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

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ABSTRACT. A new genus of tapinocephaline dinocephalian, Tapinocephalus pamelae, is described from the lowermost bizone of the Beaufort Group in South Africa. Tapinocephalus is older than any dinocephalian previously discovered in Africa, being early Late Permian (Ulimian–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 (Ulimian–Kazanian) times. They were present among the earliest therapsid fauna of the San Angelo Formation of Texas (Olson 1962) and the Russian Ocher Formation (Chudinov 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 (Boostra 1969, 1971; Kitching 1977; Keyser and Smith 1978).

The Dinocephalians are the earliest group of therapsids for which a significant adaptive radiation can be identified (Rubide 1986), but for all their early success, they became completely extinct by the close of the Tapinocephalus Zone (Dinocephalian Assemblage Zone) times, leaving no descendant groups (Boostra 1971; Kemp 1982). The infra-order Dinocephalia was considered to consist of six families, namely Estemmenosuchidae, Brithopodidae, Anteosauridae, Titanosuchidae, Tapinocephalidae and Styracosuchidae (Boostra 1963a; Kemp 1982). More recently, King (1988) reclassified these as subfamilies of the three families Estemmenosuchidae, Brithopodidae and Titanosuchidae, and regarded Styracosuchidae, the only genus in the family Styracosuchidae, 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 interlocking incisor teeth in the upper and lower jaws (Boostra 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 Edicynodon Zone, a newly identified bizone 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. Three of these 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 Rieblon 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 PALAEONTOLOGY**

Subclass **Synapsida** Osborn, 1903

Order **Therapsida** Broom, 1905

Infraorder **Dinocephalia** Seeley, 1894

Family **Titanosuchidae** Boonstra, 1972

Subfamily **Tapirocephalinae** Lydekker, 1890

*Tapinocephalus* gen. nov.

Type species. *Tapinocephalus pamelae* sp. nov.

**Diagnosis.** Large tapirocephaline dinocephalian. Moderate pachyostosis with broad postorbital bar. Temporal opening relatively large for tapirocephaline, 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 palateine 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 *tapios*, humble; Latin *canis*, 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 Tapirocephalinae.

*Tapinocephalus pamelae* 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.** *Eodicydon* Zone (Rubidge 1987) at the base of the Beaufort Group (Ufifian-Kazanian age) on Modderdrift farm, Prince Albert, South Africa (map sheet: South Africa 1: 50000, Sheet 3322 BA Seekoeigat, 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

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**Text-fig. 1.** *Tapinocephalus pamela*, 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
sural 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 sural 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 dinoccephalians (Boonstra 1962).

As in all known South African dinoccephalians, 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 sural 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 sural contact with the posterior edge of the maxilla. Behind this contact, the ventral
margin of the skull curves posteroverntrally 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 antero-dorsal 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 postdorsal 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 fenestra. 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 quadratojugal. Postero-medially 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 3904. 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 dinoccephalians, 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 quadratojugal to the
external auditory meatus. Although the lateral and dorsal contacts of the occipital and otic bones with the
tubular 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 sural contact with the parietal posterodorsally. The tubular 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.
**Palate**

In the palate, the premaxilla overlies the anterioventral 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 nares. 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 *nosea* are narrow, vertically expanded bones which form a median trough between them. They make up the medial and postero medial 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 nares. Postero medially, 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 region 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 oriented 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 interpterygoid alveolus is present and extends posteriorly from the level of the lateral flanges of the pterygoid. The pterygoid meets the basi sphenoïd immediately behind the interpterygoid 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 stapedial foramen.

The basi sphenoïd is a relatively small triangular-shaped bone with its apex pointing anteriorly to meet the pterygoid immediately posterior to the interpterygoid 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 basi sphenoïd 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 dorsomedial 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 postero medial 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 postero dor sally and has two prominent depressions which relate to the quadrates 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. Tapinocaninae 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 splenial is widely exposed on the medial side of the lower jaw. It attains its greatest width near its posterior end and is in contact with the prearticulare posteroventrally, and the angular posteroventrally. The splenial 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 specimen 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 that 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 and van der Heyden 1954). The dental formulae of the various specimens studied are: NMQR 2985 I$^1$ C$^1$ P$^2$, NMQR 2986 I$^1$ C$^1$ P$^2$; NMQR 2987 I$^1$ C$^1$ P$^2$; ROZ K95 I$^1$ C$^1$ P$^2$.

**Comparison with other Dinocephalians**

**Skull roof**

In general shape, the skull of *Tapinocephalus* resembles that of a tapinocephalian 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 *Tapinocephalus* are relatively large with a resultant narrow intertemporal region when compared with other forms of the Tapinocephalinae, although there are genera such as *Avenantsia* 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 tapinocephalian dinocephalians, except *Ulemosaurus*, but is not as long as that of the Titanosuchinae.

The quadrate jugal of *Tapinocephalus* 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 quadrate jugal was a surface bone of the posterostral 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 articular surface of the quadratojugal 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).

**Pahtal**

In the palate, the premaxilla forms a large proportion of the anterolateral margin of the internal nares as in the Titanosuchinae and the Estemmenosuchidae. In the Tapinocephalinae and in Anteosaurus, the premaxilla has only a small contact on the anteromedial side of the internal naris. The vomers are thin bones, as in the Brithopodinae (Orlov 1958), and not broad and flat as in all other South African dinosuchians, 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 Styracotherium, which is now considered to be a sister taxon of the tapinocephalines. Small clusters of palatal teeth are known in the Brithopodinae, Anteosaurinae, and in Styracotherium, which is now considered to be a sister taxon of the tapinocephalines. Small clusters of palatal teeth are known in the Brithopodinae, Anteosaurinae, and in Styracotherium, which is now considered to be a sister taxon of the tapinocephalines. Small clusters of palatal teeth are known in the Brithopodinae, Anteosaurinae, and in Styracotherium, which is now considered to be a sister taxon of the tapinocephalines.

**Dentition**

One of the diagnostic features of dinosuchians is the denticulabial, but in Tapinocephalinae the 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 petrifaction most frequently in the Tapinocephalinae. In the Titanosuchinae the teeth are generally preserved in the alveoli even though the crowns are frequently broken off at the level of the alveolar border either before petrifaction 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 dinosuchian 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 dinosuchians, the first pair of upper incisors of Tapinocephalinae is more lightly built than the others and they are laterally compressed, they lie close together and, in occlusion, they pass 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 dinosuchian, the lower canine in specimen NMR 2986 (the only one where it is preserved) is situated more in the titanosuchine position, passing in front of the upper canine (Text-fig. 1c). The size of the upper canine of Tapinocephalinae (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 dinoccephalians (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 dinoccephalians (Boonstra 1962), the postcanines of the lower jaw
of Tapinocephalus are situated on the lingual side of those of the upper jaw when the jaws are closed,
and do not intermesh as in tapinocephaline dinoccephalians. 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 Tapinocephalus 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 quadrates (Boonstra 1963b), and
orientation of the tabular bone. It is thus reasonable to consider this dinoccephalian as belonging to
the Tapinocephalinae but still retaining some pleisomorphic characters which are not present in any
other known tapinocephaline dinoccephalian.

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 dinoccephalians, 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 Estemmenosuchoida. 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, Tapinocephalus 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).
CONCLUSION

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