

A NEW PRIMITIVE DINOCEPHALIAN MAMMAL-LIKE REPTILE FROM THE PERMIAN OF SOUTHERN AFRICA

by BRUCE S. RUBIDGE

ABSTRACT. A new genus of tapinocephaline dinocephalian, *Tapinocaninus pamela*, is described from the lowermost biozone of the Beaufort Group in South Africa. *Tapinocaninus* is older than any dinocephalian previously discovered in Africa, being early Late Permian (Ufimian–Kazanian) in age. It is considered to belong to the subfamily Tapinocephalinae but retains plesiomorphic features which are absent in the Tapinocephalinae and were previously considered characteristic of the more primitive Titanosuchinae. The Titanosuchinae are distinguished from the Tapinocephalinae in the form of the postcanine teeth (leaf-shaped and serrated in the former and bearing a lingual heel in the latter) and in the pachyostotic thickening of the skull roof of the latter.

DINOCEPHALIANS were a group of medium to large mammal-like-reptiles which included the largest land-living animals to have existed up to Late Permian (Ufimian–Kazanian) times. They were present among the earliest therapsid fauna of the San Angelo Formation of Texas (Olson 1962) and the Russian Ocher Formation (Tchudinov 1983), and also formed an important part of the therapsid fauna of the *Tapinocephalus* Zone (Dinocephalian Assemblage Zone) of the Beaufort Group in South Africa (Boonstra 1969, 1971; Kitching 1977; Keyser and Smith 1978).

The Dinocephalia are the earliest group of therapsids for which a significant adaptive radiation can be identified (Ruben 1986), but for all their early success, they became completely extinct by the close of *Tapinocephalus* Zone (Dinocephalian Assemblage Zone) times, leaving no descendant groups (Boonstra 1971; Kemp 1982). The infra-order Dinocephalia was considered to consist of six families, namely Estemmenosuchidae, Brithopodidae, Anteosauridae, Titanosuchidae, Tapinocephalidae and Styracocephalidae (Boonstra 1963a; Kemp 1982). More recently, King (1988) reclassified these as subfamilies of the three families Estemmenosuchidae, Brithopodidae, and Titanosuchidae, and regarded *Styracocephalus*, the only genus in the family Styracocephalidae, as *incertae sedis*. Of the three families recognized by King, only the Estemmenosuchidae have not yet been found in Africa. The classification of King (1988) is used in this study. Apomorphic features which characterize the Dinocephalia as a distinct infraorder are the presence of intermeshing incisor teeth in the upper and lower jaws (Boonstra 1962, 1963a; Hopson and Barghusen 1986; King 1988), and incisor teeth with lingual heels (Hopson and Barghusen 1986).

MATERIALS AND METHODS

Five dinocephalian skulls, which are considered to belong to the same genus, have recently been collected in rocks of the Late Permian *Eodicynodon* Zone, a newly identified biozone at the base of the Beaufort Group (Rubidge 1987). All but one of these fossils were found on Modderdrift farm, three from the same sandstone outcrop in close proximity. These three specimens were found by Mr John Nyaphuli and are housed in the Karoo fossil reptile collection of the National Museum, Bloemfontein (specimens NMQR 2985, 2986, 2987), while the fourth specimen (ROZ K95), although found by the author, is housed in the private fossil collection of Mr Roy Oosthuizen on his farm, Zwartskraal, in the district of Prince Albert. The fifth specimen (NMQR 3097), which consists only of a skull roof and some isolated teeth, was found on Swartgrond farm in the Rietbron district and is now housed in the National Museum in Bloemfontein.

The lower jaws are preserved in all but one of the specimens, but those of ROZ K95 and NMQR 2986 were too firmly appressed to the skull prior to fossilization to prepare on the lingual side. Although the right ramus of the lower jaw of the specimen NMQR 2985 could be dissociated from the skull, the bones of the lower jaw on the medial side were damaged and disoriented prior to fossilization. By far the best preserved lower jaw is that of NMQR 2987 which is undistorted and still bears several teeth *in situ*.

All the skulls were prepared with the aid of air-driven engravers. A hammer and chisel and small angle grinder were used in areas where there was an excess of matrix covering the bone and where there was no chance of damage to the bone. Glyptal 1276 Lacquer Cement, supplied by General Electric, was used as an adhesive.

Institutional abbreviations are: NMQR, National Museum, Bloemfontein; ROZ K, Roy Oosthuizen Collection, Klaarstroom.

SYSTEMATIC PALAEOLOGY

Subclass SYNAPSIDA Osborn, 1903

Order THERAPSIDA Broom, 1905

Infraorder DINOCEPHALIA Seeley, 1894

Family TITANOSUCHIDAE Boonstra, 1972

Subfamily TAPINOCEPHALINAE Lydekker, 1890

Tapinocaninus gen. nov.

Type species. Tapinocaninus pamela sp. nov.

Diagnosis. Large tapinocephaline dinocephalian. Moderate pachyostosis with broad postorbital bar. Temporal opening relatively large for tapinocephaline, and hence relatively narrow intertemporal region. Premaxilla forming anterior and antero-lateral border of the internal nares. Maxilla with very short contact on lateral side of internal nares such that the palatine and premaxilla almost meet. Vomer narrow in ventral view. Heterodont dentition with medium-sized canine tooth lacking definite crushing heel in both upper and lower jaw. Lower canine passing in front of upper canine rather than on lingual side. Five larger incisor teeth in premaxilla, all with crushing heel. Quadrate condyles situated below posterior border of orbit. Several small palatal teeth on palatine boss.

Etymology. Greek *tapino*, humble; Latin *caninus*, canine. The name refers to the reduced size of the canine tooth relative to that of the Titanosuchinae and indicates that the genus belongs to the subfamily Tapinocephalinae.

Tapinocaninus pamela sp. nov.

Text-figures 1–3.

Diagnosis. As for genus.

Etymology. The species is named in honour of my mother Pam Rubidge who encouraged my interest in palaeontology and was with me in the field when this fossil was discovered.

Holotype. Specimen NMQR 2987. Skull and mandible. Left side of skull well preserved with several teeth; parietal and occipital regions on right side damaged as a result of weathering.

Paratypes. Specimens NMQR 2985 (skull and mandible), NMQR 2986 (skull and mandible), ROZ K95 (skull and mandible).

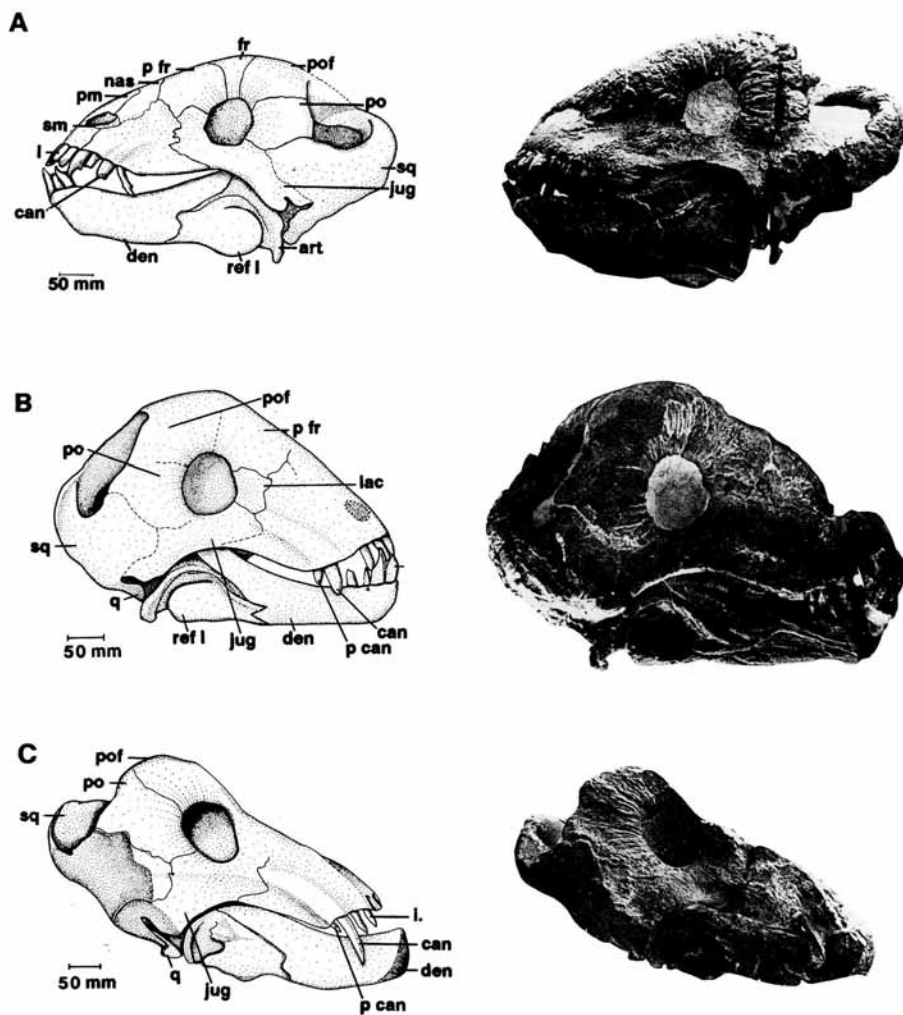
Type horizon and locality. *Eodicynodon* Zone (Rubidge 1987) at the base of the Beaufort Group (Ufimian–Kazanian age) on Modderdrift farm, Prince Albert, South Africa (map sheet: South Africa 1:50000, Sheet 3322 BA Seekoegat, first edition).

DESCRIPTION

Skull Roof

In their general shape the newly discovered dinocephalian skulls resemble those of other tapinocephaline dinocephalians in that the skull roof is greatly pachyostosed and the postorbital bar is extremely thick.

The anterior portion of the snout is formed by the *premaxilla* which also forms the anteroventral, anterior, and dorsal border of the external nares. The premaxilla extends posterodorsally as a narrow projection on the



TEXT-FIG. 1. *Tapinocaninus pamelaе*, lateral view. A, NMQR 2987; B, NMQR 2986; C, ROZ K95.

roof of the snout to a point approximately halfway between the external nares and the orbit where it is in sutural contact with the nasals. The contact of the premaxilla with the maxilla on the lateral side of the snout is an obliquely orientated suture which extends ventrally from approximately one-third of the way along the antero-ventral side of the external nares to the front of the canine alveolus.

Anteriorly, the *nasal* is in contact with the posterior border of the external naris and the septomaxilla, while it is in contact with the maxilla on the antero-ventral side and the prefrontal on the postero-ventral side. On the dorsal side of the skull the nasals extend posteriorly as a narrow projection medial to the enlarged prefrontal bone and meet the frontals in line with the anterior limit of the orbits.

The *maxilla* forms the greater portion of the lateral surface of the snout. Dorsally it is in sutural contact with the nasal, and posteriorly with the prefrontal, lachrymal, and jugal in an almost straight vertical line anterior to the orbit. The lateral surface of the maxilla, above the alveolus of the canine, is swollen laterally to accommodate the root of the canine as in titanosuchine dinocephalians (Boonstra 1962).

As in all known South African dinocephalians, the *prefrontal* is a prominent bone and forms the antero-dorsal border of the orbit. Posteriorly and posterodorsally, the prefrontal is in contact with the frontal, antero-dorsally with the nasal and antero-ventrally with the maxilla. Almost halfway down the front of the orbit, the prefrontal is in sutural contact with the *lachrymal* which extends on the lateral side of the skull anterior to the orbit. The suture between the lachrymal and *jugal* is situated slightly less than one-third of the way up from the base of the orbit and slopes anteroventrally.

The *jugal* is a prominent bone which forms the ventral margin of the orbit and of the lateral side of the cranium in the suborbital region. It extends slightly anteroventrally of the orbit on the lateral surface of the snout and has a long sutural contact with the posterior edge of the maxilla. Behind this contact, the ventral margin of the skull curves posteroventrally until it reaches its most ventral point below the postorbital bar lateral to the articulatory condyles of the quadrate. From here, the ventral margin is notched posterodorsally so that the jugal forms the anterior and dorsal walls of the notch. The posterior edge of the notch is formed by the quadratojugal.

The postorbital bar, which is broad, is made up of the *postfrontal* dorsally and the *postorbital* ventrally. The dividing suture between the postorbital and postfrontal is orientated horizontally about halfway up the orbit. The postorbital forms the anterodorsal and anteroventral borders of the temporal fenestra and the posteroventral border of the orbit.

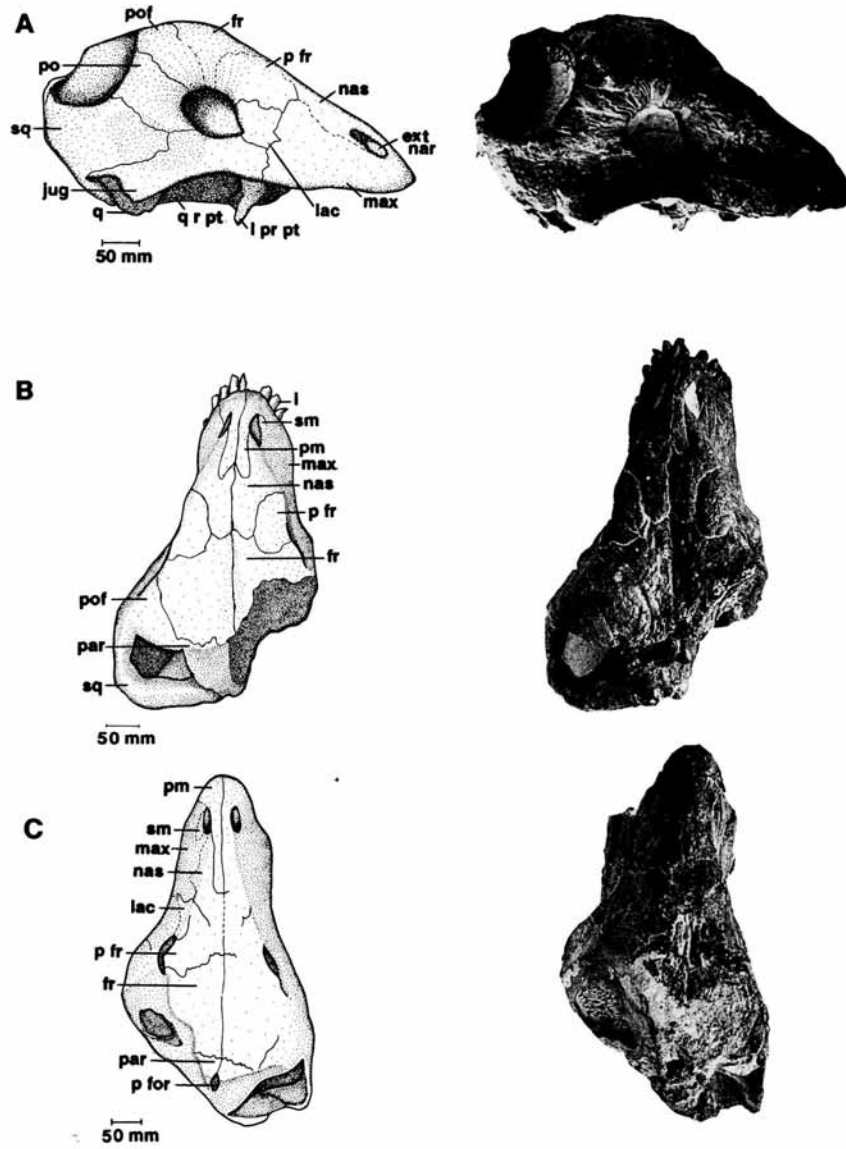
It appears that the postfrontal forms most of the dorsal margin of the temporal fenestra, with the parietal forming the posterodorsal margin. However, the suture between the postfrontal and parietal could not be identified. The *frontal* forms most of the skull roof between the orbits and temporal fenestrae. It has a laterally tapering process which forms a small portion of the dorsal border of the orbits between the prefrontal and postfrontal bones.

The *squamosal* forms the entire ventral and posterior borders of the temporal fenestra. On the ventrolateral side of the external auditory meatus the squamosal is in contact with the *quadratojugal*, while on the ventral side it meets the ascending ramus of the quadrate. Posteromedially the squamosal is in contact with the bones of the occipital region. The quadratojugal, in posterior view, is seen to form the ventrolateral corner of the skull. Dorsally its posterior surface is overlapped by the squamosal.

Dorsally, the squamosal is in contact with the *parietal*, which is badly weathered in all the specimens except NMQR 3094. A large rounded pineal foramen is situated between the temporal fenestrae. The intertemporal region becomes very narrow behind this foramen.

Occiput

As in most tapinocephaline dinocephalians, the occipital region of the skull slopes posterodorsally. The occiput is roughly flat and rectangular in shape, with the ventro-lateral regions of the *opisthotics* curving ventrally to meet the ventro-medial process of the squamosal and the dorsomedial portion of the quadrate medial to the external auditory meatus. Although the lateral and dorsal contacts of the occipital and otic bones with the tabular and postparietal bones are prominent, the sutures between the various occipital and otic bones are not easily distinguishable. The *postparietal* is an unpaired element situated dorsomedially in the occipital plate and forms a horizontal sutural contact with the parietal posterodorsally. The *tabular* is a roughly triangular bone between the postparietal, squamosal, and occipital bones with its apex extending ventrally to the point of contact between the opisthotic and squamosal. Medially it is in contact with the occipital bones.



TEXT-FIG. 2. *Tapinocaninus pamelae*. A, lateral view of NMQR 2985; B, dorsal view of NMQR 2987; C, dorsal view of NMQR 2985.

Palate

In the palate, the *premaxilla* overlies the anteroventral surface of the maxilla on the ventral side. Its posterior border extends posteromedially from a point just in front of the canine to form the anterolateral border of the internal naris. The *maxilla* forms only a small portion of the lateral border of the internal nares on the medial side of the canine and prevents contact between the palatine and premaxilla. From here it forms a thin alveolar margin which extends posteriorly to the level of the lateral flange of the pterygoid. Medially, the maxilla forms an extensive contact on the palatine and also meets the ectopterygoid.

The *vomers* are narrow vertically expanded bones which form a median trough between them. They make up the medial and posteromedial walls of the internal nares and are in contact with the premaxillae anteriorly and the palatines posterolaterally. Posteriorly they have a short pointed contact with the pterygoids.

An anteriorly directed process of the *palatine* extends almost as far as the canine tooth and forms the posterolateral, and part of the lateral, border of the internal naris. Posteromedially, the palatine forms a ventrally projecting boss which is transversely sutured to the medial pterygoid boss. The roots of several palatine teeth are situated on the anterior regions of the palatine portion of this boss in specimen NMQR 2985, and alveoli are present in specimens NMQR 2986 and NMQR 2987.

The *pterygoid* accounts for more than half the length of the palate, and the lateral flanges stretch ventrally and transversely across the palate. Posterior to the lateral flanges, the pterygoid meets its mate in the midline to form a sharp median keel. Lateral to the median keel the pterygoid is deeply excavated ventrally. On the lateral side of this wide and posteriorly flared groove, the vertically orientated quadrate ramus of the pterygoid extends posterolaterally to meet the medial condyle of the quadrate. The quadrate ramus does not extend as far as the posterior edge of the quadrate. A narrow interpterygoidal vacuity is present and extends posteriorly from the level of the lateral flanges of the pterygoid. The pterygoid meets the basisphenoid immediately behind the interpterygoidal vacuity.

Braincase

The *stapes* extends medially from the posterior surface of the quadrate, immediately behind the quadrate ramus of the pterygoid, to the fenestra ovalis. In ventral view, its distal end is expanded anteroposteriorly where it meets the quadrate. It becomes thinner towards the medial end which extends to the fenestra ovalis. In posterior view, the stapes is also narrower medially than laterally, and is pierced anteroposteriorly by a stapedia foramen.

The *basisphenoid* is a relatively small triangular-shaped bone with its apex pointing anteriorly to meet the pterygoid immediately posterior to the interpterygoidal vacuity. A keel extends ventrally down the midline of this bone. On either side of the keel are two foramina for the carotid arteries. Posteriorly, the basisphenoid is in contact with the *basioccipital* in the anterior region of the fenestra ovalis to form the anterior edge of the fenestra.

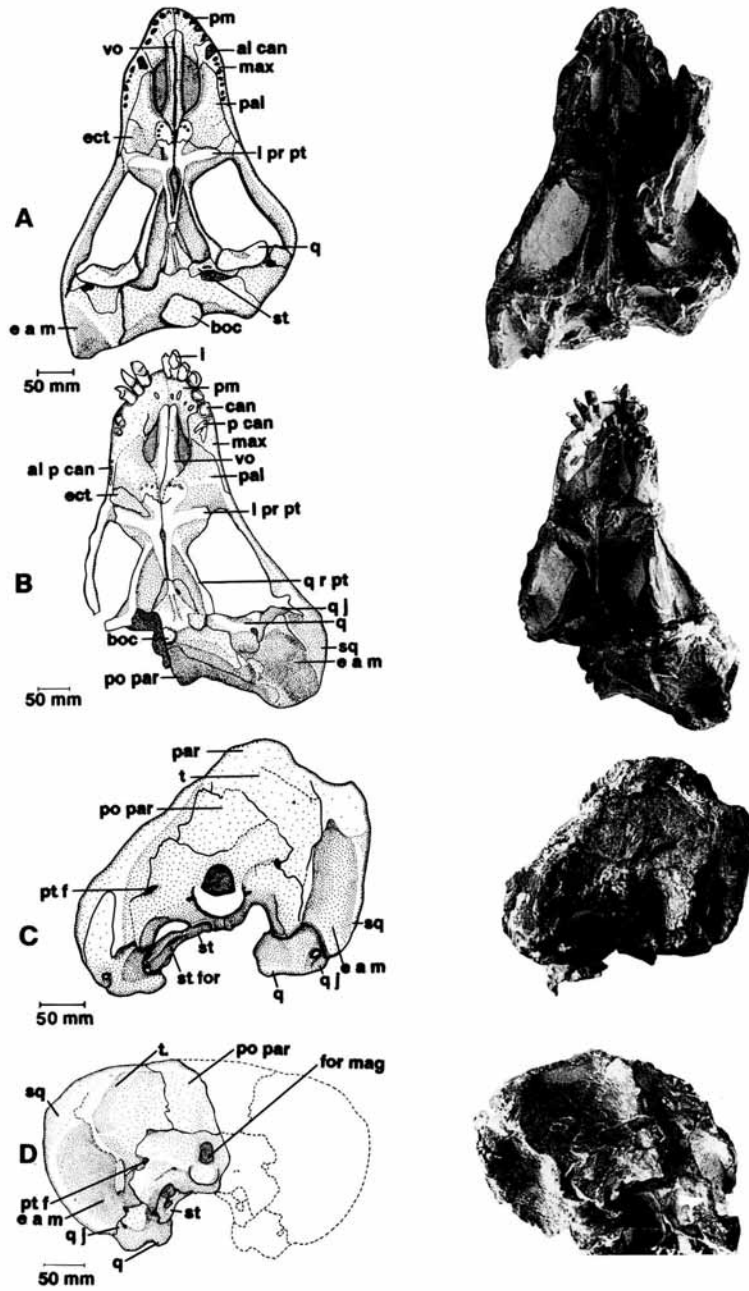
Lower jaw

The lower jaw consists of the dentary, splenial, angular, surangular, prearticular, and articular bones, but no coronoid could be recognized.

The *dentaries* are united by a symphyseal suture in the anterior midline which is very clearly defined in specimen NMQR 2987. The dentary forms the greater portion of the lower jaw. Posteriorly, it meets the *surangular* at the top of the coronoid eminence. The surangular has its greatest surface exposure on the dorso-medial side of the lower jaw, but also forms a laterally projecting ridge on the dorsolateral surface of the lower jaw. This ridge continues posteriorly as far as the ventral tip of the retroarticular process of the articular bone.

The *articular* is situated on the posteromedial side of the surangular and angular bones, and is in sutural contact with the posterior edge of the *prearticular*. The articulatory surface of the articular is orientated posterodorsally and has two prominent depressions which relate to the quadrate condyles. The more laterally situated depression is slightly larger than the medial one.

The *angular* meets the surangular on the dorsolateral side of the lower jaw immediately ventral to its laterally extending ridge. A prominent reflected lamina is formed by the angular and extends ventrally as far as the ventral margin of the jaw. Anteriorly, the angular is in contact with the dentary by means of a suture which slopes anteroventrally such that the angular forms a pointed contact on the ventral margin of the lower jaw between the dentary on the lateral side and the splenial on the medial side. The angular is also exposed on the ventromedial side of the posterior end of the lower jaw.



TEXT-FIG. 3. *Tapinocaninus pamelae*. A, ventral view of NMQR 2985; B, ventral view of NMQR 2987; C, occipital view of NMQR 2985; D, occipital view of NMQR 2987.

The *splénial* is widely exposed on the medial side of the lower jaw. It attains its greatest width near its posterior end where it is in contact with the prearticular posterodorsally, and the angular posteroventrally. The splénial tapers anteriorly as the dentary becomes broader.

Dentition

Teeth are generally poorly known in South African dinocephalians (Boonstra 1962), and the dentition is not perfectly present in any of the specimens studied. In one of the skulls (NMQR 2985), all the teeth had fallen out of the alveoli prior to fossilization.

A maximum of five *incisor* teeth, all of which have talons and heels, are present in the premaxilla. A single *canine*, with no heel, is present as the first tooth in the maxilla (Text-fig. 3A, B). The crown of the canines curves backwards and the posterior edge is rounded with no sharp edge or serrations.

The canine of specimen ROZ K95 is mediolaterally compressed when compared with that of specimens NMQR 2986 and NMQR 2987 which are more rounded in section. Boonstra (1953a) records in a specimen of *Anteosaurus* that a canine close to replacement is also flattened. This may well be the situation in the present instance as the preserved canine of specimen ROZ K95 is longer than those of the other individuals. This canine is thus possibly more mature than the others, and at the point of being replaced.

The canine is followed, on the posterior side, by at least eight *postcanines* (twelve in specimen NMQR 2986, and eight in specimen NMQR 2985). The postcanine teeth have arrow-shaped crowns with small heels on the lingual side.

In the lower jaw, four incisors with crushing heels are present anteriorly in each dentary and intermesh with the incisors of the upper jaw when occluded. A single canine is present which passes on the anterior side of the canine of the upper jaw when the jaws are occluded, in the same fashion as in the Titanosuchinae. At least 15 smaller postcanine teeth are also present on the dentary, and lie lingually of the upper set when the jaws are closed.

In summary, this new dinocephalian has a heterodont dentition, consisting of incisors, canine, and postcanines, as in the Anteosaurinae and Titanosuchinae, and not homodont, as in the Tapinocephalinae (Boonstra 1953a). The dental formulae of the various specimens studied are: NMQR 2985 $I_4^1 C_1^1 PC_{14}^8$; NMQR 2986 $I_4^3 C_1^1 PC_7^{12}$; NMQR 2987 $I_4^5 C_1^1 PC_{9-10}^5$; ROZ K95 $I_7^{4?} C_7^1 PC_7^5$.

COMPARISON WITH OTHER DINOCEPHALIANS

Skull roof

In general shape, the skull of *Tapinocaninus* resembles that of a tapinocephaline dinocephalian as described by Boonstra (1969) and King (1988). The skull roof is greatly pachyostosed, and the postorbital bar is extremely thick, as in all the Tapinocephalinae. Because the postorbital and posttemporal bars of the Anteosaurinae and Titanosuchinae are relatively slender, the temporal fossa of these subfamilies has a relatively greater anteroposterior diameter than in the Tapinocephalinae. In the last, the thickening of these two bars produces a narrowed dorsoventrally elongated slit-like posttemporal fossa. As in anteosaurines and tapinocephalines, the temporal openings of *Tapinocaninus* are relatively large with a resultant narrow intertemporal region when compared with other forms of the Tapinocephalinae, although there are genera such as *Avenantia* and *Ulemosaurus* which do have a narrow intertemporal region. In the Tapinocephalinae, a narrow intertemporal region is considered to be primitive (Hopson and Barghusen 1986).

In dorsal view, the snout is much thinner than that of other tapinocephaline dinocephalians, except *Ulemosaurus*, but is not as long as that of the Titanosuchinae.

The quadratojugal of *Tapinocaninus* is a relatively small bone which forms part of the ventrolateral surface of the skull. In the early therapsids this bone has variable relations. However, in all of them it is much reduced in size and never enters the lower temporal arch as it does in some of the Pelycosauria. Primitively, the quadratojugal was a surface bone of the posterolateral corner of the skull flanking the quadrate. It is reduced in size and displaced medially in some of the higher sphenacodonts to rest on the quadrate dorsal to the lateral condyle (Boonstra 1971). This medial displacement is continued in the Gorgonopsia, Therocephalia, Brithopodinae, and Anteosaurinae.

In the Titanosuchinae and Tapinocephalinae the quadratojugal, variable in size and shape, still forms part of the lateral skull surface (Boonstra 1971).

The articulatory surface of the quadrate is situated ventrally below the posterior border of the orbit, a relatively anterior position which corresponds more closely with the Tapinocephalinae than the Titanosuchinae, where it is situated further posteriorly.

Occiput

In the occiput, the tabular is a triangular-shaped bone which comes to a point between the squamosal and opisthotic on the ventral side, well below the post-temporal foramen. This configuration is not present in any of the Titanosuchinae or Anteosauridae, while a similar configuration is present in some of the tapinocephalines.

Braincase

A prominent stapedial foramen is present. Among the Dinocephalia, where the stapes is known, this structure is not present in the Anteosaurinae and Brithopodinae (Boonstra 1971), but is present in some other species of the Tapinocephalinae (Boonstra 1956, 1957, 1965).

Palate

In the palate, the premaxilla forms a large proportion of the anterolateral margin of the internal nares as in the Titanosuchinae and the Estemmenosuchoidea. In the Tapinocephalinae and in *Anteosaurus*, the premaxilla has only a small contact on the anteromedial side of the internal nares. The vomers are thin bones, as in the Brithopodinae (Orlov 1958), and not broad and flat as in all other South African dinocephalians, especially the Tapinocephalinae.

A single row of palatal teeth is present on the anterior margin of the palatine bosses. Small clusters of palatal teeth are known in the Brithopodinae, Anteosaurinae, and in *Styracocephalus*, which is now considered *incertae sedis* (King 1988). Palatal teeth are normally thought not to occur in tapinocephalines: Boonstra (1936 p. 97) states 'in the gorgonopsians the palatines and pterygoids carry dentigerous ridges, whereas *no* such teeth are known in my tapinocephalid'. Boonstra (1953b) does however mention indications of roots of small palatal teeth on a rounded mound on the palatine of *Struthiocephalus*. As far as the titanosuchines are concerned, Boonstra (1963b) could not find any palatal teeth in the type of *Jonkeria ingens*.

Dentition

One of the diagnostic features of dinocephalians is the dentition, but in *Tapinocaninus* the premaxillary-maxillary dentition is not perfectly preserved in any of the specimens. Boonstra (1962) states that the entire tooth (crown plus root) falls out of the alveolus before petrification most frequently in the Tapinocephalinae. In the Titanosuchinae the roots are generally preserved in the alveoli even though the crowns are frequently broken off at the level of the alveolar border either before petrification or during weathering. He considered this to be because of the difference in implantation and the mode of replacement of teeth in these two subfamilies.

The newly-discovered dinocephalian skulls have incisors with talons and crushing heels, a single canine with no heels, and numerous postcanine teeth; features of the Titanosuchinae (Boonstra 1963a). As in titanosuchine dinocephalians, the first pair of upper incisors of *Tapinocaninus* is more lightly built than the others and they are laterally compressed, they lie close together and, in occlusion, they passed their talons together between the pair of lower incisors (Boonstra 1953a).

In the Titanosuchinae, the fifth upper incisor has the rear face of the talon modified to receive the lower canine with which it intermeshes. In the lower jaw, the fourth incisor is somewhat weaker than the anterior ones (Boonstra 1962). In the Anteosaurinae, the fifth upper incisor passes labially to the lower canine during occlusion and not anteriorly, and the two teeth consequently do not intermesh (Boonstra 1962). In the new dinocephalian, the lower canine in specimen NMQR 2986 (the only one where it is preserved) is situated more in the titanosuchine position, passing in front of the upper canine (Text-fig. 1B). The size of the upper canine of *Tapinocaninus* (diameter at

alveolar border, 19–21 mm anteroposteriorly, and 13–18 mm mediolaterally; crown length, 46–52 mm) is much smaller than that of equivalent-sized titanosuchine dinocephalians (diameter at alveolar border, 35–50 mm anteroposteriorly, and 21–36 mm mediolaterally; crown length, 60–110 mm) (Boonstra 1962).

As is the case in titanosuchine dinocephalians (Boonstra 1962), the postcanines of the lower jaw of *Tapinocaninus* are situated on the lingual side of those of the upper jaw when the jaws are closed, and do not intermesh as in tapinocephaline dinocephalians. The number of postcanine teeth in the Anteosaurinae and Titanosuchinae varies greatly, from one to nineteen, and is of doubtful systematic value as it can even vary from the left to right side of the jaw (Boonstra 1953a).

The postcanines of the lower jaw of *Tapinocaninus* more closely resemble those of the Tapinocephalinae than the Titanosuchinae in that the labial portion of the crown is slightly bulbous, and there are small heels on the lingual side.

Despite having heterodont titanosuchine-like dentition, the skulls display many tapinocephaline features such as postcanines with talon and heel (Boonstra 1963a), the pachyostosed skull roof and form of the postorbital bar, relatively anterior position of the quadrate (Boonstra 1963b), and orientation of the tabular bone. It is thus reasonable to consider this dinocephalian as belonging to the Tapinocephalinae but still retaining some plesiomorphic characters which are not present in any other known tapinocephaline dinocephalian.

TAXONOMIC IMPLICATIONS

Several palaeontologists have addressed the problem of classification of the Dinocephalia, but only recently has a cladistic approach been used. Kemp (1982) was the first to use such an approach but did not give characters relating to the sister groups contained in his cladogram. Hopson and Barghusen (1986) undertook a cladistic analysis of therapsid relationships and included the various dinocephalian infraorders, while King (1988) also drew up a cladistic analysis of the Dinocephalia. All consider, as was previously stated by Boonstra (1965), that the Anteosaurinae are the most primitive of the South African dinocephalians, and the Tapinocephalinae are the most derived. The Titanosuchinae fall between the two. The scheme proposed by Hopson and Barghusen (1986) differs from that of Kemp (1982) and King (1988) in the position of the Estemmenosuchoidea. This however does not have any bearing on this paper and will not be discussed further.

Hopson and Barghusen (1986) use the following apomorphies of the Tapinocephalinae to separate them from the Titanosuchinae:

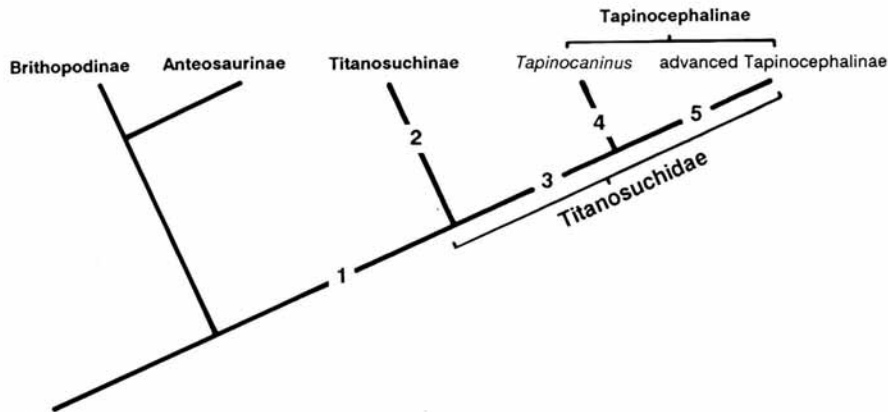
1. canines incisiform;
2. pattern of interlocking extends to canines and postcanines;
3. anterior end of postcanine row does not extend lingual to the canine.

A reassessment of material of the Tapinocephalinae and Titanosuchinae housed in South African Institutes has revealed that character 3 is shared by both of these groups and is not an apomorphy of the Tapinocephalinae alone.

King (1988) uses the following apomorphies of the Tapinocephalinae to separate them from the Titanosuchinae. Character 2 corresponds with that of Hopson and Barghusen (1986):

1. heels on the incisor teeth expanded;
2. all teeth interdigitating;
3. size of temporal fossa reduced due to pachyostosis.

Of all these characters, *Tapinocaninus* possesses only the first character of King (1988), and hence it is considered the most primitive representative of the Tapinocephalinae known. As a result, it is necessary to broaden the concept of what is presently considered to be a tapinocephaline dinocephalian (Text-fig. 4).



TEXT-FIG. 4. Cladogram illustrating the relationships of *Tapinocaninus* to the Titanosuchinae and Tapinocephalinae (modified after King 1988). Apomorphies for each node are: 1 (defining Titanosuchidae), enlarged heel on incisor teeth; jaw hinge slightly anteriorly placed to be positioned below postorbital bar; lower canine reduced in height; lower canine positioned anterior to upper one when jaws closed. 2 (defining Titanosuchinae) (after King 1988), many leaf-shaped and serrated postcanine teeth. 3 (defining Tapinocephalinae), heel on postcanine teeth; pachyostotic thickening of postorbital bar and skull roof. 4 (autapomorphies of *Tapinocaninus*), vomer narrow in ventral view; premaxilla extends far posteriorly to almost touch palatine resulting in maxilla having very short contact on lateral border of internal nares. 5 (defining advanced Tapinocephalinae), reduced canine tooth; quadrate further anteriorly positioned to be situated below orbit; all teeth interdigitating; size of temporal fenestra reduced due to pachyostosis.

CONCLUSION

A new genus and species of tapinocephaline dinocephalian, *Tapinocaninus pamela*, has been discovered from the lowermost rocks of the Beaufort Group in the same zone as the primitive dicynodont *Eodicynodon* (Rubidge 1987), and *Patranomodon*, the most primitive anomodont known (Rubidge and Hopson 1991). *Tapinocaninus pamela* is the most primitive member of the Tapinocephalinae yet discovered and retains several plesiomorphic titanosuchine-like characters which are not present in any other known tapinocephaline dinocephalians. This has led to modifications of cladistic characters previously used (Hopson and Barghusen 1986; King 1988) to separate the Tapinocephalinae from the Titanosuchinae.

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ABBREVIATIONS USED IN THE TEXT FIGURES

al.can.	alveolus for canine	p.can.	postcanine
al.p.can.	alveolus for postcanine tooth	p.fr.	prefrontal
art.	articular	p.for	pineal foramen
boc.	basioccipital	pm.	premaxilla
can.	canine	po.	postorbital
den.	dentary	pof.	postfrontal
e.a.m.	external auditory meatus	po.par.	postparietal
ect.	ectopterygoid	pt.f.	posttemporal foramen
ext.nar.	external nares	q.	quadrate
for.mag.	foramen magnum	q.j.	quadratojugal
fr.	frontal	q.r.pt.	quadrate ramus of pterygoid
i.	incisor	ref.l.	reflected lamina
jug.	jugal	sm.	septomaxilla
lac.	lachrymal	sq.	squamosal
l.pr.pt	lateral process of pterygoid	st.	stapes
max.	maxilla	st.for.	stapedial foramen
nas.	nasal	t.	tabular
pal.	palatine	vo.	vomer
par.	parietal		