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THE ADVENT OF HERBIVORY IN CERTAIN REPTILIAN LINEAGES DURING THE TRIASSIC

by

C. E. Gow

ABSTRACT

The dentitions of several presumed herbivorous Triassic reptiles are described and discussed. Some changes in dentitions with growth suggest that juveniles were insectivorous. The appearance of these forms may have been facilitated by floral changes which took place in the early Triassic.

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INTRODUCTION

General

The Karoo fauna is overwhelmingly dominated by the therapsids or mammal-like reptiles. For most of the Upper Permian the therapsids comprise two main groups: the carnivorous theriodonts which typically had large incisors and canines and few cheek teeth, and the herbivorous anomodonts which all had a horny beak and some a pair of tusks (primitive anomodonts had post-canine teeth). Anomodonts are exceedingly abundant while the theriodonts are rather rare, the proportion of carnivores to herbivores approaching that found in present-day mammalian faunas (Bakker, pers comm.).

At about the Permian–Triassic boundary profound changes occur in the Karoo fauna (fig. 1). The anomodonts all but disappear (though some are present in the Triassic). At the same time the theriodonts gave rise to several forms which were probably herbivorous. Not only the theriodonts did this, however, but also two unrelated reptilian groups did the same thing. Thus rather than there being a simple ecological replacement of anomodonts by cynodonts, it appears as if there may also have been a change in the flora which encouraged these developments, a change which the anomodonts could not exploit but which encouraged the emergence of several new forms of herbivores other than anomodonts.

There are several aspects of diet, feeding and mastication which are a necessary background to this discussion.

Here will be considered reptiles with a wide range of physiologies, from primitive reptilian to near mammalian. Plant food requires to be crushed very finely, and chewing is presumably easier for an advanced cynodont with separate respiratory and oral tracts than for a rhynchocephalian that has to stop chewing in order to breathe and vice versa.

A point which is not examined here is the manipulation of food in the mouth. In mammals this is done by the tongue and cheeks. The possible presence of muscular checks in some of the animals under consideration is a study in itself.

Work on gomphodont dentitions has tended to

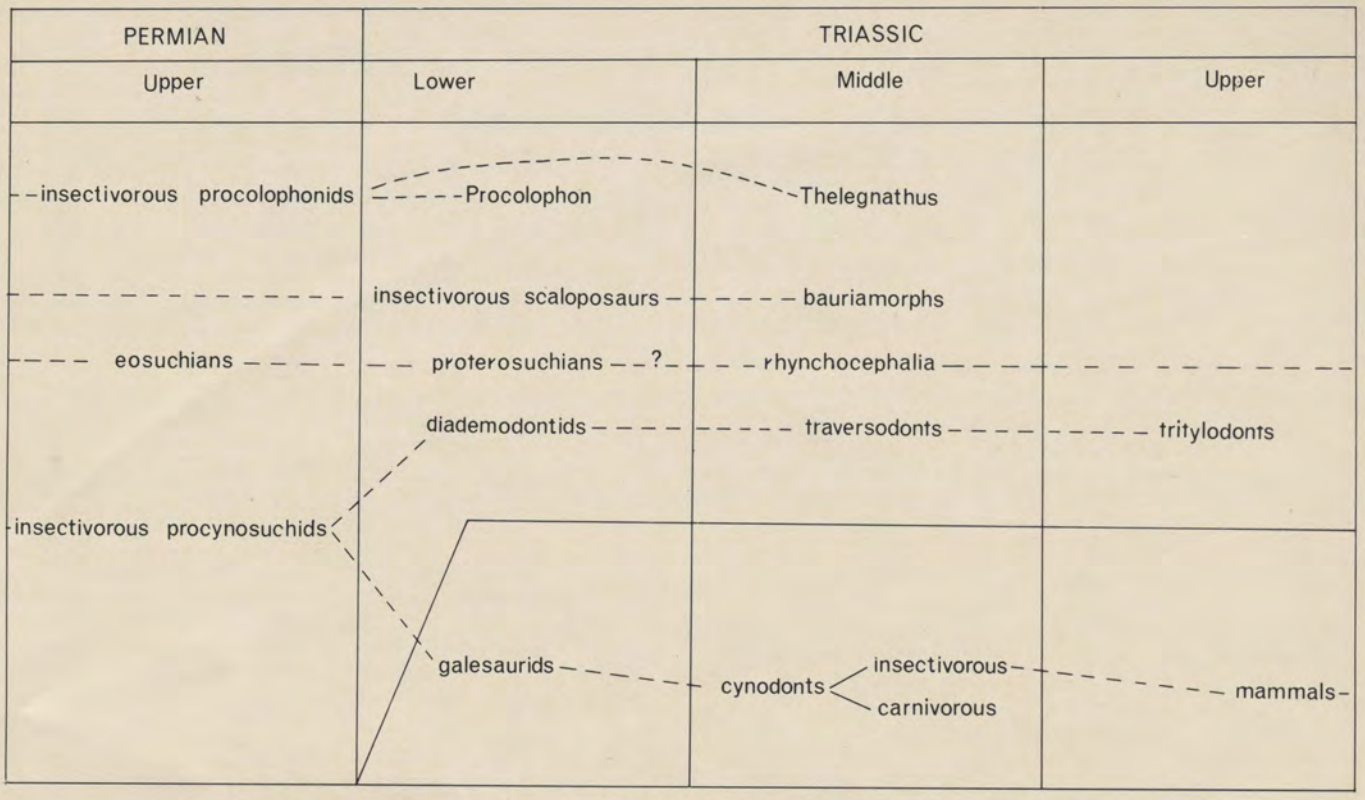


Figure 1. Appearance in time of the herbivorous reptiles discussed in this paper.

concentrate on cheek teeth to the exclusion of incisors and canines. This is unfortunate, though the fossils are largely to blame. The morphology and the degree and nature of wear of incisors in particular could tell a lot about diet and manner of feeding, e.g. the aardwolf *(Proteles)* which snuffles in the dirt after roots and insects, wears down these teeth considerably.

In considering possible diets an important factor is body mass. For example Pough (1973) has pointed out that while small species of lizards (or juveniles of larger species) are insectivorous, mature members of larger species are herbivorous, except in a few cases (e.g. *Heloderma, Varanus* spp., especially *V. komodoensis*). This is because with increased size, the energy expended catching insects becomes too great for the reward obtained.

The function of teeth

Primitive reptiles typically have undifferentiated peg-like gripping teeth and the lowers close within the arc of the uppers without the teeth actually meeting. Such teeth replace alternately throughout the life of the animal. On the other hand, in mammals the teeth meet precisely when the jaws close and typically teeth replace only once. In the fairly extensive literature on early mammals, it is generally assumed that one of the important attributes which gave mammals the potential to radiate and occupy so many niches, once the dinosaurs had left the scene at the end of the Cretaceous, was their possession of what is known as the tribosphenic molar (fig. 2), that is, a molar tooth which can puncture, crush

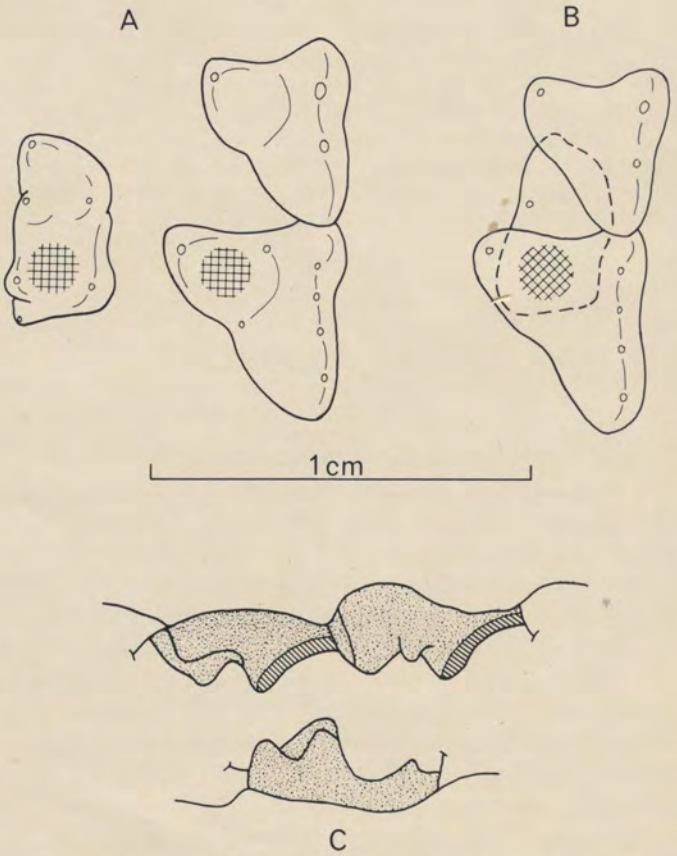


Figure 2. Essential features of the tribosphenic molar *(Didelphis marsupialis)*.
A. Lower, left, and upper, right, molars.
B. The same in occlusion.
C. Lingual view of same teeth. Cross hatched areas indicate grinding surfaces, parallel lines shear surfaces.
(After Crompton and Hiiemae, 1970.)

and cut, so that food is reduced to fine fragments in the mouth. In this way digestive juices can act rapidly, allowing the animal to derive the maximum amount of energy in the shortest possible time. It is axiomatic that there should be precise occlusion for such teeth to function properly; this demands anatomical refinement, precise neuromuscular control, and a pattern of tooth replacement which will cause the least disruption to the optimal functioning of the teeth. Of these factors it is only the complexities of neuromuscular control of the bite which cannot be studied directly in fossils. This then gives us a useful basis for comparing the performance of fossil dentitions.

DESCRIPTIONS

Procolophon trigoniceps (*Lystrosaurus* zone)

Permian procolophonids were all small (lizard sized) animals with fine sharp peg-like teeth; they were undoubtedly insectivorous. The lower Triassic *Procolophon*, though somewhat larger, is probably just within the limit of size for an insectivore, but its postcanine teeth are very different; they became heavily worn and replacement was almost eliminated (Gow, 1978b) (fig. 3).

Procolophon is always found preserved with the mouth closed and the cheek teeth intermeshed. This was just the resting position; the teeth met during use in crown to crown contact. Postcanine teeth are transversely widened and in very young animals the crown consists of two points connected by a sharp ridge. The points wear away and eventually only broad flat crushing surfaces remain. There is also considerable wear of the tips of the incisors. This wear, coupled with reduced replacement, is most sensibly interpreted as the result of a herbivorous diet in the adults. Juveniles were very likely insectivorous.

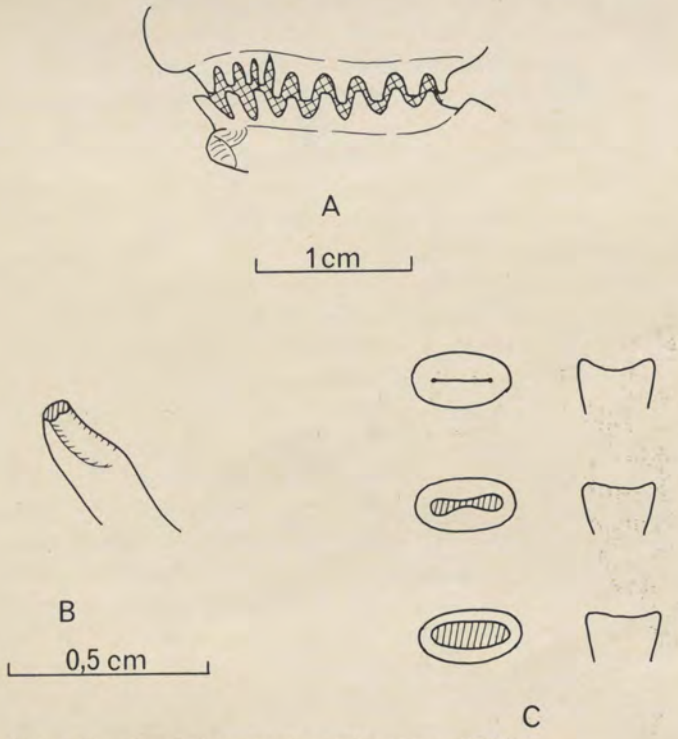


Figure 3. *Procolophon trigoniceps* (after Gow, 1978b)
A. Lingual view of dentition as preserved.
B. Incisor showing worn tip.
C. Wear stages in occlusal and mesial view. Lateral thickening of the occlusal surface ensures retention of concave shape for as long as possible.

Thelegnathus species (*Cynognathus* zone)

Triassic procolophonids are regarded as relic cotylosaurs, so it is remarkable that we should suddenly find five species of one genus in the *Cynognathus* zone (Gow, 1978a). Despite incompleteness of the fossil record one cannot avoid the inference that some factor or suite of factors suddenly presented themselves and that small morphological responses resulted from rapid speciation. Under such conditions speciation can be very rapid, perhaps of the order of a few thousand years.

These *Thelegnathus* species (fig. 4) have dental specialisations which invite speculation as to their use. Three are sufficiently distinctive to mention briefly here.

T. oppressus (fig. 4) has very robust pointed molars so heavily worn that it could only have been a crusher

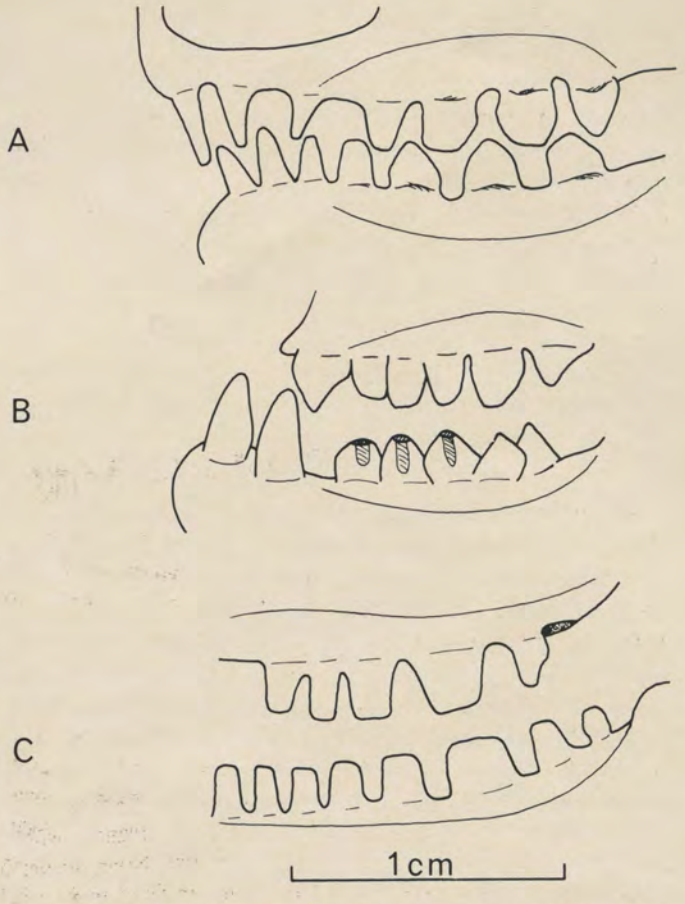


Figure 4. *Thelegnathus* species. Teeth in labial view. (After Gow, 1978a.)
A. *T. oppressus*
B. *T. perforatus*
C. *T. contritus*

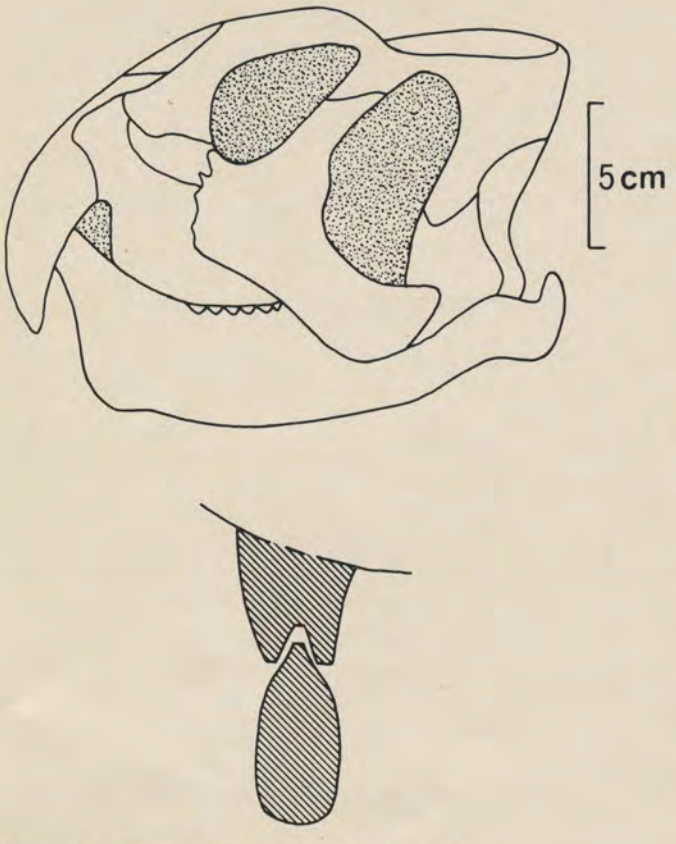


Figure 5. Top: *Scaphonyx* (after Romer, 1956). Bottom: Section through jaws and teeth. Common to all rhynchocephalians.

feeding on hard seeds; the postcanine teeth are far more robust than would be required of an insect crusher.

T. perforatus (fig. 4) had equally good crushing postcanine teeth and, in addition, greatly enlarged incisors which must have been important in procuring the food.

T. contritus (fig. 4) with its antero-posteriorly widened postcanines heavily worn to a smooth occlusal plane was most probably a root or foliage crusher.

Rhynchocephalia (*Cynognathus* zone)

These merit passing mention for the sake of completeness, though their dentitions are unique. There are two main branches, the sphenodontids, represented by the still living *Sphenodon*, which are or were insectivorous, and the rhynchosaurs of which we have cranial remains of two genera in the Karoo beds (*Mesosuchus* and *Howesia*), but which flourished in the South American Triassic, e.g. *Scaphonyx* (fig. 5). These latter were much larger animals which could only have been herbivorous. None survived the Triassic. Sphenodontids had incisor teeth while rhynchosaurs had bony beaks. Both families had a double row of cheek teeth in the upper jaw separated by a longitudinal groove (fig. 5) into which the dentary teeth occluded. It is thought that propalinal movement of the lower jaw produced a slicing action (Robinson, 1976).

Bauriidae (*Cynognathus* zone)

Bauriids, of which there are probably not more than a dozen known specimens, were the last surviving therocephalians, a distinction that may well be due to their adaptation to a herbivorous diet. The only previous work of any consequence on the teeth of bauriamorphs is contained in Crompton's paper of 1962, in which he described two dentitions in considerable detail.

Therocephalians typically have a battery of long, sharp pointed, robust incisors, well developed canines, and cheek teeth that are rudimentary or absent. Bauriids have the same prominent incisors with apparently little wear; they retain canines, but they have developed up to eleven crushing and cutting "molars", which intermesh during occlusion. Postcanine teeth were probably added at the back of the row and possibly lost in front with age, as in procolophonids and gomphodont cynodonts. The single replacing tooth in Crompton's *Bauria* may be an aberrant occurrence as is sometimes seen in procolophonids (Gow, 1978b).

During the course of this investigation I prepared a small bauriid snout, BPI FN 4655. In this specimen (fig. 6) the molar teeth unquestionably intermesh. The crowns of uppers and lowers are very similar, with prominent labial cusps and an arc of crenellations lingually. The crown surface enclosed by these structures is slightly raised in the middle. Wear on these teeth is minimal, being confined to the edges of the mesial and distal depressions either side of the labial cusp. This state of affairs contrasts so sharply with the heavy wear on, for instance, the larger specimen described by Crompton, that again there is the tendency to believe that small individuals (or species) might have been insectivorous and the adults (larger species) herbivorous.

That is the condition in an unworn and probably not fully erupted bauriamorph dentition. How does this fit with the situation described by Crompton in *Bauria*? In that specimen the lower teeth, though heavily worn, retain the large labial cusp, while in the uppers this cusp has been worn away so that these teeth have a flat labial crushing surface and a prominent lingual cusp (fig. 7B). The only apparent exceptions to this are the replacing tooth at position 5 and the young unworn tooth at position 10. This necessitates a certain amount of reinterpretation of Crompton's work. Most importantly Crompton suggested, to account for the crown patterns, that the upper and lower molar rows actually crossed each other. That this hypothesis is not necessary is borne out by the next specimen.

BPI FN 2837 is another previously unprepared snout preserved with the teeth in occlusion. So tightly are the teeth intermeshed that it proved impossible to separate them; they broke instead at the level of the crushing surfaces, giving a transverse section through the main cusps (fig. 7C). These cusps are lingual below and labial above, i.e. the

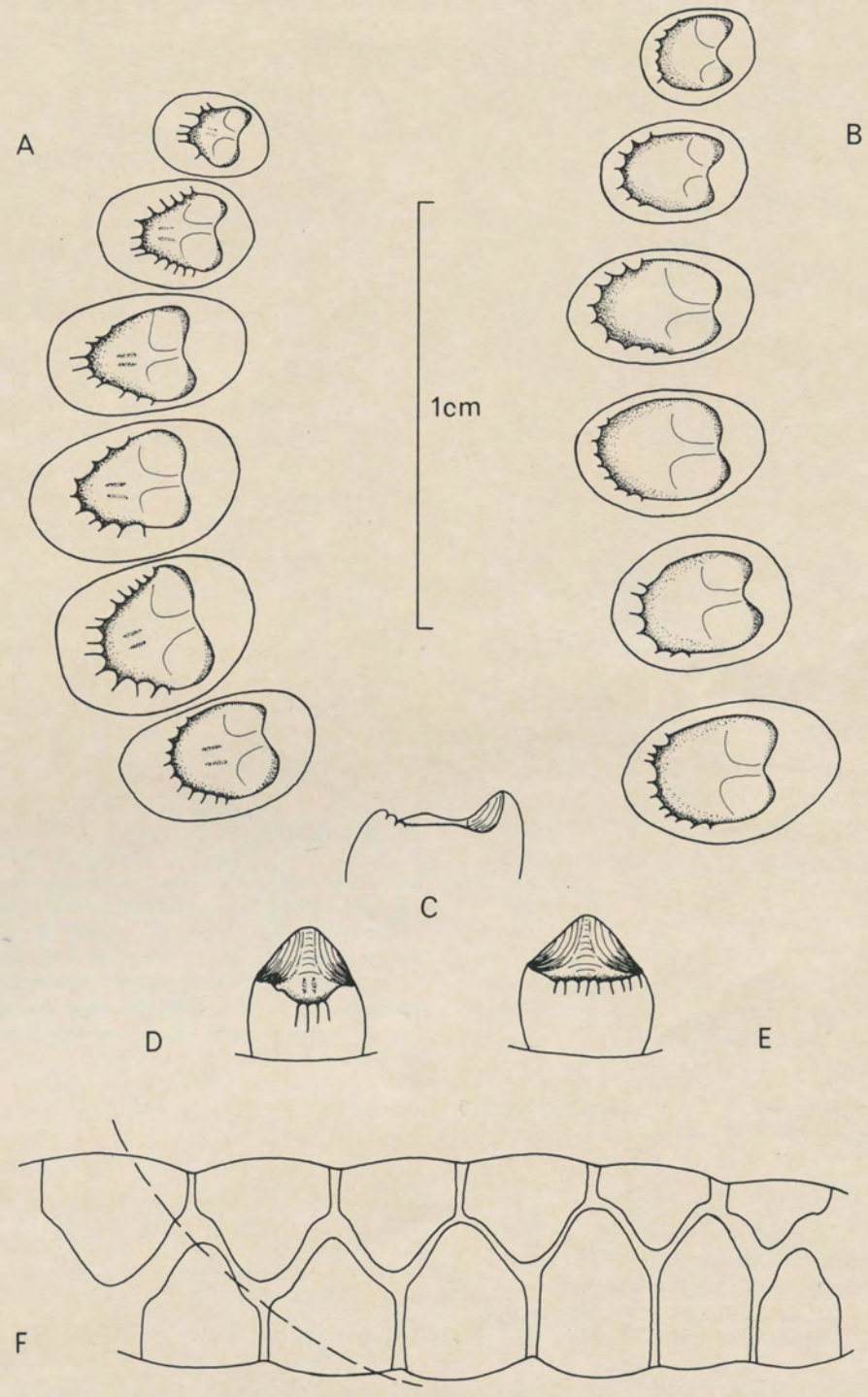


Figure 6. Small ? *Bauria* species. BPI FN. 4655.
A. Lower cheek teeth
B. Upper cheek teeth
C. Mesial view of cheek tooth
D. Lower tooth in lingual view
E. Upper tooth in lingual view
F. Cheek teeth in occlusion. Position of ascending ramus of jaw indicated by dashed line. Lower teeth are distinguished by the presence of two ridges on the occlusal surface.

dentition is well worn. The shear surfaces form a sinusoidal curve and would function rather like the pinking shears used for cutting cloth. (Edmund, 1969, has drawn the same analogy with respect to the dentition of the Australian agamid *Moloch horridus* where it is even more apt. *Moloch* is a 15 cm long ant eater.) This type of dentition, aside from gripping the object to be cut, would have a distinct advantage in cutting any material with linearly arranged fibres; on the other hand it could simply have the effect of lengthening the shearing surface.

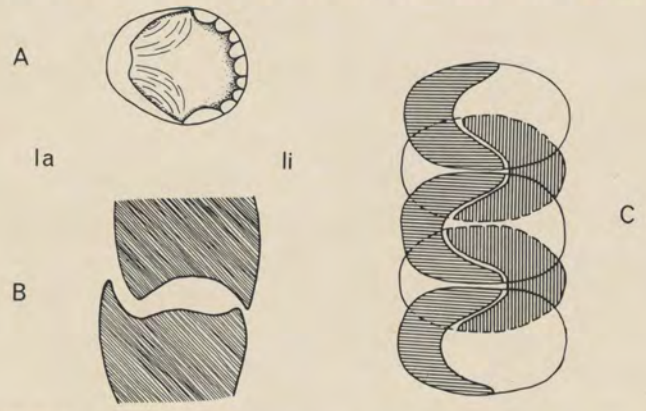


Figure 7. *Bauria cynops*
A. Unworn "molar" crown (after Crompton, 1962).
B. Section through upper and lower "molars" with wear well advanced: the large labial cusp of the upper tooth has been worn down and the lingual rim now provides the dominant cusp.
C. Section through occluded teeth at the level of the crushing surfaces. la = labial; li = lingual.

Gomphodont cynodonts

Gomphodont here refers to those cynodonts, most of which were herbivorous, in which some or all of the cheek teeth are transversely widened and meet during occlusion. Gomphodonts initially separate crushing and cutting functions into different regions of the tooth row. Later these functions are combined in individual teeth.

Trirachodontidae (*Cynognathus* zone)

Trirachodon can probably be regarded as the most primitive of the gomphodont cynodonts. The dentition is not known in detail as there are probably very few skulls known and the teeth are invariably tightly occluded.

Trirachodon has smallish complex unworn incisors, robust canines with serrated posterior edges, five large piercing and crushing postcanines and two sectorial (slicing) teeth at the back of the maxilla. The postcanines (fig. 8) are transversely widened and intermesh. There are three main piercing cusps, arranged transversely; distal and mesial ridges consist of numerous small cusps.

Though very similar to *Diademodon*, even to the characteristic jugal boss, *Trirachodon* is a much smaller animal (a big one would have weighed less than 10 kg). Lack of tooth wear suggests it was a carnivore.

In the possibly congeneric *Cricodon* from East Africa, in which the jaws could be separated, Crompton (1955) attributed decreasing complexity of the more anterior crowns to wear. If it is wear it is very slight.

Diademodontidae (*Cynognathus* zone)

In *Diademondon* the incisors are poorly known, as snout tips are usually weathered away, but they are small and so are the canines: both replaced frequently. The postcanine teeth are well known (figs. 9 and 10) though the exact sequence of replacement is still debated; basically they are lost in front and added at the back. They are differentiated into peglike "premolars", complex postcanines which get worn flat, and sectorials, the uppers and lowers of which slice past each other but do not touch.

It is difficult to suggest a diet for adult *Diademodon*. For their size (50–70 kg) and dentition, fairly hard nutritious plant foods are indicated, but due to the fairly unspecialised nature of the teeth compared to later gomphodonts, a certain amount of omnivory is possible. *Diademodon* is far more common than the contemporaneous carnivore *Cynognathus*, which was about the same size, which might indicate that the former was a herbivore and the latter a carnivore which preyed on it.

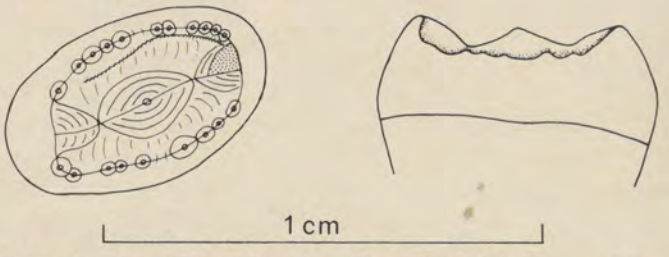


Figure 8. *Trirachodon*. BPI FN. 4659. Isolated left lower molar. Crown view left, mesial view right.

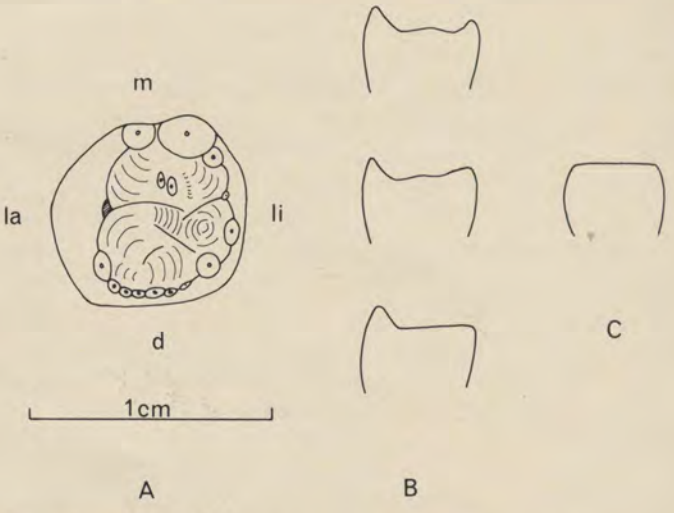


Figure 9. *Diademodon*
A. An isolated lower molar hardly worn, to show the extraordinary complexity of the crown.
B. Top to bottom: stages in the wear of an upper molar, mesial view.
C. Terminal wear on lower molar, mesial view.
d = distal: li = lingual; la = labial; m = mesial.

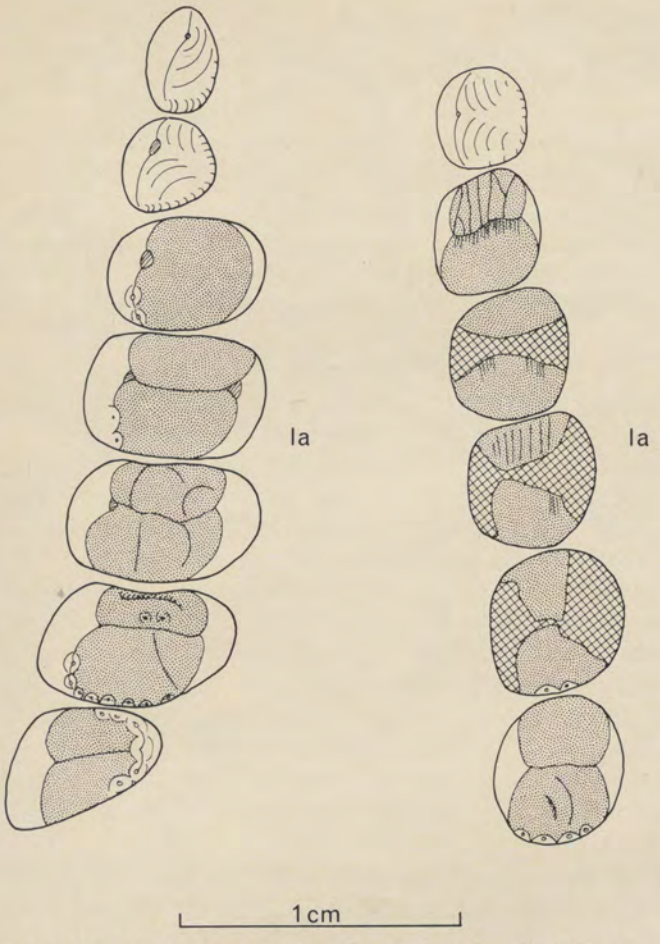


Figure 10. *Diademodon*. Geol. Surv. 483. Molar dentition, uppers left, lowers right. la = labial.
This shows a complete and well worn upper and lower molar dentition. The lower teeth, which are not nearly as broad, occlude between the uppers. All molars tend to wear to an inverted V shape, with a transverse median ridge. With this type of occlusion and the wear facets formed, the bite was clearly a simple pounding action with no or very little propalinal movement possible. Scratches on the lower teeth were probably caused by sand grains taken in with the food being pushed downslope during chewing.

Traversodontinae

This subfamily of advanced gomphodonts is best represented in the South American middle Triassic.

Scalenodon from East Africa illustrates an advance on the condition in *Diademodon*. By breaching the transverse ridge in the molars they have achieved a significant degree of propalinal movement, as borne out by wear facets on the teeth (fig. 11).

A further improvement is seen in *Massetognathus* (fig. 12) in which considerable precise propalinal shear produces vertical wear facets on the postcanines. This system reaches its greatest elaboration in the tritylodontids (fig. 13) which, as shown by Crompton (1972), have a postcanine cusp morphology similar to the pattern worn into *Massetognathus* teeth. These teeth acted rather like running two rasps past each other.

Massetognathus has heavily worn chisel-shaped incisors much like those of modern mammalian herbivores. Its canines are half as long, relative to the skull length, as those of *Trirachodon* and *Diademodon*. Tritylodonts lack canines and have incisors rather like rabbits. *Massetognathus*, according to Bonaparte (1970), is exceedingly abundant and found in groups, perhaps representing natural populations.

Romer (1972) gives a list of skull lengths of combined *Massetognathus* species in which the majority fall below 100 mm with some individuals going to 200 mm. It is a typically reptilian size distribution with growth continuing throughout the life of the individual. This last remark has recently been shown to apply to *Diademodon* as well (Grine and Hahn, 1978).

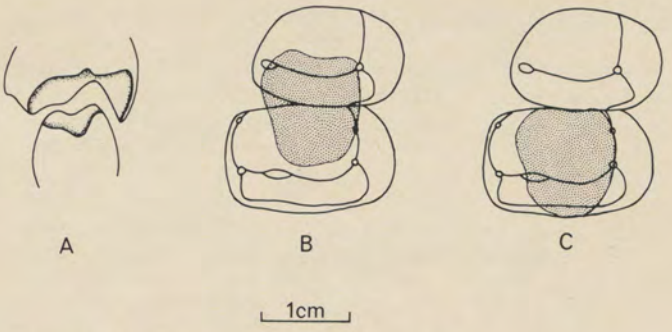


Figure 11. *Scalenodon*
A. Upper and lower molars in mesial view.
B. Two uppers and one lower at the beginning of the bite stroke.
C. The same teeth at conclusion of the bite.
(After Crompton, 1972).

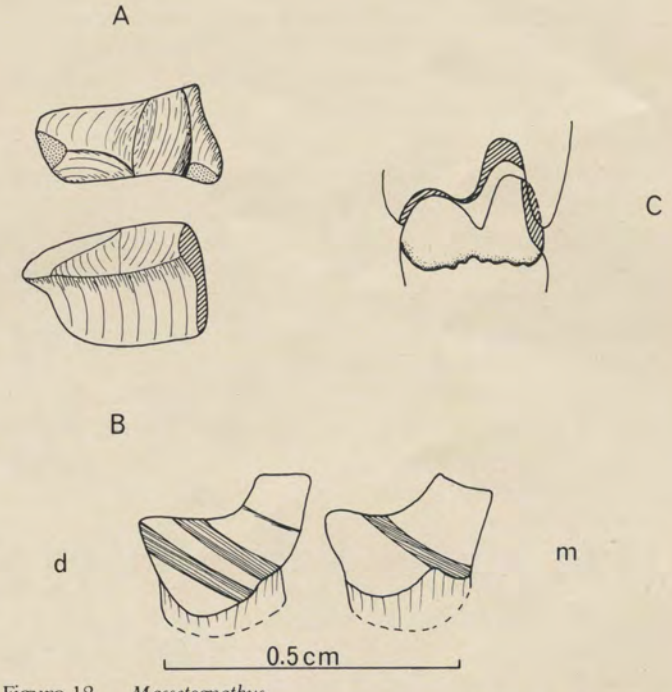


Figure 12. *Massetognathus*
A. Upper molar above, lower below; sketched from photographs published by Crompton (1972).
B. Labial view of two heavily worn lower molars showing scratch fields due to shear.
C. Teeth in occlusion, distal view (from Crompton, 1972).
d = distal: m = mesial.

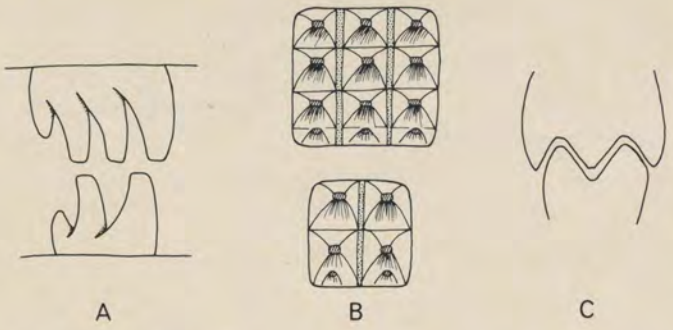


Figure 13. *Tritylodon*
A. Upper and lower molars, labial view.
B. Upper (above) and lower molars in occlusal view.
C. Distal view of occluding teeth.

DISCUSSION

For a reptile to qualify as an efficient herbivore the following conditions should, *inter alia*, be met:

The cheek teeth should be predominantly designed for crushing, or better, grinding, with a shear component as well. (Certainly there are some reptilian herbivores with serrated leaf-like teeth. In the case of some of the ornithopod dinosaurs grinding "molars" evolved from such a pattern.)

There should be loss of alternate replacement in the molar series so as not to impair the efficiency of the crushing/grinding mechanism.

Heavy wear of postcanine tooth crowns in adult animals is evidence of a herbivorous habit.

Relative abundance in the fauna is also very important. There is always a preponderance of herbivores over carnivores in any fauna. This will no doubt be an important aspect of future palaeoecological studies.

In palaeontology we often have small samples to deal with and the reasons for this are frequently open to speculation. In some cases inferences about diet based on dentition may be equivocal, but the point which study brings out is that all these reptilian lines were doing much the same thing with their teeth, so that with some being undoubted herbivores it is very likely that they all were.

How well do the animals described above meet these criteria?

Procolophon trigoniceps has crushing postcanine teeth and no alternate replacement. The teeth wear heavily and the animal is locally very abundant. Juveniles may well have been insectivorous.

Thelegnathus species are a new discovery and may have been more abundant than the ten specimens known to date would suggest. They were specialised for various plant diets but are otherwise similar to *Procolophon*. Again juveniles were probably insectivorous.

The rhynchosaurs are a special case. Like turtles, they used basically the same feeding mechanism whether carnivorous or herbivorous. The large exceedingly common *Scaphonyx* of South America was undoubtedly herbivorous.

Bauria has crushing and cutting molars subject to heavy wear in the adult. Tooth replacement is reduced but not fully understood. The animal is far less common than *Diademodon* from the same beds. This may suggest a specialised and restricted diet. Heavy postcanine wear and the retention of cutting edges and the large incisors and weak canines suggest that adults were herbivorous. The complexity of unworn teeth suggests juveniles may have been insectivorous. Change in tooth morphology with age in procolophonids and bauriids is probably indicative of change in diet. By contrast, herbivorous mammals do not have carnivorous milk dentitions.

Of the gomphodont cynodonts, *Trirachodon* is rare, the teeth do not, as far as is known, wear appreciably, and they are designed for piercing and cutting. These animals were insectivorous to carnivorous.

It is possible that *Diademodon,* as the first of the herbivorous cynodonts, may not completely have forsaken other items of diet. It is the only one of the herbivores under consideration which delegated crushing and cutting functions to different regions of the tooth row. The sophisticated tooth replacement pattern is consistent with a herbivorous habit and "molar" wear was heavy. The animal was far more common than the carnivorous *Cynognathus*.

There is no doubt that the traversodonts and tritylodonts were specialised herbivores.

Some of the Triassic herbivores may have specialised on the more nutritious parts of plants such as seed coatings, seeds and roots. (All probably derive from insectivores. It is common to find animals switching from insectivory to herbivory either seasonally or at different stages of growth.) In energetic terms seed contents, for example, have the same nutritive properties as meat, so that an efficient dental battery would be the main refinement needed in adapting to such a diet. These sorts of food would have been available in the form of dispersed conifer seeds, the fleshy coating of cycad seeds, the seeds themselves and the entire reproductive structures of some of the pteridosperms, and ginkgophyte ovules.

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