ .
- (3) The shape - and relative length - of its intact root.
- (4) The mesial extent of the distal section of the cingulum.
- (5) The shape, in occlusal view, of the equivalent part of the tooth.

Although cusp  $\bar{c}$  is broken off above the level of its junction with cusp  $\bar{a}$  in U675, the relative length of its base matches that of the equivalent cusp in 'E' problematicus. The missing cusp  $\bar{b}$  of 'E' problematicus evidently divided from cusp  $\bar{a}$  at the same low level as cusp  $\bar{b}$  does in U675. The only morphological feature of 'E' problematicus which is completely lacking in the Welsh tooth is the modest Kuhnecone mentioned and figured by Parrington (1941, 1971). Hopefully, it will be possible to determine whether or not such a cusp was originally present by the careful removal of matrix at a future date. Despite the uncertainty surrounding the question of the original presence of a Kuhnecone in U675, the agreement between this tooth and 'E' problematicus is sufficiently extensive for it to be reasonably referred to the same genus. It is worth emphasising again that Eozostrodon is not the valid name of this genus.

U675 is almost identical in size to 'Eozostrodon' problematicus. If the former tooth had been obtained from the fissure in Holwell quarry which yielded the latter one, it would undoubtedly have been referred to the same species. As this is not the case, however, and as the complete morphology of neither of the teeth is known, it is perhaps best to adopt a conservative approach and refrain from referring the Welsh molar to problematicus.

## 2. Familial positions

Any discussion of the familial positions of the Welsh morganucodonts inevitably involves a discussion of the familial positions of all morganucodont genera. It is necessary to preface such a discussion by briefly considering certain questions of cusp homology, and also by considering the systematic position of the problematic Chinese animal Sinoconodon rigneyi, which is often classified as a morganucodont.

### (i) Cusp homologies

The most distinctive feature of the lower molars of Morganucodont A is the presence of a Kuhnecone which, in all but one specimen, arises wholly or partly from the side of cusp  $\bar{a}$ . A clearly homologous cusp is present in the lower molar belonging to Morganucodont C. We may begin by considering the question of whether the Kuhnecone in these forms is homologous to the 'true' Kuhnecone in other morganucodonts. The position of the cusp in the larger lower molars of Morganucodont A leaves no doubt that it originated in the antecedents of this form of splitting out of the side of cusp  $\bar{a}$ . Homology with the Kuhnecone of Morganucodon, Megazostrodon and Erythrotherium would therefore require that the latter cusp migrated to its present position on the cingulum during the course of evolution. The fact that the Kuhnecone in Morganucodont A progresses from being wholly a crown cusp in the largest molars, to being largely (and in one case wholly) a cingulum cusp in the smallest ones, shows that such a migration would have been feasible. It is notable that in many of the more mesial lower molars of Morganucodon watsoni (the  $M\bar{1}$  and  $M\bar{2}$ ) the Kuhnecone leans slightly lingually, away from the crown, unlike the other lingual cusps of the cingulum, and that the mesial side of its base is partly confluent with cusp  $\bar{a}$ , above the level of the rest of the cingulum. Both of these features recall the situation in Morganucodonts A and C. Still more pertinently, in a few molars of M. watsoni - including the type (see Kuhne, 1948, figure 1C and E) and the specimen shown in figure 74 - the Kuhnecone leans away from the crown almost as markedly as in Morganucodont A, whilst the mesial part of its base is confluent with cusp  $\bar{a}$ , almost to the same extent as in Morganucodont A molars belonging to morphological category three (e.g. U657, figure 55). Essentially, all that is necessary to convert the type of Kuhnecone present in the latter teeth into that present in the former ones is for the cusp to migrate slightly distally. In the light of

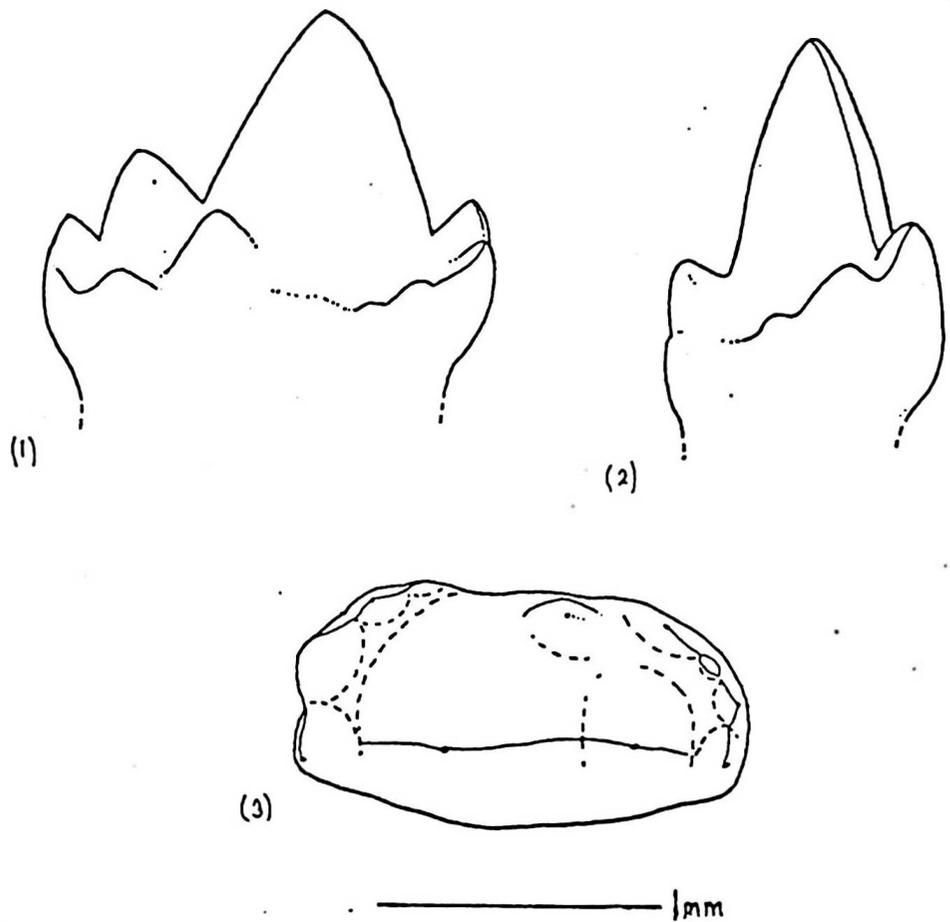


Figure 74. Morganucodon watsoni, left lower molar from Pontalun quarry (1) Lingual, (2) mesio-lingual and (3) occlusal views. Note the arrangement of the kuhnecone (especially its relationship with cusp  $\bar{a}$ ) and the extent of the division between cusps  $\bar{a}$  and  $\bar{c}$ .

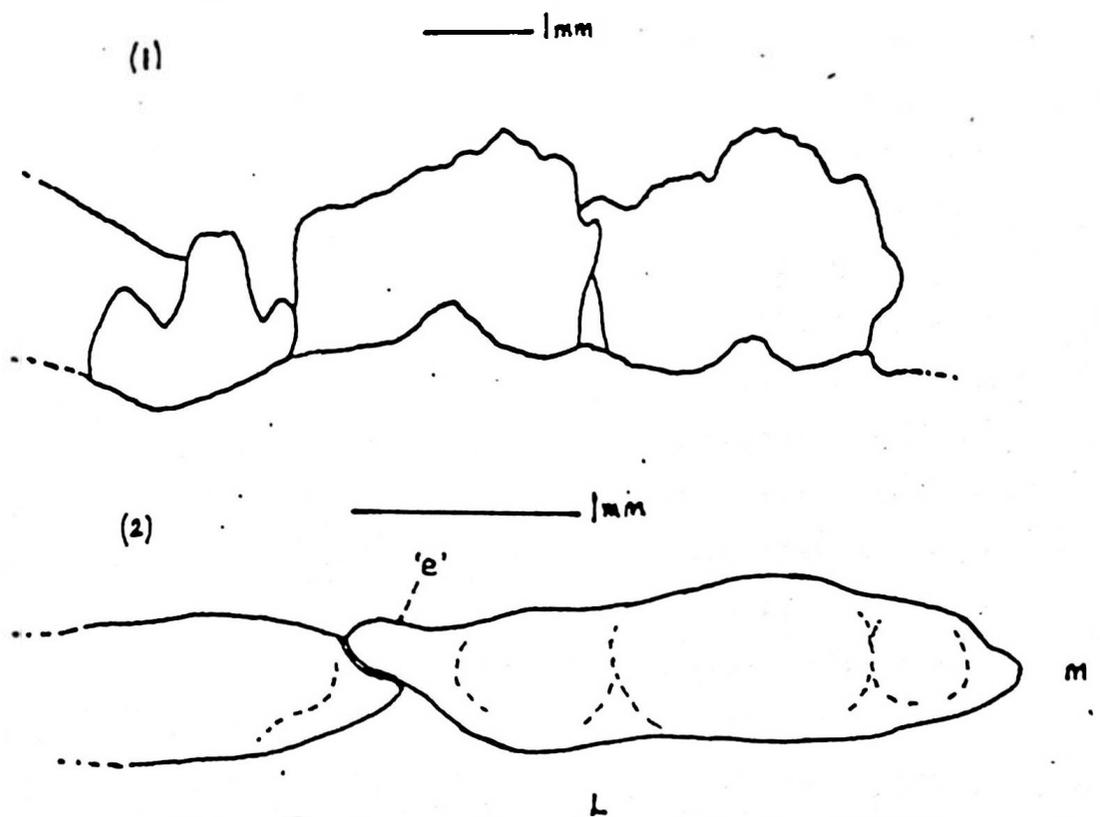


Figure 75. Sinoconodon rigneyi. Lower molars. (1) Lingual view of lower molars of specimen C U P 1. (2) Occlusal view of two adjacent molars. Note interlocking mechanism. L = lingual side.

these observations I think there can be little doubt that the cusp in Morganucodonts A and C is the homologue of that in Morganucodon, Megazostrodon and Erythrotherium. Its position in the two former genera is simply more conservative than its position in the three latter ones.

Mills (1971) has suggested - as part of a hypothesis to account for the different occlusal patterns in Morganucodon and Megazostrodon - that cusp  $\bar{c}$  in Morganucodon and Erythrotherium (his morganucodontids) is homologous with cusp  $\bar{d}$  in Megazostrodon, Sinoconodon and 'Eozostrodon' (his sinoconodontids), and that cusp  $\bar{c}$  in the latter genera is a new cusp not present in the former ones. In Megazostrodon, Sinoconodon and 'Eozostrodon' cusps  $\bar{a}$  and  $\bar{c}$  divide at a relatively high level above the cingulum, indicating that cusp  $\bar{c}$  has split off from cusp  $\bar{a}$  during the course of evolution, whilst in Morganucodon the cusps divide at a relatively low level, giving the impression that they have both arisen independently from the crown base. With regard to Erythrotherium, however, it is interesting to note that the arrangement is - according to the figures in Crompton's paper of 1972 - very similar to that in Megazostrodon: cusp  $\bar{c}$  is relatively incompletely separated from cusp  $\bar{a}$ . If Mills is correct in suggesting that cusp  $\bar{c}$  in Morganucodon and Megazostrodon are not homologues, then Erythrotherium would seem, on this evidence, to be allied with the Megazostrodon group of genera, rather than with Morganucodon. Amongst the new Welsh genera, Morganucodonts A and B resemble Megazostrodon in that cusp  $\bar{c}$  is divided from cusp  $\bar{a}$  at a relatively high level, whilst Morganucodont C resembles Morganucodon in that the cusps are divided at a low level. The new material has an important bearing on the credibility of Mills hypothesis. According to this hypothesis the common ancestor of Morganucodon and Megazostrodon had upper and lower molars which were like the posterior pre-molars of Morganucodon, possessing a large principal cusp and small mesial and distal cusps. With the commencement of occlusion the principal cusps alternated so that the tip of the lower cusp (cusp  $\bar{a}$ ) sheared directly against the mesial cusp of the upper tooth (cusp B). Mills believes that this occlusal arrangement was unsatisfactory, and he postulates that the difficulty was resolved differently in the lines leading to Morganucodon and Megazostrodon. In the former lineage, cusp B shifted mesially as it increased in size, until it came to occlude anterior to cusp  $\bar{a}$ . In the latter lineage, a groove appeared in the tip of

cusp  $\bar{a}$ , which served to accommodate cusp B. The distal part of the bifurcated tip of cusp  $\bar{a}$  was the progenitor of the Megazostrodon cusp  $\bar{c}$  (see figure 76). If Mills is correct in correlating the origin of the Megazostrodon cusp  $\bar{c}$  with the need to remedy an occlusal inefficiency caused by cusp  $\bar{a}$  shearing directly against cusp B, one would obviously not expect to find a clearly homologous cusp  $\bar{c}$  in a form in which the latter occlusal arrangement pertained. Yet this is exactly what we find in the case of Morganucodonts A and B. It is therefore clear that the origin of the Megazostrodon-type of cusp  $\bar{c}$  had nothing to do with a necessity to prevent the mutual contact of cusps  $\bar{a}$  and B and Mills argument for the non-homology of cusp  $\bar{c}$  in Morganucodon and Megazostrodon is invalid. It is interesting that in a few Morganucodon watsoni lower molars - including the type, and the specimen shown in figure 74 - the division between cusps  $\bar{a}$  and  $\bar{c}$  is slightly less complete than is usually the case, the relationship between the cusps being a little more like that encountered in the lower molars of Megazostrodon, Sinoconodon, 'Eozostrodon' and Erythrotherium. I have no doubt that cusp  $\bar{c}$  is homologous in all morganucodonts, and that in the lower molars of Morganucodon, and in the only known molar of Morganucodont C, the cusp has simply separated more completely from its parent cusp - cusp  $\bar{a}$  - than it has in the lower molars of other genera.

Mills (1971) identified cusp b in Morganucodon and Erythrotherium as a cingulum cusp, and the equivalent cusp in Megazostrodon and Sinoconodon as a 'true' cusp (= crown cusp in this account).

In the two former genera the cusp is continuous, lingually, with the cingulum, as in the case of the distal cingulum cusp  $\bar{d}$ . In the more anterior molars of Morganucodon the cusp is almost as small as cusp  $\bar{d}$  and the same appears to be true in the molars of Erythrotherium. In Megazostrodon and Sinoconodon cusp  $\bar{b}$  is larger although it is still smaller than cusp  $\bar{c}$ . In the Chinese form the cusp is relatively incompletely divided from cusp  $\bar{a}$  and it is preceded by a small cusp, which may be homologous to cusp  $\bar{e}$  of undoubted morganucodonts (see figure 75). It is therefore apparent that Mills is correct in regarding cusp  $\bar{b}$  as a crown cusp in this species.

The corresponding situation in Megazostrodon was not clear at the time when Mills wrote his paper. Crompton (1974) has subsequently shown that it is not the same as in Sinoconodon. Cusp  $\bar{b}$  is as

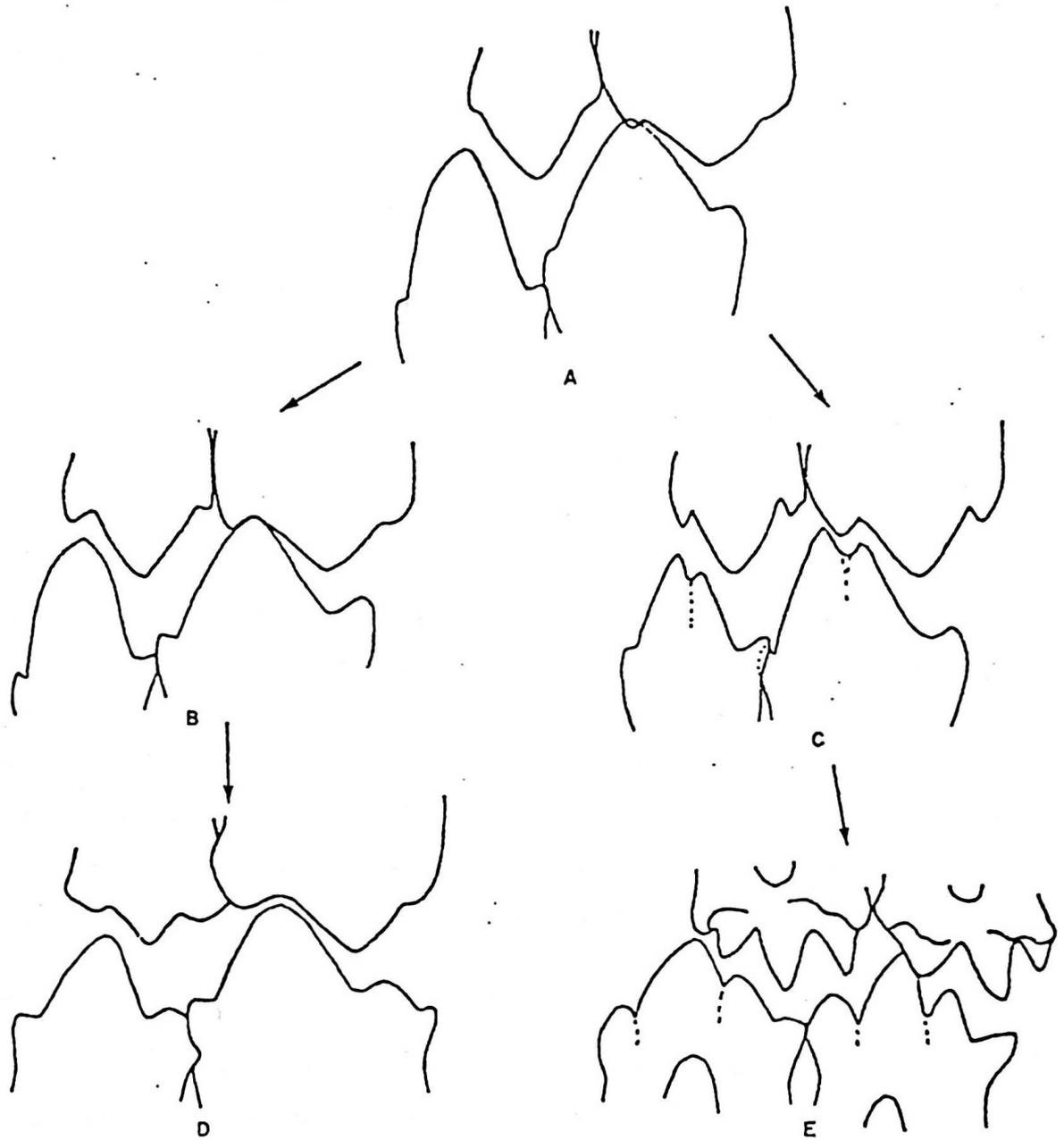


Figure 76. Evolutionary stages in the development of Morganucodon and Megazostrodon molars according to Mills hypothesis. A, hypothetical common ancestral stage at which shearing is first developed. B and C hypothetical intermediate stages. D, Morganucodon watsoni and E, Megazostrodon molars.

( From Mills 1971 )

completely divided from cusp  $\bar{a}$  as is in Morganucodon, it is not preceded by a cusp, and its relationship with the cingulum and with cusp  $\bar{a}$  is exactly the same as in Morganucodon. The morphology of the cusp also appears to be the same as in Morganucodon, so that it differs from cusp  $\bar{b}$  in the latter genus only in being a little larger. In these circumstances it seems much more reasonable to regard cusp  $\bar{b}$  in Megazostrodon as the homologue of cusp  $\bar{b}$  in Morganucodon rather than as a cusp which has arisen from a different part of the tooth. Cusp  $\bar{b}$  the new morganucodonts is clearly homologous to that in Morganucodon, Erythrotherium, and Megazostrodon. There remains the question of whether the cusp arose from the cingulum or from the crown. The former possibility is suggested by the lingual continuity of the cusp with the cingulum, and by its relatively small size in Morganucodon and Erythrotherium. The latter possibility is suggested by its larger size in the other genera. The problem may be resolved by considering the arrangement of the cusp in Morganucodonts A and B. In all but the largest lower molars of Morganucodont A, and in the sole known specimen of Morganucodont B, cusp  $\bar{b}$  is less completely divided from cusp  $\bar{a}$  than it is in the other undoubted morganucodont genera. It is apparent from the arrangement of cusp  $\bar{b}$  in these molars, that the cusp originated by splitting off from cusp  $\bar{a}$ , as both cusp  $\bar{c}$  and the Kuhnecone did.

(ii) The systematic position of Sinoconodon rigneyi

This form, which comes from the Lufeng Beds of Yunnan, China, is one of the two largest mammals known prior to the triconodontids of the upper Jurassic (the other one is Morganucodont B). Its molars exhibit a triconodont-like arrangement of their main cusps and they are morphologically conservative in that the accessory cusps are relatively incompletely divided from the principal cusp. Sinoconodon was first described by Patterson & Olson (1961), who referred it to the Triconodontidae. Subsequently, Hopson & Crompton (1969) suggested that it was an aberrant morganucodont, and this view has since been generally adopted (see, for example, Mills, 1971; Simpson, 1971; Kermack, Mussett and Rigney, 1973).

Hopson and Crompton have pointed out that Sinoconodon resembles Morganucodon watsoni more closely than any triconodontid in the presence of an angular process on its dentary, and in the number and relative sizes of the longitudinal row of cusps of its lower molars. It is also more like Morganucodon than a triconodontid in that during

ontogeny its premolars were lost by resorption.

Regarding the first of these points of resemblance, however, it should be borne in mind that many cynodonts have an angular process of the dentary, as do pantotheres (Kuehneotherium excepted) and later therians. None of these forms is closely related to the Morganucodonta. The presence of an angular process in Sinoconodon is thus in itself indicative of a close relationship with Morganucodon. With regard to the second point of resemblance, it may be noted that lower post canines which bear longitudinally arranged cusps of similar number and relative size to those which occur in the lower molars of Morganucodon, are found in the galesaurid Thrinaxodon, and the recently discovered carnivorous cynodont Therioherpeton which comes from the Middle Triassic Santa Maria Formation of Southern Brazil (Bonaparte & Barberena, 1975). Triconodont-type lower molars in which the longitudinal cusps are Morganucodon-like in their relative sizes might thus quite plausibly occur in early mammals which are not particularly closely related. This is, moreover, an especially likely occurrence if - as seems probable from the morphological evidence afforded by Bonaparte & Barberena (1975) - Therioherpeton belongs to a group of cynodonts which was immediately ancestral to the Triconodonta. With regard to the third point of resemblance the evidence for a close affinity between Sinoconodon and Morganucodon is still less conclusive. The loss, by resorption, of unreplaced post canines is a widespread phenomenon amongst cynodonts (cf. Crompton, 1964), and it has also been documented in the early Therian Kuehneotherium (Gill, 1974). It was thus probably common to all very early mammals, and hence has little bearing on the closeness of the relationship between them. It might be argued that whilst each of the three features referred to above is insufficient of itself to establish that Sinoconodon is closely allied with Morganucodon, their evidence taken together is sufficient to do so. This argument has little substance, however. All three features are features which could very plausibly have coexisted in an advanced cynodont. In this context it is worth recalling that the jaw articulation of Sinoconodon is not known. In consequence the mammalian status of the form is inferred rather than unequivocally established.

Sinoconodon differs from Morganucodon and all undoubted morganucodonts in several important respects. Most conspicuously, its lower molars

lack the prominent lingual cingulum which characterises the lower molars of these forms. An exceedingly narrow, barely discernible cingulum is present on the lingual side of the partly erupted third molar of the type specimen, and there are no cingulae at all on the two preceding teeth. In this respect, therefore, Sinoconodon is less like a typical morganucodont than the triconodontids and early therians are. The situation regarding the cingulae in the sole known upper molar of Sinoconodon is less clear than that in the lowers. As Mills (1971) has stated, there is a small cusp directly in line buccally with cusp B, but the buccal cingulum behind this, if originally present, is broken away. There is quite clearly no lingual cingulum on the distal half of the tooth, so that here again the Chinese form differs from both typical morganucodonts and triconodontids.

Sinoconodon also differs from undoubted morganucodonts in that its lower molars bear a small cusp mesio-lingual to cusp  $\bar{b}$ . This cusp may be homologous with cusp  $\bar{e}$  in the latter forms, although it does not arise from a cingulum. Whilst it is true that the mesial part of cusp  $\bar{e}$  in both Megazostrodon and Morganucodont A projects forward of cusp  $\bar{b}$ , it is never situated anything like as anteriorly as the mesio-lingual cusp in Sinoconodon.

Finally, Sinoconodon differs from undoubted morganucodonts in the very marked lateral compression of the crowns of its molars. As a result of this compression the crests which divide the linearly arranged cusps into buccal and lingual sides are much sharper in the Chinese animal than they are in the morganucodonts. In the morganucodonts and also in the triconodontids, the crests on the molar cusps played little or no part in cutting the food. Their principal role was probably in crushing and puncturing, and shearing was mainly effected by edges which were produced on the teeth through wear. In Sinoconodon, by contrast, it would appear, from the relative sharpness of the molar crests that these played a major, and perhaps predominant part in shearing the food. In other words, it would appear that the actual method of chewing in this form differed from that in typical morganucodonts and triconodontids. No wear is discernible on the three molars of the type specimen of Sinoconodon. Unfortunately the damage to the cusps of the two fully erupted molars of this jaw means that it is impossible to determine whether or not they originally bore facets. What is clear, however, is that the relative

narrowness of the crowns of the molars effectively precludes the possibility that these teeth could have become remodelled by wear to the extent that the more worn molars of Morganucodon, Megazostrodon and Morganucodont A were. This supports the inference drawn from the molar crests. In the light of the absence of conclusive evidence for a close affinity between Sinoconodon and Morganucodon, and of the striking differences which exist between the Chinese form and all undoubted morganucodonts, there can be no real justification for allocating the form to the Morganucodonta. If Sinoconodon is excluded, the Morganucodonta constitute a clearly definable, manifestly natural group of early mammals. If Sinoconodon is included, this is no longer the case. Whilst the possibility that Sinoconodon is an aberrant morganucodont cannot be entirely ruled out, I think that it is remote. On purely dental grounds Sinoconodon appears to be less closely related to both the morganucodonts and triconodontids than either group is to the other, and the form is most reasonably classified simply as 'Triconodonta incertae sedis'.

(iii) The familial positions of the undoubted morganucodont genera. In their general review of the relationships of early mammals, Hopson & Crompton (1969) placed all of the undoubted morganucodonts together with Sinoconodon in a single family. This they called the Eozostrodonidae in the mistaken belief that Morganucodon, the type genus of the family Morganucodontidae defined by Kuhne (1958), was a junior synonym of Eozostrodon, although as Hopson later pointed out, under the International rules governing nomenclature, the name Morganucodontidae has priority irrespective of whether Morganucodon and Eozostrodon are synonyms (Hopson, 1970). In his paper of 1971, Mills proposed a different classification of the morganucodonts. He removed Sinoconodon and Megazostrodon from the Morganucodontidae and placed them in a new family, the Sinoconodontidae, in which he also, rather tentatively, placed 'Eozostrodon' problematicus. The exclusion of Sinoconodon from the Morganucodonta for the reasons given above, does not, of course, necessarily invalidate Mills case for removing Megazostrodon and 'Eozostrodon' from the Morganucodontidae. It is therefore pertinent to examine this case in the light of the new information on the Morganucodonta which has been afforded by the genera from Part 4.

Mills believed that the non-morganucodontid genera, Megazostrodon and 'Eozostrodon' differ from the true morganucodontids, Morganucodon and

Erythrotherium, in the following respects:

- (1) Their lower molars have three aligned crown cusps, unlike the morganucodontids where cusp  $\bar{b}$  is a cingulum cusp.
- (2) Cusps  $\bar{a}$  and  $\bar{c}$  of the lower molars are less completely divided from one another reflecting the non-homology of the latter cusp with cusp  $\bar{c}$  of morganucodontids.
- (3) At the point of contact between adjacent lower molars, cusp  $\bar{d}$  of the more anterior tooth lies on the lingual side of cusp  $\bar{b}$  of the following tooth, whereas in morganucodontids the former cusp fits below the latter one.
- (4) During occlusion cusp A of the upper molar sheared between cusp  $\bar{c}$  and  $\bar{d}$  whereas in morganucodonts it sheared between  $\bar{a}$  and  $\bar{c}$ .

Of these supposed differences (1) has already been shown to be quite invalid; cusp  $\bar{b}$  is homologous in all morganucodonts and it is a crown cusp. (2) has also been shown to be invalid in so far as it involves the belief that the Megazostrodon and 'Eozostrodon' cusp  $\bar{c}$  is not homologous with cusp  $\bar{c}$  in the other genera. The difference in the relative extent of the division between cusps  $\bar{a}$  and  $\bar{c}$  is hardly of taxonomic importance at familial level when divested of this significance. With regard to (3) Crompton (1974) has shown that the relationship between cusps  $\bar{d}$  and  $\bar{b}$  in Megazostrodon is actually the same as that in Morganucodon. The nature of the contact between the adjacent lower molars of 'Eozostrodon' is not known, but there is no reason to suppose that it is any different from that in the other genera as regards the relationship between the aforementioned cusps.

This leaves us with (4). Of the genera considered by Mills only Morganucodon and Megazostrodon can be distinguished on the basis of their occlusal patterns as the occlusal patterns of the other genera (vis. 'Eozostrodon' and Erythrotherium) are not definitely known. Mills believed that the difference in occlusion between Morganucodon and Megazostrodon was a fundamental one. In order for the Megazostrodon type of occlusal pattern to have been derived from the Morganucodon type or vice versa there would have to have been an intermediate stage in which cusp A of the upper tooth occluded

directly with cusp  $\bar{c}$  of the lower whilst cusp  $\bar{a}$  of the latter tooth similarly occluded with cusp B of the former one, and Mills has stated "It is very difficult to believe that such an arrangement would be advantageous or even viable in a shearing dentition. Although less so it seems unlikely in a non-shearing reptilian dentition. Such a dentition, used for siezing a struggling prey requires upper and lower teeth to be quite close together, and this can be better achieved if the larger cusps alternate. If cusp stood opposite cusp there would be a greater danger of food jamming the jaw." He therefore concluded that the Morganucodon and Megazostrodon lineages must have diverged "at the very development of a shearing action". It will be recognised however, that the hypothetical occlusal pattern necessary as an intermediate stage if either of the Morganucodon or Megazostrodon types of occlusion were to have been derived from the other, matches exactly the occlusal pattern of Morganucodont A. Obviously, the manifest viability of this occlusal pattern obviates any necessity to believe that the Morganucodon and Megazostrodon lineages must have diverged at the point when occlusion first appeared in a mutual ancestor. The differences in occlusal pattern between Morganucodon and Morganucodont A on the one hand and Morganucodont A and Megazostrodon on the other essentially reflect only very slight differences in the positions of the upper and lower molars relative to one another. They certainly cannot be considered sufficient grounds for refereing these genera to different families.

Thus, of the reasons given by Mills (1971) for dividing off Megazostrodon and 'Eozostrodon' from the family Morganucodontidae, none now withstands critical examination. Both genera are very reasonably accommodated within this family, as are the new Welsh genera. As so constituted, the Morganucodontidae is a narrow family and one which is clearly distinct from all other families of early mammals.

Class	<u>MAMMALIA</u>
Subclass	<u>ATHERIA, Kermack, Mussett &amp; Rigney, 1973</u>
Order	<u>TRICONODONTA, Osborn, 1888</u>

PROBLEMATIC CHEEK TEETH

There are nine isolated molariform cheek teeth in the assemblage which are of triconodont type but which cannot be referred with facility to any of the established triconodont suborders (viz. the Morganucodonta, Eutriconodonta & Docodonta). The teeth exhibit a considerable size range and all are unique in their morphological details. All, however, share the same basic and distinctive morphological pattern, and it is clear that they belong to the same, or to closely related, species. Almost all the crowns are damaged, and, whilst the majority of specimens show evidence of two completely divided roots, little is preserved of these in most cases.

Before commencing the description of the teeth it is necessary to point out that the identification of specimens as either upper or lower teeth is problematic. Also, whilst the mesio-distal axes of the teeth can be readily distinguished from their bucco-lingual axes, more detailed orientation is not obvious on the basis of crown or root morphology. In describing the teeth, I will therefore follow the practice used in orientating haramiyid cheek teeth and adhere to an arbitrary convention where one end of the long axis of the crown is designated the 'anterior' end. The use of such a convention necessarily precludes the use of the nomenclature of Crompton & Jenkins (1968) when referring to the main crown cusps. It should be emphasised that the failure to use this nomenclature is emphatically not intended to imply the possibility that these cusps are not homologous to those of other triconodont molariform teeth.

Description

U676 (figure 77): The crown of this specimen is almost completely intact but the roots are broken off shortly below the crown base. The length of the crown measures 1.25mm whilst its breadth at the level of the midpoint of the tooth measures 0.6 mm. The specimen is devoid of wear or of pressure marks caused by the contact of neighbouring teeth. As definite evidence of wear can be discerned on some of the other specimens this suggests that the tooth had incompletely, or only recently erupted prior to the death of the animal to which it belongs.

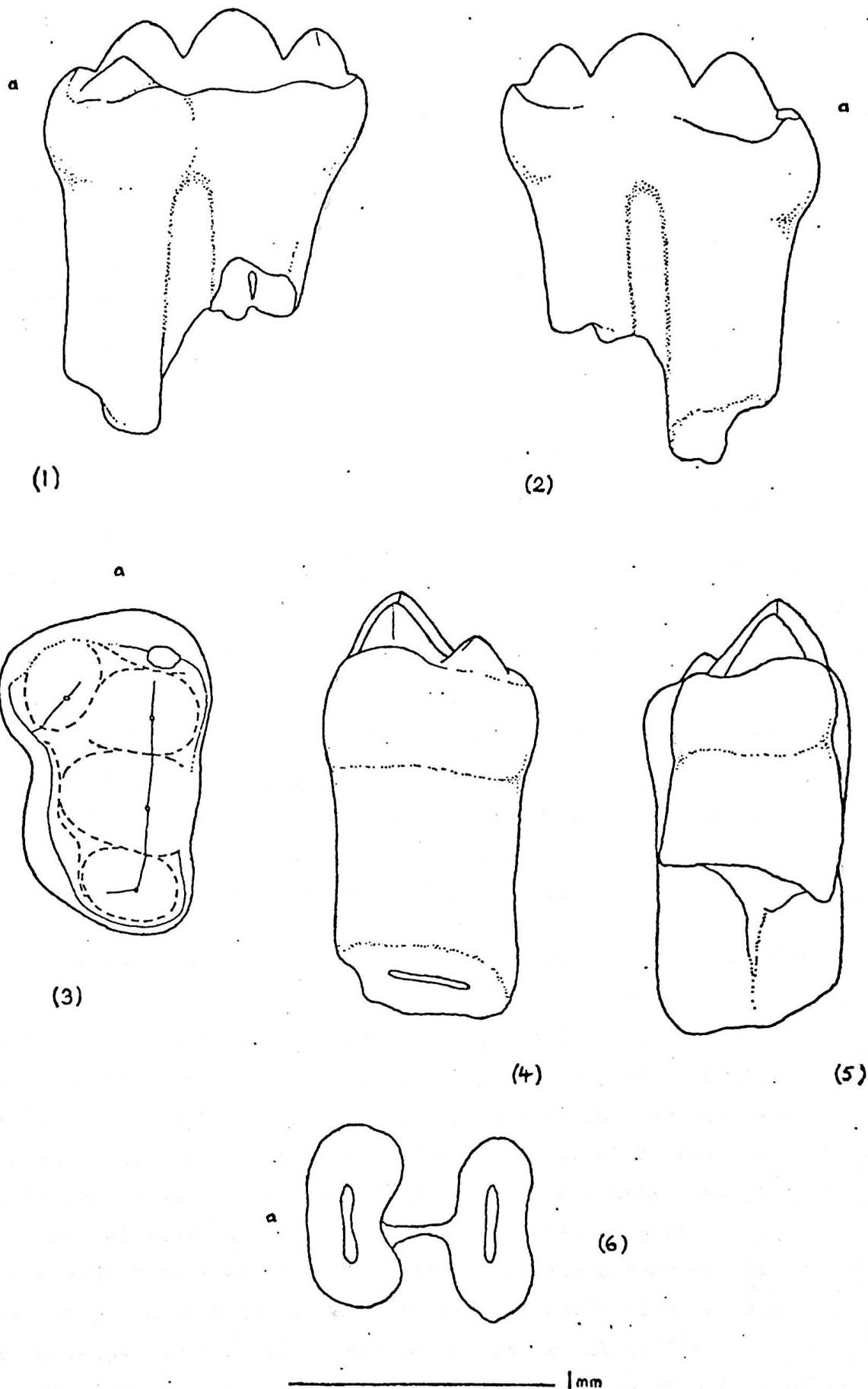


Figure 77 Problematic triconodont tooth U676.

(1) and (2) lateral views, (3) oclusal, (4) anterior and (5) posterior views and (6) end view of roots.

'a' denotes the anterior end of the tooth as in all succeeding figures.

In occlusal view the outline of the tooth is irregularly oval, one end being rather broader than the other. This broader end will be called the anterior end. The crown is almost entirely surrounded by a cingulum. As in other specimens, there are three 'crown' (as opposed to cingulum) cusps, which are linearly arranged. The anterior and posterior crown cusps are of about equal size and they are only slightly smaller than the central cusp, so that, in this respect, the crown resembles that of a triconodontid molar. The anterior and posterior crown cusps are divided from the central cusp to a low level. The three cusps are of similar form. In lateral view each is low and has a rounded profile. In vertical section, the right side of each is slightly convex whilst the left side is straight or even a little concave near the cusp base. The breadth of the cusps is greater than the length, and in occlusal view each cusp has an elliptical or oval shape. The apices of the crown cusps are situated slightly to the right of their midline. Each cusp bears two crests which descend from its apex. In the case of the first two cusps, these crests are in line with the long axis of the crown. The anterior crest on the first cusp does not quite reach the cusp base. One of the crests on the third cusp is anterior, but the other is laterally situated, descending leftward. This crest fails to reach the base of the cusp so that the crests on the crown cusps do not contact the cingulum either anteriorly or posteriorly.

The cingulum is continuous and very prominent on the left side of the crown. It is extremely broad opposite the first crown cusp, its maximum breadth here almost equalling that of the latter. This part of the cingulum bears a very prominent, elongated cusp which I will designate 'L'. The base of this cusp is as long as that of the first crown cusp although its apex is rather lower. In profile, the anterior, posterior and lateral sides of cusp L are nearly straight whilst, in occlusal view, the outline of the cusp is elliptical. Medially the widest part of the cusp base contacts the base of the first crown cusp. Cusp L is situated rather obliquely with respect to the crown cusps, so that its anterior end is medial to its posterior end. Its anterior end is also further forward than that of the first crown cusp. The apex of the cusp is situated rather medial to its midpoint and its external surface is more extensive than its internal one. A crest descends postero-laterally from the apex to the cusp base, whilst in line with this a second crest descends

anterio-medially almost to the cusp base. There is a narrow but well defined cingulum ledge external to the posterior half of the cusp. The edge of this ledge bears a crest and this terminates just forward of the cusp apex. The cingulum ledge is almost obsolete here, but it continues incipiently, and with interruptions, around the anterior part of the cusp where it joins the cingulum in front of the first crown cusp. In being almost completely bordered externally by a cingulum, cusp L is less obviously a cingulum cusp in U676 than it is in some of the specimens described below. However, it will be noted that the crests on the cusp are not continuous with those on the true crown cusps. The posterior lateral crest on cusp L is connected by a short crest to the crest on the external cingulum ledge. The cingulum ledge external to cusp L is continuous posteriorly with the remaining section of the left lateral cingulum. The breadth of this section of the cingulum is never more than about half of the maximum breadth of the more anterior section. Its upper surface takes the form of a bulbous ridge, the highest part of which bears a crest. Medially, the base of this ridge contacts the widest parts of the second and third crown cusps. Opposite the junction of these cusps the ridge is slightly expended into an incipient cusp. The cingulum passes round the back of the third crown cusp where it becomes a relatively narrow, featureless ledge. This continues on the right side of the tooth except alongside the second crown cusp where it is obsolete. The right cingulum reappears opposite the first crown cusp and it passes round the front of this cusp, where it becomes relatively broad and bears a low elongate cusp. The apex of this cingulum cusp is missing - the only area of damage on the crown. The cusp bears left and right crests. The latter is continuous with the crest on the right lateral cingulum; the former terminates just medial to cusp L.

The roots are completely separated and relatively stout. A thin web of dentine passes between them, and this clearly originally persisted for at least the length of the preserved part of the anterior root. The roots differ from those in eutriconodont and morganucodont molars in that both are very compressed antero-posteriorly. Their anterior and posterior surfaces are about twice as broad as their lateral surfaces, and they are about as broad as the crown. The anterior root is slightly broader than the posterior one. Its sides are almost straight. In their marked antero-posterior (= mesio-distal)

compression, the roots are reminiscent of the roots of some of the isolated paulchoffatiid cheek teeth described by Hahn (1969).

U677 (figure 78): This is one of the largest specimens. The crown has been damaged: the apices of the first and second crown cusps are missing and only part of the left side of the third crown cusp is preserved. Both roots are substantially intact; this is the only specimen in which this is the case. As preserved the crown measures 1.35mm by 0.8mm. The vertical distance from the broken tip of the second crown cusp to the end of the anterior root is 2.8mm.

The crown pattern is the same way round as in the previous specimen, the prominent uninterrupted lateral cingulum being on the left. The crown cusps are proportionally even broader than in the previous specimen. The right side of the crown cusp has been somewhat abraded, but in spite of this a prominent and clearly defined worn area can be discerned here. This is made up of two adjoining wear facets, one anterior and one posterior, the two sloping towards one another to form a groove into which the relevant cusp of the opposing tooth sheared. The anterior facet was formed by the antero-lateral surface of this cusp and the posterior facet by its postero-lateral surface. In lateral view (figure ) it can be seen that the deepest part of the groove formed by the two facets is slightly obliquely orientated, its upper end being posterior to its lower end. The upper end is situated behind the broken tip of the cusp so that it is clear that, during occlusion, the cusp did not meet the opposing cusp which wore the facets apex to apex. In bucco-lingual cross-section the angle which the wear facets make with the horizontal axis of the tooth is markedly more acute than that made by the original, unworn surface of the cusp. This means either that there was a large ectental component to the power stroke of the lower jaw or that the tooth was held at an angle to its opponent in the same way as the upper molars of Morganucodon watsoni and Morganucodont A were.

The highest part of the second crown cusp comprises a flat surface which slopes slightly postero-rightward. In view of the orientation of the facets on the preceding cusp it would seem unlikely that this surface was produced through wear.

Cusp L is situated rather more obliquely than in U676. The antero-median and postero-lateral crests on the cusp both reach the cusp

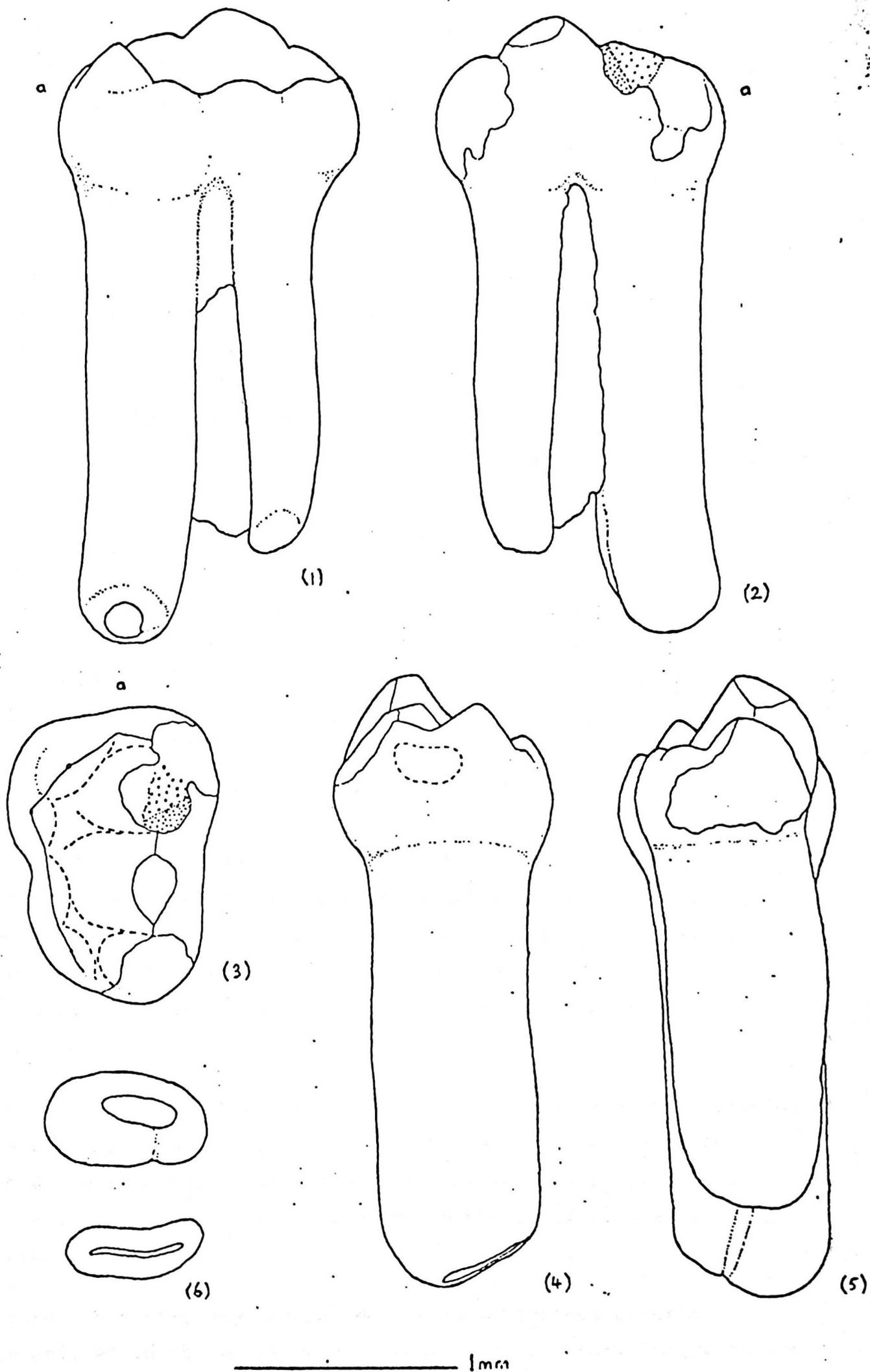


Figure 78. Problematic triconodont tooth U677 (1) and (2) lateral views (3) occlusal (4) anterior and (5) posterior views (6) End view of roots. Note the wear facet on the first crown cusp (views (2) and (3) - stippled area). Note also that the scale for the figure differs

base and are continuous with crests on the adjacent parts of the cingulum. There is no cingulum external to the cusp so that it is quite clearly a cingulum cusp in this specimen. Immediately below the left side of the cusp base the surface of the tooth forms a prominent shoulder, so that its junction with the cusp base is discernible although not sharply defined.

Behind cusp L, and opposite the junction of the first and second crown cusps, there is a low bulbous cingulum cusp. This is smaller than cusp L but it is situated slightly further laterally so that the cingulum does not narrow immediately behind cusp L as it does in U676. Between the base of this cingulum cusp and the bases of the first and second crown cusps there is a small basinid area. Posterior to the cingulum cusp the cingulum narrows somewhat and bears two cusps of similar prominence. The first of these is opposite the second crown cusp and the second opposite the third crown cusp. The bases of these cingulum cusps contact the widest parts of the bases of the crown cusps. The more posterior of the two cingulum cusp is situated rather obliquely with its posterior end medial to its anterior end, so that in this respect it mirrors cusp L. The damage to the posterior end of the crown means that it is impossible to determine whether or not the cingulum continued further round the third crown cusp. As in U676 there is no cingulum on the right side of the second crown cusp. There is the suggestion of a cingulum on the right side of the posterior part of the first crown cusp, but the situation has been obscured more anteriorly by abrasion. The right side of the anterior cingulum cusp which precedes the first crown cusp has been obliterated. The left side of this cusp contacts cusp L.

On the front surface of the tooth a short distance below the junction of the anterior cingulum cusp and cusp L there is a large medially situated pressure mark. When the tooth was in situ it clearly did not interlock with the neighbouring tooth which was responsible for this pressure mark.

The roots are completely separated and are compressed antero-posteriorly as in the previous specimen. Both are very long although more is preserved of the anterior root than of the posterior one. The sides of the anterior root are straight and parallel in lateral view except near its apex where the root curves slightly anteriorly.

The root apex is slightly abraded and the pulp canal is open so that it is not certain that the original length of the root is preserved, although it probably is. The posterior root tapers slightly in lateral view. Just above the point where its end has been broken off it begins to curve slightly anteriorly so that when the root was intact it probably imitated the anterior root. Matrix completely fills the space between the roots on the right side, and I have not attempted to remove it for fear of damaging them. On the left side the matrix does not pass all the way up to the crown, and above it the roots can be seen to be joined by a thin web of dentine.

U680 (figure 79): This is about the same size as the previous specimen. The crown cusps have been almost entirely obliterated and much of the remainder of the crown is rather water worn. The roots are broken off just below the crown base. As preserved the crown measures 1.35mm by 0.75mm. The crown pattern is the opposite way round to that in the previous specimen. In occlusal view the outline of the tooth is an almost perfect mirror image of the outline of this specimen. The whole left side of the occlusal surface of the crown comprises a dentine plateau which slopes slightly to the left and slightly posteriorly. The right edge of the plateau is only a little higher than the adjacent lateral cingulum. Nothing remains of the first crown cusp, and only a small part of the right side of the succeeding cusps is discernible. The surface of the plateau is not smooth and it is clear that the plateau has been produced, at least in part, as a result of posthumous abrasion. The fact that the original topography of the right side of the crown has not been similarly obliterated, however, suggests that the crown cusps were already somewhat worn prior to the death of the animal.

The form of the prominent lateral cingulum is almost identical to that in U677, with the exception of cusp L. This is situated slightly more posteriorly than in U677 so that it is level with the position which the anterior crown cusp would have occupied. Cusp L is bordered externally by an incipient cingulum ledge so that it appears to be partly a crown cusp as it does in U676. The apex of the cusp is missing. Anterior to the base of the cusp the surface of the tooth forms a very broad shoulder. The cingulum continues round the back of the crown, where it is very narrow. Nothing is preserved of the form of the cingulum on the left side of the tooth. The roots are of the same type as in the previous specimens.

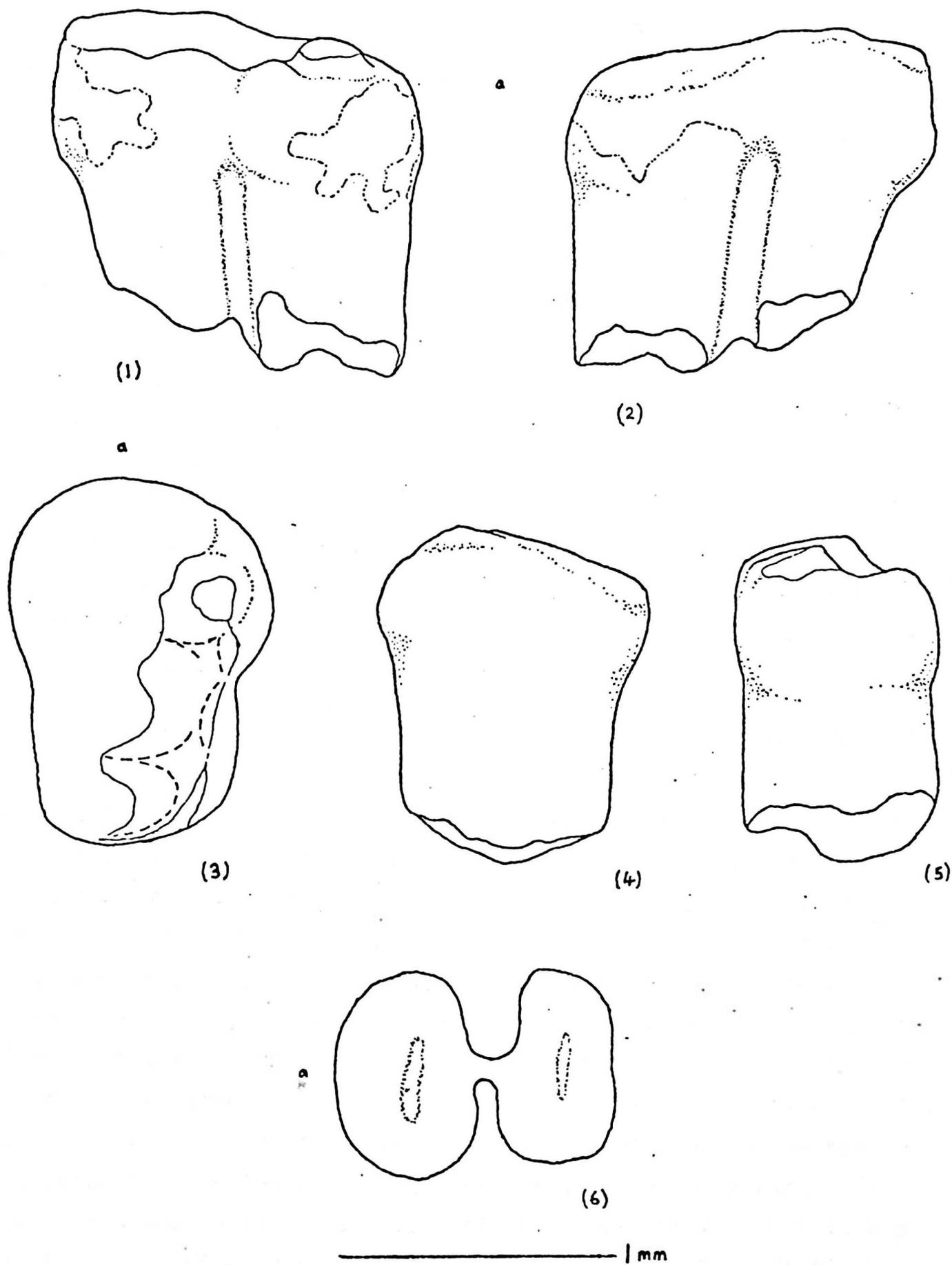


Figure 79 Problematic triconodont tooth U680.

(1) and (2) lateral views, (3) occlusal, (4) anterior and (5) posterior views and (6) end view of roots.

U679 (figure 80): This is a large specimen. The crown is damaged: the apices of the first and second crown cusps have been posthumously worn and the posterior end of the crown, including almost all of the third crown cusp, is missing. The roots are broken off just below the crown base. As preserved the crown measures 1.2mm by 0.8mm.

The prominent, continuous lateral cingulum is on the left side of the crown. The second crown cusp is proportionally slightly taller, relative to the first, than in the most complete specimen which has been described, U676. In contrast to the situation in the latter tooth the anterior crest on the first crown cusp reaches the cusp base, and it is continuous with a posterior crest on the anterior cingulum cusp. Cusp L is smaller than in any of the previous specimens, and it is situated almost exactly level with the first crown cusp. It is only slightly obliquely orientated and is rather widely separated from the anterior cingulum cusp. The surface of the tooth between these cingulum cusps forms a broad shoulder in front of the first crown cusp. This shoulder is continued more narrowly round the external side of cusp L so that the junction of the cusp with the lower part of the tooth is clearly defined.

Behind cusp L the cingulum bears three cingulum cusps as in U677. The first two of these cusps are very low but the third, although missing its apex, is almost as high as cusp L. The cusp immediately following cusp L is situated almost directly posterior to it rather than somewhat laterally as in U677, and the next cingulum cusp is in line with its predecessor. In consequence in occlusal view the more anterior part of the prominent cingulum does not bulge distinctly lateral to the more posterior part, as it does in the previous specimens and the outline of the tooth is more regular. On the right side of the crown part of the posterior section of the lateral cingulum can be discerned against the remnant of the third crown cusp. Anterior to the second crown cusp the anterior section of the right cingulum appears and passes forward as a narrow ledge. This continues even more narrowly along the right side of the anterior cingulum cusp. The anterior cingulum cusp is not as laterally elongated. The apex and the right side of the cusp have been abraded.

The roots are of the same type as in the previous specimens except that they are connected by a very thick web of dentine. They therefore appear to be incompletely separated.

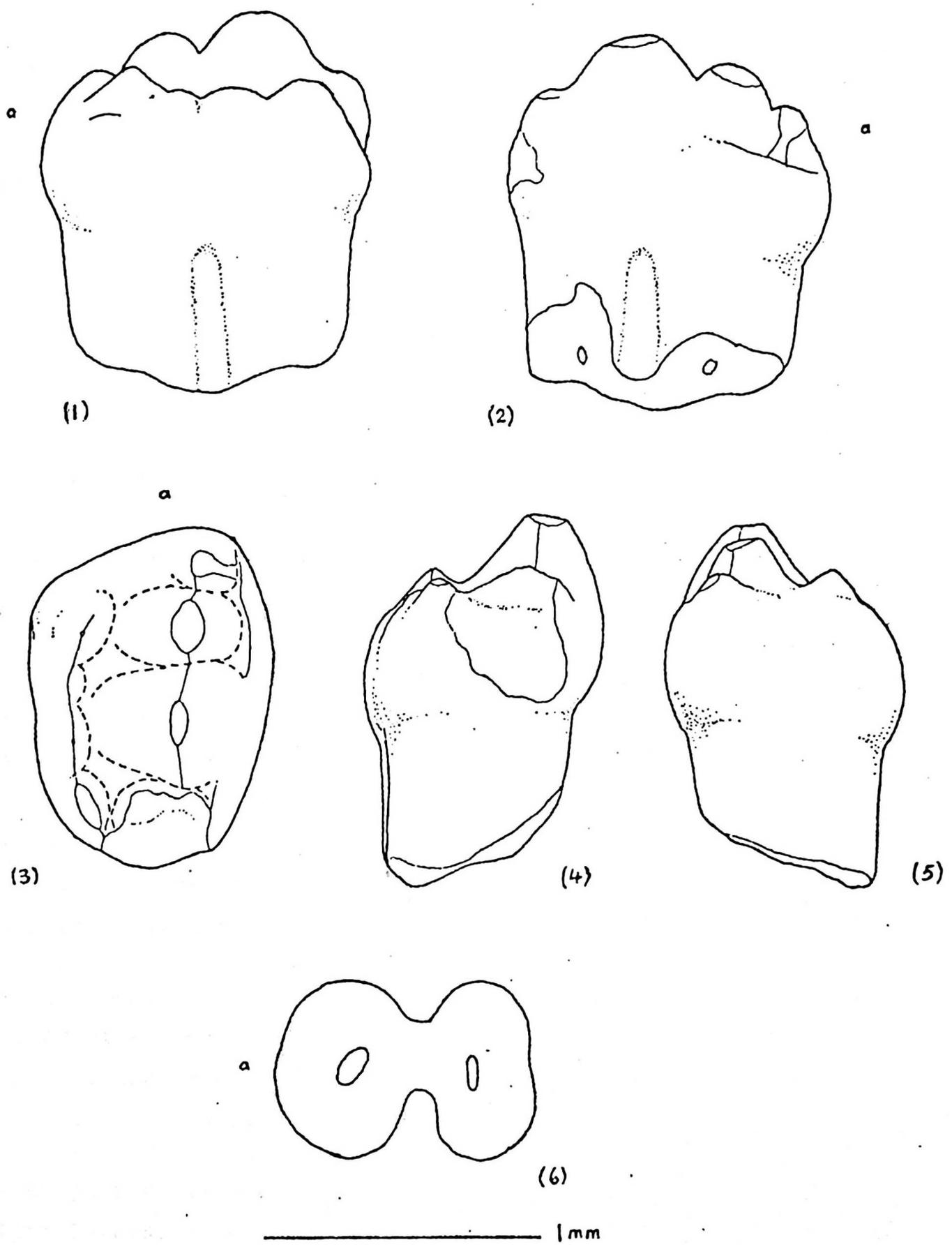


Figure 80 Problematic triconodont tooth U679.  
(1) and (2) lateral views, (3) occlusal, (4) anterior and (5) posterior views and (6) and view of roots.

U685 (figure 81 ): This is one of the smallest specimens. The apices of the crown cusps are missing. The tooth bears a single root which corresponds in its antero-posterior breadth to the double roots of other specimens. The root has been broken off at a point which was probably about half way along its original length. The crown measures 0.81mm by 0.55mm.

The crown pattern is the opposite way round to that in the previous specimen and in occlusal view the shape of the tooth mirrors that of this specimen. Cusp L - which is damaged - is situated almost exactly on a level with the first crown cusp. Behind cusp L the cingulum bears two low rather poorly defined cusps. It does not pass round the back of the crown and there is no cingulum on the left side of the third crown cusp. The anterior cingulum cusp is damaged. To the left of this the cingulum turns and passes backward as a narrow ledge alongside the first crown cusp in the usual way. The cingulum continues back to the level of the damaged apex of the second crown cusp; this is the only specimen in which this is the case.

In end view the root tapers somewhat, although this is less marked near its broken end. The tip of the root is compressed laterally. On the right side the surface of the root is smooth. On the left side it bears a median groove, so that it appears to be incipiently divided into two. There is, however, only one pulp canal. The form of the root and the relative size of the tooth suggest that the specimen comes from the distal end of the tooth row.

U684 (figure 82 ): This is of similar size to the previous specimen. The posterior end of the crown is missing as are the apices of the first and second crown cusps. The roots are broken off some distance below the crown. As preserved the crown measures 0.75mm by 0.55mm.

The crown pattern is the same way round as in the previous specimen. The right lateral cingulum differs from that in the previous specimen in that it does not bear any distinct cusps behind cusp L.

The roots are incompletely divided but are otherwise of normal type.

U683 (figure 83 ): This is slightly larger than the previous specimen. The crown has been heavily worn anteriorly and also slightly damaged. The roots are broken off some distance below the crown. The latter measures 0.9mm by 0.6mm.

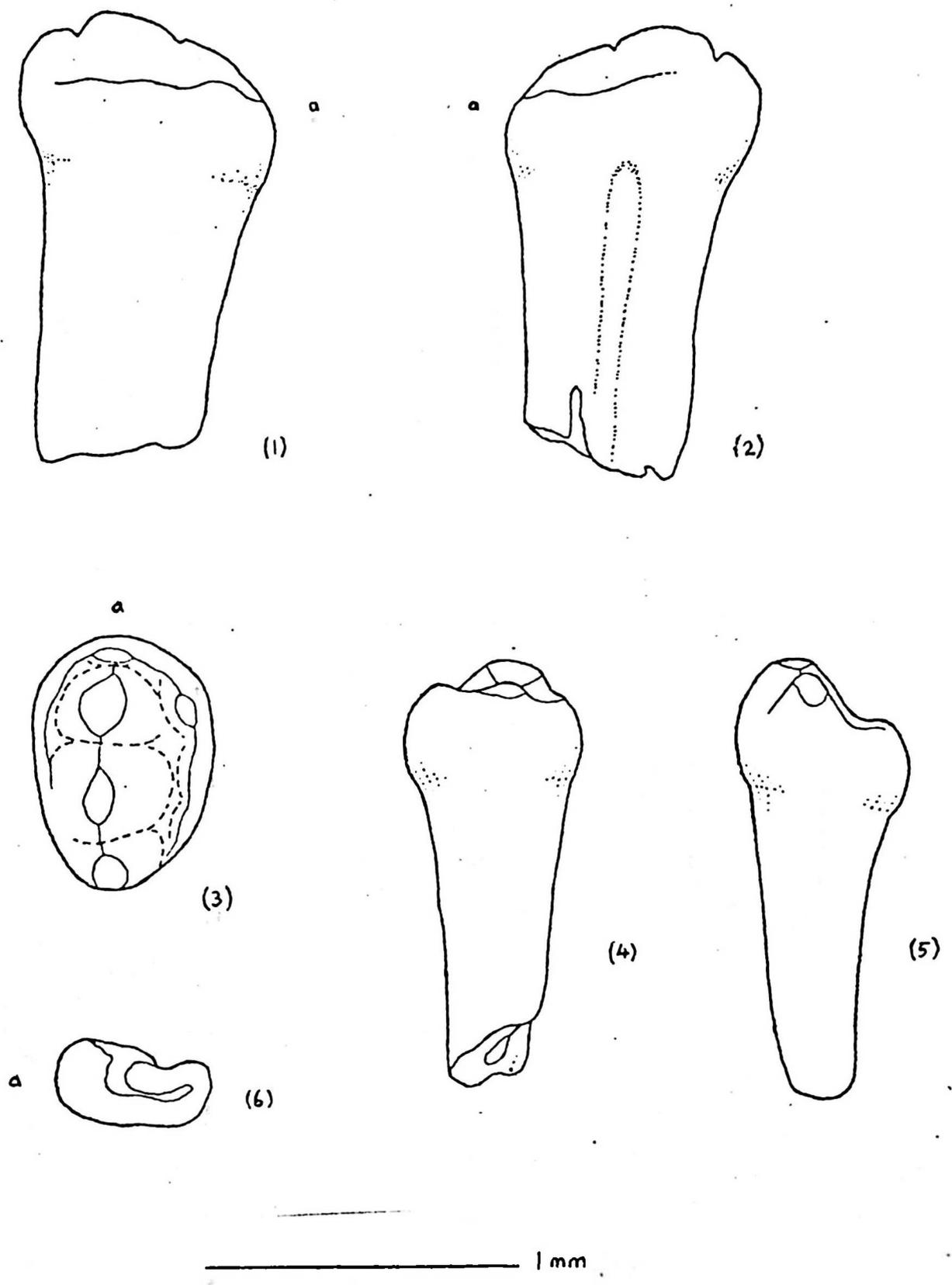


Figure 81 Problematic triconodont tooth U685.  
(1) and (2) lateral views, (3) occlusal, (4) anterior and (5) posterior views and (6) end view of roots.

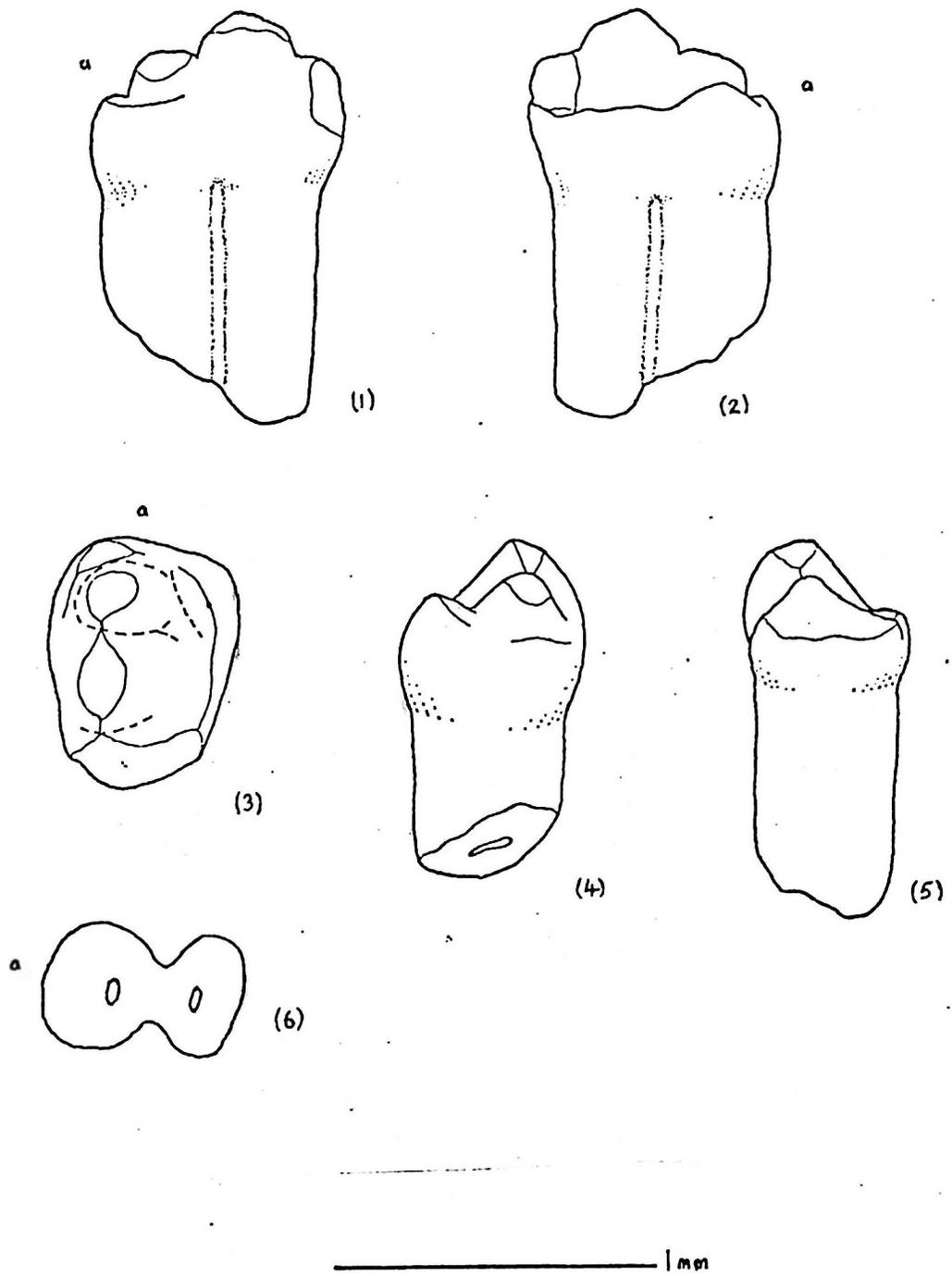


Figure 82 Problematic triconodont tooth U684.

(1) and (2) lateral views, (3) occlusal, (4) anterior and (5) posterior views and (6) end view of roots.

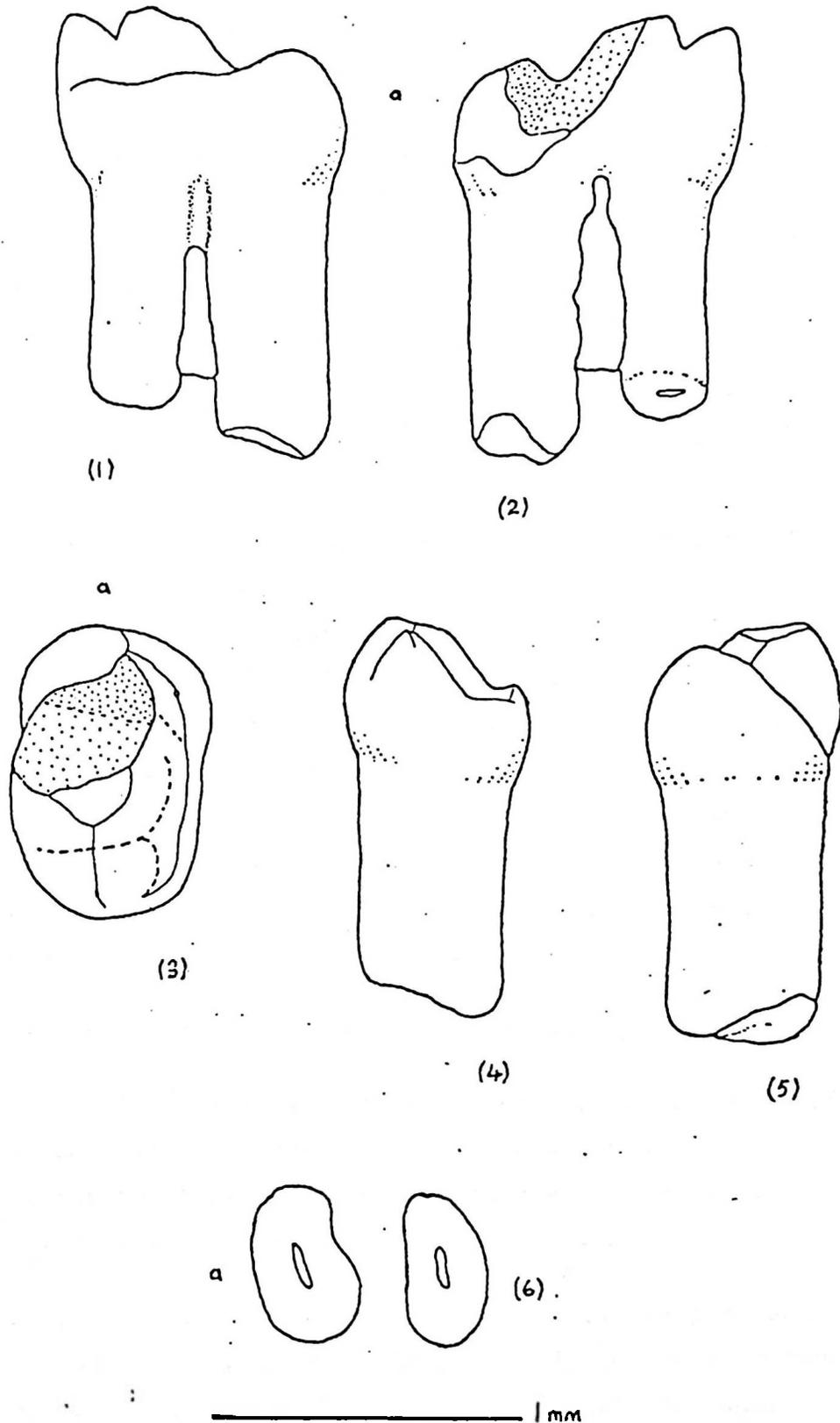


Figure 83 . Problematic triconodont tooth U683.  
 (1) and (2) lateral views, (3) occlusal, (4) anterior and (5) posterior views and (6) end view of roots.  
 Note very large wear facets (views (2) and (3) - stippled area).

The crown pattern is the same way round as in the previous specimen. In occlusal view the outline of the tooth is rectangular. The left anterior corner of the crown is damaged.

The first crown cusp and the anterior half of the second - except for a small part of its right side - have been worn away to produce two extremely large wear facets which are homologous to the facets on U677. On the left side of the tooth the groove which the facets form extends down almost to the crown base. In bucco-lingual cross-section the angle which the facets make with the horizontal axis of the crown is much more acute than that made by the original surfaces of the cusps, as in U677. There is no functional wear on the crown posterior to the two described facets.

The apex of the third crown cusp is situated behind the midpoint of the cusp base. In lateral view the posterior edge of the cusp is almost vertical. The disparity in size between this cusp and the preceding cusp would appear to have been greater than in U676 - the only other specimen so far described in which the third crown cusp is intact. In contrast to the situation in U676, a short posterior crest descends from the cusp apex. The right cingulum is almost identical, morphologically to that in U684. The cingulum does not continue round the back of the crown and there is no cingulum on the left side of the third crown cusp.

The roots are completely separated and are of normal type.

U681 (figure 84): This is a relatively large specimen. The apex of the second crown cusp has been broken off and the anterior and posterior ends of the tooth are damaged. There are no remains of roots. As preserved, the crown measures 1.15mm by 0.7mm.

The crown pattern is the opposite way round to that in the previous specimen. The second crown cusp is slightly larger, compared to the other crown cusps, than it is in U676. There is a small but well developed wear facet on the right side of the first crown cusp which descends from the cusp apex. In bucco-lingual cross-section the facet is steeply orientated relative to the horizontal axis of the tooth (the angle of slope must be about the same as that made by the original, unworn, cusp surface). The occlusal stroke of the lower jaw in the animal to which the tooth belongs must therefore have been predominantly orthal. On the right side of the second crown cusp

there are two elongated, adjoining wear facets which descend from the broken cusp tip. The posterior facet is narrow, the anterior one a little broader. The enamel has not yet been completely worn away from the surface of either. The two facets slope slightly away from one another, in horizontal section, following the original shape of the cusp surface. A little below the level of the notches between the second crown cusp and the other crown cusps the two facets begin to diverge, the anterior one turning anteriorly and the posterior one posteriorly. The posterior facet becomes indistinct at the level of the cingulum. The anterior facet is terminated at this level by a small area of damage. As will be appreciated, the form of the wear on the second crown cusp closely matches that on cusp  $\bar{a}$  of a moderately worn Morganucodont A lower molar. It does not match the wear found on the cusp of any known triconodont upper molar.

In contrast to the two preceding cusps the third crown cusp is completely unworn. The form of this cusp is very similar to that in U683, its posterior edge (when viewed laterally) passing down nearly vertically from the cusp apex. There is no posterior crest but a crest descends postero-leftward from the apex.

Anterior to the first crown cusp the cingulum is broken. Opposite the junction between the first and second crown cusps on the left side of the tooth there is a low cingulum cusp. The relative size and position of this cusp suggest that it is probably not cusp L-but a more posterior cingulum cusp, cusp L having been broken away. Behind the cusp the cingulum narrows slightly. It does not bear any well defined cusps. The cingulum passes narrowly round the back of the crown and its edge here has been abraded away, the damaged area extending almost to the crown base. On the right side of the crown the narrow, interrupted lateral cingulum takes the usual form.

U682 (figure 85): This is a large, rather distinctive, specimen. The apices of the first and third crown cusps are missing and the prominent lateral cingulum is damaged anteriorly. The roots are broken off just below the crown base. As preserved the crown measures 1.35mm by 0.7mm.

The crown pattern is the opposite way round from that in the previous specimen. The crown is proportionally narrower and the second crown cusp proportionally longer and higher than in any of the other teeth. The anterior and posterior edges of the second crown cusp are straight

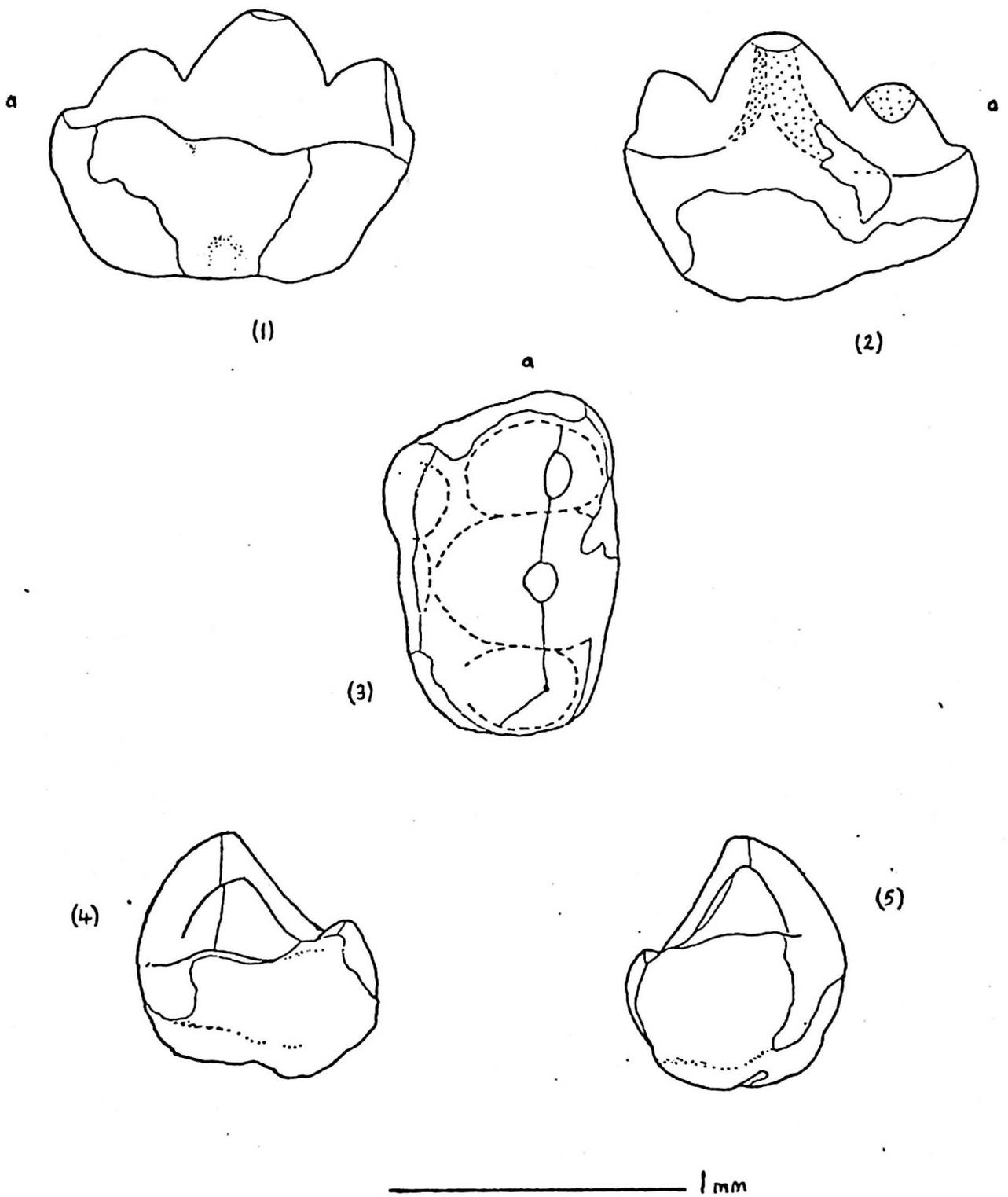


Figure 84 Problematic triconodont tooth U681.

(1) and (2) lateral views, (3) occlusal, (4) anterior and (5) posterior views.

Note the wear on the first and second crown cusps (view 2 - stippled area)

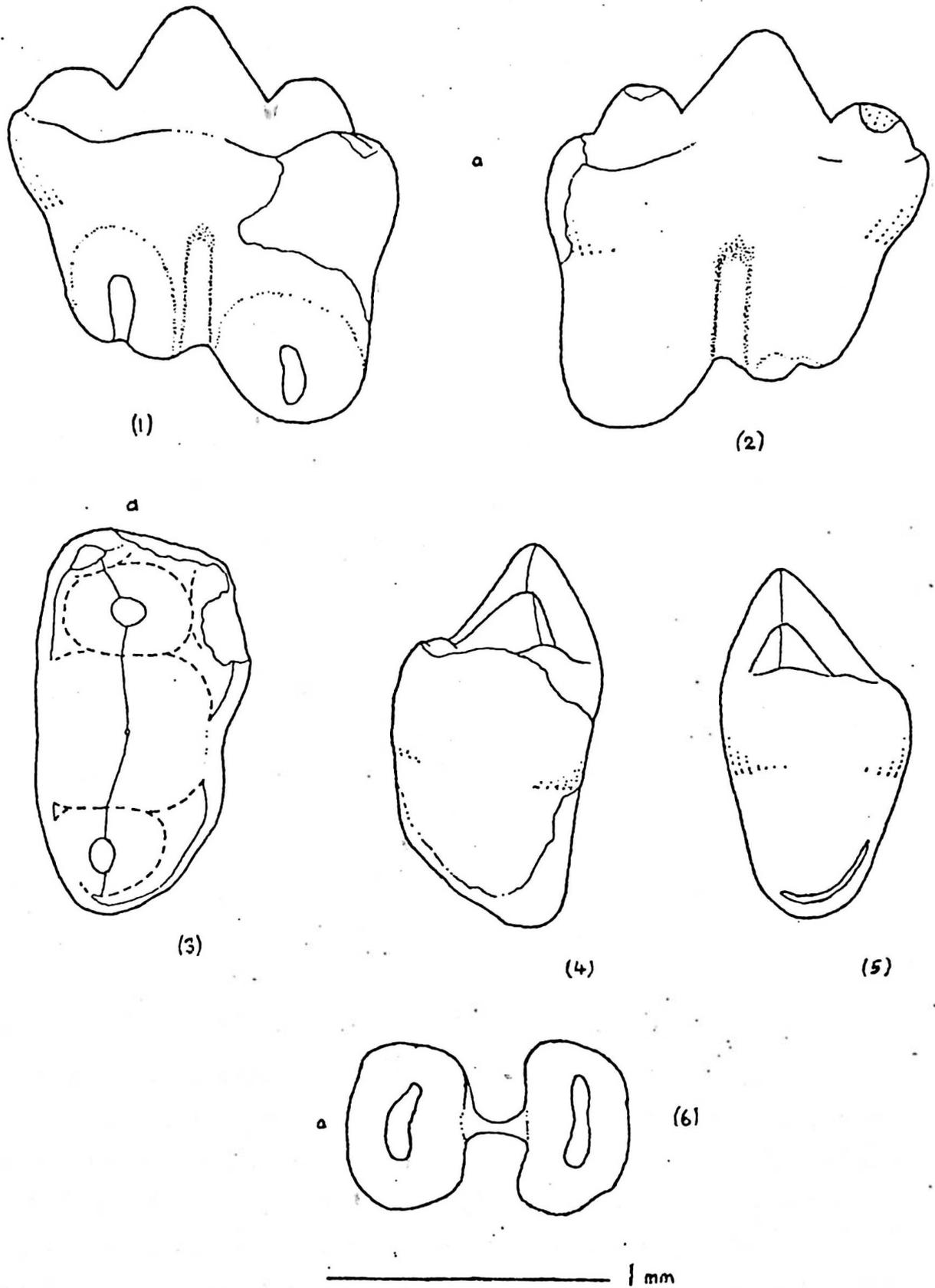


Figure 85 Problematic triconodont tooth U682.

(1) and (2) lateral views, (3) occlusal, (4) anterior, (5) posterior views and (6) end view of roots.

Note wear facet on the third crown cusp (view 2 - stippled area).

rather than convex in lateral view - except near the cusp apex, which is blunt. The first and third crown cusps are of normal size and shape. The anterior crest on the former cusp is slightly obliquely orientated, passing slightly leftward as well as forward. The latter cusp bears a well defined posterior crest instead of a lateral crest as in U676. There is a small wear facet on the left side of the tip of the first crown cusp. In bucco-lingual cross-section the angle which the surface of the facet makes with the horizontal axis of the crown would appear to be nearly the same as that made by the original cusp surface.

A substantial part of cusp L has been broken away. There is no cingulum cusp immediately behind cusp L and the cingulum here forms a featureless shelf. More posteriorly it narrows, becoming almost obsolete against the widest part of the second crown cusp, where it is incipiently continued as a bulge at the cusp base. Thereafter it widens again, passing backward without bearing any cusps. It continues round the back of the crown, where it is very narrow. The anterior section of the narrow, interrupted, lateral cingulum on the left side of the tooth is of normal form. The posterior section is interrupted by the widest part of the third crown cusp.

The roots are completely separated immediately below the crown, and are of normal type. As usual, a thin web of dentine passes between them.

#### The mutual relationships of the teeth

As the teeth exhibit variations in size and morphological detail and as their basic morphology is rather different from that of any other triconodont cheek teeth, their mutual relationships are problematic. If the variations in size and morphological detail alone are considered, there is no evidence that more than one species is represented: both can be quite adequately accounted for by postulating that the teeth belong to different positions in the dentition of a single form. However, it will be shown in due course that the wear patterns on the four worn specimens (U677, 681, 682 and 683) preclude the possibility that the teeth belong to a dentition in which the positions of all the opposing cheek teeth, relative to one another, were the same. This could be interpreted as evidence that we are dealing with more than one species. It should be added that

the fact that at least one of the nine specimens (U676) is completely unworn whilst another (U683) has been very heavily worn, minimises the possibility that the teeth belong to the dentition of a single individual.

#### The dental positions of the teeth

Any discussion of the dental positions of the teeth is obviously hampered by the uncertainty over whether or not the specimens belong to a single form. However, it is clear from the morphological similarities between the teeth that they cannot belong to species which are not closely related, and it is therefore reasonable to consider them in terms of a single morphological type of dentition. The most basic question which arises in respect of this dentition is : are both upper and lower teeth represented amongst the nine specimens? The teeth resemble the upper molariform teeth of other triconodonts in that they possess (in those specimens where the relevant region is preserved) cingulae on both sides of the crown. This naturally invites the interpretation that they are all upper molariform teeth. Although, on purely numerical grounds, it seems improbable that the teeth could belong exclusively to the upper dentition, nine is not a sufficiently large number to definitely preclude this possibility. It is pertinent at this point, however, to recall the fact that the wear facets on two of the worn teeth - U677 and 683 - are distinctly more transversely orientated (in bucco-lingual cross-section) than the facets on the two remaining worn specimens - U681 and 682. In order to maintain that all of the teeth are from the upper dentition (or, for that matter, from the lower dentition) it would therefore be necessary to postulate either that the mandibular power stroke which resulted in the wear on U677 and 683 was markedly more transverse than that which resulted in the wear on U681 and 682, or - if the mandibular power stroke was the same with respect to both pairs of teeth - that U677 and 683 leaned more markedly towards their opponents than did U681 and 682. There are no other possibilities. In either case it would obviously also be necessary to posit that the two pairs of teeth belong to different species.<sup>1</sup> It is unlikely, however,

<sup>1</sup>If they belong to the same species the difference in the transverse orientation of the wear facets would prove beyond doubt that the two pairs of teeth belong to opposing dentitions.

that closely related species would differ fundamentally in the nature of their mandibular power stroke or in the bucco-lingual orientation of their upper (or lower) cheek teeth. We may much more plausibly interpret the disparity in the transverse orientation of the wear facets on the two pairs of teeth as evidence that they belong to opposing dentitions (re upper and lower dentitions), the components of the dentition to which U677 and 683 belong having leaned more markedly towards their opponents than the components of the dentition to which U681 and 682 belong. This interpretation receives strong support from the fact that in all triconodonts where the dentition as a whole is at all adequately known - including the dentally specialised Docodon - the upper molars lean lingually in the maxilla whilst the lower molars are arranged relatively vertically in the dentary. In the light of the situation in other triconodonts it is therefore justifiable to conclude that U677 and 683 are very probably upper teeth and U681 and 682 very probably lower teeth.

With regard to the remaining specimens, U685 and 684 are sufficiently morphologically similar to U683, and U680 is sufficiently similar to U677 to be regarded as components of the same tooth row type. In other words they are probably upper teeth. U676 and 679, by contrast, are rather too morphologically different from the two pairs of worn teeth to be reasonably identified as either probable upper or lower teeth.

We may now consider the relative mesio-distal positions of some of the specimens. The incompletely divided roots of U684 and the single root of U685 suggest that these teeth belong to the distal end of the dentition. This would accord with their relatively small size. The crown of the only other relatively small tooth, U683, is so like that of U684 that the specimen would appear on this basis to belong to a similar region of the dentition. In fact, the nature and distribution of the wear on U683 clearly demonstrates that this tooth comes from the distal end of a mature tooth row. The only wear facets on the tooth are situated anterior to the midpoint of the crown, and a substantial part of the original topography of the crown has been obliterated during the course of their formation. The absence of more posterior wear is unequivocal and it shows that the specimen only ever occluded with one, rather than two opponents. If the end of the tooth which I have called 'anterior' is, in reality, the mesial end, then this opponent must have been a more mesially situated tooth. If, on the other hand, the anterior end is the distal end, the

opponent was a more distally situated tooth. However, even allowing for the possibility of the posteriad ontogenetic loss of unreplaced molariform teeth (as occurred, for example in Morganucodon watsoni dentitions) the hypothesis that U683 only ever occluded with a more distal opponent is, in the light of the heavy wear on the specimen, so implausible as to be safely dismissed. The opponent of U683 must have been a more mesially situated tooth, and the anterior end of U683 must be its mesial end. The level of the mesial wear on the specimen shows that it enjoyed a long functional life. In these circumstances, the absence of a more distally situated opponent can only be the result of U683 having been situated at the distal end of the mature tooth row, its more mesially situated opponent having been the last functional tooth of the opposing row.

Little can be said concerning the relative mesio-distal positions of the remaining teeth. U682, which is rather different from all of the other specimens in the relative narrowness of its crown and height of its second crown cusp, might perhaps be a premolariform tooth.

Orientation

As the wear facets on all of the worn specimens occur on the other side of the crown from the prominent, continuous lateral cingulum, it is evident that this cingulum is on opposite sides of the crown in opposing teeth. In the lower teeth it must be on the lingual side, whilst in the uppers it must be on the buccal side.

It has been shown above that the anterior end of U683 is the mesial end of the tooth, and the same must be true of the other presumed upper teeth. The mesio-distal orientation of the presumed lower teeth and the other remaining teeth is quite uncertain, however. This is irrespective of whether cusp L is homologous in upper and lower teeth.

Occlusion

The first specimens to be discovered exhibited no definitive evidence of wear and the relatively low, broad form of their crowns suggested that occlusion probably involved substantial crown-crown contact (or 'opposition', to use the terminology of Simpson (1936) ) - in other words it suggested that the principal function of occlusion was the crushing of the food. The nature of the wear on U677, 683, 681 and

682, however, demonstrates that the basic type of occlusion was the same as that in Morganucodonts and Eutriconodonts. The buccal surfaces of the lower teeth moved past the lingual surfaces of the upper teeth to effect a double shear. As in the aforementioned groups, matching shearing surfaces were not present on unworn opposing teeth, but were produced as a result of mutual wear. The anterior (mesial) pressure mark on one of the presumed upper teeth, U677, shows that neighbouring teeth were held under mesio-distal pressure. As stated previously, this is an adaptation to the maintenance of precise occlusal relations, as it serves to prevent the longitudinal drift of the members of opposing cheek teeth rows. The peculiar shape of the roots is very probably also correlated with occlusion. Their relatively great bucco-lingual width would have served as an alternative to crown buttressing as an insurance against their breakage when transversely directed displacement forces were exerted on the crowns of opposing teeth during occlusion.

We may now consider the occlusion of the two presumed upper teeth which exhibit wear, U677 and 683. The positions of the only discernible facets on these specimens are identical and they were clearly formed in each case by a cusp of an opposing tooth which commenced shearing slightly mesial to the junction of the first and second cusps. The slightly oblique mesio-distal orientation of the groove formed by the facets indicates that the mandibular power stroke included a small anterior component, as it did in Morganucodont A. The second and third crown cusps of U677 are too damaged for it to be clear whether they were originally worn or not, although if the second crown cusp was worn, the level of this wear cannot have equalled that on the first. The absence of wear behind the two adjoining mesial facets in U683 is definitive, as stated above. The two facets on this tooth must therefore have been produced by the distal cusp on the opposing tooth. This means that if U683 is in reality an upper tooth, its occlusal relations and - by implication - those of U677 were significantly different from those of any other known triconodont upper molariform teeth.

Turning now to the two presumed lower teeth which exhibit definite wear, U681 and 682, it has been noted that the most prominent facet on the former specimen is on the first crown cusp whilst the third crown cusp is completely unworn. On the latter specimen, however, the only identified facet is on the third crown cusp; the second

crown cusp is unworn, and whilst it is possible that there was originally a facet on the first crown cusp this cannot have been as prominent as that on the third. There is thus a significant difference in the wear patterns on the two teeth. This difference may perhaps be the result of U682 being a premolariform tooth.

In contrast to the positions of the facets on U677 and 683, the facets on U681 are situated on the median parts of the relevant lateral surfaces of the first and second crown cusps. There is no wear in the areas between the cusps. From this it is clear that during occlusion, the appropriate opposing cusps must have sheared directly against each of the worn cusps. The occlusal relations of U681 are thus incompatible with those of the two presumed upper teeth considered above; it cannot have occluded with either of them. One possible explanation for this discrepancy is that the teeth belong to different species, as we have already noted. An alternative possibility is that occlusal relations varied within a single species from individual to individual, U681 coming from a different individual from the two presumed upper teeth. There is insufficient evidence for the issue to be resolved.

#### Taxonomic position and affinities within the Triconodonta

In the possession of three axially arranged crown cusps, lateral cingulae, and (in the majority of specimens) divided roots, the teeth appear to belong to one or more species of triconodont mammal. In the possession of both buccal and lingual cingulae they resemble the upper molars of other triconodonts more closely than the lowers. This resemblance is enhanced by the relative lowness of the principal crown cusp. The teeth are rather more like the upper molars of eutriconodonts and morganucodonts than they are like the specialised upper molars of docodonts. They are distinct from both eutriconodont and morganucodont upper molars however in (1) the relatively great breadth of the crown cusps (the principal cusp of U682 excepted) (2) the presence together a very prominent lateral cingulum and a narrow featureless and interrupted one, and (3) the marked mesio-distal compression of both of the roots.

Even if all the specimens were upper teeth their distinctive features would, I think, warrant the allocation of the form (or forms) to which they belong to a new triconodont suborder. The fact however that

they appear - on the evidence of wear - to include both upper and lower teeth, makes the case for such an allocation overwhelming. No component species of the established triconodont suborders possesses lower molariform teeth which so closely resemble the upper molariform teeth, or in which a clearly defined cingulum is present on the buccal side of the accessory crown cusps, or in which the principal crown cusp is as low (or broad) as it is in all but one of the present specimens.

The teeth are advanced over the molars of Sinoconodon and dentally conservative morganucodonts such as Morganucodont A in that the division between the principal crown cusp and the accessory crown cusps are at a low level. They are surely specialised in the relatively low, broad form of the crowns.

The presence of buccal as well as lingual cingulae on the lower teeth may be interpreted either as a peculiar, specialised feature, or, as a conservative one that was lost in the morganucodont-docodont and triconodontid lineages, being retained in a vestigial form in the amphilestids.<sup>1</sup> There is insufficient evidence to decide between these alternatives.

The unusual morphology of the teeth, and our very incomplete knowledge of the dentition, make the relationships between the form (or forms) to which the teeth belong and other triconodonts (essentially the morganucodonts and eutriconodonts) very problematic. The absence of a Kuhnecone in the lower teeth suggests that the antecedents of the species may have divided off from the morganucodont-docodont stock before this cusp originated, as the antecedents of the eutriconodonts may have done. The relatively large, subequal size of the accessory crown cusps - and the subequal size of all the crown cusps in some specimens - recalls the situation in eutriconodont molars. On the other hand, the teeth resemble, in certain respects, the upper molars of morganucodonts, and particularly of Morganucodont A, more closely than they do any other triconodont teeth: Cusp L is reminiscent of the prominent cingulum cusp F in Morganucodont A upper molars, and the anterior cingulum cusp is similarly reminiscent of cusp E. In neither sets of teeth is there a clearly differentiated posterior cingulum cusp, and in Morganucodont A the accessory crown cusps are

<sup>1</sup> If the amphilestids are, in fact triconodonts (see Mills, 1971).

like those in the present form in that they are subequal. As described in the previous chapter, there are two Morganucodont A upper molars in which the lingual cingulum does not continue past the widest part of the principal crown cusp, so that - in this respect - it resembles the narrow, interrupted lateral cingulum of the present teeth. The overall resemblance between these two Morganucodont A teeth and the present specimens is very striking.

In the case of the two Morganucodont A upper molars, it is clear that the interrupted lateral cingulum arose, as a non-adaptive variation, from the continuous cingulum of normal specimens. It is tempting to suppose that the interrupted lateral cingulum of the present, problematic teeth arose, during the course of phylogeny, in a similar manner, although there is no direct evidence to support this supposition.

It is probably not without significance that the teeth which bear the closest resemblance to the present specimens are the upper molars of one of the dentally most conservative morganucodonts, Morganucodont A. The similarities between the two sets of teeth have, of course, to be viewed in the light of the significant differences between them. They must also be viewed in the light of the very striking differences between the lower molars of Morganucodont A and the teeth which are here identified as lowers. Nevertheless, the similarities do suggest, albeit rather tentatively, that the relationship between the suborder to which the present, problematic teeth belong and the Morganucodonta may be closer than that between this suborder and the other known triconodont suborders.

Class	MAMMALIA
Subclass	THERIA
Order	EUPANTOTHERIA, Kermack, Kermack & Mussett, 1968
Family	KUEHNEOTHERIIDAE, " " " "

This early pantothere family is represented by isolated teeth and a few small dentary fragments. All the material belongs to the only currently viable genus and species of the family.

Genus	KUEHNEOTHERIUM, Kermack, Kermack & Mussett, 1968
Species	KUEHNEOTHERIUM PRAECURSORIS " " "

This is the third most abundantly represented mammalian species of the assemblage. Its relative abundance can be gauged from the number of molars: there are twenty one lowers and fifteen uppers.

The Kuehneotherium material from the Welsh localities has been studied by Miss P. M. Gill. All that needs to be stated here regarding the present material is that the teeth do not appear to differ in any significant respect from the specimens from Pontalun quarry which were described by D.M.Kermack, K.A.Kermack & F.Mussett in 1968.

The synonymy of *Kuehneotherium praecursoris*

The first pantothere tooth from South Wales was found in the fissure material which Kuhne collected from the floor of Dutchy quarry (Kuhne, 1950). This specimen, which is probably an upper molar (D. M. Kermack et al, 1968), was given the binomial Kuhneon duchyense by Kretzoi in a paper published in 1960. In 1968 D. M. Kermack, K. A. Kermack and F. Mussett published a description of a collection of isolated pantothere teeth and jaw fragments from a second Hirmeriella quarry: Pontalun. This publication has already been referred to above. Kermack et al, considered the affinities of Kuhneon duchyense indeterminate, and they therefore coined the new names Kuehneotherium praecursoris for the species represented in their material. In the light of our greater knowledge of this species and also of the Hirmeriella association itself, however, there can now be no real doubt that Kuehneotherium praecursoris is a junior synonym of Kuhneon duchyense. The names Kuehneotherium praecursoris are now well established in the literature, having been used for the Welsh pantothere in all publications subsequent to 1968. In the interests of simplicity and utility I have therefore used these names here, although this is not strictly in accordance with the rules of nomenclature.

MAMMALIAN-TYPE TEETH OF UNCERTAIN AFFINITIES

Thirteen teeth of mammalian type remain to be considered. At least some of these specimens probably belong to forms which have already been described.

(a) Premolars

U673 (figure 86 ). This is a tricuspid, double rooted tooth. The crown of the specimen is damaged and only part of the roots are intact. As preserved, the crown measures 1.45 by 0.8mm, dimensions slightly greater than for any Morganucodon watsoni premolar. The crown is entirely dominated by a trenchant principal cusp, the apex of which is missing. The mesial and distal edges of this cusp are straight in both side and end views. The mesial edge is longer than the distal, and is damaged at its base. Evidently a small mesial cusp was originally present here. There is a modest distal cusp in line with the principal cusp. It is damaged and incompletely divided from the principal cusp. Below the level of the distal cusp the back of the crown is also damaged, and a smaller still more distal cusp may have been broken away here. The two preserved cusps of the crown bear mesial and distal crests. On one side of the crown a very weak distal cingulum passes forward to about midway along the principal cusp where it becomes obsolete. There is no mesial component of the cingulum and no trace of a cingulum on the other side of the crown. Here a large wear facet descends the principal cusp from its tip.

The presence of a cingulum on only one side of the crown suggests that the tooth is a lower premolar, the cingulum being lingual and the wear buccal. The degree of complexity of the crown would appear to preclude the possibility that the tooth is a preultimate Morganucodont lower premolar. Its size is perhaps appropriate for an ultimate lower premolar of Morganucodont A. However, as the tooth cannot be identified with certainty as either an upper or lower premolar, and as it lacks any preserved feature which is characteristic of Morganucodont A cheek teeth (for example, very long straight non-tapering roots), the allocation of the specimen to this species is not justifiable.

U678 (figure 87 ). This is a very much smaller specimen. The crown bears three main cusps and there is evidence that the tooth originally possessed two roots, although these are broken off immediately

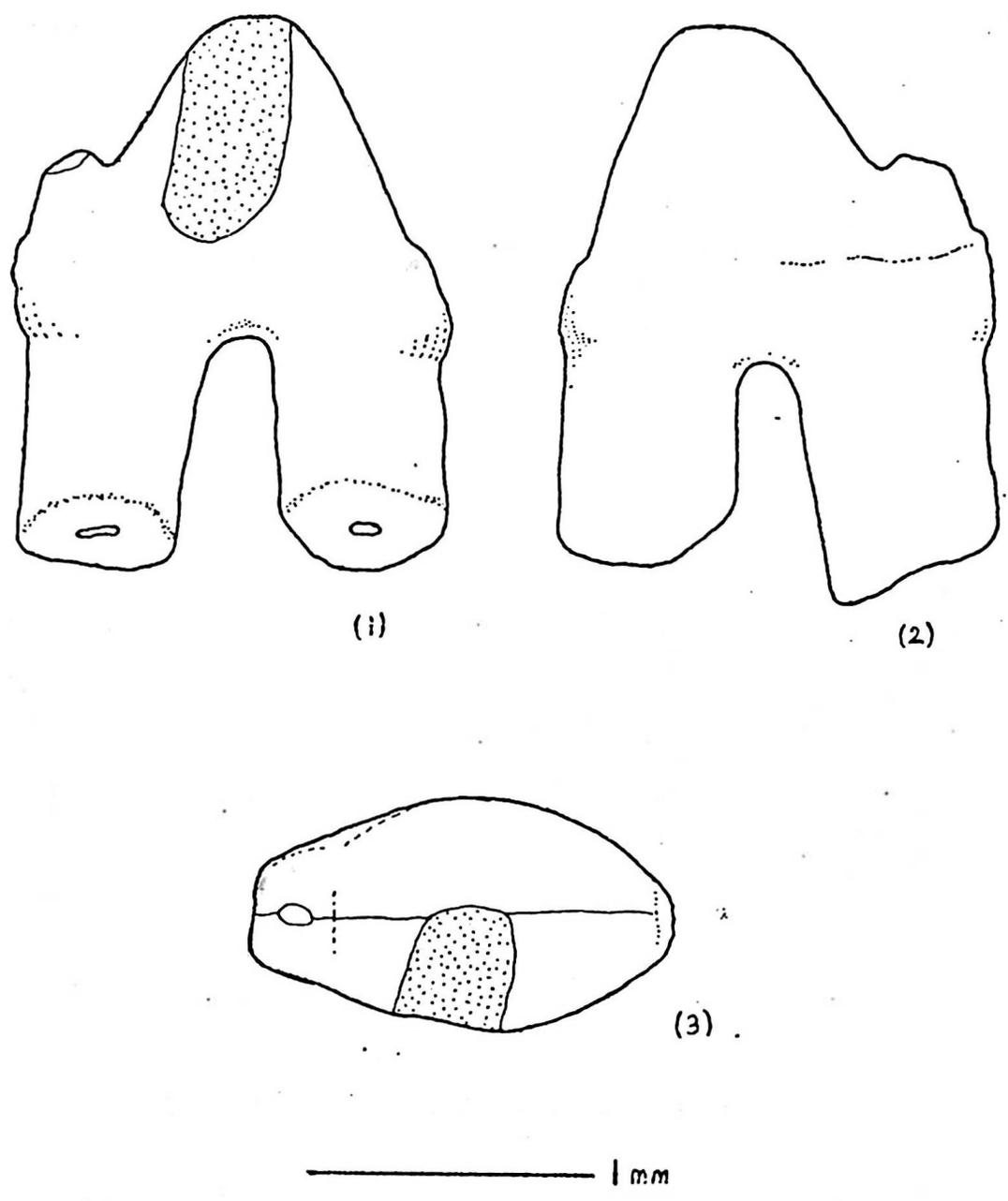


Figure 86 Premolar of uncertain affinities, U 673. (1) and (2) lateral views ; (3) occlusal view. Note the large wear facet on one side of the principal cusp (view (1) ).

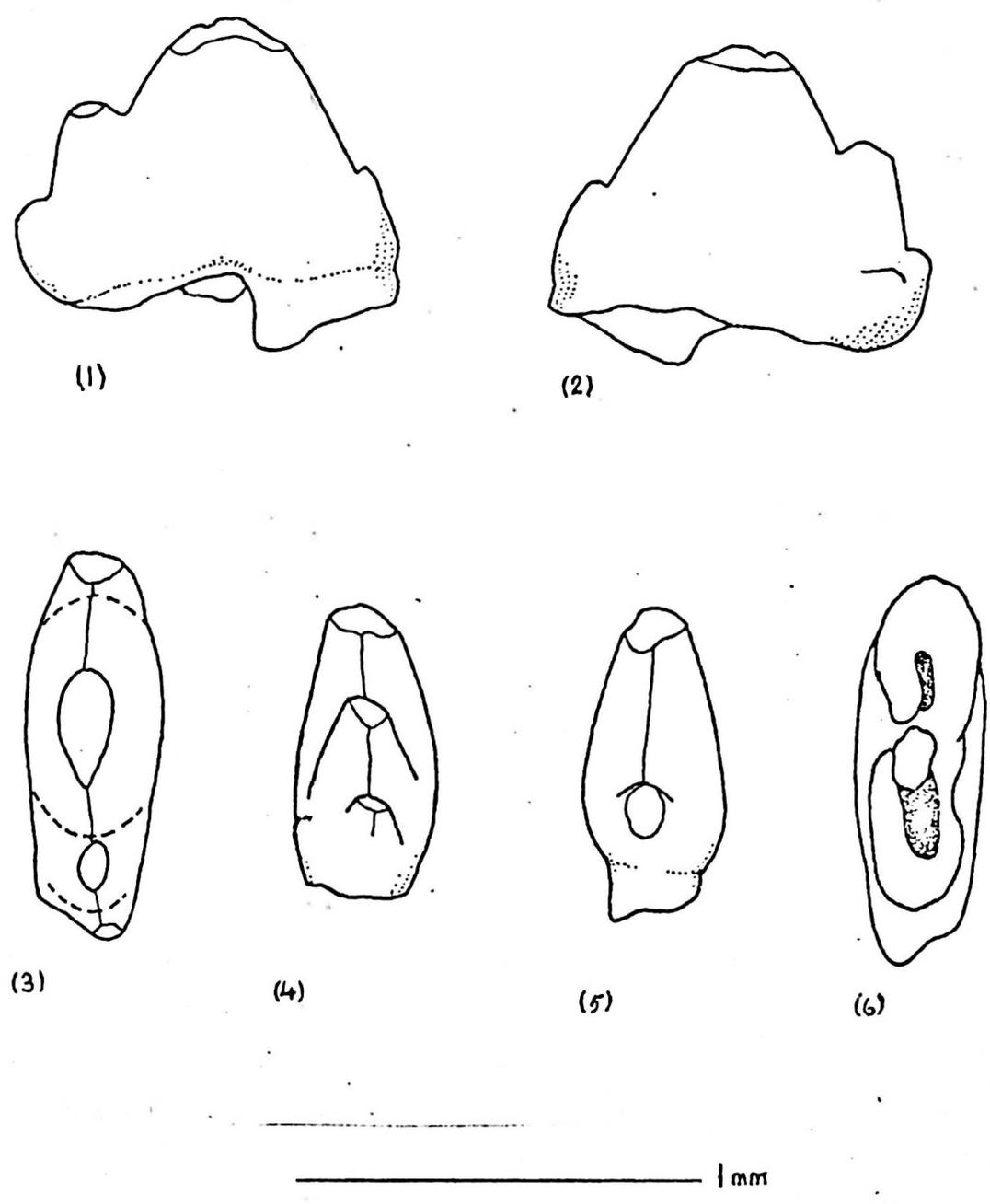


Figure 87 Very small premolar of uncertain affinities, U 678.  
(1) and (2) lateral views, (3) crown, (4) distal, (5) mesial and (6) root views.

below the crown. As preserved the crown measures 0.9mm by 0.3mm.

As in the previous specimen, the crown is dominated by a principal cusp. The apex of this cusp has been broken away and its preserved mesial and distal edges are straight in both side and end views. When the cusp was intact it would not have been proportionally as tall as the principal cusp of the previous tooth. In front of the principal cusp is a remnant of a small mesial cusp. Behind the principal cusp is a modest cusp, the apex of which is missing. The latter cusp is incompletely divided from the former, and it is followed by a very much smaller cusp which is also damaged. The principal cusp and the two following cusps all bear mesial and distal crests. On the right side of the crown (orientating the specimen as in figure 87 ) there is no trace of any cingulum. On the left side, there is a very short incipient cingulum opposite the posterior crest of the distal cusp. This does not continue to the back of the tooth.

The crown is markedly laterally compressed and it evidently had a cutting rather than a piercing function. The tooth matches the previous specimen in its degree of complexity. It cannot be reliably identified as either an upper or a lower tooth. It is clearly too small to be an ultimate premolar of any of the morganucodonts represented in the collection. The possibility that it might be a more mesial premolar of Morganucodont C or D would seem to be precluded by the fact that the more mesial premolar of other morganucodonts are of rather simpler form. It is possible that the tooth is a haramiyid premolar although its small size makes this improbable. The fact that no similar premolars have come from the Holwell fissures which produced haramiyid teeth also militates with this possibility. The tooth might be a premolar of the new type of triconodont which is represented by the problematic cheek teeth described earlier. Equally, however, it might be a premolar of some form not represented by any other tooth in the collection.

(b) Lower incisors

These are of two morphological types. The first type, of which there are six specimens, is very similar to the first lower incisor of Morganucodon watsoni. The second, of which there are four specimens, is similar to the second lower incisor in this species. None of the specimens is intact. Figure 88 shows a relatively well

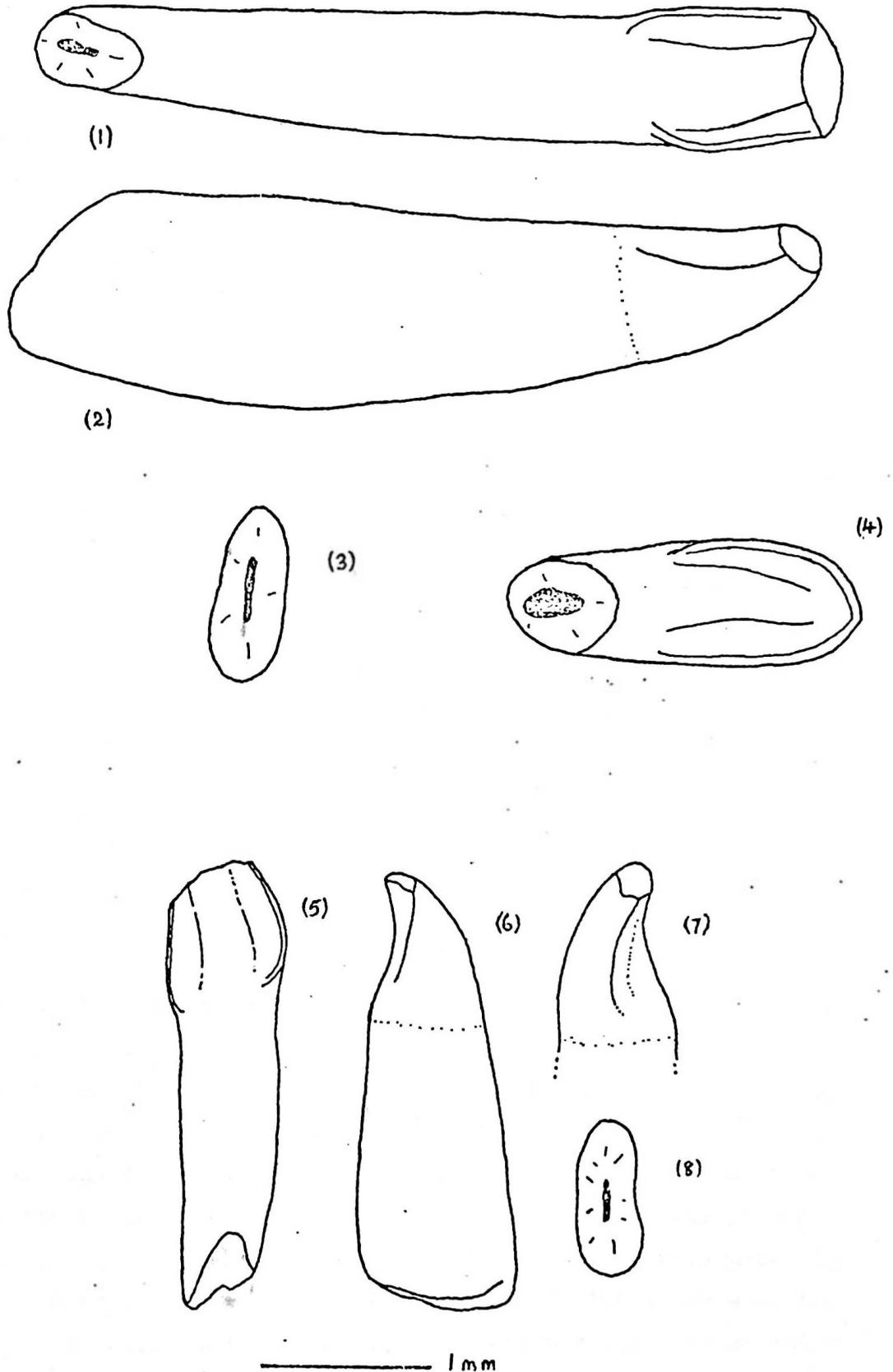


Figure 88 Large lower incisors of uncertain affinities. (1) Dorsal and (2) buccal views of a left I<sub>1</sub>. (3) End view of the root of the same specimen, (4) complete crown of a second left I<sub>1</sub>. (5) dorsal, (6) buccal and (7) lingual views of a right lower incisor from a more distal position. (8) end view of the root of this specimen.

preserved specimen of each type. The illustrations need few supplementary remarks. It will be noted that in lateral view the crowns of both specimens pass imperceptibly into the roots. The roots in each case expand in the lateral plane as they pass backward. These features are not found in the equivalent Morganucodon incisors.

The figured specimens are representative of the sizes of the specimens in each morphological group. As preserved, the specimen illustrated in figure 88a has a maximum length of 4.8mm, whilst that illustrated in figure 88b has a length of 2.6mm. These incisors are clearly too large to belong to Morganucodont A or D. They appear to be slightly too small to belong to Morganucodont B, although the possibility that they belong to this form cannot be entirely ruled out. If the molar which represents Morganucodont C is from the distal end of the dentition, and hence a relatively small component of the cheek tooth row (and there are some points of evidence in favour of this view) the incisors might not be too large to belong to this form.

(c) Incisiform tooth of unique morphology

This specimen, U714, is shown in figure 89. The root is broken off just below the crown but the latter is perfectly preserved.

The root passes smoothly and almost imperceptibly into the crown (the line delimiting the extent of the enamel is barely discernible). In cross section the preserved part of the root resembles an equilateral triangle with rounded corners.

The crown will be described in the orientation in which it is shown in figure 89. It is approximately twice as long as it is broad and it is distinctly tricuspid. Most of the crown is made up by a very stoutly built cusp. This ends in a well defined, though relatively blunt apex, and it bears two clearly defined surfaces. In horizontal section, one of these is nearly straight - and will be designated the anterior surface for convenience - whilst the other is markedly convex. The edges of the upper half of the anterior surface of the main cusp are sharp, and they curve towards one another in anterior view, meeting at the cusp apex. In side view the left of these edges is concave and the right one is straight. The sides of the lower half of the anterior surface of the main cusp are straight and parallel in anterior view. This half of its anterior surface bears two elongated, ridge-like cusps, one on each side. These cusps decrease in prominence as they pass downwards, and each is marked by an elongated crest which passes along its length. These crests

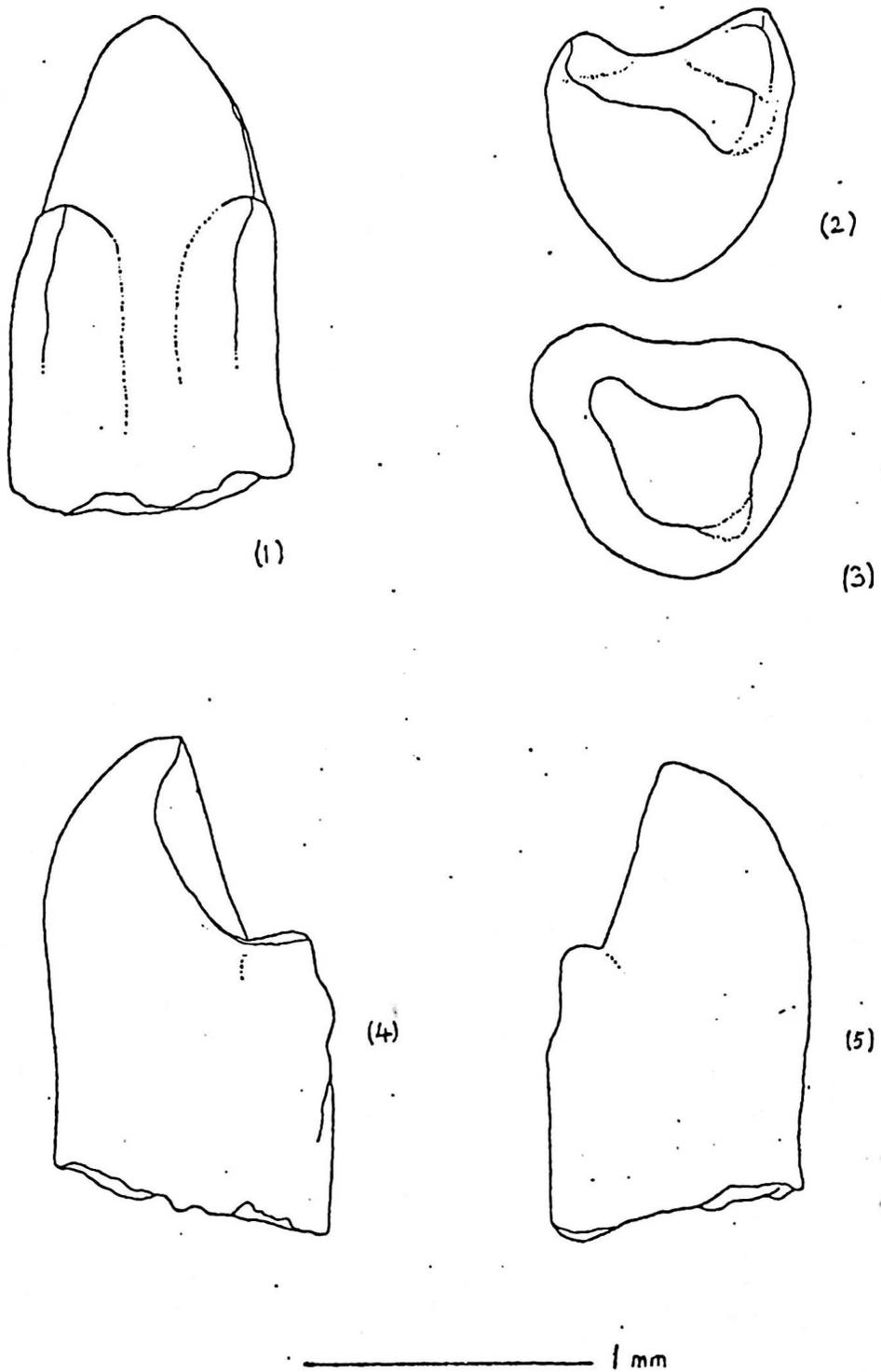


Figure 89. Incisiiform tooth of unique morphology and uncertain affinities, U714. (1) anterior view (2) apical view of crown; (3) end view of root; (4) and (5) lateral views.

are continuous with the sharp edges of the upper half of the anterior surface of the main cusp. In side view, the outline of the lower half of the posterior surface of the main cusp is slightly concave, and it is parallel to the crests on the ridge-like cusps. Above this level, it curves smoothly towards that of the anterior surface, and it meets the latter at an angle of about  $90^{\circ}$ . In apical view (figure ) the right half of the anterior surface of the main cusp slopes slightly downwards from the horizontal plane of the left half. The crown is completely unworn. Its maximum breadth measures 0.9mm whilst the length of the tooth, as preserved measures 1.6mm.

It is impossible to determine whether the specimen is an upper or lower tooth. It might be a haramiyid incisor although it does not resemble any of the incisiform teeth from either Holwell or Hallau. It might equally be an incisor belonging to the new type of triconodont represented by the problematic cheek teeth described earlier. There is also the possibility that it might belong to some unknown mammal or therapsid reptile: the inclusion of the specimen in this section is purely a matter of convenience; it does not involve a decision that the tooth is necessarily mammalian.

THE AGE OF THE ASSEMBLAGE

It is appropriate to begin a discussion of the age of the new assemblage by placing it within the context of the other tetrapod assemblages which have come from Mesozoic fissures in the Bristol Channel area. These may be divided into four principal types. The oldest and most widespread comes from mature fissures of continental origin which are found on both sides of the Bristol Channel, and it consists exclusively of the remains of sauropsid reptiles. A list of the pertinent localities, together with the vertebrates which have been obtained from them is given in table 6. Robinson (1957) has considered the probable history of the formation and infilling of these fissures and has convincingly argued that they filled in late Norian times, immediately prior to the Rhaetic transgression. The 'normal' facies of the Keuper Marls of the Bristol Channel area show some evidence of having been laid down in shallow transitory saline lakes (Robinson, 1957, George, 1970) so that it would appear that the prevailing climate of Norian times was hot with only very intermittent rainfall. Robinson (1971) has correlated the complete absence of mammals and mammal-like reptiles from the late Norian assemblages with this relatively stringent environment, noting that in arid and semi arid regions of the world today sauropsid reptiles (lepidosaurs) are more numerous than mammals - a fact which probably reflects the greater powers of water conservation and the higher core temperature tolerance of the majority of these forms. It will be observed from table that two of the genera which are listed have been found at more than one locality; the sphenodontid Glevosaurus has been found at both Slickstones in Gloucestershire and Pant-y-ffynon in Glamorgan, whilst the paralacertid Kuehneosaurus has been found at Batscombe and Emborough in Somerset and also at Slickstones. As Robinson (1957) has pointed out, the occurrence of the same genera in more than one deposit, together with the fact that all of the late Norian assemblages are of approximately the same age, suggest that the assemblages have been drawn from a single sauropsid fauna which occupied the uplands of the Bristol Channel area immediately prior to the incursion of the Rhaetic sea.

A second type of tetrapod assemblage has come from Neptunian dykes at Holwell in Somerset. The most characteristic feature of this type of assemblage is the presence of haramiyid teeth. The first collection of

TABLE 6

SAUROPSID ASSEMBLAGES FROM FISSURES IN THE BRISTOL CHANNEL AREA

<u>Locality</u>	<u>Assemblage</u>
Ruthin Quarry, St. Marys Hill, nr. Cowbridge, Glamorgan	<u>Tricusposaurus thomasi</u> (Robinson, 1957 b)
Pant-y-ffynon Quarry, nr. Bonvilston, Glamorgan	<u>Thecodontosaurus</u> (Kermack, 1973) <u>Glevosaurus ?hudsoni</u> (Halstead and Nicoll, 1971) Un-named paracrocodyle (Kermack, 1956) Two un-named reptiles (Robinson, 1957 a)

Continued overleaf...

Slickstones Quarry, nr. Cromhall,  
Gloucestershire

Kuhneosaurus )  
?Tricuspososaurus ) (Halstead &  
Un-named procolophonid) Nicoll, 1971)  
Un-named thecodont )  
Glevosaurus hudsoni (Swinton, 1939)  
Two un-named pleurodont lepidosaurs  
(Robinson, pers. comm.)  
Un-named prosauropod (Robinson, pers. comm.)

Emborough Quarry, Old Down,  
nr. Wells, Somerset

Variodens inopinatus (Robinson, 1957 b)  
Kuhneasaurus latus (Robinson, 1962 )  
Un-named archosaur (Robinson, 1957a)  
Un-named reptile (Robinson, 1957a)

Batscombe Quarry,  
nr. Cromhall, Gloucestershire

Kuhneosaurus latissimus (Robinson, 1962 )

tetrapod material from Holwell was made by Charles Moore, circa 1858, who obtained twenty-nine haramiyid teeth together with unidentified reptilian remains from three cartloads of infilling which he removed from a single fissure (Moore, 1867; Simpson, 1928). A second collection of material was made by Kuhne in 1939. From one fissure - 'Holwell 1' - he obtained a single haramiyid tooth, whilst from a second - 'Holwell 2' - he obtained a further twenty-nine specimens, together with the two triconodont teeth called Eozostrodon parvus and 'Eozostrodon' problematicus, and the teeth of a crocodylian and placodont (Kuhne, 1946; Parrington, 1949)<sup>1</sup>. It is possible that the latter fissure is the same as the one from which Moore obtained his specimens, although this cannot now be established. There are real difficulties in dating the Holwell assemblages. The fissure 'Holwell 2' yielded, in addition to the teeth of tetrapods, the teeth, fin spines and scales of Rhaetic fishes and the remains of marine invertebrates which range in age from the Rhaetic to the Bajocian or Vesulian (Kuhne, 1946). All the tetrapod fossils are well mineralised, and their state of preservation is such that they could very plausibly have been reworked, as the fish remains must have been. On the evidence of the invertebrates the age of the tetrapod teeth could therefore be anything from Rhaetic to Lower Inferior Oolite. The earlier work of Moore does not help us to reduce this time span. Although it is known that he obtained the remains of Rhaetic fish from his haramiyid fissure we do not know whether or not he also obtained younger faunal elements (Kuhne, 1946). Some circumstantial evidence favouring a Rhaetic age for the Holwell tetrapods comes from the fact that 'Holwell 1' yielded only the remains of Rhaetic fish, in addition to the haramiyid tooth

<sup>1</sup> In 1966 Savage and Waldman described a dentigerous fragment of a tritylodont maxilla from a fissure at Holwell which they considered was very probably Kuhne's 'Holwell 1'. They identified the specimen as a maxilla of Oligokyphus, although as Savage (1971) later pointed out this identification was incorrect; the exact affinities of the Holwell tritylodont are uncertain, but it is definitely not a species of Oligokyphus. The argument that the specimen comes from 'Holwell 1' appears to be based upon its state of preservation - evidence which, of itself, is hardly conclusive. The age of the specimen and of the deposit in which it was found are unknown.

mentioned above. Again however, the possibility of some, or all of the fossils from this fissure having been reworked is a real one, and, this being so, the possibility of the haramiyid tooth being of a different age from the fish remains cannot be entirely excluded. In his paper of 1946 Kuhne argued that the haramiyid and triconodont teeth from 'Holwell 2' were most probably of Rhaetic age on the grounds that similar teeth occur in the Upper Rhaetic Bonebed of Hallau in Switzerland. With regard to this argument, however, it is important to bear in mind that the stratigraphical range of the Haramiyidae is not known. The family might easily have extended into the Lower Liass. It should also be noted that none of the morganucodont molars from Hallau which are figured and described by Peyer (1956) resemble 'Eozostrodon' problematicus as closely as does the 'Eozostrodon' tooth from Pant 4. None can safely be referred to the same genus. Whilst the tetrapod assemblages from Holwell are, on the available evidence, more likely to be of Rhaetic than Jurassic age, this evidence is insufficient for their age to be determined unequivocally. The only really defensible date which can therefore be given to them is the relatively conservative one of 'Rhaeto-Liassic'.

A third type of tetrapod assemblage is that which has been obtained from the fissures of the Hirmeriella association in South Wales. As stated earlier, the geological history of the area in which these fissures occur precludes the possibility that the assemblages which they have yielded are of post basal Sinemurian age. It does not, however, determine a credible maximum possible age for the assemblages. The only identified components of the Hirmeriella association which are represented in other deposits are the genus Morganucodon, the plant species Hirmeriella muensteri and Triletes tylotus and the gastropod Nattica oppeli. Morganucodon, in the form of M. oehleri, has been found in the Lufeng Beds of Yunnan, China, the particular stratum from which it comes being of Rhaeto-Liassic age (Kermack, Mussett & Rigney, 1973). As the Chinese specimen is not conspecific with the Welsh species its value in correlation is, of course, strictly limited, but it nevertheless provides a broad indication of the age of the Hirmeriella association. The potentially more valuable correlative evidence of the plants has been discussed by Lewarne & Pallot (1957) and by Harris (1957). These authors have shown that it militates against the possibility of the Hirmeriella association being of pre-Rhaetic age. Unfortunately, it is not sufficient to show whether the association is of

Rhaetic or Lower Liassic age. The evidence of the gastropod -which is given in Kermack, Mussett & Rigney (1973, page 101) - corroborates the floral evidence. Again, however, it does not allow the age of the association to be narrowed down more closely than 'Rhaeto-Liassic'.

The fourth type of tetrapod assemblage to have been obtained from a Mesozoic fissure in the Bristol Channel area - prior to the discovery of the Pant 4 material - is the monogeneric Oligokyphus assemblage from the Neptunian dyke at Windsor Hill, in Somerset. This is the only one of the assemblages which can be accurately dated. Kuhne (1956) has shown that the unworked remains of Oligokyphus must be the same age as the youngest marine invertebrates which have been obtained from the fissure. The latter are of basal Pleinsbachian age (jamesoni zone).

The overall faunal composition of the new assemblage, with mammals and tritylodonts forming a significant component in marked contrast to the situation in the Late Norian assemblages, clearly indicates that it is of post-Norian age. The evidence for a post-Norian age is corroborated and strengthened beyond doubt by the fact that the tritylodonts include the Windsor Hill species of Oligokyphus. The Windsor Hill deposit is stratigraphically separated from the Norian by the entirety of the Rhaetic, and by the combined Hettangian and Sinemurian stages of the Lower Liass, the whole representing a time interval during which the Bristol Channel area underwent the profound topographical and climatic changes which transformed it from a semi arid, interior Continental region, to a region in which an archipelago of small tropical or semi tropical islands lay in a warm, coral bearing sea.

In attempting to narrow down the age of the assemblages more closely than 'Rhaeto-Liassic' we are obviously confined to the correlative evidence which is afforded by those genera which also occur in deposits of known age; in other words to the evidence which is afforded by Thomasia and Oligokyphus. Unfortunately the limits of the stratigraphical ranges of neither of these genera, nor any of their constituent species, is known. The oldest known tooth of Thomasia is a recently discovered specimen which comes from the Knollenmergel of Halberstat (Hahn, 1973). The youngest Thomasia teeth, which can be dated more accurately than 'Rhaeto-Liassic' are from the Upper Rhaetic of Hallau (Peyer 1956). Since there is no

reason to suppose that a genus which persisted from the upper Norian to the upper Rhaetic could not also have survived into the Lower Liassic, the evidence which is afforded by Thomasia is negligible. In the case of Oligokyphus, the situation is more promising as we are here able to compare the relatively abundant remains of one of the Pant forms - O. minor - with similarly abundant remains of this species from Windsor Hill. As has been shown, there is no evidence of any divergent micro evolution between the two populations of O. minor which are represented in the Welsh and English assemblages. Whilst our knowledge of these populations is, of course, far from complete, it is particularly striking that three of the non-adaptive variations which are present in the Windsor Hill material are also encountered in the material from Pant 4. These comprise two of the morphological types of O. minor ultimate upper cheek teeth, and the upper cheek tooth which bears a supernumerary cuspule on the buccal side of its crown (see page ). In populations of vertebrates which inhabit small islands, and which are thus genetically isolated and of very limited size, non adaptive or neutral characters tend to become eliminated or fixed through the operation of genetic drift. That none of the three variantes mentioned above had become eliminated from, fixed within, or even predominant within the population of Oligokyphus minor which is represented in the Windsor Hill material therefore indicates that this population was not separated by a substantial time interval from the population which is represented in the Pant 4 material. Here, however, a difficulty arises. Although the age of the Triassic - Jurassic boundary has been reasonably estimated on the basis of radiometric data, no absolute dates at all are available for any of the divisions of the Rhaetic or the Liass (Howarth, 1964; Tozer, 1964). We are, consequently, unable to assess the evidence which is afforded by Oligokyphus minor within the context of a reliable Rhaeto-Liassic time scale. Nevertheless, if we make the reasonable assumption that the combined Hettangian and Sinemurian stages represent a time interval of a similar order of magnitude to that which separates the present from the Astain, a Liassic (Hettangian or basal Sinemurian ) age for the Pant 4 assemblage is, on the evidence afforded by this species, much the most plausible one.

As the new assemblage comes from South Glamorgan and contains the three principal Hirmeriella tetrapods, there naturally arises the question of its temporal relationship with the Hirmeriella association. The tetrapods themselves are of little value in determining this relationship. On the one hand, the presence of more species within the Pant 4 assemblage than occur within the Hirmeriella type of tetrapod assemblage cannot be regarded as evidence that the two types of assemblage are of a different age since neither is necessarily representative of the fauna from which it has been drawn. On the other hand, the presence of the normal Hirmeriella species within the Pant 4 assemblage no more establishes its contemporarity with the Hirmeriella association than the presence of Oligokyphus major, minor and A establishes its contemporarity with the assemblage from Windsor Hill. Of much more significance is the fact that the fissure, Pant 4, is situated in the same quarry as a fissure which, in 1955, yielded the abundant remains of the Hirmeriella tetrapods ('Pant 2', cf: Kermack, Mussett and Rigney, 1973, page ). Both fissures are, like the majority of those from which elements of the Hirmeriella association have been obtained, narrow slots which constitute very immature solution phenomena. Their development was clearly arrested by their infilling and, ultimately, by their submergence beneath the Liassic sea in lower Sinemurian times. The change from solution to sedimentation within these fissures must have taken place when the Rhaeto-Liassic water table had risen to a level at which it checked the velocity of inflowing drainage waters sufficiently to cause the precipitation of any sediments which they were carrying. The deposition of the very fine sediments which occur in the fissures can only have taken place in water that was actually standing within them. Whilst it is possible that, at any given time, the height of the Rhaeto-Liassic water table varied somewhat over the whole of the area in which the Hirmeriella quarries are now situated, the important point is that the two Pant fissures are on approximately the same level and are only about 100 yards apart. Clearly, the water table must have attained the critical level which effected the change from solution to sedimentation at approximately the same time with respect to each. In other words, they must have filled approximately synchronously. As none of the tetrapod remains from the two fissures are derived, the two assemblages must therefore be of about the same age. The tetrapods from Pant 4 have thus been drawn from the same fauna as the tetrapods of the Hirmeriella association. We may refer to this fauna as the 'Hirmeriella fauna'.

The question of why the Pant 4 assemblage is a more representative sample of this fauna than the normal type of Hirmeriella assemblage may now be considered. The state of preservation of the fossils which make up both types of assemblage is essentially similar. In each case, fully macerated skeletal material was washed into the fissure system on numerous separate occasions, probably by flash-floods which occurred during a rainy season. The different compositions of the two types of assemblage must therefore be due to some difference in the particular circumstances which led to the original accumulations of these skeletal remains, prior to their fluvial transportation.

Kermack, Mussett and Rigney (1973) have suggested two alternative hypotheses which they consider might account for the original accumulation of the remains which make up the normal type of Hirmeriella assemblage. Firstly, they suggest the possibility that the primary collection was made by a carnivore. Predation is the most frequent cause of the primary collections of the faunally mixed microvertebrate assemblages which occur in Tertiary and Quaternary underground watercourses (see for example Kurten, 1968), and Kuhne (1956) has shown that the primary collection of the Oligokyphus remains which were buried in the Windsor Hill fissure was made by a carnivore. Such a collecting agency would account for both the limited size and number of the tetrapod species which are present in the normal type of Hirmeriella assemblage, as Kermack, et al (1973) have pointed out. It would also be consistent with the condition of the tetrapod remains. Bones which pass through the digestive systems of modern carnivores, or which are regurgitated by owls, are normally completely cleared of soft tissue, but they often show little evidence - other than breakage - of what they have undergone.

The second hypothesis suggested by Kermack et al arises from a theory which Harris (1958) advanced to account for the fusainized state of most of the plant remains from the fissures. Harris argued that the carbonisation of these remains can only have been effected through the action of forest fires. Kermack, et al suggest that such fires might have destroyed most of the small vertebrates which lived in the locality whilst larger forms were able to escape. They also point out that as the fires destroyed the vegetation cover they would have produced the conditions in which cloud-bursts could have swept great masses of soil along with the tetrapod

remains into the fissures. There are, however, at least three serious objections to this hypothesis. In the first place, it is difficult to see how fires which converted plant material into fusain and destroyed the bodies of small vertebrates sufficiently to make their dissociated bones available for transportation would have left the organic content of these bones intact, thereby enabling them to survive the rigours of the transportation without disintegrating. Secondly, if the hypothesis were correct, one would naturally expect to find fusain frequently intermixed with bone in the fissure deposits. Yet this is hardly ever the case; the fusain normally occurs in discrete pockets of fissure deposit which contain little or no bone. Finally, the hypothesis is quite inadequate as an explanation for the small number of tetrapod species which are present in the normal type of Hirmeriella assemblage. Quite clearly, forest fires which destroyed Morganucodon, Kuehneotherium and the pleurodont lepidosaur would also have destroyed at least some of the other small tetrapods which we now know were also present in the Hirmeriella fauna.

Of the other potential causes of the mass deaths of small tetrapods - flooding, drought, lack of food and disease - none appears to be capable of satisfactorily accounting for the accumulation of the fully macerated bones of a mixture of different species. We are therefore left with the predator-collector hypothesis as the only tenable explanation for the primary accumulation of the remains which make up both the normal type of Hirmeriella assemblage, and that obtained from Pant 4. In the case of the Pant 4 assemblage, a strong indication that the primary collection was made by carnivorous archosaurs is afforded by the presence of numerous teeth of these reptiles amongst the remains which have been obtained from the fissure. The larger of the species to which these teeth belong would have been amply large enough to have preyed upon the other tetrapods which are represented in the assemblage. They were quite possibly the dominant carnivores of the Hirmeriella fauna. The occurrence of the teeth of these archosaurs together with the bones and teeth of their prey can be adequately accounted for by the fact that they possessed dentitions with rapid tooth replacement. As Kuhne (1956) has pointed out, crocodiles often leave some of their teeth with the remains of their meals. With regard to the normal type of Hirmeriella assemblage, the general absence of archosaur teeth would seem to preclude the possibility that the primary collection was made by these predators. Since the predator of the tetrapods which make up this type of assemblage has not left any of

its teeth together with the remains of its prey, it presumably had a dentition in which teeth were infrequently replaced, or in which there was no replacement. This suggests that it may have been a mammal, a mammal-like reptile, or an acrodont lepidosaur -perhaps a sphenodontid. The presence of the relatively large morganucodont, Morganucodont B, in the assemblage from Pant 4 demonstrates that there was at least one species of mammal in the Hirmeriella fauna which was of sufficient size to have been the predator of the species which make up the normal type of Hirmeriella assemblage. As the species which are exploited by a given predator will depend upon the taste preferences, ecological behaviour, size, and predatory capacity of the predator, the conclusion that different predators were probably responsible for the primary aggregations of tetrapod remains which make up the two types of Hirmeriella assemblage provides an obvious and simple explanation for the differences which exist in the faunal composition of these assemblages.

CONCLUDING REMARKS

The new assemblage from Pant 4 greatly increases our knowledge of the Hirmeriella fauna, providing ample evidence that it was a rich and varied one. The occurrence within the fauna of Oligokyphus major, minor and A, together with forms that are almost certainly specifically identical to 'Eozostrodon' problematicus and Thomasia anglica, demonstrates that there was a distribution of at least some of the post-Norian Mesozoic tetrapod species of the Bristol Channel area throughout the archipelago which existed in the Rhaeto-Liassic sea. This suggests that many of the other components of the Hirmeriella fauna lived on the contemporaneous Mendip islands which lay adjacent to the Holwell and Windsor Hill localities. The new Welsh material certainly precludes the possibility that the complete generic disparity in the faunal compositions of the Holwell and Windsor Hill assemblages is the result purely of palaeogeography. The question of whether this disparity is due to a difference in age or in palaeofaunal sampling factors cannot be answered conclusively in our present state of knowledge. If, however, the Holwell tetrapods are of Rhaetic age - as seems most probable on the basis of such evidence as is available - the occurrence of two of these forms together with Oligokyphus in the Hirmeriella fauna would accord with this fauna being intermediate in age between the Holwell and Windsor Hill assemblages. In other words, it would be in accordance with the postulated Lower Liassic age of the fauna, 'Eozostrodon' and Thomasia representing within it relicts of an earlier Rhaetic fauna.

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