

THE AFFINITIES OF THE EARLY CYNODONT REPTILE, *NANICTOSAURUS*

by

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ABSTRACT

This investigation into the anatomy of the four extant specimens of *Nanictosaurus* has revealed that there is one valid species, viz. *N. kitchingi* Broom 1936 which has two junior synonyms, viz. *N. robustus* Broom 1940 and *N. rubidgei* Broom 1940. The closest known relative of *Nanictosaurus* is the well-known cynodont *Thrinaxodon liorhinus*. The differences from *Thrinaxodon* and other early cynodonts are discussed and illustrated.

INTRODUCTION

The cynodonts made their first appearance in the South African fossil record in strata of the *Aulacephalodon-Cistecephalus* Assemblage Zone (Kitching, 1977; Keyser and Smith, 1978). They became more abundant in the overlying *Dicynodon lacerticeps-Whaitsia* Assemblage Zone (formerly called the *Daptocephalus* Zone), where *Procynosuchus*, *Cynosaurus* and *Nanictosaurus* are found. At the beginning of the Triassic one cynodont, *Thrinaxodon*, is sufficiently abundant to be regarded as a zone marker (the zone now called the *Lystrosaurus-Thrinaxodon* Assemblage Zone), which is a rare distinction for a non-herbivore; it speaks volumes for its adaptation to the environment.

Thrinaxodon is represented by a large number of specimens and is well-known. Lately our knowledge of the cranial anatomy of the earlier cynodont *Procynosuchus* has been substantially improved by the work of Kemp (1979). *Nanictosaurus* and *Cynosaurus*, on the other hand, are known only on the basis of a few imperfect skulls and the majority of these have not been adequately described to date.

MATERIAL

Four specimens have been assigned to the genus *Nanictosaurus*, and these were referred to three different species:

TM 279 Small skull from Wapadsberg, Bethesda Road, Graaff-Reinet district; *Dicynodon lacerticeps-Whaitsia* Assemblage Zone (Late Permian). Holotype of *Nanictosaurus kitchingi* Broom 1936.

RC47. Small skull (the smallest of the four) from Wellwood, Graaff-Reinet district; *Dicynodon lacerticeps-Whaitsia* Assemblage Zone. Holotype of *Nanictosaurus rubidgei* Broom 1940 (p. 190).

RC48 Incomplete skull from Hoeksplaas, Murraysburg district; *Dicynodon lacerticeps-Whaitsia* Assemblage

Zone. Holotype of *Nanictosaurus robustus* Broom 1940 (p. 192).

RC 133 Fairly small skull from Wellwood, Graaff-Reinet district; *Dicynodon lacerticeps-Whaitsia* Assemblage Zone. This specimen was provisionally referred to *Nanictosaurus rubidgei* by Brink & Kitching (1953) and Van Heerden (1976).

RC47 and RC 133 were prepared prior to 1976. RC 133 was prepared further for the present study; it proved to be rather disappointing because the palate was not preserved. RC 48 and TM 279 were also prepared and have thereby yielded very useful information. The snout of TM 279 was weathered and therefore it was decided not to prepare the dorsal surface, but rather the palate and basicranium. All preparation work was carried out by the technical staff of the Palaeontology Department of the National Museum, Bloemfontein.

Earlier Work:

Broom (1936; 1940) did not assign *Nanictosaurus* to a particular cynodont family. He focussed attention on the long main cusps of the postcanine teeth and also noted a similarity with *Thrinaxodon* (1940: 192). Brink & Kitching (1953) briefly described a second specimen of *N. rubidgei* (RC 133, not RC 307 as in their paper) and assigned the genus to the Galesauridae. Many authors have followed this classification (cf. Haughton & Brink 1955; Romer 1966; Van Heerden 1976; Brink 1983).

Hopson & Kitching (1972) included one species of *Nanictosaurus* in the Procynosuchidae (*N. robustus* = *Procynosuchus delaharpeae*) another in the Galesauridae (*N. kitchingi* = *Cynosaurus suppostus*); no mention was made of *N. rubidgei* but Kitching (pers. comm. 1971) was of the opinion that it is a junior synonym of *Thrinaxodon liorhinus*.

The only detailed description of the *Nanictosaurus* material was given by Van Heerden (1976) who described

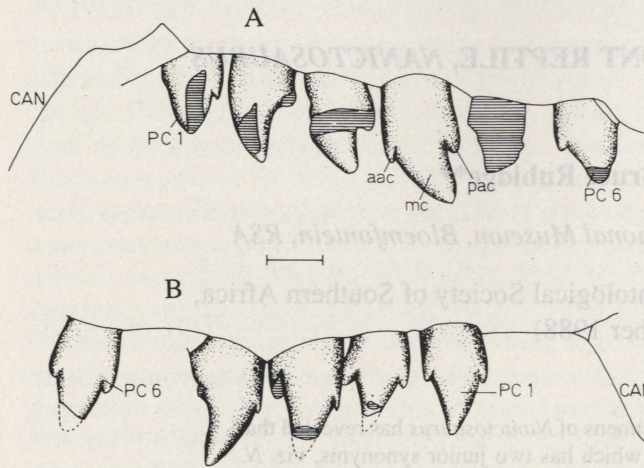


Figure 1. Upper postcanines of TM 279 (holotype of *Nanictosaurus kitchingi*) in labial view: A, left side. B, right side. Scale is 1 mm. Damaged areas are hatched. CAN = canine, aac = anterior accessory cusp, mc = main cusp, pac = posterior accessory cusp.

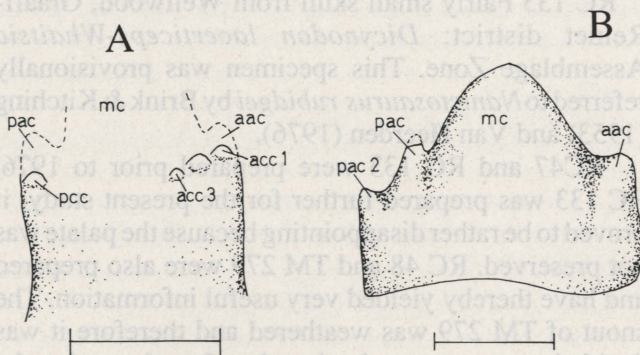


Figure 3. A, lingual view of 4th lower left postcanine of RC 47, redrawn after Van Heerden 1976. B, 4th or 5th lower postcanine of RC 48 in lingual view. Scale in each case 1 mm. acc = anterior cingulum cusp (1-3), mc = main cusp, pcc = posterior cingulum cusp.

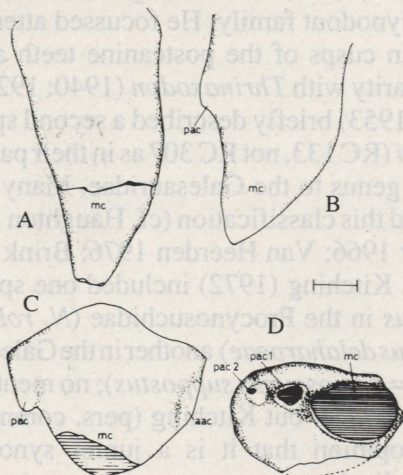


Figure 5. Some postcanines of SAM 4333 (*Cynosaurus suppostus*): A-C, labial views. D, 7th in crown view. Redrawn after Van Heerden 1976.

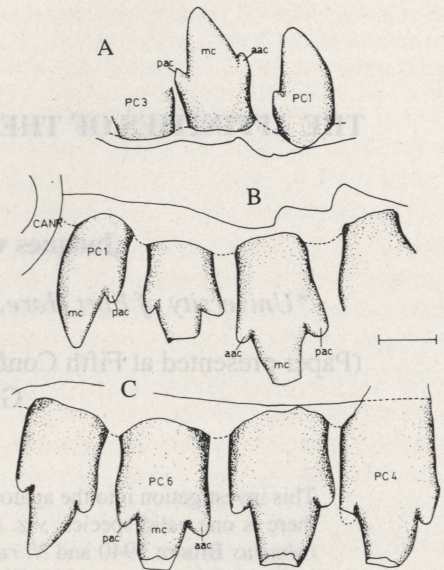


Figure 2. Postcanines of RC 47 in labial view: A, first three lower right postcanines. B, first four upper left. C, 4th to 7th upper right. Scale is 1 mm. CANR = canine root. Damaged areas are hatched. Redrawn after Van Heerden 1976.

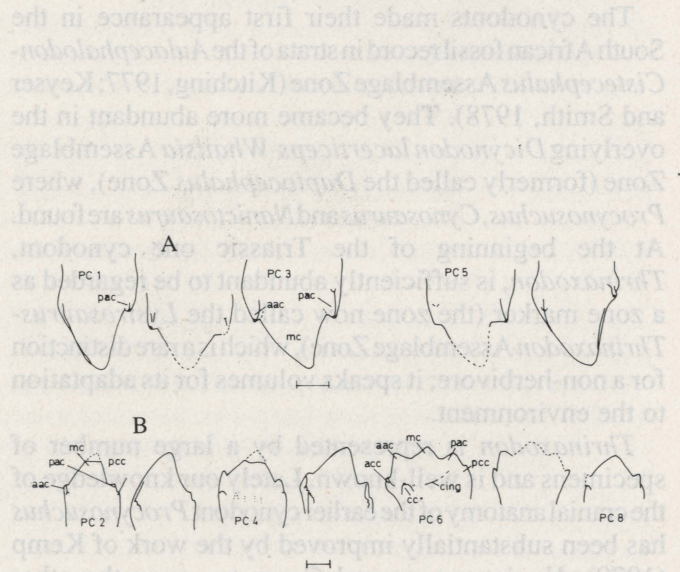


Figure 4. Left upper and lower postcanines of SAM K377 (*Thrinaxodon liorhinus*). Scale 1 mm. Redrawn after Crompton 1963.

RC 47 and RC 133. The present paper is a general comparison of *Nanictosaurus* and allied early cynodonts; a more detailed description of especially TM 279 is at present in preparation.

ANATOMY OF NANICTOSAURUS

In the earlier description (Van Heerden 1976) it was noted that in general structure "*N. rubidgei*" agrees closely with *Thrinaxodon liorhinus*. Some possible differences were observed at the time, but these were not all substantiated by the present investigation. The preparation of TM 279 has yielded valuable additional information. On the basis of the four specimens the

following differences from other early cynodonts were noted:

In its general skull proportions and the positions of the sutures (where visible), *Nanictosaurus* appears to be similar to *Thrinaxodon*. The snout is transversely broadened in the canine region and the orbits are relatively large with slender postorbital bars, while the suborbital bars are relatively deep. The secondary palate is complete and reaches posteriorly to the level of about the penultimate upper postcanines. In TM 279 it was noted that the pterygo-palatine ridges are rounded, i.e. lacking the distinct crest found in *Thrinaxodon*; at this stage it is not possible to say whether this is really a distinctive feature, because this area is damaged in RC 47 and completely missing in RC 133. In *Nanictosaurus* the pterygoid flanges reach down far ventrally, to the lower edge of the mandible when this is closed (in *Thrinaxodon* the flanges are only about half as deep.) There is no interpterygoid vacuity in TM 279. It has not been possible to clear this area in RC 47 completely of matrix, but there is a possibility of a small vacuity; if present, it would parallel the condition described for *Thrinaxodon* juveniles (Estes 1961).

With reference to the lower jaw, it was previously noted (Van Heerden 1976) that the postdentary elements of RC 47 are relatively slightly larger than in *Thrinaxodon*. This is probably also true of TM 279: what is visible on the left side indicates that the postdentary elements of the right side have been moved anteriorly. The coronoid process (only complete in RC 47 and now exposed on the right side) is the same height as in *Thrinaxodon*. In TM 279 the insertion of the temporalis muscle on the coronoid process very clearly reaches to the base of this process, just behind a vertical line that passes just posterior to the last exposed postcanine.

Each upper jaw half has four incisors, one large canine, and six to seven postcanines, while the lower jaw ramus has three incisors, one canine and probably seven or eight postcanines. In almost all the postcanines there are smaller anterior and posterior accessory cusps and a centrally placed main cusp, visible in labial view (figs 1, 2). The exceptions are some of the anterior postcanines, where the anterior accessory cusp is often suppressed. As noted by Broom (1936), the upper postcanines all have relatively long main cusps. There is no marked decrease in the size of the main cusp from front to back in the tooth row.

The lower postcanines (where these are exposed) exhibit a dominant main cusp, but this is not quite as high as in the case of the upper postcanines (fig. 3B); some lower postcanines also have small cingulum cusps (fig. 3A).

DISCUSSION

There seems to be no reason to recognize three different species of the genus *Nanictosaurus*. Moreover, even though RC 48 (the holotype of *N. robustus*) and RC 133 (paratype of *N. rubidgei*) are incomplete, sufficient

detail is preserved in each case to refer both to the genus *Nanictosaurus*. The name that has priority is *N. kitchingi*, which was given by Broom in 1936 to TM 279; *N. robustus* and *N. rubidgei* are to be regarded as junior synonyms.

The complete secondary palate and the height of the coronoid process indicate that *Nanictosaurus* belongs to the Galesauridae rather than the Procynosuchidae. An interpterygoid vacuity, if present in juveniles, is closed in adults, as is the case in *Thrinaxodon* (contrary to the condition in *Procynosuchus*). *Procynosuchus* also has a longer tooth row, with eight incisiform teeth in front of the canine (i.e. incisors and precanines) and ten postcanines in each upper jaw ramus (Kemp 1979).

Nanictosaurus can easily be distinguished from the other (sufficiently known) galesaurids on the basis of its postcanine structure: in *Cynosaurus* (fig. 5) the anterior upper postcanines resemble those of *Thrinaxodon* and *Nanictosaurus* in that there are two cusps of which the anterior one is by far the largest; in contrast, the posterior upper postcanines of *Cynosaurus* have three main cusps, of which the anteriormost one is the largest (Van Heerden 1976). In Figure 5B and C the main cusp is reconstructed fairly conservatively, with a mild curvature posteriorly. A specimen collected in September 1988 by J W Kitching at New Bethesda had a number of upper postcanines with markedly recurved main cusps situated on the anterior margins of the teeth.

In *Galesaurus* the anterior cusp is very large and recurved to form a long cutting edge; the posterior cusp is small and "hidden" under the recurved main cusp (Van Heerden 1976).

In both *Nanictosaurus* and *Thrinaxodon* the postcanines are tricuspidate with the central cusp as the main one. In *Nanictosaurus* the main cusp is proportionately larger than in *Thrinaxodon* when compared to the width of the tooth; it also tends to be rather straight, whereas in *Thrinaxodon* the main cusp length is at least a little curved posteriorly (cf. Crompton 1963; Osborn & Crompton 1973). The differences between cusp lengths in *Nanictosaurus* and *Thrinaxodon* cannot be accounted for simply by tooth wear. Firstly, no postcanines of *Thrinaxodon* have main cusps which are as long as those of *Nanictosaurus*; this applies both to newly erupted teeth and the teeth of younger specimens. Secondly, although there must have been some tooth wear, the teeth did not occlude and therefore tooth wear must have been relatively slow – it is then all the more relevant that *Nanictosaurus* has long main cusps.

Other notable differences between *Nanictosaurus* and *Thrinaxodon* are the relatively larger postdentary elements, the deeper pterygoid flanges, and the rounded pterygo-palatine ridges of the former taxon (cf. Van Heerden 1976; in prep.)

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