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SKULLS OF THE PROSAUROPOD DINOSAUR *MASSOSPONDYLUS CARINATUS* OWEN IN THE COLLECTIONS OF THE BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH

by

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ABSTRACT

Description of the skull of *Massospondylus* (Prosauropoda, Anchisauridae) is largely unnecessary since excellent descriptions now exist of *Plateosaurus* (Galton 1984, 1985a) which, though larger and of slightly different proportions, is anatomically almost identical. This paper presents comprehensive illustrations of the *Massospondylus* skulls in the Bernard Price Institute collections and discusses only those aspects of this material in which *Massospondylus* differs from *Plateosaurus*, or which further add to our knowledge of the prosauropod skull. It is shown that Attridge *et al.* (1985) give spurious reasons for considering the recently discovered *Massospondylus* skull from Arizona to differ from the southern African taxon, and that the suggestion of Crompton and Attridge (1986) that this animal may have had a horny beak on the tip of the lower jaw is unnecessary and improbable.

INTRODUCTION

Owing to the superbly detailed accurate work of Galton (1984, 1985a) the skull of the European late Triassic prosauropod *Plateosaurus* is well known. Galton lists seven crania of which two are complete. We have nine skulls of the related form *Massospondylus* in this country, six at the Bernard Price Institute for Palaeontological Research and three at the South African Museum. Several of these are associated with fairly complete articulated postcranial skeletons; in addition there are several bits of crania and partial articulated skeletons in collections, and a lot more material has been recorded but not collected, because of poor preservation or bad erosion or both. It is perhaps worth noting that although *Massospondylus* remains may be common in most localities where they occur, they are almost invariably found individually and are not concentrated in large numbers as is the case with *Plateosaurus*, and indeed several occurrences of euskelosaurids in our basal Elliot Formation. A *Massospondylus* skull has recently been announced from the Kayenta Formation of North America (Attridge, Crompton and Jenkins 1985) which we believe to be the same taxon as ours. *Massospondylus* is also known from Zimbabwe (Cooper 1981 and references cited therein). Cooper has suggested that the Chinese *Lufengosaurus* may be *Massospondylus*; we consider this possible but unproven at this time.

Plateosaurus beds are firmly established as of upper Triassic age (Galton 1984). The Kayenta and Elliot Formations are considered lower Jurassic (Olsen, Shubin and Anders, 1987).

Plateosaurus grew to one and a half times the size of *Massospondylus*, and its teeth were smaller in proportion and more numerous. When it comes to the detailed osteology and the sutural relationships of the skull bones, Galton's (1984, 1985a) description of *Plateosaurus* could have been written for *Massospondylus*. The two genera even exhibit the same kinds of variation; Galton conservatively ascribed this to individual variation, but we believe that the increased sample allows us to suggest that the accentuated features of larger skulls may reflect sexual dimorphism. These two prosauropod genera are so similar that common ancestry is certain, if not an ancestor-descendant relationship.

MATERIAL

BP/1/4934 (figs l and 7a).
The largest skull and part of an articulated skeleton lacking only hindlimbs and tail. From the farm Bormansdrift (133); upper part of Elliot Formation: 28° 57'S 27° 26' E. Map reference 2827CD Mekoatlengsnek.

BP/1/5241 (figs 2 and 7b).
Next largest relatively undistorted skull, also has much articulated postcranial skeleton. Farm Upper Drumbo; ± 6 metres below Elliot/Clarens Fm. contact: 30° 50'S; 27° 45' E. Map reference 3027DC Barkly East.

BP/1/4376 (figs 3 and 7c).
The smallest skull, also has considerable associated postcranial material. Blikana mountain, Herschel district

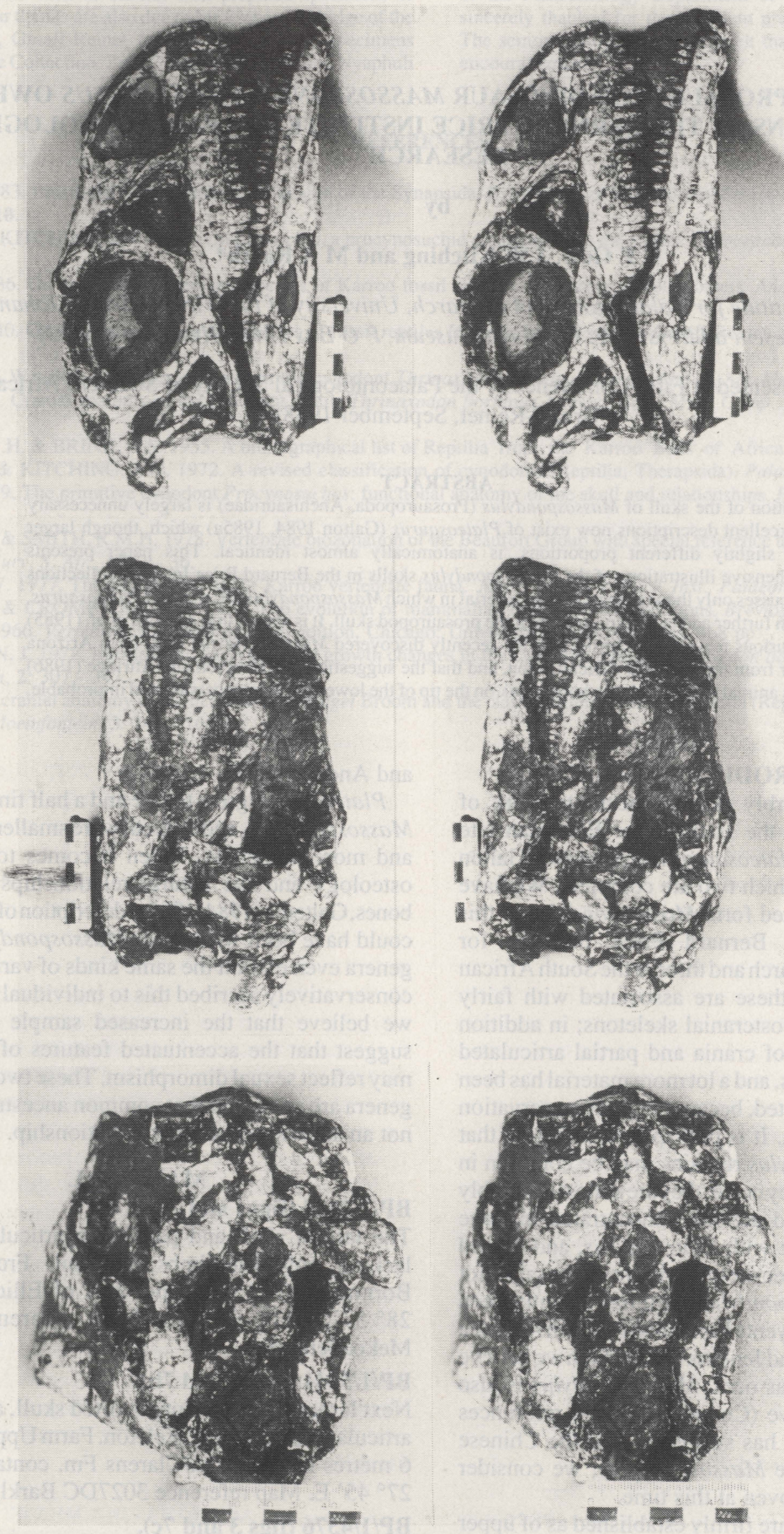


Figure 1. BP/1/4934 Stereophotographs of both sides and the occiput. From the latter the degree of sagittal flexure to which the specimen was subjected can be seen.

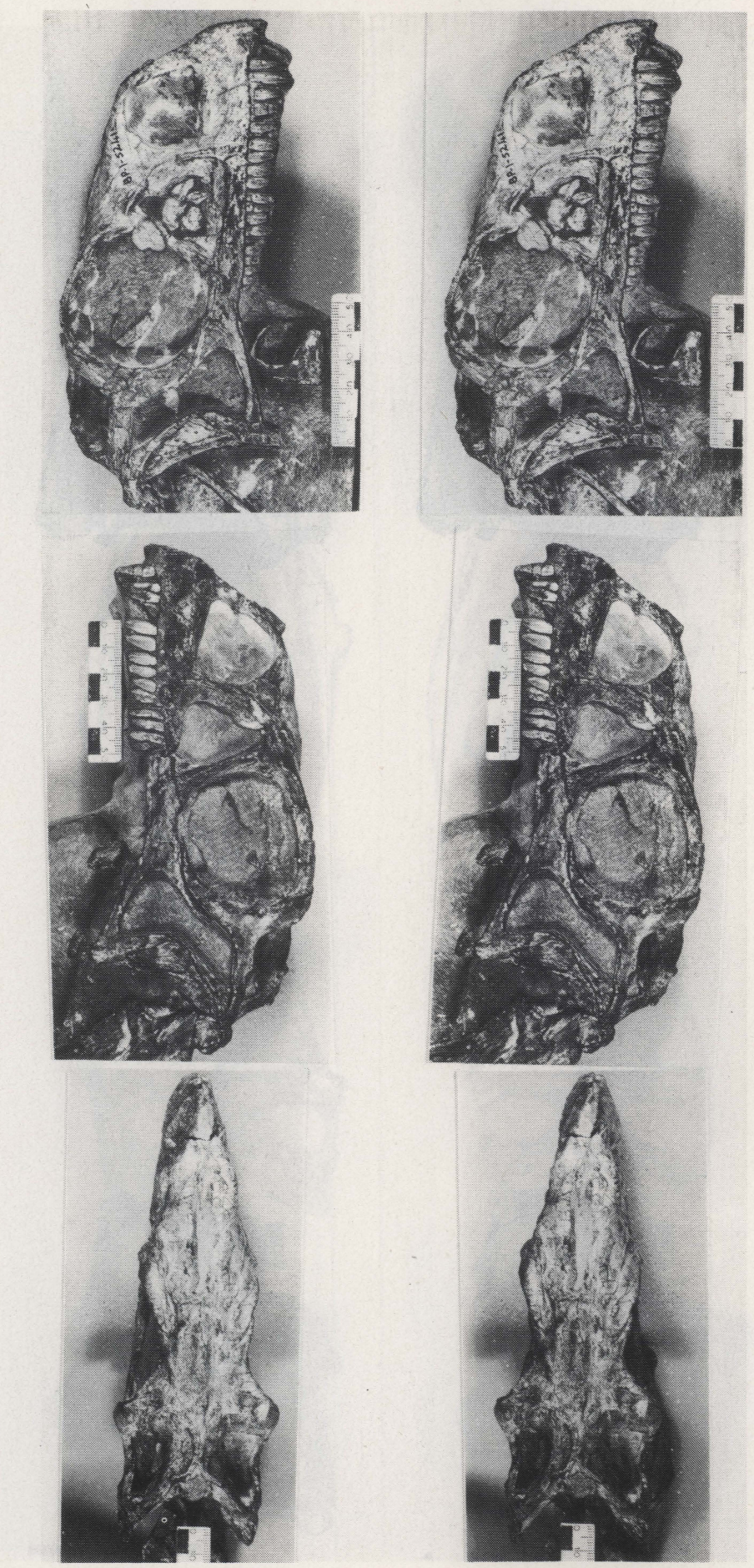


Figure 2. BP/1/5247 Stereophotographs of both sides and the dorsal aspect, the latter showing the very considerable lateral compression of the specimen. On the right side scleral plates lie in the antorbital fenestra and a loose ectopterygoid below the skull.

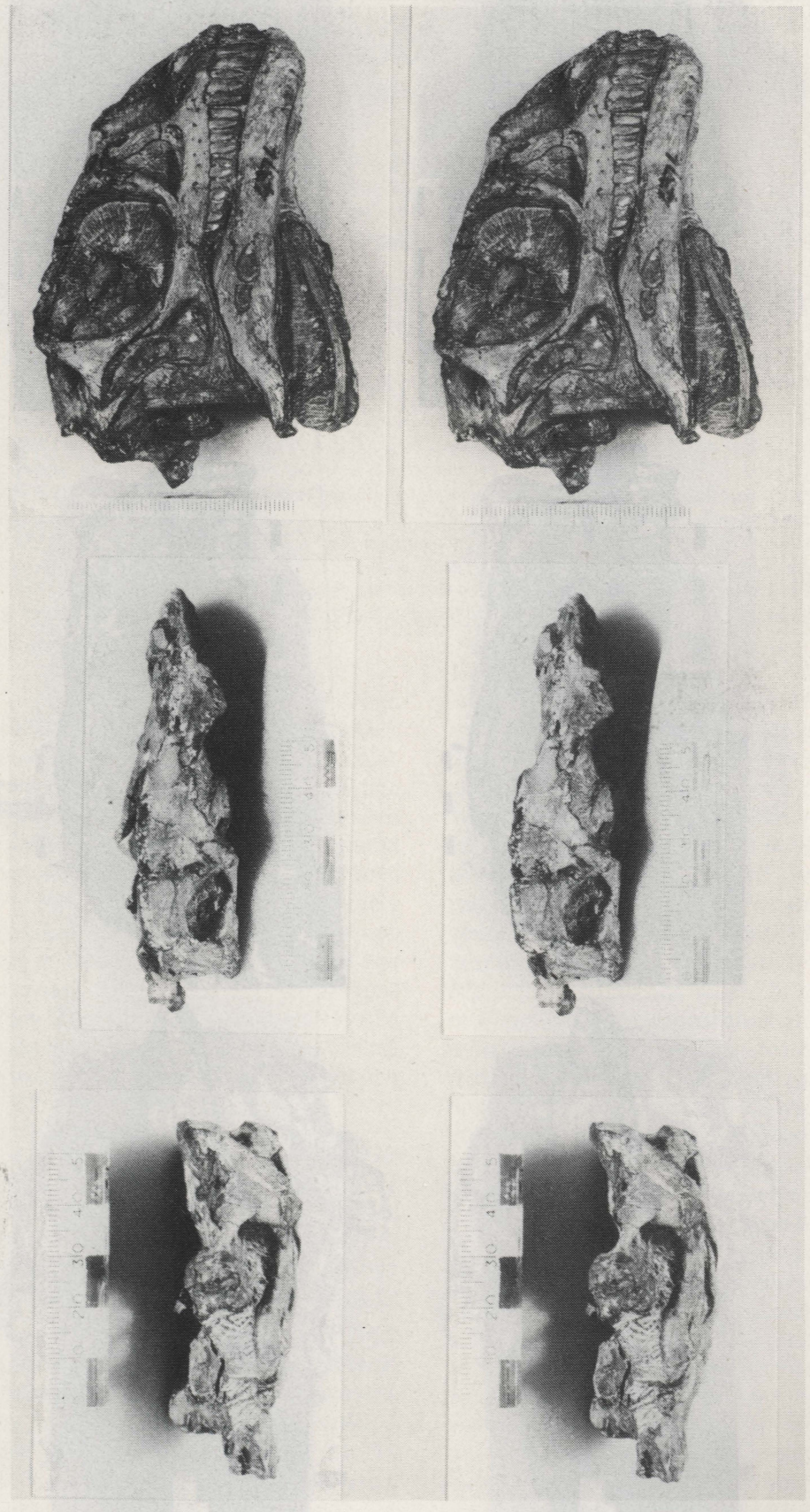


Figure 3. BP/1/4376 Lateral, dorsal and occipital stereophotographs. Only the right half of this skull is intact.

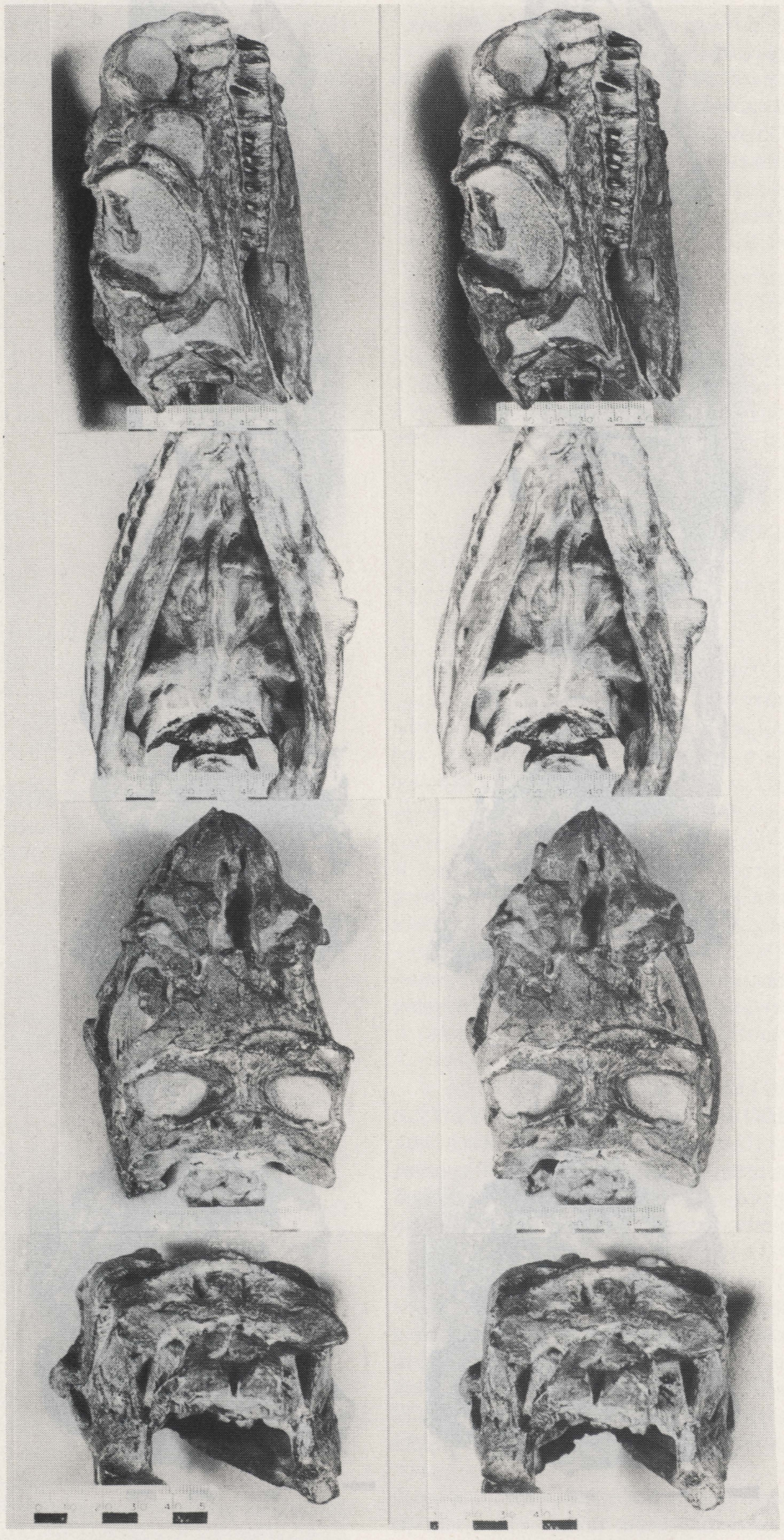


Figure 4. BP/1/4779 Stereophotographs of lateral, palatal, dorsal and occipital views. This specimen has suffered antero-posterior compression as can be seen from the distortion of the orbits and upper temporal fenestrae, and the bulbous nasal region.



Figure 5. BP/1/4930 Lateral, palatal and dorsal stereophotographs. This specimen has suffered antero-posterior shortening which has obliterated the temporal openings and caused considerable plastic deformation of the rest of the skull.

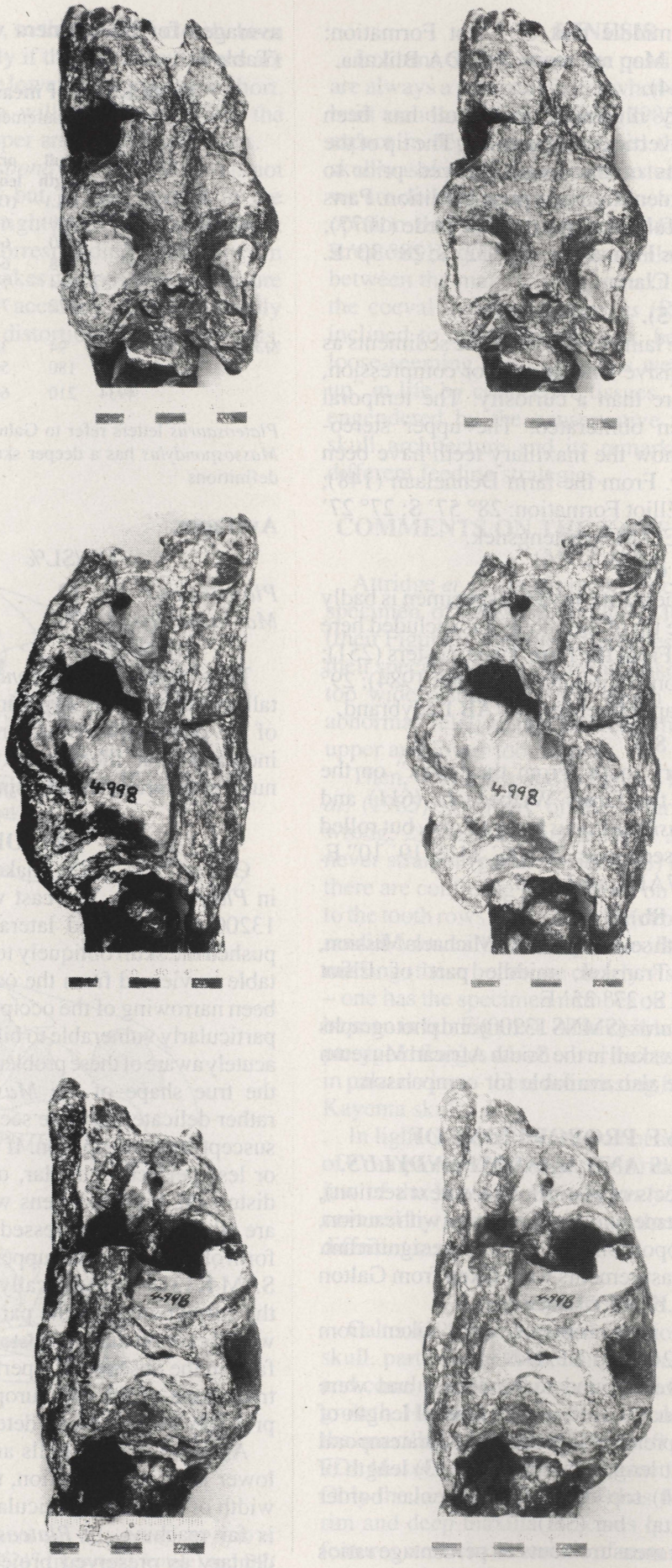


Figure 6. BP/1/4998 Dorsal and lateral stereo views of badly preserved and eroded skull.

of Transkei; from middle part of Elliot Formation: 30° 36'S; 27° 37'E. Map reference 3027DA Blikana.

BP/1/4779 (Figure 4).

As the orbit clearly illustrates, this skull has been distorted by oblique vertical compression. The tip of the lower jaw and parts of the snout decayed prior to fossilisation and the dentition is in poor condition. Parts of the palate are useful. From the farm Tevrede (1077); lower part of Clarens Formation: 28° 32' S; 28° 30' E. Map sheet 2828CB Clarens.

BP/1/4930 (Figure 5).

This skull must have lain nose down in the sediments as it has suffered extensive anteroposterior compression, making it little more than a curiosity. The temporal openings have been obliterated. The upper stereophotograph shows how the maxillary teeth have been compacted together. From the farm Dennelaan (148); from upper part of Elliot Formation: 28° 57' S; 27° 27' E. Map sheet 2827CD Mekoatlengsnek.

BP/1/4998 (Figure 6).

This sun-cracked, haematite-invaded specimen is badly eroded and lacks the tip of the snout; it is included here for the record only. From the farm Twee Zusters (251); *Tritylodon* Acme Zone (Kitching and Raath 1984): 29° 03'S; 27° 26' E. Map reference 2927AB Ladybrand.

BP/1/4952 (Figure 8c).

Isolated premaxillary tooth. From the "neck" on the boundary between the farms Welbedacht (611) and Edelweiss (698); *Euskelosaurus* Range Zone, but rolled from higher up the sequence: 29° 06' 24"S 19' 10" E. Map reference 2927AB Ladybrand.

BP/1/5293 (Figure 8b).

Dentary fragment with several teeth. St. Michaels Mission, Herschel district, Transkei; middle part of Elliot Formation: 30° 30' S; 27° 25' E.

A cast of *Plateosaurus* (SMNS 13200) and photographs of a *Massospondylus* skull in the South African Museum (SAM K1314) were also available for comparison.

RELATIVE PROPORTIONS OF *PLATEOSAURUS* AND *MASSOSPONDYLUS*.

Owing to the effects of distortion (see next section), comparative measurements must be regarded with caution, but the following proportional differences are significant.

Plateosaurus measurements were taken from Galton (1985: figs 8, 9 – n.b. reconstructions).

Massospondylus measurements were taken from BP/1/4376, BP/1/5241 and BP/1/4934.

Measurements were found to be erratic and were discarded. Those finally used were: 1) total length of skull – from tip of premaxilla to tip of supratemporal (SL). 2) mid height length of orbit (OL). 3) length of premaxilla (PL). 4) top of skull to alveolar border through the preorbital bar (SH).

Expressing these measurements as percentage ratios of skull length gave consistent results that could be averaged for both genera with the following results (Table I):

Table 1. List of measurements & ratios

Measurements in mm

		skull length (SL)	orbit length (OL)	premax length (PL)	skull height (SH)	% OL/SL	% PL/SL	% SH/SL
Plateosaurus	A	340	64	52	88	19	15	25
	D	340	64	48	96	19	15	28
	F	348	64	48	86	29	15	25
	G	344	72	44	96	19	15	28
	J	372	72	44	92	19	15	25
Massospondylus	4376	94	30	10	32	32	15	34
	5241	180	50	25	60	28	14	33
	4934	210	60	32	78	29	14	38

Plateosaurus letters refer to Galton 1985 Figures 8 and 9.
Massospondylus has a deeper skull and larger orbit. See text for definitions

Averages:

	OL/SL%	PL/SL%	SH/SL%
Plateosaurus	19	15	25
Massospondylus	29	14	35

Thus clearly *Massospondylus* has a larger orbit in a taller skull. Perhaps surprisingly, the proportional length of the premaxilla is the same in both genera, but this indicates that the premaxillary teeth, though more numerous, are relatively smaller in *Plateosaurus*.

DISTORTION

Galton (1984, 1985a) makes scant mention of distortion in *Plateosaurus*. The cast we have examined (SMNS 13200) has suffered lateral compression, which has pushed the skull obliquely to the left relative to the skull table as viewed from the occiput. Inevitably there has been narrowing of the occiput, whose V-shape makes it particularly vulnerable to bilateral compression. We are acutely aware of these problems when trying to understand the true shape of the *Massospondylus* skull, whose rather delicate structure seems to have made it equally susceptible to distortion. If the orbit is preserved more or less perfectly circular, one can assume no vertical distortion, but specimens which satisfy this condition are all laterally compressed, so the problem of the true form of the occiput and upper temporal opening remains. SAM K1314 was vertically compressed, so may show the correct angle of the paroccipital processes, but we would caution that the postorbital region is too broad. In fact, in the absence of a perfectly undistorted skull, the true shape of the prosauropod skull in dorsal view is probably impossible to determine.

As prosauropod skulls are often preserved with the lower jaws in articulation, the effect of changes in the width of the skull (particularly in the quadrate region), is far reaching. In *Plateosaurus* (SMNS 13200) the dentary as preserved projects as far as the tip of the premaxilla; we know that the lower teeth occluded

within the arc of the uppers, so this jaw has clearly been pushed forward. Conversely if the jaw articulations are unnaturally splayed out, the lower jaw appears too short. This artefact of distortion will obviously affect the relative positions of the upper and lower tooth rows.

The best skull of *Massospondylus* (BP/1/4934) is not only laterally compressed but is also curved in the sagittal plane, resulting in a right premaxilla fully 10 mm longer than the left, with a corresponding discrepancy in mandible length. Damage makes it impossible to measure the left maxilla with any accuracy, but it certainly appears shorter. This plastic distortion is seldom obvious, but is quite common.

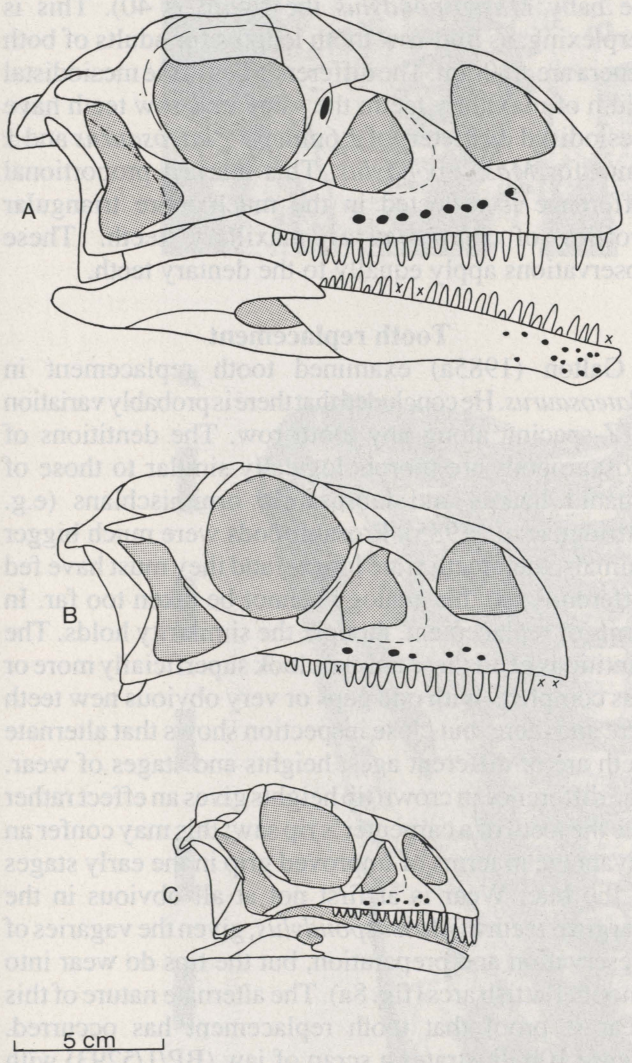


Figure 7. Outline drawings of (from top to bottom): BP/1/4934 (presumed male), BP/1/5247 (presumed female) and BP/1/4376 (juvenile). Matrix shade, "X" indicates vacant tooth positions).

KINESIS

In terms of distortion, the possible effects of kinesis are always a potential factor when dealing with a lightly built archosaur skull. Galton (1985a) has discussed this aspect in depth and concluded that the *Plateosaurus* skull was akinetic; from our own study of *Massospondylus* we are divided on this issue. One of us (MAR) is of the opinion that at the very least *Massospondylus* had a streptostylic quadrate, and a similar loose kinetic union between the maxilla and premaxilla to that reported in the coeval theropod *Syntarsus* (Raath 1977). CEG is inclined to agree with Galton, believing that several loose-seeming bony junctions were probably "locked up" in life by connective tissues. The disagreement is engendered by the conservative nature of archosaur skull architecture and its remarkable adaptability to different feeding strategies.

COMMENTS ON THE KAYENTA SPECIMEN (MCZ 8893)

Attridge *et al.* (1985) reconstruct the occiput of their specimen of *Massospondylus* (MCZ 8893) too wide (their Figure l), thus the differences they detect between their specimen and ours are all linked. An occiput that is too wide results in a jaw which is too short and an abnormal relationship between the posterior ends of upper and lower tooth rows.

Then, with reference to Figures l and 2 of Attridge *et al.* (1985): 1) many of the sutural relationships are wrong; 2) the maxillary teeth of *Massospondylus* are never straight (parallel) sided; 3) in their palatal view there are confusing lines drawn on the maxillae medial to the tooth rows which should not be there; 4) the paired medial vomers between premaxillae and palatines are missing (these bones are clearly visible in SAM K1314 – one has the specimen number on it). Vomers can also be seen in our Figure 4. Also visible in that figure are the pterygoid flanges which cover the basipterygoid processes in palatal view – these are missing from the figure of the Kayenta skull.

In light of the above we do not accept the suggestion of Crompton and Attridge (1986) that the tip of the lower jaw of the Kayenta *Massospondylus* could have been covered by a horny beak, and that it may represent a different taxon.

VARIATION

Galton (1985a) mentioned variation in the *Plateosaurus* skull, particularly thickening of the dorsal orbital rim, and concluded that this was individual variation due to growth. He did not remark on the deep posterior end of the maxilla seen in AMNH 6810 (Galton, 1985: fig. 7D). *Massospondylus* exhibits exactly the same variation. Only the largest (BP/1/4934) has the thickened orbital rim and deep maxilla. It seems quite likely that these features were characteristic of mature males – assuming the sex ratio to favour a preponderance of females.

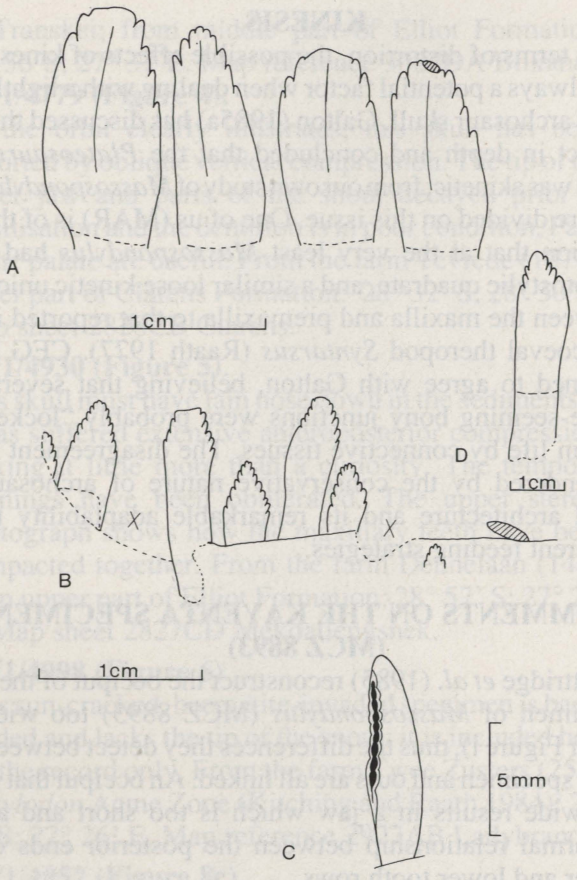


Figure 8. *Massospondylus* teeth. A. Evidence of replacement:BP/1/5247 tips of alternate teeth are worn, that on extreme right has a recent (pre-fossilisation) chip. B. Evidence of replacement. BP/1/5293 Hatching indicates broken mature tooth, "X" indicates empty tooth position; a mature tooth on the right and a small replacing bud on the left would complete the pattern of near perfect alternate replacement. C. Edge of an isolated (shed) premaxillary tooth; wear has exposed dentine. (BP/1/4952). D. Unworn tooth of sauropod *Brachiosaurus* (from Janensch, 1935).

DENTITION

Tooth morphology

The first impression of *Massospondylus* teeth is their considerable length (the same length as those of *Plateosaurus*, hence relatively longer, and several times longer than those of the functionally similar Elliot fabrosaurs). Then there is marked morphological differentiation between premaxillary and maxillary teeth in *Massospondylus*, and a greater gradation in tooth length from the front to the back of the upper tooth row than in *Plateosaurus*. Dentary teeth are of nearly uniform height. In *Massospondylus* there is a constant number of four premaxillary tooth positions. In *Plateosaurus* the number ranges from five to seven (Galton 1985a). These are the longest and most robust teeth; when serrations are present they are confined to the tips of these teeth. The lingual surfaces of premaxillary teeth have longitudinal grooves separating the sharp edges from the more rounded body of the tooth; they are thus essentially piercing and cutting teeth.

In the available specimens, the number of maxillary tooth positions ranges from 14 to 22 with increasing skull size (*Plateosaurus* can have as many as 30 maxillary tooth positions). There are 26 dentary tooth positions in the largest specimen of *Massospondylus*. These lateral teeth have flattened leaf-like crowns thickening towards the roots and slightly waisted where the enamel ends. On their labial surfaces they go from rounded to having two barely perceptibly, longitudinally offset, flattish surfaces towards the tips. Lateral teeth are slightly offset and overlapping in such a way as to ensure a continuous cut. The number of "serrations" is variable within and between specimens (three to eight) and doubtless also between different generations of teeth. "Serrations" extend further down the posterior edge than the anterior, as is sometimes the case with carnivorous reptile dentitions as well.

An apparently contradictory aspect of the dentition is that *Massospondylus* has relatively more teeth per unit length of maxillary row than does *Plateosaurus* (the ratio % figures for adults are 24 and 16 respectively; for the baby *Massospondylus* the figure is 40). This is perplexing, as mid-row tooth lengths for adults of both genera are ± 10mm. The difference lies in the mesiodistal width of maxillary teeth: the same mid-row teeth have mesiodistal diameters of ± 6mm for *Plateosaurus* and ± 4mm for *Massospondylus*. This marked proportional difference is reflected in the much more triangular profiles of *Plateosaurus* maxillary teeth. These observations apply equally to the dentary teeth.

Tooth replacement

Galton (1985a) examined tooth replacement in *Plateosaurus*. He concluded that there is probably variation in Z-spacing along any tooth row. The dentitions of prosauropods are morphologically similar to those of iguanid lizards and fabrosaurid ornithischians (e.g. Attridge *et al.*, 1985). Prosauropods were much bigger animals, their teeth were longer, and they must have fed differently, so this analogy cannot be taken too far. In terms of replacement, though, the similarity holds. The dentitions of all these animals look superficially more or less complete, with odd gaps or very obvious new teeth here and there, but close inspection shows that alternate teeth are of different ages, heights and stages of wear. The difference in crown tip heights gives an effect rather like the teeth of a carpenter's rip saw; this may confer an advantage in terms of improved grip in the early stages of the bite. Wear is at first not at all obvious in the marginal teeth of *Massospondylus*, given the vagaries of preservation and preparation, but the tips do wear into smooth flattish arcs (fig. 8a). The alternate nature of this wear is proof that tooth replacement has occurred. Figure 10b illustrates a scrap of jaw (BP/1/5293) with active alternate replacement affecting a sequence of ten tooth positions. In the absence of dentitions prepared from the lingual surface, the order of eruption of teeth cannot be precisely determined.

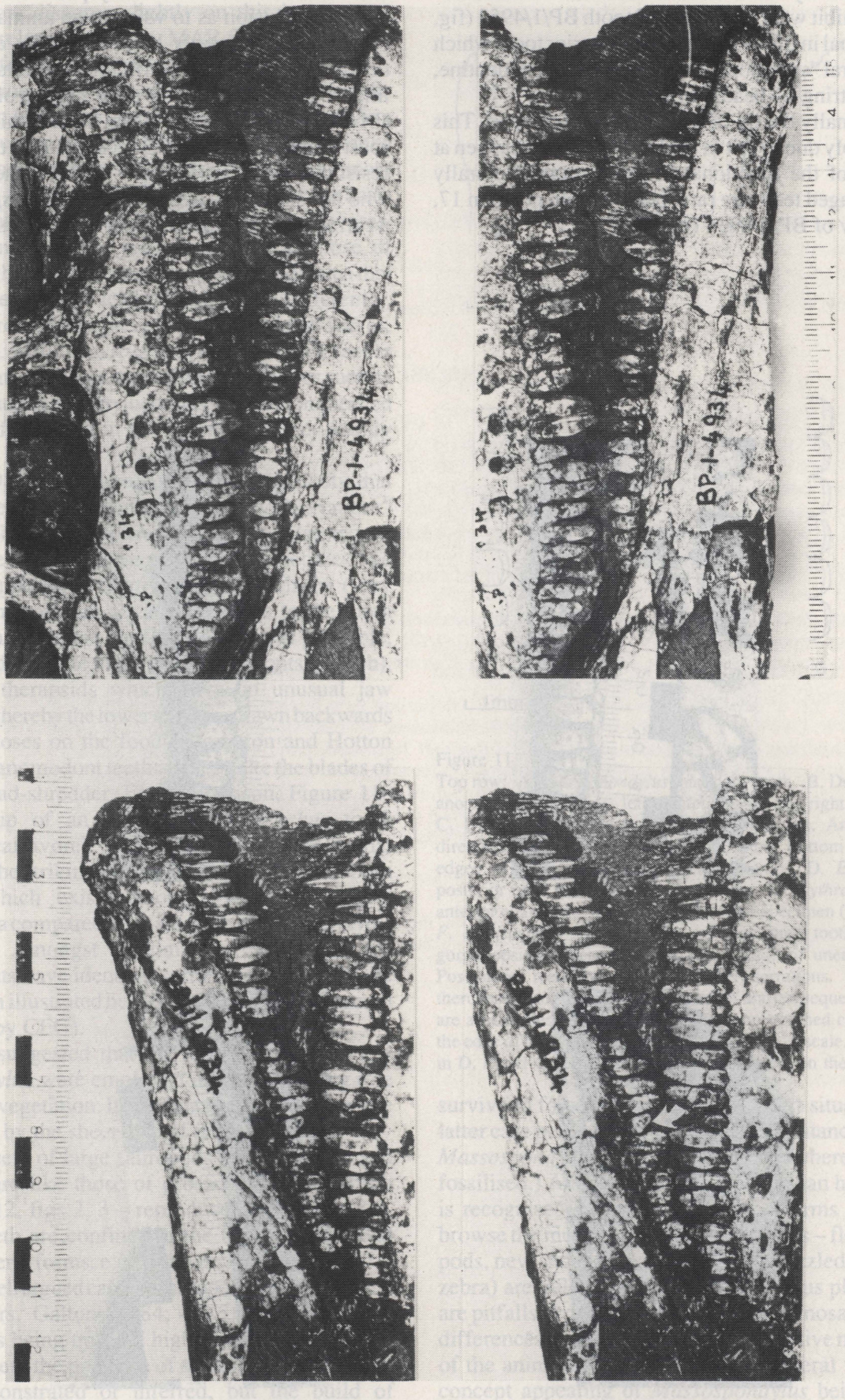


Figure 9. BP/1/4934 Stereo views of left and right dentitions. Arrow indicates tooth broken prior to fossilisation.

Replacement turnover was clearly rapid, as one does not find heavily worn teeth. The lateral "serrations" seldom exhibit wear. The isolated tooth BP/1/4952 (fig. 8c) is unusual in this respect; it is an anterior tooth which has the lateral "serrations" worn away to expose dentine, giving a "string-of-beads" effect.

Occasionally the tip of a tooth may be chipped. This was probably due to grit in the food and could happen at any stage of the functional life of a tooth. Naturally badly damaged teeth are rare, but see tooth position 17, left dentary of BP/1/4934 (fig. 7).

DIET OF *MASSOSPONDYLUS*

In broad terms it is usually possible to arrive at a sound conclusion as to whether an animal was mainly carnivorous or mainly herbivorous by examining its dentition. What is more difficult is to exclude all sorts of improbable items from the potential diet of either group. (MAR once kept a squirrel that liked nothing better than roast chicken, while CEG recalls a dog that could not resist raw tomatoes). Cooper (1981) is the only worker who has seriously suggested that *Massospondylus* was a carnivore. The chief merit of this suggestion has been

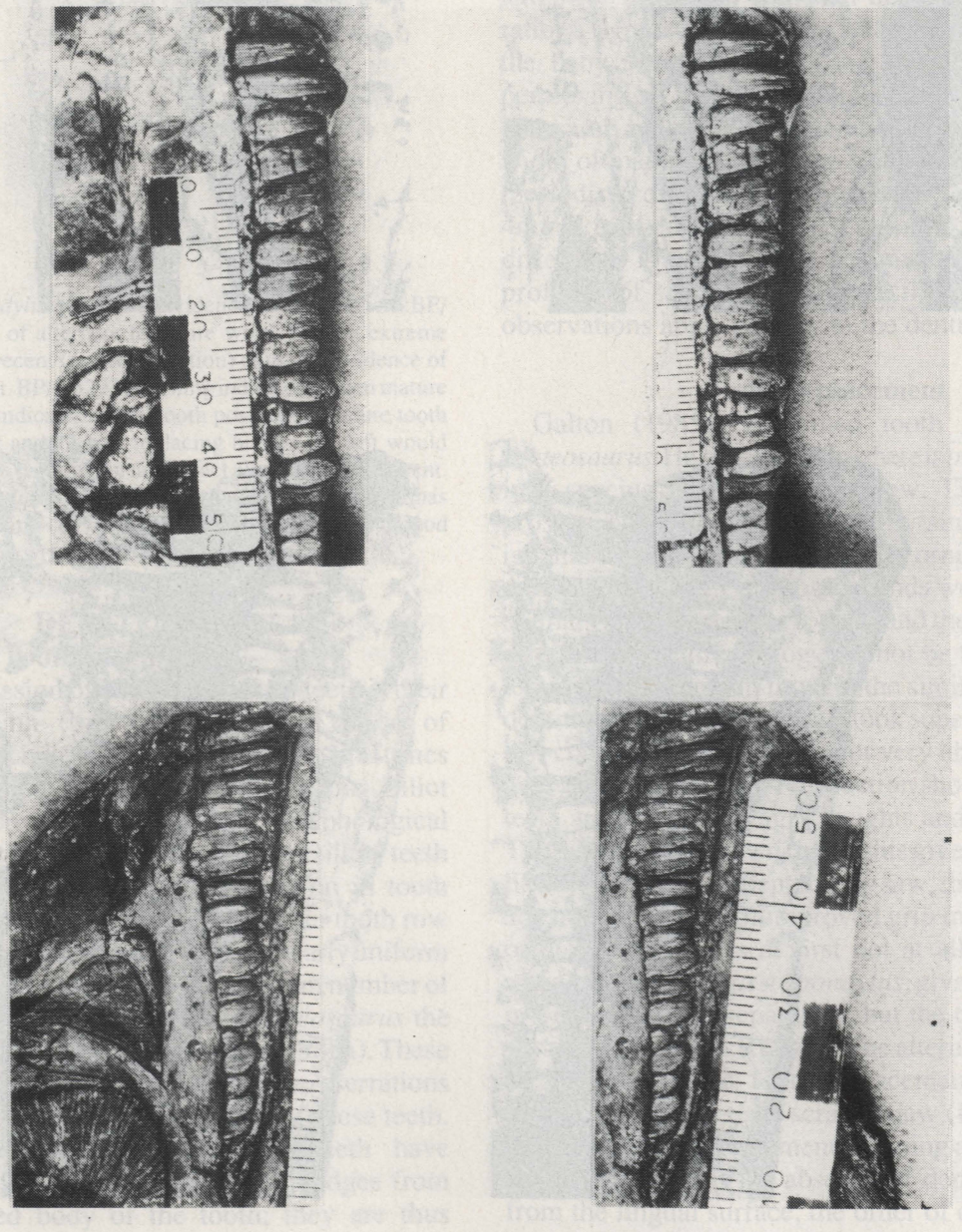


Figure 10. BP/1/5247 above; BP/1/4376 below. Stereo photographs of dentitions of best side.

to elicit the exhaustive refutations of Galton (1984, 1985), who has laboured the case for herbivory. The present authors disagree slightly on this issue, CEG agreeing entirely with Galton, MAR favouring a more catholic diet for *Massospondylus*.

The question of the diet of *Massospondylus* can be approached in several different ways. Most compelling is the ecological approach. Galton (1985b) has claimed that prosauropods account for at least 95% of the biomass of the known faunas in which they occur. On the basis of this estimate they could only have been herbivores. The great length of the teeth compared to those of fabrosaurs, which are structurally similar, indicates that these two herbivores utilised the flora differently. Fabrosaurs probably bit pieces out of individual leaves, as do iguanas, while *Massospondylus* was a bulk feeder on soft vegetation. (More specialised herbivores such as heterodontosaurids and tritylodontids – which commenced breakdown of the food in the mouth – are not readily comparable).

Galton (1985b) has demonstrated conclusively that the marginal teeth of reptilian herbivores have "serrations" angled to follow the direction of bite (he claimed 45 degrees to the tooth axis; we prefer 10 - 20 degrees, see fig. 8a), as opposed to carnivores, in which the (very different) serrations are set at 90 degrees to the tooth axis. As an independent confirmation of this principle, we illustrate dentary teeth of two anomodonts (fig. 11b), herbivorous therapsids which have an unusual jaw mechanism whereby the lower teeth are drawn backwards as the jaw closes on the food (Crompton and Hotton 1967). These anomodont teeth are very like the blades of a kitchen salad-shredder. For comparison, Figure 11c shows the tip of an unworn *Erythrosuchus* tooth (undoubted carnivore). The lower illustrations in that figure show the striking uniformity in the shape of tooth serrations which exists amongst widely divergent carnivore taxa compared, to scale, with *Massospondylus* "serrations". Amongst mammalian carnivores, the sabretooth cats have identical serrations to those of the gorgonopsian illustrated here (Martin 1980 and personal observation by CEG).

We have suggested that the long delicate teeth of *Massospondylus* were employed in a bulk feeding role utilising soft vegetation. Indeed such a bulk feeding role is predicated by the sheer size of the animal.

Unworn teeth of large sauropods in the Jurassic and Cretaceous are like those of prosauropods (Janensch 1935: Plate 12, figs 2, 3 – reproduced as our fig. 8d). Sauropod teeth are confined to the front of the broad mouth in several forms, e.g. *Diplodocus*. Bakker (1971) presented a well argued case for sauropods being terrestrial high browsers. Galton (1984, 1985) has argued for prosauropods being tripodal high browsers. This is all very well where the presence of suitable tall vegetation can be demonstrated or inferred, but the build of prosauropods would make them ideal survivors in badly degraded habitats as well. (African elephants at present

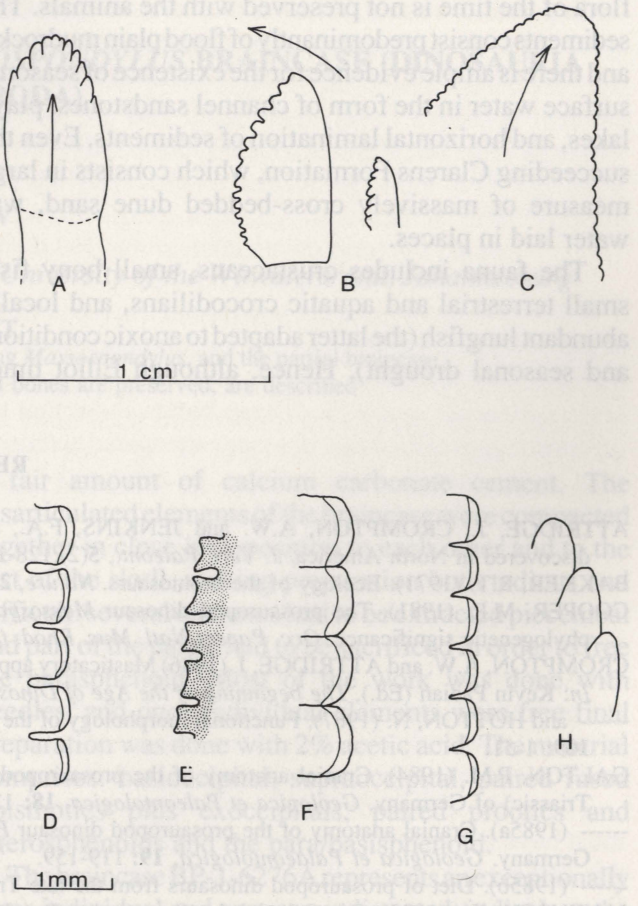


Figure 11.
Top row: A. *Massospondylus* maxillary tooth. B. Dentary teeth of anomodont therapsids: left, *Endothiodon*; and right, *Pristerodon*. C. Unerupted dentary tooth of *Erythrosuchus*. Arrows indicate direction of movement during jaw closure. Bottom row: serrated edges of teeth of several unrelated taxa: D. *Erythrosuchus*: posterior edge of unworn dentary tooth. E. *Erythrosuchus*: worn anterior edge of another tooth in the same specimen (tooth shaded). F. *Rauisuchus*: posterior edge of unerupted tooth. G. Indet. gorgonopsian (Therapsida): posterior edge of unerupted canine. Postcanine teeth have slightly finer serrations. The teeth of therocephalians do not have sharp edges and consequently serrations are absent. Serrations also appear in sabre-toothed cats. H. Part of the edge of tooth figured in A for comparison of scale. The fine lines in D, F and G delimit the translucent enamel on the cutting edge.

survive in forest, bush and semi-desert situations – the latter case perhaps closest to the circumstances in which *Massospondylus* existed in those areas where its remains fossilised.) Amongst modern mammalian herbivores it is recognised that narrow muzzled forms (e.g. kudu) browse the more nutritious parts of trees – flowers, seed pods, new shoots etc., while broad muzzled forms (e.g. zebra) are bulk feeders on less nutritious plants. There are pitfalls in drawing analogies with dinosaurs, such as differences in plant foods, and the digestive mechanisms of the animals themselves, but in general we find the concept appealing of *Massospondylus* being, at least seasonally, a fastidious feeder. Actual breakdown of the food took place in the stomach, aided by gastroliths

(Raath 1974). In respect of the environment in which *Massospondylus* lived, we still know too little. The flora of the time is not preserved with the animals. The sediments consist predominantly of flood plain mudrocks, and there is ample evidence for the existence of seasonal surface water in the form of channel sandstones, playa lakes, and horizontal lamination of sediments. Even the succeeding Clarens Formation, which consists in large measure of massively cross-bedded dune sand, was water laid in places.

The fauna includes crustaceans, small bony fish, small terrestrial and aquatic crocodilians, and locally abundant lungfish (the latter adapted to anoxic conditions and seasonal drought). Hence, although Elliot times were relatively dry, there is good evidence for seasonal rain and a scattering of permanent water sources. Perhaps subsurface water supported vegetation in river courses. *Massospondylus* probably fed on the growth in and around various bodies of water, dispersing after rains and coming together in larger herds during the drier months.

ACKNOWLEDGEMENTS

We would like to acknowledge the help of Rupert Wild in arranging to obtain a cast of *Plateosaurus* (SMNS 13200) from Stuttgart for the Bernard Price Institute, and the hospitality and help extended to JWK by the various farmers on whose land he collected most of the specimens. CEG wishes to record his appreciation of the kind hospitality of the Hepburns of Fort Hook which made possible the collection of BP/1/4376 and BP/1/5293.

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