

A NEW GALESAURID (THERAPSIDA: CYNODONTIA) FROM THE LOWER TRIASSIC OF SOUTH AFRICA

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ABSTRACT. A new galesaurid cynodont, *Progalesaurus lootsbergensis* gen. et sp. nov., is described on the basis of a well-preserved skull, lower jaw, right scapula and left atlantal neural arch. Autapomorphies of *Progalesaurus* include postcanine teeth bearing numerous mesial and distal accessory cusps that flank a recurved main cusp, a post-temporal fenestra bordered by the squamosal ventrally and a large external naris. *Progalesaurus* is similar to *Galesaurus* in possessing a poorly defined masseteric fossa on the dentary, a strongly recurved main cusp of the postcanine dentition, an incomplete secondary palate and a similar basisphenoid-parasphenoid morphology. A cladistic analysis of ten early cynodont genera resolves a monophyletic Galesauridae encompassing *Cynosaurus*, *Progalesaurus* and *Galesaurus*, although support for this clade is weak. *Procynosuchus* and *Dvinia* are placed at the base of Cynodontia whereas *Thrinaxodon* and *Platycraniellus* are positioned higher, but outside of Eucynodontia. The holotype and only known specimen of *Progalesaurus* was collected during systematic prospecting of Permo/Triassic boundary strata at New Lootsberg Pass, Graaff-Reinet District, South Africa. The discovery of *Progalesaurus* increases the number of valid Early Triassic cynodonts to four and sheds light on the tempo of early cynodont diversification after the end-Permian mass extinction.

KEY WORDS: Cynodontia, Galesauridae, South Africa, Permo/Triassic, Balfour Formation, phylogeny, mass extinction.

MAMMALIAN hallmarks such as a bony secondary palate, multicusped postcanine teeth, double occipital condyles and jaw adductor musculature differentiated into temporalis and masseter components first appeared in Late Permian (c. 255 Ma) cynodont therapsids (Hopson 1994; Rubidge and Sidor 2001), the richest fossil record of which hails from the Beaufort Group of South Africa (Kitching 1977; Rubidge 1995).

Cynodonts from the Upper Permian and Lower Triassic rocks of South Africa are represented by a handful of genera traditionally divided into two families, Procynosuchidae and Galesauridae (Hopson and Crompton 1969; Kemp 1982). The former includes only *Procynosuchus delaharpeae*, whereas the latter includes *Bolotridon frerensis*, *Cynosaurus suppostus*, *Galesaurus planiceps*, *Platycraniellus elegans* and *Thrinaxodon liorhinus*. Although numerous coeval cynodont taxa were initially recognized (e.g. Haughton and Brink 1954), more recent taxonomic work has demonstrated that the above taxa are the only valid South African forms (Hopson and Kitching 1972). Moreover, phylogenetic studies have shown that *Thrinaxodon* is more closely related to mammals than it is to *Galesaurus*, and the family Galesauridae is therefore paraphyletic as traditionally defined (Hopson 1991).

This paper has two aims. The first is to document the morphology of a new Triassic cynodont collected within 36 m of the Permo/Triassic boundary. The second is to place this taxon within the context of early cynodont diversification by incorporating it into a lower-level cladistic analysis of cynodont relationships. Because this analysis principally deals with cynodonts that fall phylogenetically outside of Eucynodontia (i.e. non-eucynodont cynodonts), we will use the terms 'basal, early, or primitive' to refer herein to this paraphyletic assemblage of cynodonts.

Principal measurements of the holotypic skull are given in Table 1.

Institutional abbreviations. AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; SAM, South African Museum, Cape Town; TM, Transvaal Museum, Pretoria.

TABLE 1. Principal measurements of the holotypic skull of *Progalesaurus lootbergensis* in mm. Asterisk indicates an approximate value based on the left side only.

Basal skull length	93.5	Maximum width across zygomatic arches	70*
Preorbital length	34.5	Width across pterygoid transverse flanges	27.0
Width of snout between canines	24.7	Depth of zygomatic arch at midlength	13.6
Diameter of orbit	16.1	Length of temporal fossa	30.6
Length of postorbital bar at midheight	3.2	Width across occipital condyles	14.8
Minimum interorbital width	21.6	Height of foramen magnum	9.1
Temporal width at parietal foramen	4.7	Width of foramen magnum	10.5

MATERIAL AND METHODS

The specimen was found by RMHS in November 1998 in a small drainage gully on the slopes of the Sneeberg mountains near New Lootsberg Pass (Text-fig. 1). The skull was completely contained within a dark reddish brown calcareous nodule; only when the nodule was excavated and broken open was the fossil revealed. The specimen was mechanically prepared by Annelise Crean of the South African Museum using air scribe and mounted needles under a binocular microscope. To enhance the sutures and prevent scratches during handling, the surface of the fully prepared skull was hardened with 5 per cent Paraloid B72 thinned in acetone.

The following specimens were used as comparative material to construct the data matrix presented in the Appendix: *Cynosaurus suppostus* (BMNH R1718, BP/1/3926, BP/1/4469, SAM-PK-4333); *Galesaurus platyceps* (AMNH 2223, BP/1/4281, BP/1/4714, SAM-PK-K1119, SAM-PK-K9956, TM 24, TM 83); *Lumkuia fuzzi* (BP/1/2669); *Platycraniellus elegans* (TM 25); *Procynosuchus delaharpeae* (BP/1/226, BP/1/591, BP/1/1545, BP/1/1559, BP/1/2600, BP/1/3758, BP/1/5832, SAM-PK-K338, SAM-PK-K8511); *Thrinaxodon liorhinus* (SAM-PK-K1498, SAM-PK-K10016, SAM-PK-K10017, TM 80, TM 81, TM 180); *Trirachodon kannemeyeri* (SAM-PK-K11481). Data for *Dvinia prima* were based on Tatarinov (1968) and the unpublished research of J. A. Hopson and R. R. Reisz (pers. comm. 2002). Codings for *Bolotridon frerensis* were taken from Broili and Schröder (1934). Kemp (1979) was consulted for supplementary data on *Procynosuchus delaharpeae*.

SYSTEMATIC PALAEOLOGY

THERAPSIDA Broom, 1905

CYNODONTIA Owen, 1861

EPICYNODONTIA Hopson and Kitching, 2001

GALESURIDAE Lydekker, 1890

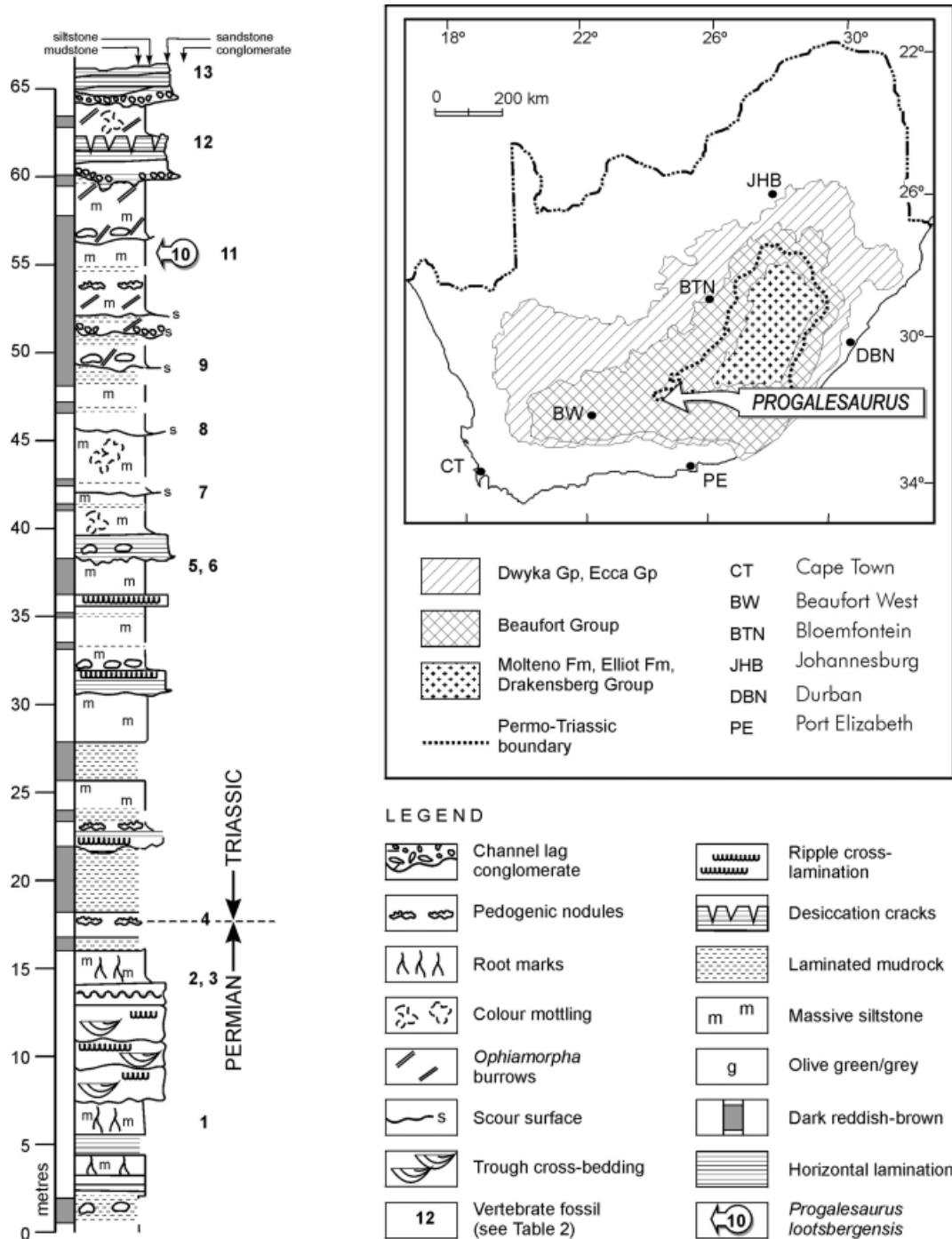
Revised definition. All cynodont therapsids sharing a more recent common ancestry with *Galesaurus* than with *Thrinaxodon*.

Revised diagnosis. Postcanine teeth lack lingual cingula; basisphenoid triangular in ventral view with long anterior projection.

PROGALESURUS gen. nov.

Derivation of name. Greek, *pro*, prefix meaning before, *gale*, weasel or cat and *saurus*, lizard or reptile. The combination of these roots refers to the antecedent nature of this taxon to the phylogenetically more derived and stratigraphically higher genus *Galesaurus*.

Diagnosis. As for species.



TEXT-FIG. 1. Sedimentological section of New Lootsberg Pass with position of the Permo/Triassic boundary as determined by Smith and Ward (2001) and all *in situ* fossil occurrences. See Table 2 for fossil records.

Progalesaurus lootsbergensis sp. nov.

Text-figures 2–6

Derivation of name. *Lootsberg* is in reference to New Lootsberg Pass, the locality from which the holotype was collected; *ensis* is Latin for ‘from’ or ‘belonging to.’

Geological context. The holotype of *Progalesaurus* was discovered within a nodule protruding from a small outcrop of reddish brown massive siltstone. Detailed logging of the sedimentary sequence above and below the fossil locality (Text-fig. 1) shows several similar nodular horizons interbedded with tabular greenish grey fine-grained sandstone bodies. These mudrocks are interpreted as proximal floodplain deposits that mainly accumulated from episodic flooding of rivers on a semi-arid alluvial plain (Smith 1995; Ward *et al.* 2000). The nodules are composed of micrite and interpreted to be of pedogenic origin formed in the B horizon of an arid zone calcic palaeosol. Preferential micritization around buried bone began with bacterial decay that produced a reduction halo around the bones some 0.5 m below the floodplain surface. Later, microcrystalline calcium carbonate was precipitated from groundwater within the reduction envelope and onto the bone surface (Konizeski 1957). The uncompressed state of the skull attests to the early lithification of the calcareous nodule, before the surrounding mud was fully compacted.

Associated sandstone bodies are up to 4 m thick and extend laterally for 1–2 km. They are predominantly horizontally laminated and contain conglomeratic lenses made up of mudrock pebbles, pedogenic nodules and fragments of bone. These are interpreted as the in-channel deposits of ephemeral, low sinuosity rivers flowing in a general northerly direction across a semi-arid, low gradient alluvial plain (Smith and Ward 2001).

Holotype. SAM-PK-K9954, nearly complete skull with lower jaws, right scapula, left atlantal neural arch and unidentified fragments.

Type horizon and locality. Coordinates South 31° 50′ 34.4″ East 24° 50′ 91.3″, New Lootsberg Pass, Tweefontein Farm (Lucerne 70), Graaff-Reinet District, eastern Cape Province, Republic of South Africa. The type locality lies near the top of the Paalingkloof Member of the Balfour Formation of the Beaufort Group, some 36 m above the Permian/Triassic boundary. Biostratigraphically, it falls in the lowermost *Lystrosaurus* Assemblage Zone (Groenewald and Kitching 1995) and is part of the Lootsbergian land vertebrate faunachron of Lucas (1998).

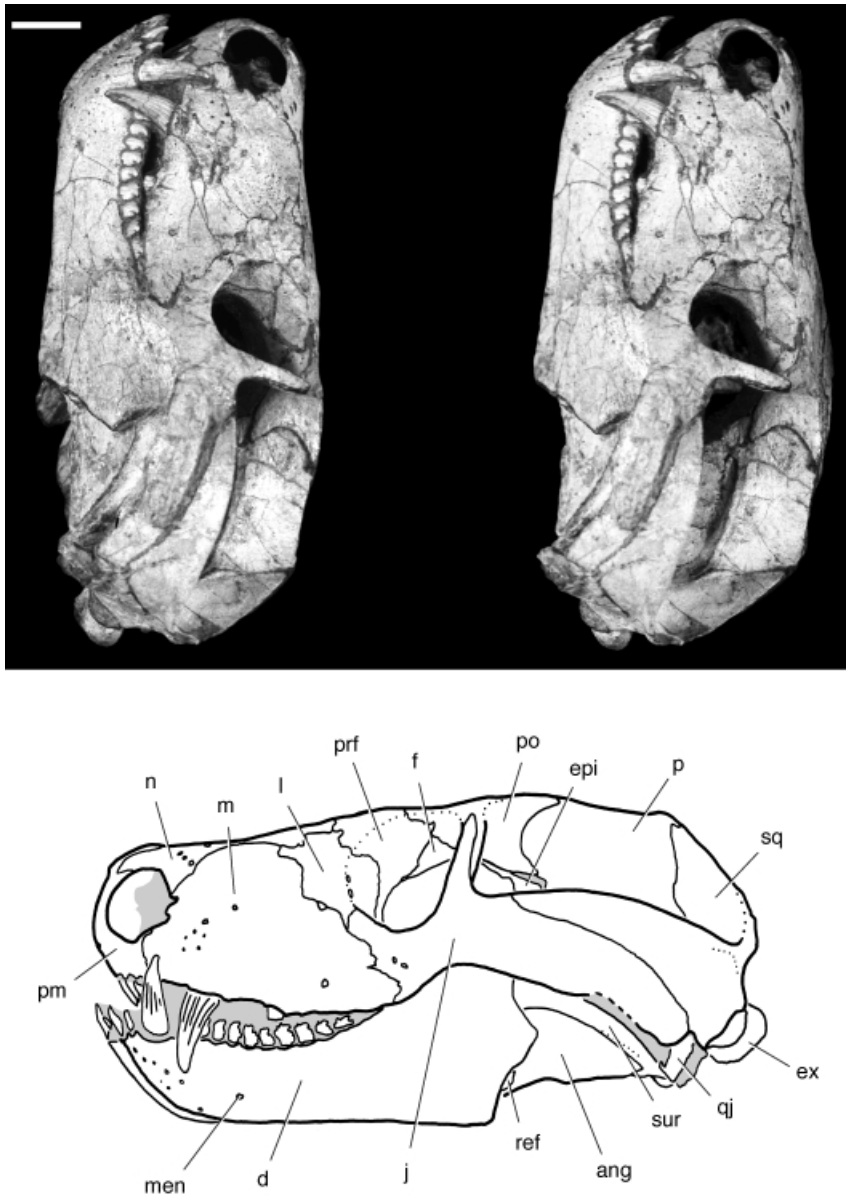
Diagnosis. Megaserrations (or cuspules) along mesial and distal carinae of lower postcanine teeth; squamosal with long medial process between tabular and paroccipital process of the opisthotic that contacts the post-temporal fenestra; external naris large; maxilla-jugal suture oriented transversely in ventral view.

DESCRIPTION

The specimen is generally well preserved, although the right zygomatic arch is broken and displaced downwards just posterior to its junction with the postorbital bar. In addition, the lower jaws have been disarticulated, laterally rotated about their long axes and pushed forwards such that the lower canines lie anterior and external to upper canines. This movement has made preparation of the anterior portion of the palate impossible. The short, robust snout is slightly wider than it is deep at its midpoint. The orbits are directed anterolaterally and placed just anterior to the midpoint of the skull. The temporal fenestrae are large and approach one another dorsally such that a sagittal crest is formed. This crest narrows posterior to the oval parietal foramen.

Skull roof

The premaxilla forms the anteromedial and ventral margins of the external naris. Compared to the condition in other early cynodonts, the external naris in *Progalesaurus* appears remarkably large, which is considered an autapomorphic condition. The ascending, or internarial, process of the premaxilla is complete and overlaps the nasal dorsally. A small, anteriorly directed foramen is present on the external surface of the premaxilla where the internarial process joins the body of this element. The premaxilla is overlapped by the maxilla ventral to the external naris. The palatal surface of the premaxilla has not been exposed.



TEXT-FIG. 2. Stereophotographs (with snout uppermost) and interpretive line drawing (with snout to the left) of the skull of *Progalesaurus lootbergensis* gen. et sp. nov. (SAM-PK-K9954), in lateral view. Scale bar represents 1 cm.

Only the right septomaxilla is preserved in place. As described by Wible *et al.* (1990) and Hillenius (2000), the septomaxilla in cynodonts may be divided into two portions: the body and the facial process. The former rests above the junction of the premaxilla and maxilla and is contained entirely within the external naris. It bears a medial lamina, which partially floors the external naris, and a horizontal, intranarial process. These two structures are separated by an anteriorly concave plate of bone that is pierced by a forwardly facing foramen, termed the opening of the septomaxillary canal by Hillenius (2000). On the lateral surface of the snout, an oval septomaxillary foramen is present between the body of the septomaxilla and the maxilla. When compared to the condition in primitive therapsids

(e.g. *Biarmosuchus*) or more basal cynodonts (e.g. *Procynosuchus*), the facial process of the septomaxilla is extremely small and extends between the maxilla and nasal for only a short distance. On the left side (Text-fig. 2), the posterior margin of the external naris bears two irregularities, the upper representing the fossa for the facial process of the septomaxilla and the lower the ventral margin of the septomaxillary foramen.

The maxilla is a large bone that forms most of the side of the face (Text-fig. 2). The external surface of the maxilla is pock-marked by numerous small foramina, especially above the upper canine. In addition, a somewhat larger, anteriorly-directed foramen is present further posteriorly, near the ventral margin of the maxilla. This foramen, which presumably transmitted branches of the maxillary portion of the trigeminal nerve, lies ventral to the anterior margin of the orbit. In lateral view, the dorsal surface of the maxilla is convex where it contacts the nasal. From its highest point midway along the snout, the posterior margin of the maxilla curves posteroventrally to contact the lacrimal and jugal along a jagged suture. The alveolar border of the maxilla is basically straight in profile. Posteriorly, the maxilla bends outwards and contacts the jugal underneath the orbit. As in chiniquodontids, this contact is transverse in ventral view (Text-fig. 4). Only a small portion of the palatal process of the maxilla can be seen. Although little can be said of its detailed morphology, the position of the maxilla-palatine contact indicates that its configuration was similar to that of *Galesaurus* and *Cynosaurus* and that the maxilla formed the majority of the choanal plate, although it did not contact its mate along the midline (Boonstra 1935; Rigney 1938; Brink 1965).

The nasal is primarily restricted to the dorsal surface of the snout, where it extends from the posterior margin of the external naris to a point in line with the anterior third of the orbit (Text-fig. 3). In the snout it is convex from side to side, but it becomes flat in the region of the lacrimal and prefrontal. As with the maxilla, numerous foramina dot the external surface of the nasal, especially on its anterior half. Anteriorly, the nasal forms the dorsal margin of the external naris between those portions formed by the septomaxilla and the ascending process of the premaxilla. As in all basal cynodonts, the nasal is expanded posterolaterally to contact the lacrimal (Hopson and Barghusen 1986). Posteriorly, the nasal contacts the prefrontal and frontal. The naso-frontal suture is transverse in *Thrinaxodon*, whereas it forms an inverted V-shape in *Progalesaurus*, *Galesaurus* (BP/1/4281; TM 24, 83, 180), *Cynosaurus* (BP/1/4496; SAM-PK-4333) and *Procynosuchus* (Kemp 1979, fig. 1). The condition in *Dvinia* is uncertain, but is probably V-shaped as well.

In dorsal view, the frontal is an elongate element that tapers posteriorly (Text-fig. 3). In *Progalesaurus*, the frontal is flat and lacks the well-developed median ridge present in eucynodonts such as *Trirachodon* and *Diademodon*. Contact between the prefrontal and postorbital precludes the frontal from contributing to the dorsal margin of the orbit. However, in lateral view, the frontal can be seen to emerge below the former two elements as a small, triangular wedge within the orbit (Text-fig. 2). As in other early cynodonts, this portion of the frontal contacts the epipterygoid by means of a long, posteroventrally directed lamina.

The prefrontal forms the anterodorsal margin of the orbit. It contacts the lacrimal along its anterior and ventral faces, whereas it contacts the nasal, frontal and postorbital on the skull roof. Inside the orbit, the prefrontal bears a long, descending flange that passes medial to the lacrimal to contact the pterygoid.

The lacrimal forms the anterior margin of the orbit. Externally, it contacts the prefrontal, maxilla and jugal. On the floor of the orbit, the lacrimal contacts the pterygoid. Two lacrimal foramina are present just inside the orbital margin. The foramina lie along the same vertical line, although the upper foramen is slightly smaller. The lower lacrimal foramen appears to communicate with a foramen positioned on the lacrimal-maxilla suture on the external surface of the face, as in *Lumkuia* (Hopson and Kitching 2001).

The postorbital supports two large processes and one small process. Its small, anterior ramus forms the posterodorsal margin of the orbit and contacts the prefrontal anteriorly. The postorbital ramus of the postorbital is gracile and descends to near the base of the postorbital bar medial to the jugal. The posterior, or temporal, ramus of the postorbital overlaps the parietal on the lateral surface of the sagittal crest and has a deeply forked posterior margin that extends to the level of the parietal foramen (Text-fig. 2). The morphology of the temporal ramus of the postorbital is variable in basal cynodonts. For example, the dorsal fork is absent in small specimens of *Thrinaxodon* (SAM-PK-K10016, 10017), whereas both forks are present in larger individuals (TM 80, 81, 180), in *Galesaurus* (AMNH 2223; BP/1/4281) and in *Cynosaurus* (BP/1/3926). The ventral fork is absent in *Trirachodon* (SAM-PK-K11481), *Procynosuchus* (SAM-PK-K8511; BP/1/226, 3748; Kemp 1979, fig. 3) and *Dvinia*. In *Progalesaurus*, the posterior ramus of the postorbital served as an origination area for temporalis musculature, but this origination area did not extend onto the dorsal surface of the postorbital bar.

Anterior to the parietal foramen on the skull roof, the parietals bear bilaterally symmetrical, anterior prongs that overlie the frontals and might be separated by a midline suture. Behind the foramen, the parietals are clearly fused on the midline, forming a short sagittal crest. As in *Galesaurus* and *Cynosaurus*, this crest narrows considerably posterior to the parietal foramen. In more advanced cynodonts such as *Platycraniellus*, *Thrinaxodon* and *Trirachodon*, the sagittal crest incorporates the parietal foramen with little discernible increase in its width. The development of the sagittal crest in cynodonts shows ontogenetic as well as phylogenetic variation (van Heerden 1972). For example, extremely small individuals of *Thrinaxodon* (e.g. SAM-PK-K-10016, 10017) lack a sagittal crest both in front of and

behind the parietal foramen, whereas those of intermediate size (e.g. TM 80) approximate the galesaurid condition, with a true sagittal crest occurring only posterior to the parietal foramen. Below the sagittal crest, the body of the parietal expands posteriorly and, in cross-section, has sides that diverge at an angle of approximately 80 degrees. In lateral view, the parietal bears a shallow groove just above its contact with the epipterygoid and proötic. This groove, termed the external orbitotemporal groove by Rougier *et al.* (1992), has been interpreted as housing the arterial ramus supraorbitalis and associated vein of the sinus canal (Rougier *et al.* 1992; Wible and Hopson 1995).

The jugal is a large, triradiate element. Its anterior ramus forms most of the suborbital bar and contacts the lacrimal and maxilla anteriorly. The jugal bears two small foramina on its external surface ventral to the orbit and a single, medial foramen within the orbit. In ventral view, the jugal can be seen to contact the maxilla along a transversely oriented suture, as in chiniquodontids (Hopson and Barghusen 1986). In other basal cynodonts, the jugal-maxilla suture is oriented posterolaterally. The postorbital ramus of the jugal ascends on the external surface of the postorbital nearly to the level of the skull roof. The posterior ramus of the jugal is deep and accommodates the zygomatic ramus of the squamosal on its dorsolateral surface. The jugal and maxilla are faintly thickened in their region of contact, but a distinct suborbital (or masseteric) process is absent.

The squamosal forms the dorsal half of the zygomatic arch. As in *Cynosaurus*, *Galesaurus* and *Thrinaxodon*, the zygomatic arch of *Progalesaurus* is a relatively robust structure that deepens posteriorly. Its dorsal margin is continuous with the dorsal ridge of the lambdoidal crest. The squamosal overlaps the parietal on the posterior face of the temporal fenestra. In posterior view, the squamosal has a well-defined fossa under the junction of the zygomatic and lambdoidal ridges. This fossa, the homologue of the external auditory meatus, presumed to house the outer ear tube (Allin and Hopson 1992), is relatively shallow when compared with cynognathian taxa such as *Cynognathus*, *Diademodon* or *Trirachodon*, but not basal probainognathians such as *Lumkuia*. An inverted V-shaped notch is present on the ventral margin of the squamosal. It typically accommodates the quadrate and quadratojugal, although these elements have been disarticulated in the *Progalesaurus* holotype. The right squamosal bears a deep, medially facing fossa for the paroccipital process of the opisthotic, the distal portion of which is broken off on this side. The occipital portion of the squamosal has a medial process that contributes to the ventral margin of the post-temporal fenestra in *Progalesaurus*. In all other basal cynodonts the tabular overlies the squamosal and completely encircles the post-temporal fenestra.

Palate

As currently preserved, the palatal portion of the vomer is visible only in its post-choanal portion (Text-fig. 4). A thin, vertical septum descends from the body of the vomer into the gap between the choanal processes of the palatines and maxillae. Breakage along its ventral edge demonstrates that this element is unpaired. The contact between the vomer and the premaxilla cannot be seen. The body of the vomer, in the roof of the choanal trough, is trapezoidal in outline, ventrally concave and tapers posteriorly between the palatines and pterygoids. Posteriorly, the post-choanal portion of the vomer contacts the pterygoids.

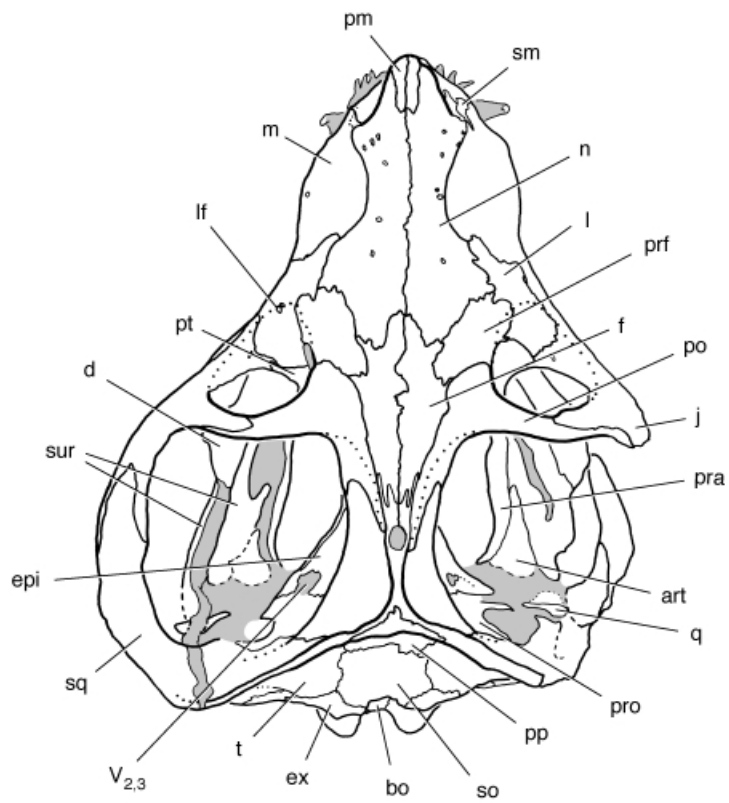
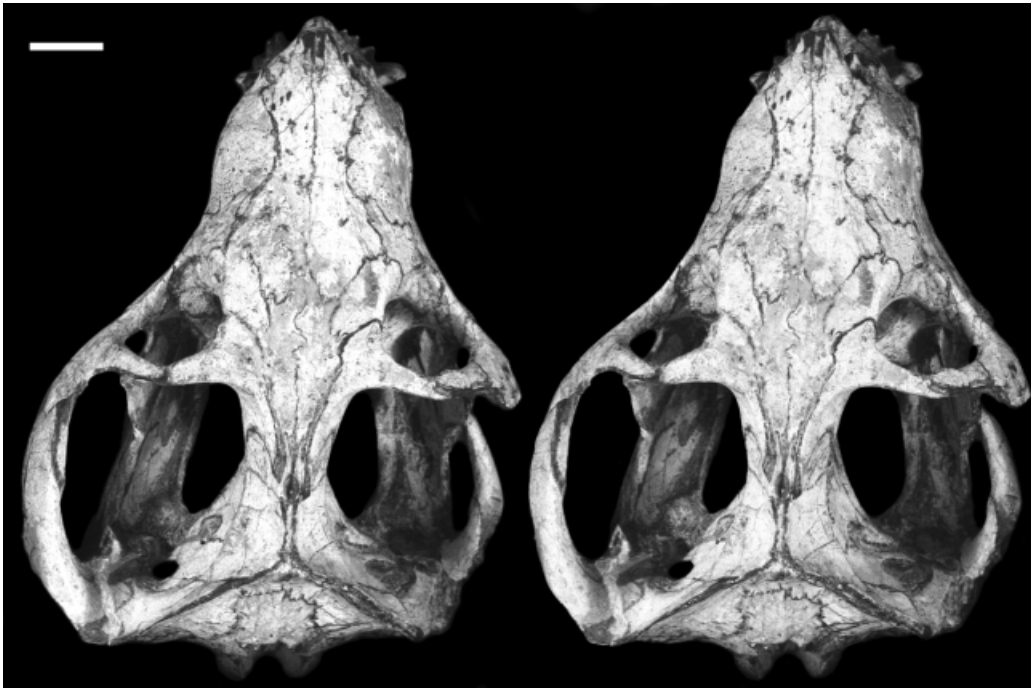
The palatine contribution to the secondary palate is poorly exposed in *Progalesaurus*. From what can be seen, it forms the posterior 2–3 mm of the incomplete secondary palate. As in *Galesaurus* and *Cynosaurus*, a complete secondary palate was not formed in *Progalesaurus*. On the roof of the primary palate, the palatine contacts that vomer and, more posteriorly, bears a posteromedially-oriented ridge that continues onto the pterygoid.

The region of the ectopterygoid is obscured by the lower jaw and covered by matrix.

The pterygoids form the roof of the choanal trough posterior to the vomer, where they contact the vomer anteriorly and the palatines anterolaterally (Text-fig. 5). Each pterygoid bears a short transverse flange, the posterior margin of which is vertical. Because of the dislocation of the mandible, it is difficult to determine how far down the inside of the lower jaw the transverse flange would have descended. The quadrate ramus of the pterygoid is reduced to a thin, posterolaterally directed strut that approaches the quadrate distally. As in large, presumably adult, specimens of *Thrinaxodon*, *Galesaurus* and *Cynosaurus*, interpterygoid vacuities are absent in *Progalesaurus*. On the sidewall of the braincase, the quadrate ramus of the pterygoid can be seen to underlie and support the epipterygoid.

Occipital and endochondral elements

The epipterygoid is best preserved on the left side. This plate-like element is anteroposteriorly long, being approximately twice the length of the proötic, and has a curved anterior margin. At its anterodorsal extreme, the epipterygoid contacts the frontal and postorbital. The footplate of the epipterygoid has a long anterior prong that extends along the dorsal margin of the quadrate ramus of the pterygoid. The latter is partially exposed on both sides and sweeps posterolaterally towards the jaw articulation. Posteriorly, the epipterygoid contacts the proötic above and below a large foramen that accommodated the maxillary (V_2) and mandibular (V_3) branches of the trigeminal nerve.



The proötic and opisthotic portions of the ossified otic capsule are almost completely fused. The opisthotic forms most of the paroccipital process, which in *Progalesaurus* is anteroposteriorly thickened. In ventral view (Text-fig. 4), the opisthotic forms the anterior half of the margin of the ventrally facing jugular foramen. Anterior to this, it presumably forms the posterior half of the fenestra ovalis. The proötic is best exposed on the sidewall of the braincase, where it contacts the squamosal posteriorly, the parietal dorsally and the epipterygoid anteriorly. It has a curved dorsal margin and two posteriorly directed struts that envelop the pterygoparoccipital foramen. In ventral view, the left proötic can be seen to suture to the opisthotic just lateral to the fenestra ovalis.

The fused basisphenoid-parasphenoid is exposed on the ventral surface of the skull as a triangular element (Text-fig. 5). The apex of this triangle tapers to a point anteriorly, where it slots between the basicranial rami of the pterygoids. The basiptyergoid processes are offset from the ventral surface of the basisphenoid-parasphenoid, which forms a shallow fossa whose lateral edges are slightly thickened and downturned. This combination of features distinguishes the basisphenoid-parasphenoid of galesaurids from that of both 'procynosuchid-' and '*Thrinaxodon*-grade' cynodonts. For example, in procynosuchids this basiptyergoid process projects forwards from the level as the basisphenoid-parasphenoid plate, whereas in '*Thrinaxodon*-grade' cynodonts the triangular plate is restricted more posteriorly and is equilateral. The internal carotid foramina of *Progalesaurus* are presumably positioned between the basisphenoid-parasphenoid rostrum and the basiptyergoid processes, as in *Thrinaxodon* and *Galesaurus*, although this area is obscured by matrix in the holotype. Posteriorly, the basisphenoid-parasphenoid contacts the basioccipital along an inverted U-shaped suture, resembling the condition in *Thrinaxodon* and *Cynosaurus* and contrasting with the more V-shaped suture in *Galesaurus*.

The ventral surface of the basioccipital bears a pair of faint, parasagittal depressions that bound a low, median ridge. These depressions are more poorly developed than in large specimens of *Thrinaxodon* or *Galesaurus*. Small individuals of *Galesaurus* have shallow depressions (e.g. SAM-PK-K9956). The basioccipital tapers in width posteriorly and contacts the opisthotic and exoccipital along its lateral margins. In occipital view, the basioccipital forms the ventral rim of the foramen magnum between the double occipital condyles.

The paired exoccipitals form the mammal-like, double occipital condyles characteristic of cynodonts (Hopson and Barghusen 1986). Each extends upwards on either side of the foramen magnum and bears a slight thickening that represents the articular surface for the proatlas. The exoccipital in *Progalesaurus*, *Cynosaurus* and *Galesaurus* is broader than in *Thrinaxodon*, which is restricted along the lateral margin of the foramen magnum. Ventrally, the exoccipital forms the posterior half of the rim of the jugular foramen. A tiny foramen opens dorsomedially from the posterior portion of the jugular foramen; it probably transmitted the hypoglossal nerve in life.

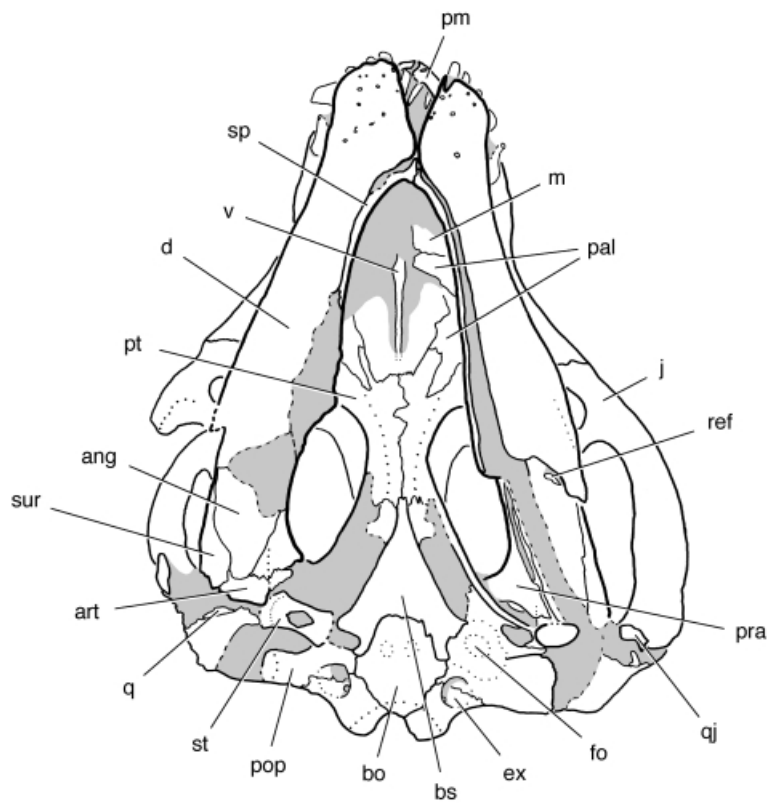
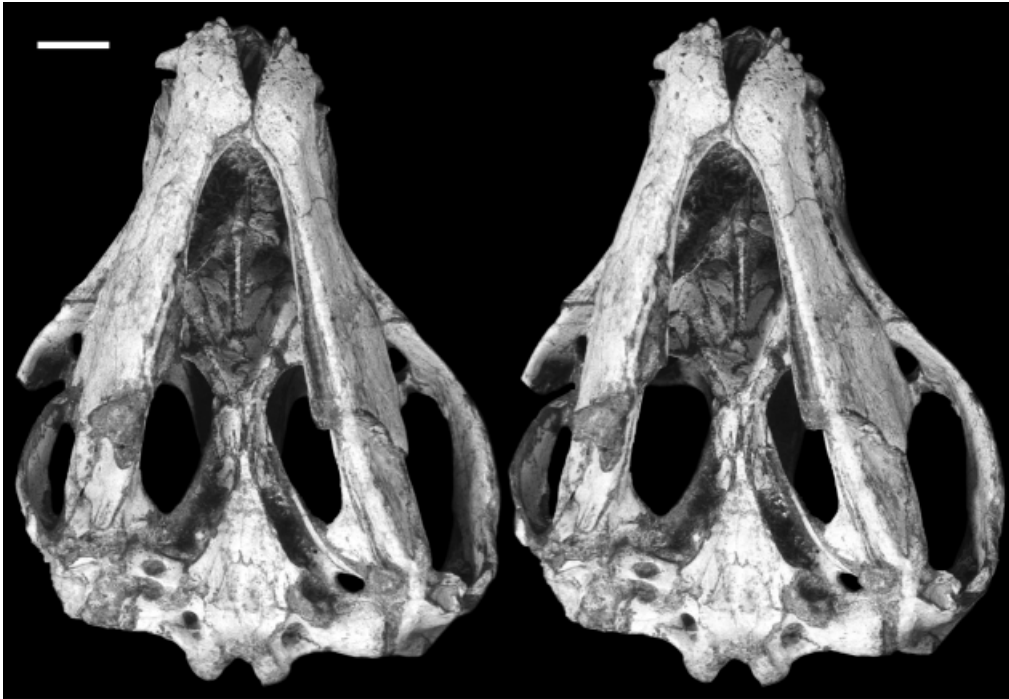
The postparietal is a vertical bone that forms the middle third of the dorsal margin of the occiput. The posterior surface of the postparietal supports a broad median ridge and shallow parasagittal fossae. It is bounded laterally by the tabulars and ventrally by the supraoccipital. The postparietal contributes a small triangular wedge to dorsal skull roof, just posterior to the parietal on the sagittal crest.

The supraoccipital forms the upper one-third of the margin of the foramen magnum. As in most cynodonts except *Procynosuchus* and *Dvinia*, the supraoccipital is relatively broad between its contacts with the tabulars and exoccipitals (Kemp 1979; Tatarinov 1979). The broad, median ridge present on the postparietal extends onto the posterior surface of the supraoccipital.

The tabular is a large bone that occupies the dorsolateral portion of the occiput and forms the majority of the occipital rim of the lambdoidal crest (Text-fig. 5). The tabular is indented ventrally by the post-temporal fenestra, which, atypically, is bounded ventrally by the squamosal. The tabular contacts the squamosal along its lateral and ventral margins and the exoccipital, supraoccipital and postparietal along its medial margin. In addition, it makes a short contact with the paroccipital process of the opisthotic between the squamosal and exoccipital.

The quadrate and quadratojugal are both difficult to observe in *Progalesaurus*. On the left side, a band of calcite passes through the region of the jaw articulation. The ventral edge of the quadratojugal has slipped laterally, exposing its articular surface for the quadrate. On the right side, the dorsal ramus of the quadrate can be seen through the temporal fenestra. It has a flat anterior face, and is relatively tall with a ventromedially sloping dorsal margin.

Only the right stapes is preserved (Text-fig. 5). It lies approximately in life position, with its proximal end resting on the eminence surrounding the fenestra ovalis and its poorly-ossified distal surface directed towards the region of the jaw articulation. As in other basal cynodonts, the stapes in *Progalesaurus* is characterized by a large, oval stapedial foramen that separates two gracile crura.



Lower jaw

The lower jaws, which are unfused at the symphysis, have been diagenetically protracted and laterally rotated about their long axes. In addition, the dentary and post-dentary portions of the jaw are slightly disarticulated on both sides; the right post-dentary bones are angled anterodorsally whereas those on the left are anteroventrally oriented. The symphysis is deep, anteriorly convex and formed by both the dentary and splenial. In overall aspect, the mandible of *Progalesaurus* is similar to that of *Galesaurus* (e.g. TM 80), but much more robust than that of primitive cynodonts such as *Dvinia*, *Procynosuchus* or *Thrinaxodon* (Tatarinov 1968; Fourie 1974; Kemp 1979).

The dentary is the largest element of the lower jaw (Text-fig. 2). Its dorsal margin is smoothly continuous between the horizontal, tooth bearing ramus and the posterodorsally sloping coronoid process. The ventral margin of the dentary behind the convex symphyseal region is subhorizontal until it bends sharply upwards at the pseudangular process. Small, randomly placed foramina adorn the external surface of the mandible in the region of the symphysis. In addition, bilaterally symmetrical mental foramina are positioned near the lower border of the jaw approximately 9 mm posterior to the lower canine. As in *Galesaurus*, the lateral surface of the coronoid process is slightly concave, although this depression, the masseteric fossa, is not well defined. In taxa such as *Procynosuchus*, *Dvinia* and *Thrinaxodon*, the anterior and ventral margins of the masseteric fossa are offset from the rest of the dentary by a well-developed edge. The preserved dorsal extent of the coronoid process indicates that it was approximately three times deeper than the horizontal ramus. The posterior margin of the coronoid process slopes posteroventrally to meet the postdentary bones. The latter are approximately half the height of the dentary.

The body of the angular is best preserved on the right side, although only a shard of a reflected lamina remains. A greater portion of a reflected lamina is preserved on the left side, where it is exposed in medial view and appears slightly deeper than that described for *Thrinaxodon* by Fourie (1974, fig. 31). Poor preservation precludes further description of this feature. In lateral view, the angular is bordered by the surangular dorsally and by the dentary anteriorly. Because of the disarticulation between the dentary and postdentary components, the orientation of the ventral border of the angular cannot be confidently ascertained. The body of the angular is rounded from side to side and forms the ventral margin of the mandible between the dentary and articular. Posteriorly, the angular overlaps the surangular and articular in lateral view.

In lateral view, the surangular is bowed posteroventrally from the dentary to the jaw articulation (Text-fig. 2). It is convex from top to bottom along its exposed length and contacts the dentary anteriorly, angular ventrally and articular posteroventrally. The medial surface of the surangular is flat and its outline resembles that illustrated for *Procynosuchus* (Kemp 1979, fig. 6) and *Thrinaxodon* (Fourie 1974, fig. 31).

The splenial is a vertical lamina of bone that is restricted to the medial aspect of the lower jaw. In ventral view, the anterior end of the splenial expands slightly to form a small, triangular wedge into the base of the symphysis. In medial view, the splenial deepens posteriorly until just in front of the transverse flange of the pterygoid. At its deepest point, the dorsal margin of the splenial is curved medially. Posterior to the level of the transverse flange of the pterygoid, the splenial continues as a shallow bone restricted to the ventromedial margin of the mandible.

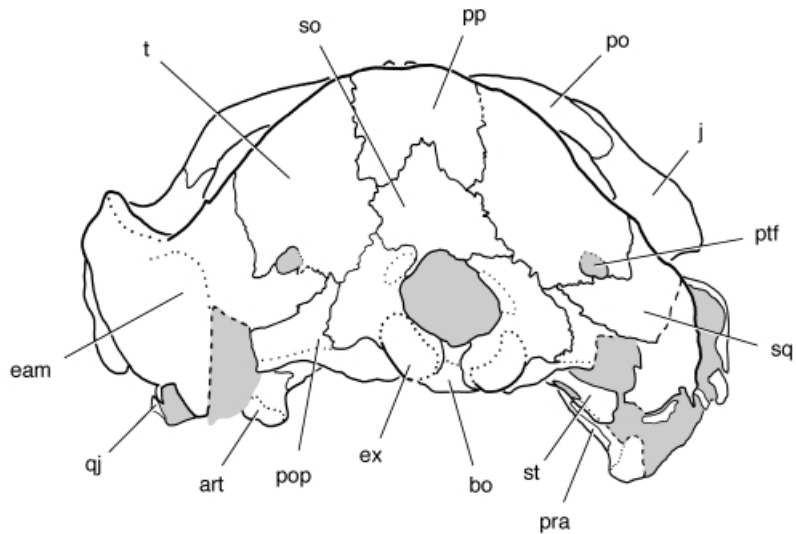
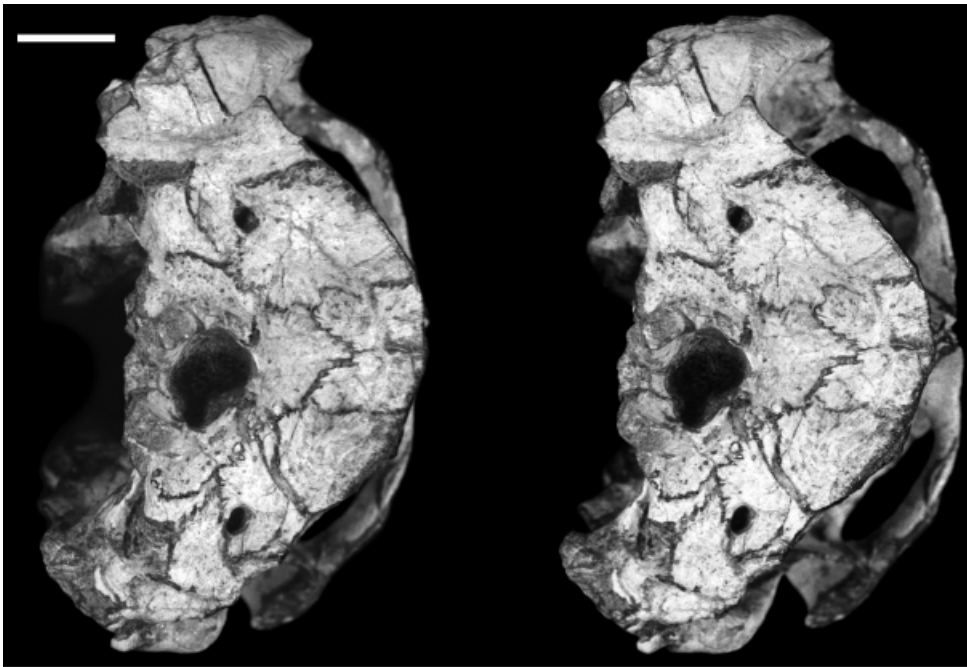
The region of the coronoid bone proved impossible to prepare free of matrix. On the right side, a thin sheet-like bone is suspended below the palate and might represent the disarticulated coronoid.

The prearticular is a rod-like element that, towards its caudal end, expands medially to accommodate the width of the articular (Text-fig. 4). In the region of the subtemporal fossa, the prearticular contacts the angular laterally, articular posteriorly and the surangular dorsally. Further anteriorly, the prearticular should contact the remaining jaw elements (i.e. dentary, splenial and coronoid), although this area is not visible in the holotype.

In dorsal view, the articular appears as an acute triangle wedged between the surangular and body of the angular (Text-fig. 3). It bears a well-developed, downturned retroarticular process that extends below the level of the body of the angular. In ventral view, the articular can be seen to possess a medial process that is positioned just posterior to the medial expansion of the prearticular.

Dentition

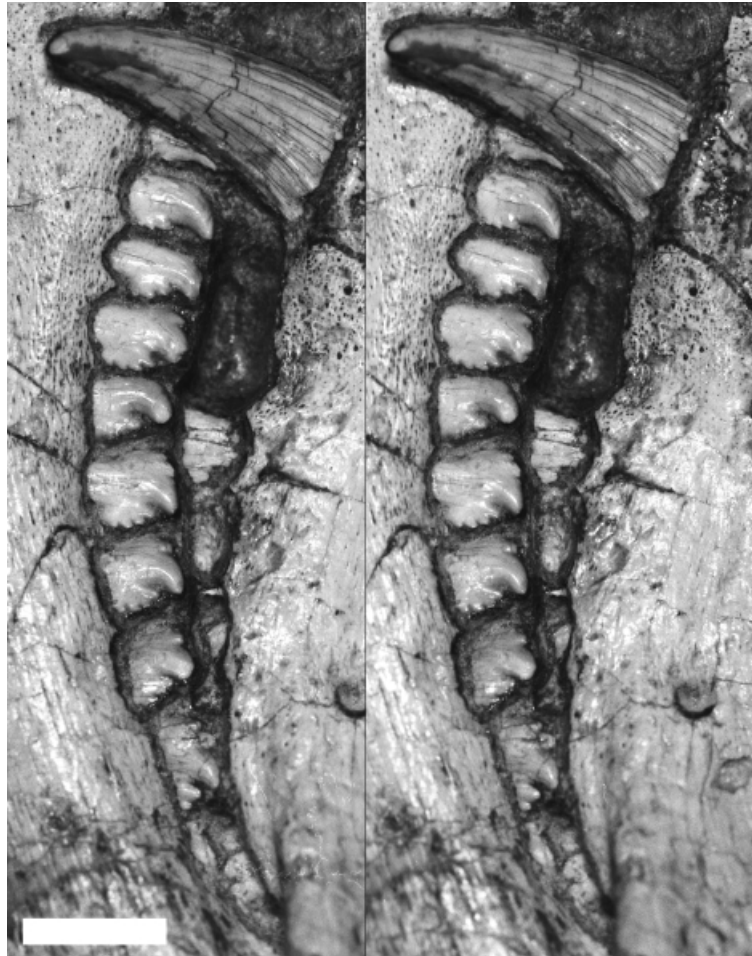
The dental formula of *Progalesaurus* is I4/3, C1/1, PC 7?/9. The upper incisors are long and needle-like, with a circular cross-section, although part of their apparent length might be the result of having slipped out of their sockets to some degree. The third and fourth upper incisors appear more robust than the more mesial teeth. The lower incisors are smaller than the corresponding upper incisors and slope along the upward curvature of the mandibular symphysis.



TEXT-FIG. 5. Stereophotographs (dorsal surface to the right) and interpretive line drawing (dorsal surface uppermost) of the skull of *Progalesaurus lootbergensis* in posterior view. Scale bar represents 1 cm.

The canines have an oval cross-section and are longitudinally striated (Text-fig. 6). The upper canines preserve posterior cutting edges, which lack serrations, whereas the condition for the lowers is ambiguous. Among early cynodonts, similar striations are present in *Procynosuchus*, *Cynosaurus* and *Galesaurus*. In *Thrinaxodon*, the surface of the canine is divided into discrete facets but lacks striations. The lower canine of *Progalesaurus* is slightly longer than the upper, although the latter has a more robust root.

TEXT-FIG. 6. Stereophotographs of the left lower postcanine dentition of *Progalesaurus lootsbergensis* in lateral view. Scale bar represents 5 mm.



The morphology of the postcanine dentition probably represents the most distinctive feature of *Progalesaurus*. It resembles that of *Galesaurus*, *Cynosaurus* (pers. obs. BP/1/3926) and *Probelesodon* in possessing a strongly recurved main cusp, but differs in the number and placement of accessory cusps (Broom 1932; Romer 1969). In contrast to *Galesaurus* and *Cynosaurus* (van Heerden 1976, figs 14–19), anterior accessory cusps are well developed in *Progalesaurus*. The upper postcanines are exposed on the right side, although their morphology is not especially well preserved. It appears that the first, second and fourth alveoli are empty on this side. The third position houses a poorly preserved crown. The fifth upper postcanine is poorly preserved, but enough is present to say that its external surface was smooth and devoid of a cingulum. The sixth tooth appears larger than the fifth and shows a strongly recurved main cusp followed by at least one accessory cusp. Upper postcanine 7 is the best preserved and has a strongly recurved main cusp. This cusp is preceded by at least one small, accessory cusp that is also recurved. No accessory cusps can be seen on the distal margin of this tooth because of poor preservation. An isolated, presumed upper, postcanine is suspended by matrix between the medial surface of the right lower jaw and palate on that side. The root of another tooth can be seen in the same position on the left side.

The lower postcanine dentition is well preserved, complete and best exposed on the left side (Text-fig. 6). The teeth become progressively lower and anteroposteriorly longer from front to back. In addition, they each angle anteromedially so that the posterior margin of one tooth lies lateral to the anterior margin of the tooth behind it. As in *Galesaurus* (Haughton 1924; Broom 1932), all of the postcanine teeth have a smooth external surface lacking cingula or cingular cusps. The first lower postcanine is obscured by the upper canine such that only its posterior edge is visible. The second tooth is more fully exposed and shows the primary features of the dentition: a strongly recurved

main cusp followed by multiple, well-developed cusps. These cusps are similar to the single posterior cusp in *Galesaurus* in that their distal margin is convex towards the gum line. As a result, all of the distal accessory cusps tend to point towards the apex of the tooth. The third tooth resembles the second. The fourth tooth is the first to display at least one cusp mesial to the main cusp. The fifth tooth is smaller than the fourth and shows only one posterior accessory cusp, although the absence of additional cusps is probably due to wear. The sixth to ninth lower postcanines become squatter as the alveolar border of the dentary swings upwards towards the coronoid process.

Postcranial skeleton

The postcranial skeleton of *Progalesaurus* includes a right scapula and left atlantal neural spine that were preserved in the same nodule as the skull. As each closely resembles the morphology described for *Thrinaxodon* by Jenkins (1971), a detailed description is not provided here.

The anterior border of the scapula is turned outward. This, in combination with a slightly thickened posterior border, produces a broad fossa on the lateral surface of the scapula. The dorsal edge of the bone extends posteriorly beyond the thickened posterior margin of the scapula to form a small posterodorsal process. The atlantal neural spine was originally found between the left lower jaw and basicranial ramus of the pterygoid. It preserves a facet for articulation with the atlantal pleurocentrum and a well developed parapophysis for the atlantal rib.

DISCUSSION

Early cynodont diversification

Cynodonts are traditionally considered to have originated during the Late Permian based on the first appearance of the two most primitive forms, *Dvinia* and *Procynosuchus*, in the fossil record. In addition, the lack of clear autapomorphies in the latter genus has suggested to some workers that it lies near the ancestry of all later cynodonts (Hopson 1991). Earlier theories deriving cynodonts from whaitsiid (Kemp 1972) or 'scaloposaur' (Brink 1960) theroccephalian ancestors have been replaced by cladistic studies that posit theroccephalians and cynodonts as monophyletic sister taxa (Hopson and Barghusen 1986; Hopson 1991).

The rarity of well-preserved Permian cynodonts, combined with the initial recognition of juvenile specimens of *Procynosuchus* and *Cynosaurus* as distinct taxa, has impeded a full understanding of the early diversification of this group (Anderson 1968; van Heerden 1976, 1988). The first major taxonomic revision of the Cynodontia was that of Hopson and Kitching (1972), who recognized *Procynosuchus* and *Cynosaurus* as the only valid cynodont genera from the Permian of South Africa. *Parathrinaxodon*, which is known from the Upper Permian Kawinga Formation of Tanzania (Parrington 1936), is considered to be indistinguishable from *Procynosuchus* by J. Hopson (pers. comm. 2002), although Battail (1982, 1991) has suggested that it is slightly more derived than either *Procynosuchus* or *Dvinia*.

Cynosaurus is arguably the most problematic Permian cynodont. Its holotype, a partial snout with lower jaws (BMNH R1718), was originally described and figured by Owen (1876, pl. 16) and given the name *Cynosuchus suppostus*. Later, Haughton (1918) added a second species, *Cynosuchus whaitsi*, and Watson (1920) briefly redescribed the type material. Schmidt (1927) recognized that the name 'Cynosuchus' was preoccupied by a crocodile and proposed *Cynosaurus* as a replacement generic name. Broom (1931) reidentified Haughton's (1918) specimen as a distinct genus, *Cynosuchoides*, to which Brink (1965) referred a second specimen. Hopson and Kitching (1972) synonymized *Cynosuchoides* (as well as *Nanictosaurus*, *Mygalesuchus* and *Baurocynodon*) with *Cynosaurus*.

The holotype of *Cynosaurus suppostus* is diagnostic by virtue of its subvertical mentum, short, broad snout and lack of lingual cingula on the postcanine teeth. Haughton's (1918) specimen (SAM-PK-4333) resembles the type in the latter two features, but does not preserve the lower jaw with its diagnostic mentum. Thus, Broom's (1931) assignment of the SAM specimen to a new genus might have been premature. Brink's (1965) referred specimen (BP/1/3926) is also problematic as it also lacks a lower jaw. Moreover, Brink (1965) stated that his specimen was recovered from *Lystronsaurus* zone rocks on the farm Tweefontein, which might make it the only Triassic representative of *Cynosaurus*. However, more recent fieldwork on Tweefontein and adjoining farms has shown a maximum of a 40-m-thick overlap in the

TABLE 2. Vertebrate fauna collected at New Lootsberg Pass. For exact stratigraphic relationship to the Permo/Triassic boundary as positioned by Smith and Ward (2001), see Text-figure 1.

No.	Identification	Metres from P/Tr boundary	Description
1	<i>Dicynodon</i> sp.	-10	Partial skull and anterior skeleton
2	<i>Lystrosaurus</i> sp.	-3	Small skull minus lower jaw
3	<i>Lystrosaurus</i> sp.	-3	Skull plus lower jaw and some disarticulated anterior postcrania
4	<i>Dicynodon</i> sp.	0	Skull plus lower jaw and some scattered postcranial elements
5	Rhinesuchid indet.	+18	Partial skull, pectoral girdle and ventral scales
6	Moschorhinid indet.	+18	Skull plus lower jaw and semi-articulated skeleton
7	Dicynodont indet.	+23	Isolated dicynodont caniniform process with tusk
8	<i>Lystrosaurus</i> sp.	+26	Articulated hind limb of medium-sized dicynodont
9	<i>Lystrosaurus</i> sp.	+30	Skull plus lower jaw
10	<i>Progalesaurus lootsbergensis</i>	+35	Skull plus lower jaw and isolated anterior postcrania
11	<i>Lystrosaurus</i> sp.	+35	Skull plus partially articulated skeleton
12	Moschorhinid indet.	+40	Lower jaw
13	<i>Lystrosaurus</i> sp.	+44	Small skull plus articulated skeleton

ranges of *Dicynodon* and *Lystrosaurus* immediately below the Permo/Triassic boundary (Text-fig. 1, Table 2; Smith and Ward 2001), so the age of this specimen remains in doubt.

Van Heerden and Rubidge (1990) reviewed the four specimens attributed to *Nanictosaurus* and considered them to represent only a single species, *N. kitchingi*. Nonetheless, we follow Hopson and Kitching (1972) in considering them to represent juvenile individuals of *Cynosaurus*.

In summary, we recognize two *Dicynodon* Assemblage Zone genera (*Procynosuchus* and *Cynosaurus*) and four *Lystrosaurus* Assemblage Zone genera (*Progalesaurus*, *Galesaurus*, *Thrinaxodon* and *Platycraniellus*) from South Africa.

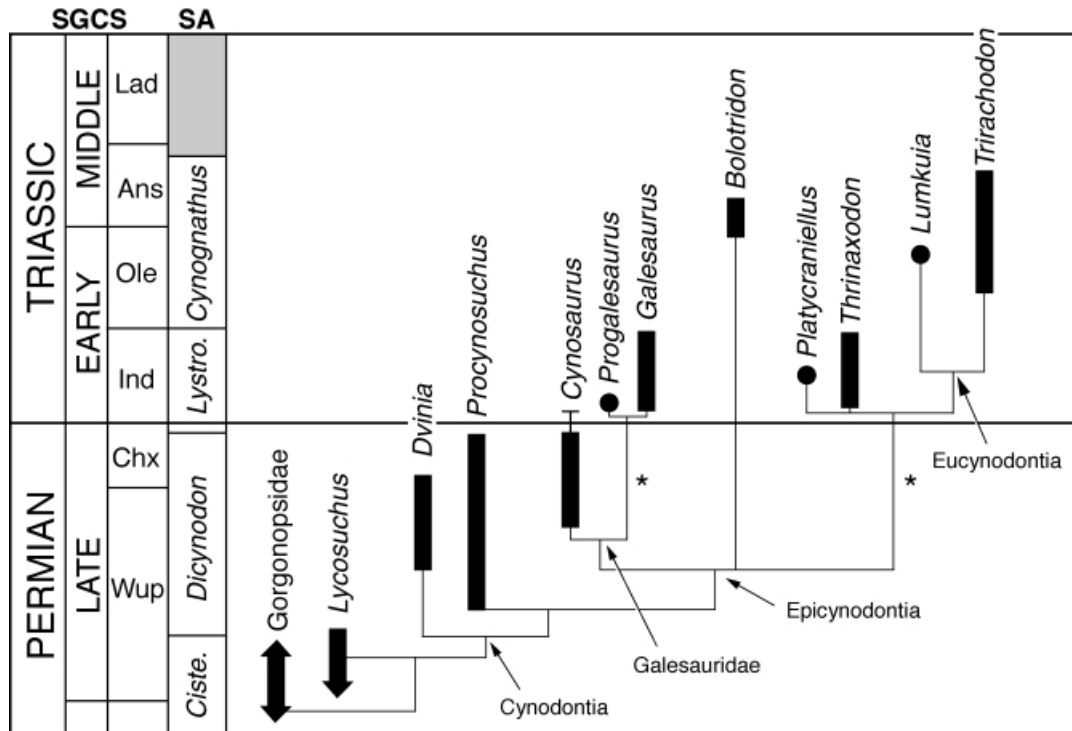
Cladistic analysis

We assessed the phylogenetic position of *Progalesaurus* by including it in a cladistic analysis of cynodont relationships (Appendix). Fifty-six characters were employed in our analysis: 32 from the skull, 12 from the mandible and 12 from the dentition. Ten of the 56 characters were original; the remainder were derived from the work of either Hopson and Barghusen (1986) or Hopson and Kitching (2001). We included eight basal cynodont genera as well as *Lumkuia* and *Trirachodon* as representative eucynodonts. A gorgonopsid and primitive therocephalian (*Lycosuchus*) served as outgroups. Other details of the methodology are given in the Appendix.

Text-figure 7 presents an Adams consensus of the 21 primary trees resulting from our analysis. A strict consensus of the 21 trees creates a large polytomy including Galesauridae, Eucynodontia, *Platycraniellus*, *Thrinaxodon* and *Bolotridon*. Rerunning the cladistic analysis with *Bolotridon* excluded yields three trees of 89 steps (CI=0.83, RI=0.85) that differ only in the position of *Platycraniellus* relative to *Thrinaxodon*. Thus, the physical incompleteness of *Bolotridon* is a likely cause for the poor resolution of our initial analysis.

Cynodont systematics

In the Appendix we present the distribution of unambiguously optimized synapomorphies for six cynodont subclades. Our analysis of early cynodont phylogenetic relationships indicates that *Progalesaurus* is nested within the Galesauridae as the sister taxon of *Galesaurus* (Text-fig. 7). Synapomorphies uniting



TEXT-FIG. 7. Adams consensus cladogram of 21 primary trees of basal cynodont relationships plotted against a generalized Permo-Triassic stratigraphy. Tree statistics: Tree length = 89 steps, CI = 0.83, RI = 0.85. Asterisks denote the two cynodont lineages that are inferred to have crossed the Permo/Triassic boundary. SGCS, abbreviation for the Standard Global Chronostratigraphic Scale; SA, the vertebrate assemblage zones recognized by the South African Committee for Stratigraphy (Rubidge, 1995). *Lystro.* and *Ciste.* denote the *Lystrosaurus* and *Cistecephalus* Assemblage Zones, respectively. Gorgonopsids are known from the *Eodicynodon* through *Dicynodon* Assemblage Zones (Middle–Late Permian). *Lycosuchus* is exclusively known from the *Tapinocephalus* Assemblage Zone (Middle Permian). The stratigraphical position of the Russian cynodont *Dvinia* is an estimate based on faunal comparisons (Modesto and Rychczynski 2000; Lucas 2002). Filled circles are used to represent the stratigraphical position of those taxa known only from a single specimen.

Progalesaurus with *Galesaurus* include the lack of a well-defined masseteric fossa on the dentary, the strongly recurved principal cusp on the postcanine dentition and the anterior curvature of the posterior accessory cusp(s). This phylogenetic position is mirrored by the intermediate stratigraphical position of *Progalesaurus*, which occurs above the first appearance of *Cynosaurus* in the Permian and below that of *Galesaurus* in the Triassic (Text-fig. 1). The remainder of our phylogenetic results corroborate the topology advanced by Hopson and Kitching (2001), although we have more complete taxon sampling. In particular, our results support *Dvinia* as the most primitive cynodont and Epicynodontia, which encompasses Galesauridae, *Thrinaxodon* and Eucynodontia, as a robust clade.

The positions of *Platycraniellus* and *Bolotridon* are less well resolved. The former can be confidently placed within the Epicynodontia and is extremely similar to *Thrinaxodon*, although it is distinct by virtue of its very small postcanine teeth and extremely wide and deep zygomatic arches (J. Hopson, pers. comm. 2002). The phylogenetic position of *Bolotridon* is particularly difficult to assess because of the physical incompleteness of the known material. The stratigraphical position of *Bolotridon*, Subzone B of the *Cynognathus* Assemblage Zone (*sensu* Hancox *et al.* 1995), makes it the only non-eucynodont genus recovered from lower Middle Triassic strata.

Permo/Triassic extinction

The end-Permian mass extinction is known to have profoundly affected the composition of terrestrial and marine faunas (Erwin 1993; Erwin *et al.* 2002). In the Beaufort Group, gorgonopsians, biarmosuchians and pareiasaurs became extinct at or near the Permo/Triassic boundary whereas dicynodonts and therocephalians, although suffering major losses, produced Triassic representatives (Groenewald and Kitching 1995; Kitching 1995; Smith and Ward 2001). Among cynodonts, our cladistic analysis requires at least two lineages to have crossed the Permo/Triassic boundary: the galesaurid lineage and *Thrinaxodon* + eucynodont lineage. Importantly, unless the precise stratigraphical position of Brink's (1965) specimen of *Cynosaurus* is determined to be Triassic, no cynodont genus has been definitively recorded from both below and above the boundary (Smith and Ward 2001).

Rubidge (1995) and King and Jenkins (1997) recorded five boundary-crossing genera (*Elonichthys*, *Lystrosaurus*, *Tetracynodon*, *Owenetta* and *Moschorhinus*), although additional collecting has cast doubt on the latter record (Smith and Ward 2001). In addition, Reisz and Scott (2002) suggested specific differentiation between the Permian and Triassic members of the procolophonoid genus *Owenetta*. Systematic fossil collecting at New Lootsberg Pass and other Permo/Triassic strata will continue to refine the stratigraphical distribution of these taxa (Table 2; Smith and Ward 2001).

Smith (1995) and Ward *et al.* (2000) studied Beaufort Group sedimentation across the Permo/Triassic boundary. Their results suggest that the mass extinction event was caused by a major injection of carbon dioxide and methane into the atmosphere, possibly from large scale vulcanism, and/or oceanic overturn. The resulting climatic warming combined with the rain shadow effect of the southern Gondwanide mountains led to extreme aridity in the central parts of the Pangean supercontinent. Prolonged drought soon decimated the end-Permian lowland ecosystems. On the floodplains, the loss of lush riverside undergrowth caused the local extinction of the small herbivores (e.g. *Diictodon* and *Pristerodon*) and small carnivores (e.g. *Cynosaurus* and *Aleurognathus*). This was quickly followed by the loss of the gallery forest trees and shrubs (*Glossopteris*) which resulted in the demise of the large herbivores (e.g. *Dicynodon* and *Pelanomodon*) with their attendant large carnivores (e.g. *Prorubidgea* and *Dinogorgon*). This marks the end of the end-Permian mass extinction. It is estimated that the approximately 15 m of strata containing the entire extinction event took between 100,000 and 500,000 years to accumulate.

The occurrence of *Progalesaurus* so soon after the extinction event, and of *Galesaurus* and *Thrinaxodon* shortly thereafter, suggests that cynodonts radiated quickly after the end-Permian extinction. Interestingly, all *Lystrosaurus* Assemblage Zone cynodonts discovered thus far have a postcanine dentition indicative of carnivory. Not until *Cynognathus* Assemblage Zone times did herbivorous cynodonts make their first appearance in the form of taxa such as *Trirachodon* and *Diademodon* (Neveling *et al.* 1999). A fuller understanding of terrestrial ecosystem recovery in the Early Triassic will require detailed fossil collecting and improved temporal resolution.

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APPENDIX

Abbreviations used in the figures

ang, angular; art, articular; bo, basioccipital; bs, basisphenoid; d, dentary; eam, fossa for external auditory meatus; epi, epipterygoid; ex, exoccipital; f, frontal; fo, fenestra ovalis; j, jugal; l, lacrimal; lf, lacrimal foramen; m, maxilla; men, mental foramen; n, nasal; p, parietal; pal, palatine; pm, premaxilla; po, postorbital; pop, paroccipital process; pp, postparietal; pro, proötic; pra, prearticular; pt, pterygoid; ptf, post-temporal fenestra; q, quadrate; qj, quadratojugal; ref, broken base of the reflected lamina; sm, septomaxilla; so, supraoccipital; sp, splenial; sq, squamosal; st, stapes; sur, surangular; t, tabular; v, vomer; V_{2,3}, foramen for the maxillary and mandibular components of the trigeminal nerve.

List of the characters and character states used to construct the cladogram in Text-figure 7

The number preceding the character definition corresponds to that of the columns in the next section. An ° preceding the character number denotes that the character was ordered. Following the last character state for each character is a citation for previous uses of the character in the literature. When an asterisk follows the citation, it indicates that the character definition or character states have been modified from their original form. Citations are in the form: (author:character number), except for those of Hopson and Barghusen (1986), which are (author:table.clade.character number). Abbreviations for authors are as follows: HB, Hopson and Barghusen (1986); HK, Hopson and Kitching (2001).

1. Length of septomaxillary facial process: long (0), or short (1)
2. Nasal-lacrimal contact: absent (0), present (1) (HB:1.11.2; HK:2)
3. Postfrontal: present (0), absent (1) (HB:1.11.22; HK:4)
4. Prefrontal-postorbital contact: absent (0), present (1) (HB:1.11.6; HK:6)
- °5. Zygomatic arch dorsoventral height: slender (0), moderately deep (1), very deep (2) (HK:18)
6. Sagittal crest development: wide temporal roof (0), broad in front of pineal but narrow behind it (1), or ridge envelops pineal foramen (2) (HB:1.11.26*)
7. Parietal region elevated high above remainder of skull profile: absent (0), present (1) (HB:4.36.2)
8. Vomer internarial shape: broad plate (0), parallel-sided keel (1) (HK:8)
9. Vertical lamina of vomer: absent (0), restricted to interchoanal region (1), or extends posteriorly onto post-choanal plate (2)
10. Palatal exposure of maxilla behind canine greater than 20 per cent distance from canine to posterior end of palatine: absent (0), present (1) (HK:11)
11. Secondary palatal plate on maxilla: absent (0), present, does not reach midline (1), present, reaches midline (2) (HB:1.11.9*; HK:12)

12. Secondary palatal plate on palatine: absent or low ridge (0), present, extends nearly to midline (1), present, reaches midline (2) (HB:1.11.9*; HK:13)
13. Interpterygoid vacuity in adult between pterygoid flanges: present (0), absent (1) (HK:10)
14. Teeth on pterygoid flange: present (0), absent (1) (HB:1.11.23; HK:16)
15. Ectopterygoid: contacts maxilla (0), does not contact maxilla (1), absent (2) (HK:9)
16. Tabular extends around post-temporal fenestra: absent (0), present (1) (HB:1.11.8*; HK:24)
17. V-shaped notch separating lambdoidal crest from zygomatic arch: absent (0), present (1) (HK:43)
- °18. Squamosal groove for external auditory meatus: shallow (0), moderately deep (1), very deep (2) (HK:22)
19. Descending flange of squamosal lateral to quadratojugal: absent (0), present not contacting surangular (1), present contacting surangular (2) (HK:25)
20. Quadrate ramus of pterygoid: present (0), absent (1) (HB:4.41.4; HK:30)
21. Quadrate posteroventral process in squamosal posterior notch: absent (0), present (1) (HB:1.11.12; HK:31)
- °22. Epipterygoid ascending process at level of trigeminal foramen: rod-like (0), moderately expanded (1), greatly expanded (2) (HB:1.11.25; HK:32)
23. Epipterygoid-proötic overlap: absent (0), present (1) (HB:1.11.11*; HK:33)
24. Epipterygoid-frontal contact: absent (0), present (1) (HB:1.11.16; HK:35)
25. Basipterygoid processes at level of basisphenoid and suture transversely to pterygoid (0) or offset dorsally with median ridge formed (1)
26. Groove on proötic extending from pterygo-paroccipital foramen to trigeminal foramen: absent (0), present and open (1), present and enclosed as a canal (2) (HB:1.11.18; HK:27)
27. Trigeminal nerve exit: between proötic incisure and epipterygoid (0), via foramen between proötic and epipterygoid (1), via two foramina (2) (HK:28)
28. Lateral flange of proötic: absent (0), present (1) (HK:34)
29. Paroccipital process of opisthotic narrow (0) or expanded anteroposteriorly (1) (HB:4.37.4)
30. Jugular foramen faces posteriorly (0) or ventrally (1) (HB:1.11.14)
31. Double occipital condyles: absent (0), present (1) (HB:1.11.7; HK:37)
32. Stapedial foramen orientation: anteroposterior (0), dorsoventral (1) (HB:1.11.13; HK:38)
33. Lower jaw positioned laterally (0) or near middle (1) of temporal fenestra (HB:1.11.2)
34. Dentary symphysis: not fused (0), fused (1) (HB:4.42.2; HK:44)
35. Symphysis in lateral view: convex anteriorly (0), or concave anteriorly with small lip (1)
36. Dentary masseteric fossa: absent (0), high on coronoid region (1), extends to lower border of dentary (2) (HB:1.11.1; HK: 45)
37. Dentary masseteric fossa: anterior and ventral margins well defined (0), or not (1)
38. Dentary overlap of dorsal surface of surangular: short (0), long (1) (HB:1.11.20; HK:46)
39. Dentary coronoid process height: below middle of orbit (0), above middle of orbit (1) (HK:47)
40. Position of dentary/surangular dorsal contact relative to postorbital bar and jaw joint: closer to postorbital bar (0), midway between (1), closer to jaw joint (2) (HK:48)
41. Foramen on external surface of mandible between dentary and angular: absent (0), present (1)
42. Postdentary rod height relative to exposed length (distance between base of reflected lamina and jaw joint): greater than half length (0), about half length (1), less than half length (2) (HK:49)
43. Reflected lamina of angular posterior extent relative to distance from angle of dentary to jaw joint: greater than half the distance (0), less than half the distance (1) (HK:51)
44. Reflected lamina of angular shape: deep corrugated plate (0), spoon-shaped plate (1), hook with depth greater than half length (2), hook with depth less than half length (3) (HK:52)
45. Upper incisor number: five or more (0), four (1), three (2) (HK:53)
46. Lower incisor number: four or more (0), three (1), two (2) (HK:54)
47. Incisor cutting margins: serrated (0), or smoothly ridged (1) (HK:55)
48. Precanine maxillary teeth present (0) or absent (1) (HB:4.38.5)
49. Canine serrations: present (0), absent (1) (HK:59)
50. External surface of canines smooth (0), striated longitudinally (1), or faceted (2)
51. Postcanine shape: single point (0), two or more cusps in line (1) (HB:1.11.28*; HK:60)
52. Central cusp on postcanines directed vertically (0) or strongly recurved (1)
53. Anterior accessory cusp(s) on postcanine teeth: present (0) or absent or very reduced (1) (HB:4.39.2)
54. Posterior accessory cusp(s) vertical (0) or curved anteriorly (1)
55. Postcanine teeth transversely expanded: absent (0), present (1) (HB:4.36.1)
56. Internal cingulum on lower postcanine teeth: absent (0), present (1)

Data matrix used in the cladistic analysis of cynodont interrelationships

Gorgonopsidae and *Lycosuchus* were used as the outgroups to polarize character state transformations. A complete list of specimens used in this analysis is provided in the 'Material and methods' section. Characters and character state definitions are provided above. '?' denotes missing data; multistate taxa indicate polymorphism. This matrix was subjected to Branch and Bound analysis in PAUP 3.1 (Swofford 1993).

	12345	1 67890	11111 12345	11112 67890	22222 12345	22223 67890	33333 12345	33334 67890
Gorgonopsidae	00001	00000	00000	00000	00001	00000	00000	0?000
<i>Lycosuchus</i>	00000	10000	00000	00000	01000	00000	0?000	0?000
<i>Dvinia</i>	01110	21111	11010	10000	12110	11101	11101	10100
<i>Procynosuchus</i>	01110	10111	11011	10000	12110	11111	11101	10100
<i>Cynosaurus</i>	11111	10121	1111?	?0??0	?2111	111?1	??100	?0???
<i>Progalesaurus</i>	11111	10121	1111?	00110	12111	11111	11100	21110
<i>Galesaurus</i>	11111	10121	11111	10110	12111	11111	11100	21110
<i>Bolotridon</i>	?111?	?????	?????	?????	?????	?????	???	20?1?
<i>Thrinaxodon</i>	11111	20121	22111	10110	12111	11111	11100	20111
<i>Platyocraniellus</i>	?1111	20121	22?1?	?01?0	121?1	?111?	1?1??	??11?
<i>Lumkuia</i>	11111	20121	22012	11121	12111	11111	11110	20112
<i>Trirachodon</i>	11112	20121	22112	11221	12111	22111	11110	20112
	44444	44445	55555	5				
	12345	67890	12345	6	per cent missing data			
Gorgonopsidae	02000	00000	001?0	0	3.6			
<i>Lycosuchus</i>	10000	00000	001?0	0	5.4			
<i>Dvinia</i>	10010	0101?	10001	1	1.8			
<i>Procynosuchus</i>	10010	01011	10000	1	0			
<i>Cynosaurus</i>	????1	??1??	10000	0	35.7			
<i>Progalesaurus</i>	01??1	11111	11010	0	5.4			
<i>Galesaurus</i>	01021	11111	11110	0	0			
<i>Bolotridon</i>	????1	1?1??	100?0	1	71.4			
<i>Thrinaxodon</i>	01021	11112	10000	1	0			
<i>Platyocraniellus</i>	????1	??1??	10???	?	46.4			
<i>Lumkuia</i>	02131	11110	11000	0	0			
<i>Trirachodon</i>	02131	1110?	11001	1	1.8			

Synapomorphy scheme for internal nodes of the cladogram shown in Text-figure 7

Clades are diagnosed by the following unambiguously optimized characters; parentheses denote which derived state of a multistate character is synapomorphic; minus signs denote reversals.

Cynodontia: 2, 3, 4, 8, 9(1), 10, 11(1), 12(1), 14, 16, 21, 22(2), 23, 24, 26(1), 27(1), 28, 30, 31, 32, 33, 36(1), 38, 44(1), 47, 52, -54

Procynosuchus + Epicynodontia: 15(1), 29

Epicynodontia: 1, 5, 9(2), 13, 18, 19, 25, 36(2), 39, -41, 42(1), 44(2), 45(1), 46, 48, 49

Galesauridae: -57

Progalesaurus + *Galesaurus*: 37, 53, 55

Eucynodontia: 15(2), 17, 20, 34, 40(2), 42(2), 43, 44(3), 53