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FEEDING ADAPTATIONS IN TRIASSIC DICYNODONTS

by

A. R. I. Cruickshank

ABSTRACT

The Dicynodontia declined markedly at the close of the Permian, entered the Triassic with very few species and had a final burst of evolutionary success in the Middle Triassic, before being overcome by archosaurian competitors in the Upper Triassic. The structure of their skull is analysed in terms of life habit and it is concluded that in all probability the most likely close analogues to the Triassic Dicynodontia were the ground sloths of the American Neogene. Browsing and grazing modes of life are recognised. It is also postulated that tusks in the Triassic Dicynodontia were used for display purposes, and that tuskless forms were either nocturnal, or lived in thick undergrowth.

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INTRODUCTION

General

The dicynodonts were the dominant herbivores of the Gondwanaland Upper Permian, were of much lesser importance in the Lower Triassic, and in the Middle Triassic had a brief resurgence. They were replaced by the end of the Upper Triassic by herbivorous dinosaurs. Their basic jaw mechanism was established very early in their history and is first seen in the Russian Middle Permian genus, *Venjukovia* (Barghusen, 1976). This unique masticatory apparatus (Crompton and Hotton, 1967) was apparently retained throughout their history.

The greatest adaptive radiation of the dicynodonts was in the Gondwanaland Upper Permian and seems to coincide with the development of the *Glossopteris* flora. At the Permo-Triassic boundary there was a change from a *Glossopteris*-dominated flora to one which became typified by *Dicroidium*. This change is marked by a parallel change in the fortunes of the dicynodonts, very few genera apparently surviving into the Lower Triassic (Middle and Upper Beaufort), and thus allowing the now vacant niches to be filled with herbivorous representatives of other groups (e.g. cynodonts, bauriamorphs and cotylosaurs (Anderson and Anderson, 1970; Gow, 1978)).

One line of dicynodonts which seem to have survived the Permo-Triassic hiatus more successfully than the others was the descendants of the genus *Odontocyclops* and its relatives (Keyser and Cruickshank, in prep.). It is assumed that they were either pre-adapted to a *Dicroidium*-based diet or actually feeding on a Permian *Dicroidium* ancestor.

The physical environment and flora of the Triassic

In South Africa the Upper Beaufort (*Cynognathus* zone) represents a flood plain deposit, typified by sediments laid down by meandering rivers, with a high proportion of interdistributory fines. It is best developed in the south, reaching a thickness of 600 m there, but thins out completely beyond Aliwal North towards Rouxville. Palaeocurrent measurements indicate a palaeoflow direction from south to north, which coincides with those of the overlying Bamboesberg member of the Molteno Formation. The terrain supplying those sediments was a granite highland off the present South African coast. Thus the *Cynognathus* zone fauna was a lowland fauna.

The position of the *Cynognathus* zone is high in the Scythian, which indicates a late Lower Triassic age (Turner, pers. comm.; Cruickshank, 1978).

The Molteno Formation, which overlies the *Cynognathus* zone and is of Carnian age and from which has come the richest and best known of the Triassic floras, represents a series of deposits typical of a braided river system of higher energy than represented by the *Cynognathus* zone. It is believed to have been laid down in a series of alluvial fans under cool, seasonal conditions with permanent ice in the mountain hinterland. The "Molteno flora" seems to coincide with an upsurge in the fortunes of the dicynodonts elsewhere and is thus of some importance. No tetrapod vertebrates are, however, known from the Molteno Formation, and the flora is dominated by the ubiquitous genus *Dicroidium* (Turner, 1969; 1971; 1975; in prep.)

TABLE 1
Triassic floras and their growth habit

Taxon	*Cynognathus* zone South Africa	Molteno Formation South Africa	Middle to Upper Trias S. America	India Rewa Basin	Growth habit
Bryophyta		2 g 2 spp			Ground cover; damp shade
Lycophyta		1 g 2 spp		3 g 3 spp	Halophyte: near sea: pollen only
Sphenophyta	1 g 1 sp	5 g 9 spp	3 g 8 spp	3 g 3 spp	Swamp dweller; bamboo-like
Filicophyta		3 g 4 spp	5 g 14 spp		Ferns and relatives; low growth
Pteridophylla	1 g 1 sp	9 g 22 spp	10 g 35 spp	2 g 6 spp	Ground cover, low growth (fern leaf)
Glossopteridophyta		1 g 2 spp	1 g 1 sp	2 g 9 spp	Deciduous trees?
Pteridospermophyta	4 g 8 spp	3 g 24 spp	2 g 19 spp	2 g 8 spp	Deciduous shrub? or low ground cover
Cycadophyta	3 g 5 spp	2 g 20 spp	6 g 20 spp	3 g 4 spp	Leaves and "fruit" growing from elevated bole
Ginkgophyta	1 g 1 sp	3 g 10 spp	8 g 20 spp	2 g 2 spp	Small trees and shrubs
Coniferophyta	1 g 2 spp	1 g 3 spp	2 g 2 spp	3 g 3 spp	Large trees

Information summarised from Anderson and Anderson (1970, Charts 11, 12, 19) and Anderson, H. M. (pers. comm.)

However, floras which grew contemporaneously with the Triassic dicynodonts have been described from India, South Africa and South America. As they are all generally similar, so the physical environment may well have been much the same as in South Africa. These floras are summarised in Table 1 with their growth habit (Anderson, H. M., 1974; 1976).

FEEDING BEHAVIOUR IN TRIASSIC DICYNODONTS

In the Triassic, the dicynodonts followed two main adaptive trends in skull morphology. The trends are typified by forms such as the *Cynognathus* zone genus *Kannemeyeria*, which has a narrow rounded snout, and others, seemingly more common, which have blunt snouts. The two groups thus defined were accorded familial status by Cox (1965) as the Kannemeyeriidae and Stahleckeriidae respectively. However, Keyser and Cruickshank (in prep.) prefer to regard all the larger Triassic dicynodonts as belonging to one family (the Kannemeyeriidae) which comprises four sub-families. A different grouping of broad-snouted forms, the Dinodontosaurinae, is the most common, with the Kannemeyeriinae reserved for narrow-snouted contemporaries.

While trying to justify the creation of these families on functional grounds, Cox compared their adaptations to those seen in modern African rhinos. These latter are broadly distinguished on lip shape, and the orientation of the occipital region of the skull. Thus the "black" rhino, *Diceros bicornis*, has a pointed prehensile upper lip and carries its head parallel to the ground, and thus has an occiput at right angles to the palate. The "white" rhino, *Ceratotherium simum,* has a broad upper lip, carries its head close to the ground and has a sloping occiput. The former is a browser, the latter a grazer.

The significance of these contrasting adaptations of the occiput lies in the relationship of the occipital plate to the line of the cervical vertebrae. In all tetrapods, and particularly the mammals, this angle is almost a constant 124 degrees (Westoll, pers. comm.). Thus in a tetrapod, by varying the angle that the occiput makes with the palatal plane, the head will be carried nearer to or farther from the ground. It is this variation which distinguishes the two rhinos and also the two major evolutionary lineages of Triassic dicynodonts.

Unfortunately, as Cox (op. cit.) noted, the broad-snouted dicynodonts have occiputs at right angles to their palates and the narrow snouted forms have sloping occiputs. There is, incidentally, no significant variation in the width to height proportions of the occiputs of both these dicynodont families. Their occiputs are almost universally low wide plates formed largely from the expanded squamosals (Keyser and Cruickshank, in prep.).

Thus the expected browser carries its head close to the ground and vice versa. Also rhinos, being mammals, have fleshy lips, but the dicynodonts seem to have had their snouts and lower jaw tips covered in horn, rather like modern turtles and tortoises. Therefore a comparison of the way of life of anomodonts and rhinos seems to be tenuous to say the least, but the broad division of the Triassic dicynodonts into functionally contrasting groups is a valid concept. However, comparison of reconstructions of Triassic anomodonts with modern rhinos demonstrates that the former are very much smaller than the latter (fig. 1). Further comparisons of size and body form seem to indicate that the anomodonts are closer to pigs in size. Choosing two modern African forms we find the warthog, *Phacochoerus aethiopicus,* with a sloping occiput and the bushpig, *Potamochoerus porcus,* with an upright occiput. The snouts of the two pigs, being used in a similar manner to turn over the soil and vegetation in search for choice pieces of food, do not contrast. The warthog is a diurnal selective grazer with fairly prominent tusks (Ewer, 1958). It uses the sloping occiput to position its incisors for carefully cropping off the growing ends of new grass. The bushpig, on the other hand, is a nocturnal browser-cum-omnivore with relatively indistinct tusks. The former

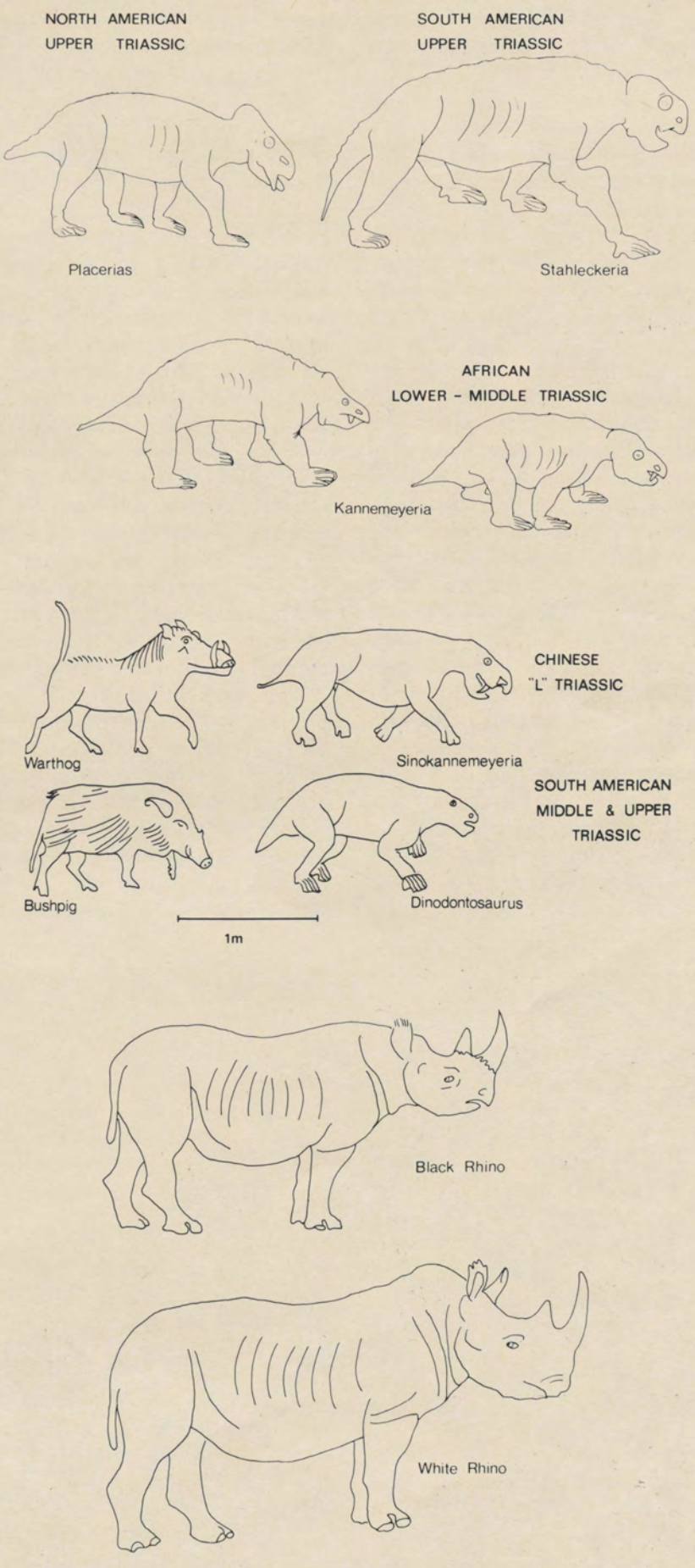


Figure 1. Reconstruction of several Triassic dicynodonts compared with two species of rhino and two species of wild pig. Details from various authors. All to same scale.

feeds very largely in the open and the latter is secretive in its habits and prefers dense cover if it is at all active during daylight hours (Smithers, 1971; Dorst and Dandelot, 1970).

If these pigs can be taken as analogues of the two main Triassic dicynodont sub-families, then it follows that the narrow-snouted dicynodonts fed close to the ground (i.e. were the selective "grazers" of the Triassic) and that the broad-snouted forms fed at head height (i.e. were "browsers"). The former could be considered selective feeders in the sense that their narrow snouts would allow them to "graze" with some precision on the ground cover or the growing tips of emerging plants or even perhaps fructifications growing low down. The others would be more likely to take their food from what was available at head height and thus they may have been entirely leaf eaters or, perhaps, adding to their diets fructifications growing at the end of branches.

Further analysis of the problem introduces, firstly, the question of whether it is possible to compare a relatively active animal like a pig with what was clearly a pretty sluggish animal, the dicynodont (e.g. *Kannemeyeria* as reconstructed by Pearson, 1924). Secondly, these comparisons ignore what was happening to the vegetation at heights greater than 1,0 m above ground (fig. 1), the normal maximum head height of a dicynodont.

The pigs under discussion here are part of a complex ecological picture in which herbivores form a community browsing and grazing on vegetation at virtually all levels, i.e. from elephants and giraffes through a range of browsers to such forms as zebras (grazing "bull-dozers") and the more selective grass eaters of the open plains. Thus each species in the African context has its own level of feeding and preferred diet (Grzimek and Grzimek, 1960).

The Triassic dicynodonts, on the other hand, were, to begin with, part of an impoverished anomodont fauna, only reaching a reasonable size in the *Cynognathus* zone. In the Beaufort, the enormous dicynodont radiation of the Permian (200 "species") gave way to the *Lystrosaurus* zone with six to nine species and then to the *Cynognathus* zone with perhaps three species. At the same time other groups (cynodonts, bauriamorphs and cotylosaurs) moved in to take over the now vacant niches, but these were all in the small-to-medium size category, much smaller than the majority of the dicynodonts (*Myosaurus* and *Kombuisia* excepted) (Gow, 1978).

These few early Triassic dicynodonts were never able to establish a lineage as dominant as their Permian ancestors, but as *Dicroidium* underwent an adaptive radiation of its own (Anderson, 1976) so the fortunes of the dicynodonts seemed to improve. However, they could never have been as active as most modern mammals, and only produced large species very late in the Triassic (e.g. *Stahleckeria*); thus the problem of the high level forager still requires solving.

Two ways in which high level vegetation can be brought down to ground level are, firstly, to push the plants over or, secondly, to pull the branches down to feeding level. Triassic dicynodonts could probably have done both. For instance, the reinforcing of the skull roof (Camp, 1956) in these forms could be an adaptation for pushing over vegetation. Likewise, the forefeet of dicynodonts in general and some Triassic forms in particular have long ungual

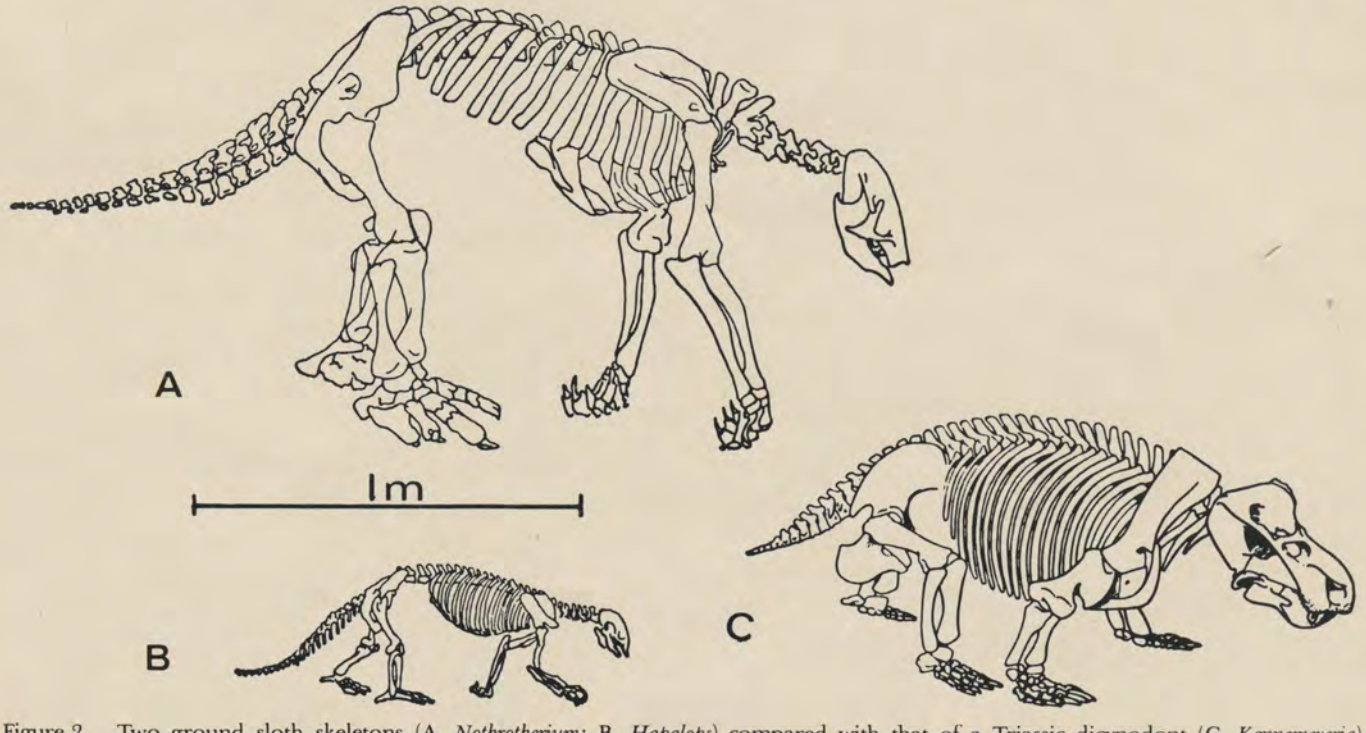


Figure 2. Two ground sloth skeletons (A, *Nothrotherium*: B, *Hapalops*) compared with that of a Triassic dicynodont (C, *Kannemeyeria*). The former from Stock (1925) and the latter from Camp (1956).

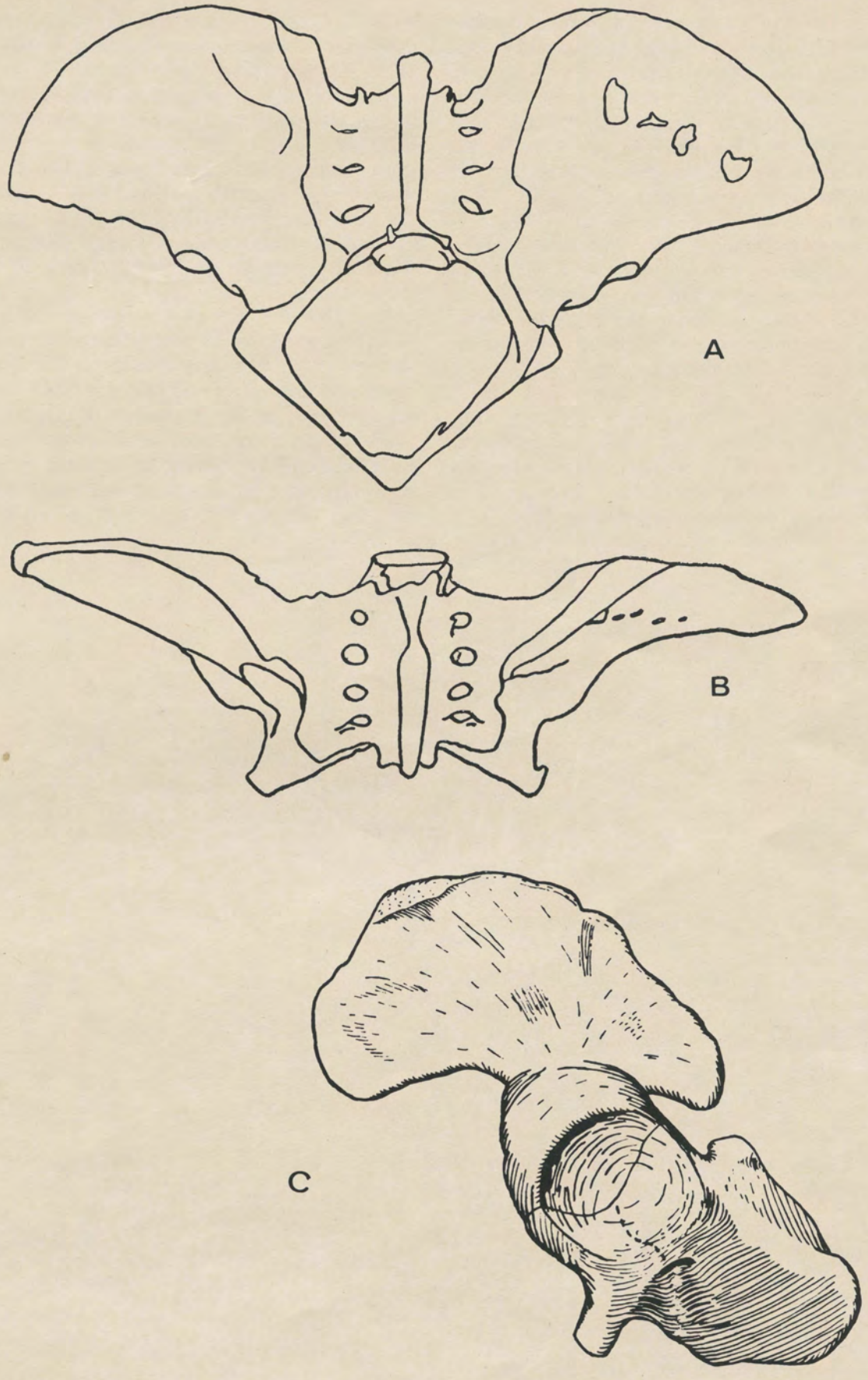


Figure 3. Pelves of a ground sloth, *Nothrotherium* (A and B), and *Ischigualastia* (C) for comparison. The expanded wing-like shape of both is undoubtedly an adaptation for the support of large digestive tracts. From Stock (1925) and Cox (1965).

phalanges capable of an extreme of flexure (Cruickshank, 1967) and which could act as powerful hooks to pull leaf bunches towards the mouth. Therefore, a search was instituted for a mammalian form which could provide a parallel for these projected functions, and, surprisingly perhaps, one was found which did seem to fill these requirements: the "ground sloths" amongst the edentates (fig. 2).

These were a group of presumably sluggish terrestrial herbivores, by analogy with the surviving tree sloths, which were extremely common in the South American Neogene, spreading into North America and the West Indian islands in the Plio-Pleistocene. Some were of moderate size *(Hapalops)* and some very large indeed *(Megatherium, Megolonyx)* (Romer, 1966).

Their post-cranial skeletons were strikingly convergent with the dicynodonts. Their vertebral columns seem to have had a similar upward sweeping smooth curve; the pelvic girdle, hind limb and fore limb and manus are also very similar (figs. 3–6). Ground sloths are frequently pictured squatting on their hind limbs and pulling branches into the reach of their long prehensile tongues (fig. 7).

Thus the picture that now emerges from this study is that the plant-eating niches of the Triassic could have been filled by a variety of reptile groups in the Lower and Middle stages (Gow, 1978). Those niches suitable for small-to-medium sized "grazers" and "browsers" were possibly filled by the gomphodont cynodonts, bauriamorphs and procolophonids, those requiring larger animals being filled by the dicynodonts.

It is clear that the dicynodonts may well have had as wide a range of feeding preferences as must have the ground sloths and that both "browsing" and "grazing" forms existed side-by-side. The former are envisaged as being capable of reaching into the lower branches of trees, while either squatting on their haunches or rearing up and dragging bunches of leaves into their mouths by means of their powerful claws (fig. 8). The latter was probably the more

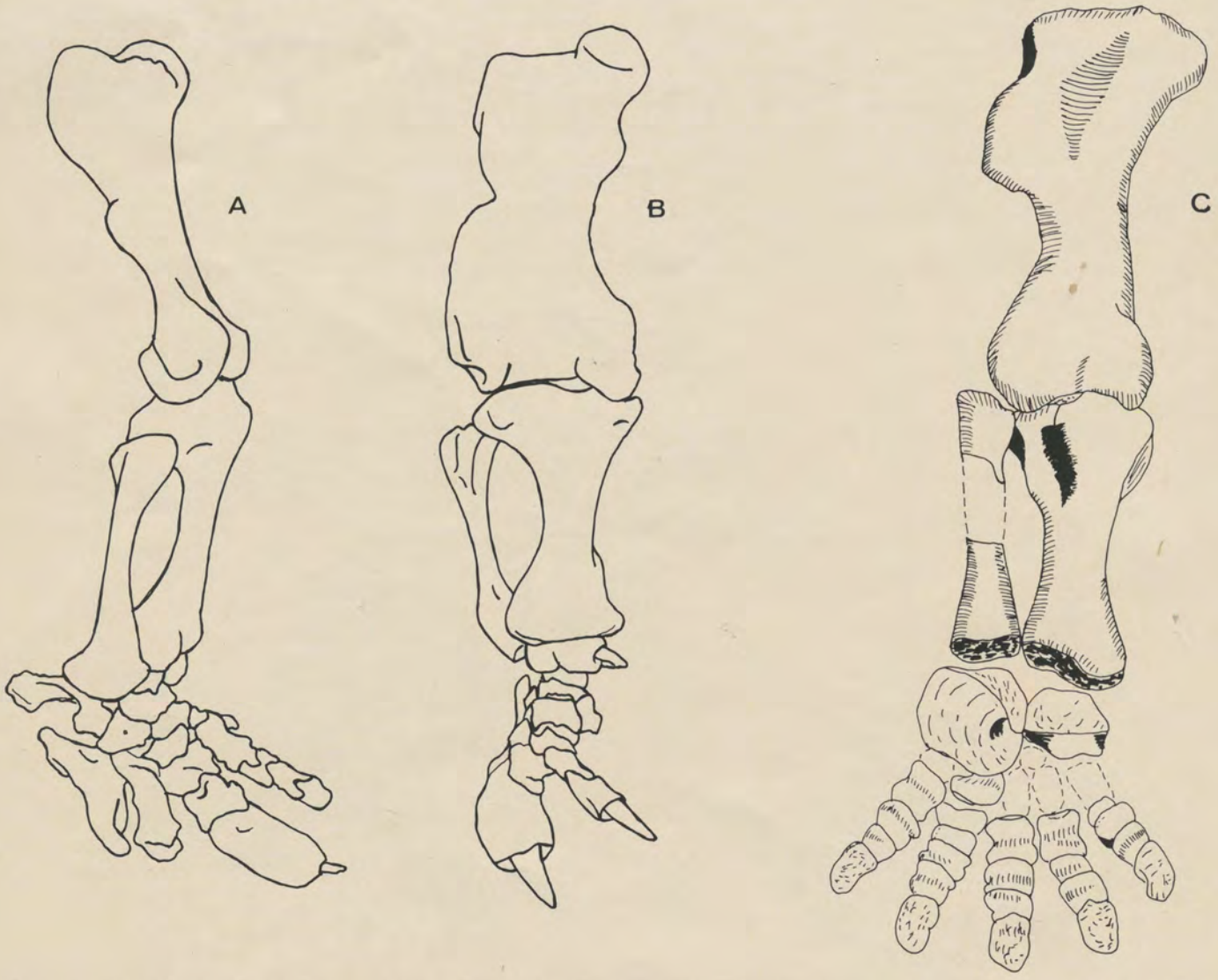


Figure 4. Hind limbs of *Nothrotherium* (left, A and B) and *Ischigualastia* (right, C) reduced to same size to show overall similarities of the pro- and epi-podials. The feet are quite distinct. From Stock (1925) and Cox (1965) respectively.

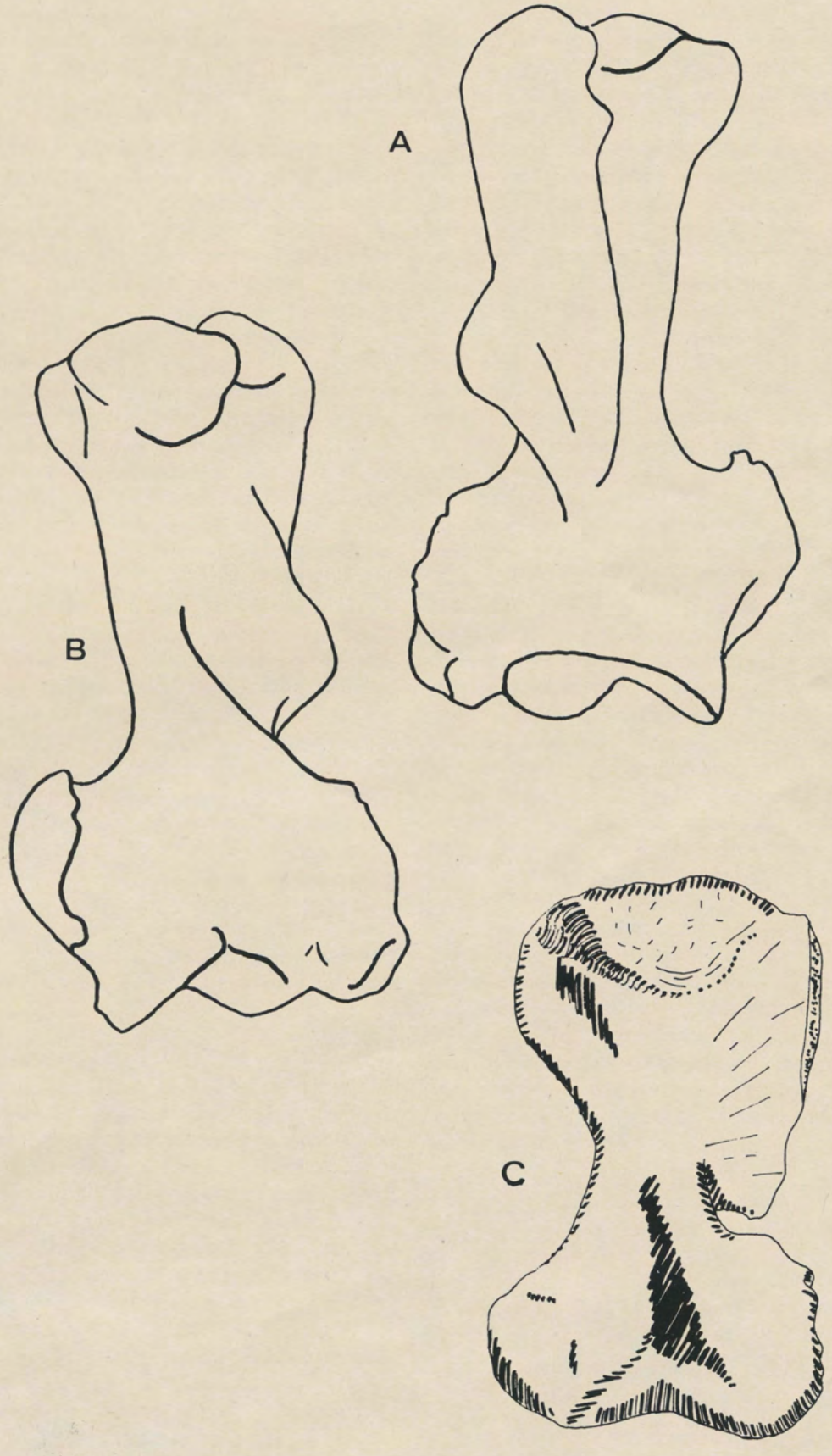


Figure 5. Humeri of *Mylodon* (A and B) and *Ischigualastia* (C) reduced to same approximate size to show the same overall pattern, with expanded distal ends and prominent delto-pectoral crests. From Stock (1925) and Cox (1965) respectively.

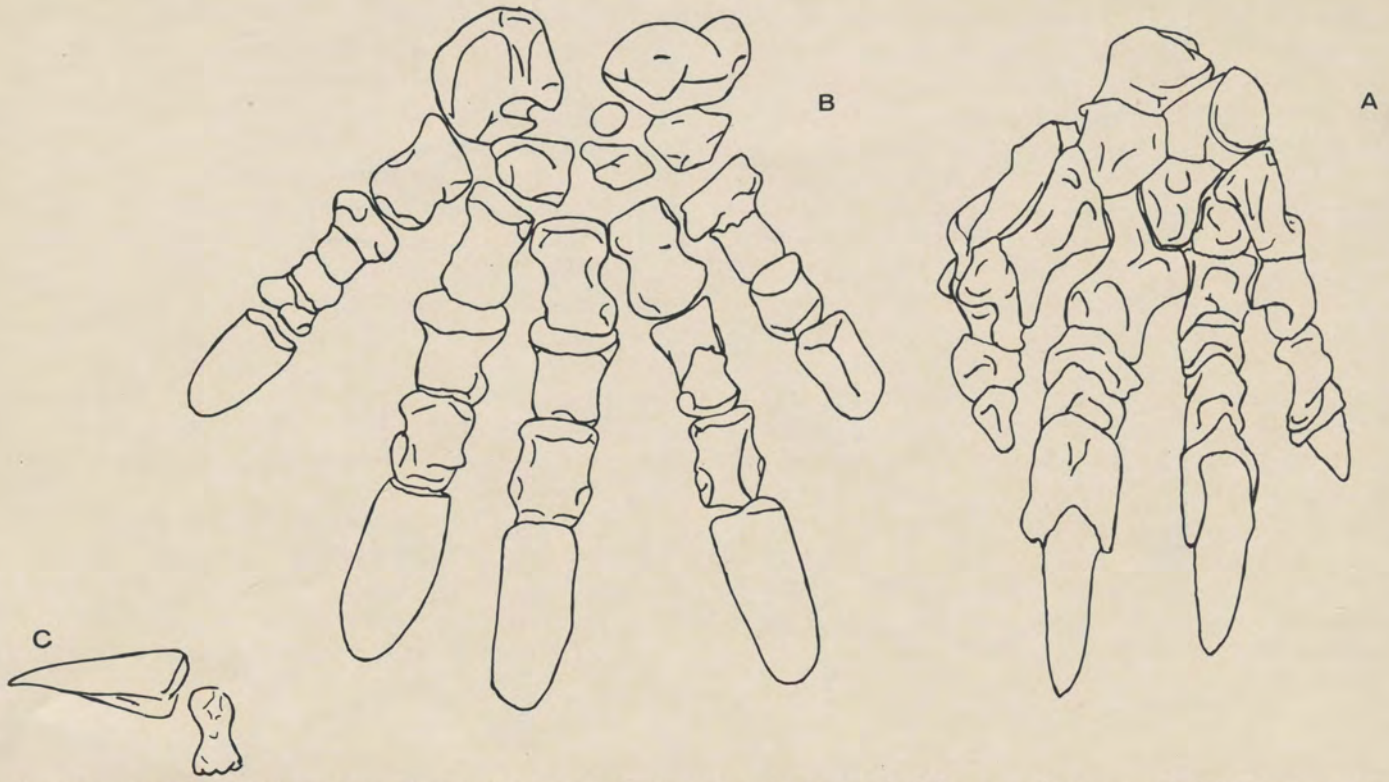


Figure 6. Forefeet of *Mylodon* (right, A) and *Tetragonias* (left, B) to show long ungual phalanges and a presumed ability in the latter (C) to flex these substantially. Reduced to same size from Stock (1925) and Cruickshank (1967).



Figure 7. Reconstruction of *Nothrotherium* (from Stock, 1925).

likely as the elongated ischium and substantially built, though short, tail could quite well have accommodated muscles sufficiently powerful to enable a dicynodont to rear up (Cox, 1965, fig. 11). The powerful hooked digits of the fore feet are also well adapted to assist in this action. Squatting may well have been a difficult action for dicynodonts with their hind limbs being orientated in a splayed pose.

Very high level vegetation would, therefore, be accessible only to small browsing arboreal tetrapods or insects or by the large ground-dwelling forms pushing or dragging over trees and bushes. The "grazers" may have been those forms with narrow snouts and sloping occiputs, but there is no certainty that this morphological type needed to have been restricted to low-level vegetation. Evidence exists in at least one genus of presumed dicynodont "browser" *(Dolichuranus)* for the presence of a long prehensible tongue (fig. 9). The similarity of the form of the dental symphysis of this genus to that of the ground sloth is marked and is taken to mean that if the ground sloth had a prehensible tongue, then so did *Dolichuranus*. A survey of the form of the symphyses of Triassic (and Permian) dicynodonts would be very illuminating, as would a study of the hyoid apparatus in these forms. However, both of these are outside the scope of this paper.

Finally, most Triassic dicynodonts are the possessors of a pair of canine tusks. As in the Permian, there were tuskless forms as well, but these in the main belong to the Upper Triassic. The function of these tusks has been variously ascribed to defence, offence and digging for roots and tubers among other activities. However, although dicynodonts could clearly open their mouths wide enough to effect a damaging bite on an enemy, it is not clear how they could use the tusks as digging implements. When the mouth is closed, the tusks protrude only very slightly below the level of the lower jaw and certainly not enough to make an effective rooting structure.

Watson (1960, p. 184) has described and discussed the significance of wear facets on the tusks of Permian dicynodonts, in particular *Dicynodon bolorhinoides*. "Large tusks . . . seem always to lack enamel. The inner surface of the crown is worn parallel to the animal's mid-plane into a facet . . . and was evidently made by wear against the horny beak of the lower jaw . . . an independent facet on the hinder surface of the tooth [meets this] facet at about 120 degrees, the ridge between them being rounded off . . . In front of and behind this [second] facet both teeth are unworn."

Watson believed (op. cit.) that the wear (and polish) on the outer surface of these tusks ". . . [implied] the presence of masses of dust-covered vegetation, close to the ground and probably reaching well above it, into which the animal thrust its head whilst feeding". He also mentions the possibility of *Diaelurodon*, a small form, not being able to rear up "more than eight inches" and continues by saying that it could not pull anything down with its fore foot.

The facets on the outside of dicynodont tusks may well have been formed as Watson believed, but it is more likely that such a resistant tissue as dentine would have required more deliberate usage than being rubbed on dust-covered vegetation to have these facets worn into them.

A study of some isolated dicynodont maxillae from *Cynognathus* zone localities in the South African Beaufort *(Kannemeyeria),* which have unusually well preserved canines in position, show that there is no wear on their tips on the outer side, but the usual facets worn through contact with the jaw are clearly present on the inner surfaces. Therefore, different life styles governed *D. bolorhinoides* and *Kannemeyeria*, and a tentative suggestion is made here to the effect that the external wear facets on the tusks of *D. bolorhinoides* could well have been made by "thegosic" actions, a display threat, and that the *Kannemeyeria* individuals noted here used their tusks differently. This point has been covered in the discussion on *Kannemeyeria* taxonomy (Keyser and Cruickshank, in prep.) where it is shown that in this genus tusk size increases markedly over the Scythian-Anisian boundary but with no more evidence of wear on the tip than is shown on the earlier forms.

It is, therefore, suggested that tusks in the Dicynodontia were used for display and/or threat purposes and that those forms with no tusks were either nocturnal or lived in deep undergrowth where visual signals were not important. This is reinforced to some extent by Keyser's analysis of the structure of *Oudenodon*, a Permian tuskless genus, which has large eyes and a highly developed olfactory tract, which he believed indicated it to be nocturnal (Keyser, 1976).

Cluver (pers. comm.) has pointed out that some birds which live in the open and which have large crests used for signalling may also have near relatives which live in close bush and which do not have the crest. He also pointed out that the race of African elephant, *Loxodonta africana,* living near Addo in the eastern Cape Province is regarded as having tusks much smaller than is thought normal for elephants. This may be due to their forest habitat exerting a selective pressure on tusk size similar to that discussed above, or perhaps, as is more likely, excessive hunting on this small population may have cleaned out all the big tuskers.

Harris (1975, p. 360) in summary pointed out that in the deinotheres "It is unlikely that the (downturned) tusks were used for digging and the most probable functions were for stripping and clearing vegetation, to provide a means of individual recognition and for providing a source of purchase for the proboscis". Perhaps the dicynodont canines could also be used for "stripping and clearing vegetation" (decorticating shoots or stripping leaves from stems). It is interesting to see how two widely



Figure 8. Reconstruction of hypothetical (Middle) Triassic scene showing three dicynodont individuals feeding. In the foreground one is using a prehensile tongue to feed on a low-growing fern-like plant. The second is pushing over a cycad-like plant to provide access to the "cone". In the background the third animal has reared up to eat an attractive shoot on a sphenophyte. The hills in the far background are part of a mature landscape with conifers growing close to the water's edge of a meandering river. The dicynodonts are based on the skeletal reconstruction of *Sinokannemeyeria* (Sun, 1963) but with the forefeet turned in, as in the ground sloths. The hind feet are turned outward as discussed by Cruickshank (1967) for *Tetragonias*. There is no evidence either way for the presence of hair on these animals.

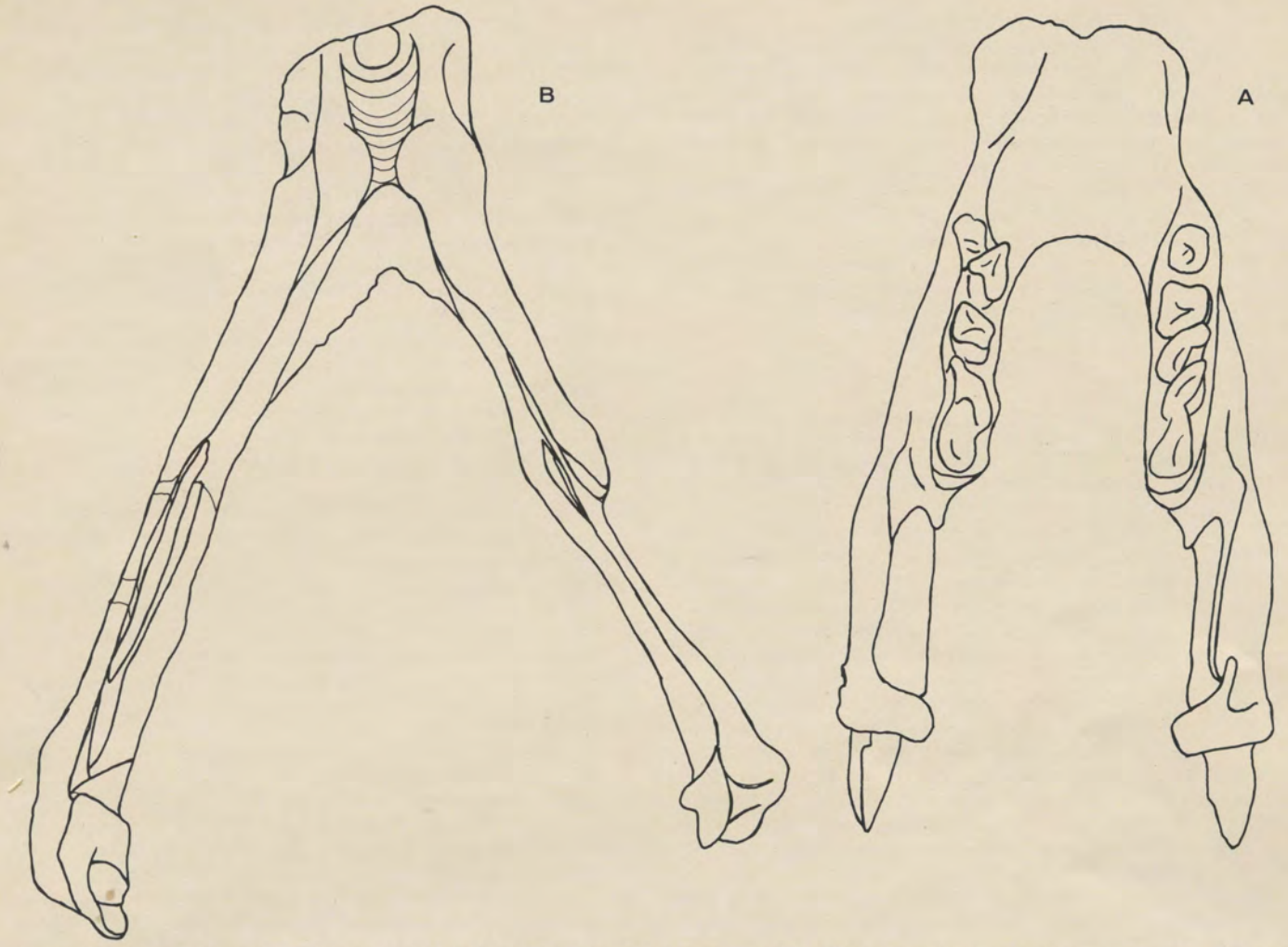


Figure 9. Dorsal views of the lower jaws of *Mylodon* (right, A) and *Dolichuranus* (left, B) to show the short widely grooved symphysis of forms believed to have had long, prehensile tongues. From Stock (1925) and B.P.I. F. No. 3636. Reduced to same size.

separate lineages have possibly used their tusks for similar functions.

SUMMARY AND CONCLUSIONS

Triassic dicynodont faunas are summarised in Table 2. If the functional analysis is accurate the situation resolves itself thus: In the Lower Triassic, one genus of "selective grazer" is found alongside four genera of "browser". This reflects the lack of diversity of the Lower Triassic *Dicroidium* flora as it affected the dicynodonts. As the *Dicroidium* flora diversified in the Middle Triassic, seven genera of "grazer" are seen with five genera of "browser". Three tuskless genera indicate that the nocturnal/deep bush niches were being systematically exploited for the first time. The "grazing" niches were now clearly very much more attractive and the dicynodonts had entered their last brief period of dominance among the herbivores.

Finally, in the Upper Triassic, the appeal of the "grazing" niche was still there, but exploited largely by tuskless forms. The "browsers" have one genus each of tusked and tuskless forms. Thus died out the Dicynodontia, lurking in semi-obscurity in the depths of the bushes and only venturing out to feed at night. The archosaurs had come into their own.

TABLE 2

	Grazers	*Browsers*
Upper Triassic	*Placerias* (reduced tusks)	*Dinodontosaurus*
	Ischigualastia (tuskless)	*Stahleckeria* (tuskless)
	Jacheleria	
	?Barysoma	
Middle Triassic	*Kannemeyeria*	*Dinodontosaurus*
	Uralokannemeyeria	*Dolichuranus*
	Rabidosaurus	*Tetragonias*
	?Rhadiodromus	
	?Rhinocerocephalus	
	Sanguasaurus (tuskless)	*Rhinodicynodon*
	Wadiasaurus (tuskless)	*Zambiasaurus* (tuskless)
Lower Triassic	*Kannemeyeria*	*Sinokannemeyeria*
		Parakannemeyeria
		Vinceria
		Shansiodon

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The reconstruction in Figure 8 was drawn by Miss Dolores Rokos and the majority of the remaining figures by Miss Julie Bunt. The final MS was typed by my wife, Enid.

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