

REDESCRIPTION OF *PLATYCRANIELLUS ELEGANS* (THERAPSIDA, CYNODONTIA) FROM THE LOWER TRIASSIC OF SOUTH AFRICA, AND THE CLADISTIC RELATIONSHIPS OF EUTHERIODONTS

by FERNANDO ABDALA

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa; e-mail: abdalaf@geosciences.wits.ac.za

Typescript received 8 March 2006; accepted in revised form 6 June 2006

Abstract: *Platycraniellus elegans* is an enigmatic Triassic cynodont from South Africa that has only been briefly described previously. New preparation of the holotype and additional unpublished material allows a detailed redescription and comparison with different cynodonts. *Platycraniellus elegans* is recognized as a valid species of basal cynodont. The distinct suborbital angulation of the zygomatic process, previously considered as a diagnostic character in chiniquodontid cynodonts, and more recently observed in some galesaurids, is also present in *P. elegans*. A larger, second specimen was initially referred to *P. elegans*, but most recently considered to belong to *Galesaurus planiceps*. Close comparison of this specimen with the holotype of *P. elegans* and with galesaurid specimens allows a tentative allocation to *G. planiceps*. A cladistic analysis of 32 taxa (two gorgonopsians, seven therocephalians and 23 cynodonts) and 96 craniodental characters places *P. elegans* as sister taxon of Eucynodontia. Results from the analysis

favour a dichotomy between (1) Cynognathia, including the sectorial-toothed cynodonts *Ecteninion*, *Cynognathus* and the gomphodont cynodonts, and (2) Probainognathia, including most sectorial-toothed eucynodonts (e.g. *Lumkuia*, *Probainognathus*, *Chiniquodon*), tritheledontids, tritylodontids and mammaliaforms. The Late Triassic sectorial-toothed *Ecteninion* is the most basal member of Cynognathia, whereas the Middle Triassic *Lumkuia* is the basal representative of Probainognathia. Tritylodontids (*Oligokyphus* and *Kayentatherium*) are placed among Probainognathia, forming a monophyletic group with the tritheledontid *Pachygenelus*, whereas *Brasilitherium* is the sister taxon of Mammaliaformes. The cladistic analysis also indicates paraphyly for Therocephalia, with the whaitsiid *Theriognathus* identified as sister taxon of Cynodontia.

Key words: *Platycraniellus elegans*, Cynodontia, galesaurids, Early Triassic, South Africa.

THE locality of Harrismith Commonage in the Free State Province of South Africa is known for its extremely rich record of Early Triassic fossil vertebrates (Kitching 1977), and is biostratigraphically included in the *Lystrosaurus* Assemblage Zone [AZ] (Groenewald and Kitching 1995). Among the therapsid fauna from Harrismith, three species of cynodont, *Platycraniellus elegans*, *Galesaurus planiceps* and *Thrinaxodon liorhinus*, have been recovered (Kitching 1977).

Platycraniellus elegans was briefly summarized and originally named as *Platycranion elegans* by van Hoepen (1916). In a second contribution, van Hoepen (1917, p. 217) renamed the species *Platycraniellus elegans*, because *Platycranium* was 'preoccupied twice in the form of *Platycranius*'. The original proposition of *Platycranion* is probably a print error in van Hoepen (1916), and Battail (1991) regarded it as a *nomen oblitum*. Haughton

(1924a) provided a description of the holotype specimen of *P. elegans*, and Broom (1932a) gave a succinct account of the species. Brink (1954a) later referred a larger specimen from Harrismith Commonage to *P. elegans*. In their revision of cynodonts, Hopson and Kitching (1972) recognized *P. elegans* as a valid species of Galesauridae, but considered the second specimen referred by Brink (1954a) to be *Galesaurus planiceps*.

Hopson and Kitching (1972) and later Battail (1982) included *Platycraniellus elegans* in Galesauridae, a family that included species with both incomplete (e.g. *Galesaurus planiceps*) and complete (e.g. *Thrinaxodon liorhinus*) osseous secondary palates. Later, only taxa with an incomplete secondary palate and sectorial postcanines, without a lingual cingulum, were included in Galesauridae (Hopson and Barghusen 1986; Battail 1991; Hopson 1991). Taking into account this diagnosis for the family,

only *Galesaurus planiceps* and *Cynosaurus suppostus* were recognized as members of Galesauridae. In addition, Batail (1991) formally resurrected the family Thrinaxodontidae of Watson and Romer (1956) to include taxa with a complete osseous secondary palate: *Thrinaxodon liorhinus*, *Nanictosaurus rubidgei*, *Nanocynodon seductus*, *Bolotridon frerensis* (= *Tribolodon frerensis*; see Coad 1977) and *Platycraniellus elegans*. Thrinaxodontidae is also a term used in phylogenetic hypotheses by Hopson and Barghusen (1986) and Hopson (1991), but in neither publication is there indication of the composition of the family.

The short account by Haughton (1924a) remains the best description of *Platycraniellus elegans*, although it lacks information on many significant regions of the skull. New preparation of the holotype specimen and unpublished additional material now permits a more comprehensive description of this species. In addition, the specimen previously referred to as *P. elegans* by Brink (1954a) was also available for this study, enabling comparison with the holotype. The new information presented here, combined with historical data, justifies a taxonomic re-evaluation of this peculiar species.

A cladistic analysis including 32 taxa and 96 craniodental characters was conducted with the aim of providing a hypothesis of relationships for *P. elegans*. In view of the current dispute about the inclusion (Kemp 1982, 1983; Rowe 1988, 1993; Wible 1991; Wible and Hopson 1993; Abdala 1996a) or exclusion (Hopson 1991, 1994; Sues 1985a; Hopson and Kitching 2001) of tritylodontids in Mammaliaforma, two tritylodontids (*Oligokyphus* and *Kayentatherium*), two basal mammaliaforms (*Morganucodon* and *Sinoconodon*) and two traversodontids (*Massetognathus* and *Exaeretodon*) were included in the data matrix to test the phylogenetic placement of tritylodontids. In addition, seven representatives of therocephalians were included to test the monophyly of cynodonts and therocephalians.

Institutional abbreviations. AM, Albany Museum, Grahamstown; AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; CGP, Council for Geosciences, Pretoria; GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; MB, Humboldt Museum für Naturkunde, Berlin; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; NMP, Natal Museum, Pietermaritzburg; NMQR, National Museum, Bloemfontein; OUMNH, Oxford University Museum of Natural History, Oxford; PULR, Museo de Antropología, Universidad Nacional de La Rioja; PVL, Colección Palaeontología de Verte-

brados Lillo, Universidad Nacional de Tucumán; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan; RC, Rubidge collection, Wellwood, Graaff-Reinet District; SAM, Iziko: South African Museum, Cape Town; TM, Northern Flagship Institution: Transvaal Museum, Pretoria; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre; UMZC, University Museum of Zoology, Cambridge; US, University of Stellenbosch.

Anatomical abbreviations. af, adductor fossa; An, angular; apf, anterior premaxillary foramen; Bo, basioccipital; ca, canine alveolus; ce, ventral opening of the cavum epiptericum; D, dentary; Ect, ectopterygoid; Ep, epipterygoid; F, frontal; fo, fenestra ovalis; H, humerus; inf, foramen incisivum; ipt, interpterygoid opening; J, jugal; jf, jugular foramen; L, lacrimal; lc, lower canine fragment; lcd, lateral crest of the dentary; lcr, lower canine root; lpr, lower postcanine roots; Mx, maxilla; N, nasal; oc, occipital condyle; of, osseous fragments; otg, orbitotemporal groove; P, parietal; Pa, prearticular; pal, palate; pci, remains of lower postcanines attached to the palate; pff, primary facial foramen; pi, pineal foramen; Pl, palatine; Pmx, premaxilla; Po, postorbital; pop, paroccipital process of the opisthotic; Pp, postparietal; prc, prootic crest; Prf, prefrontal; Pro, prootic; Pt, pterygoid; ptc, post-temporal foramen; ptf, pterygoparoccipital foramen; Q, quadrate; qf, quadrate foramen; Qj, quadratojugal; Q+Qj, quadrate/quadratojugal; qre, quadrate ramus of the epipterygoid; qrp, quadrate ramus of the pterygoid; rl, reflected lamina of the angular; rps, rostrum of the parasphenoid; Sa, surangular; ?sc, scapular blade; smf, septomaxillary foramen; Smx, septomaxilla; So, supraoccipital; Sp, splenial; Sq, squamosal; sqdp, squamosal descendent process; sqs, squamosal sulcus; St, stapes; T, tabular; tf, trigeminal foramen; upr, upper postcanine roots; V, vomer.

MATERIAL AND METHODS

The following specimens were examined for the descriptive/comparative section of this study: TM 25, holotype of *Platycraniellus elegans*; NMQR 860, specimen referred to *P. elegans* by Brink (1954a); NMQR 1633, specimen referred to *P. elegans* in this contribution (see below); TM 279, holotype of *Nanictosaurus kitchingi*; RC47, holotype of *Nanictosaurus rubidgei*. Comparative material of *Galesaurus* and *Thrinaxodon* was also consulted (see Appendix).

Cladistic analysis

A data matrix including 96 craniodental characters and 32 taxa (see Appendix) was assembled for the cladistic analysis. The characters were compiled using various sources and also include some original ones. Previous studies using data matrices and including cynodonts are those of Rowe (1988), Wible (1991), Wible and Hopson

(1993), Lucas and Luo (1993), Luo (1994), Luo and Crompton (1994), Martinez *et al.* (1996), Sidor and Hopson (1998), Flynn *et al.* (2000), Hopson and Kitching (2001), Bonaparte *et al.* (2003, 2005), Abdala and Ribeiro (2003), Sidor and Smith (2004), Martinelli *et al.* (2005), Sidor and Hancox (2006), Abdala *et al.* (2006) and Botha *et al.* (2007). Other important sources for original data collection and discussion about characters, although without provision of data matrices, are Battail (1982, 1983, 1991), Kemp (1983, 1988), Sues (1985a), Hopson and Barghusen (1986), Hopson (1991, 1994) and Rowe (1993). Syntheses such as those of Broom (1932a), Watson and Romer (1956), Hopson and Kitching (1972) and Kemp (1982) were also relevant at this stage of the study. A more comprehensive analysis of eutheriodont relationships (Abdala, work in progress) will include the rationale for characters selected for the study.

The computer program TNT (Goloboff *et al.* 2003) was used for the cladistic analyses. Considering the size of the data matrix, a heuristic searching strategy consisting of ten random addition sequences (ten Wagner trees, randomizing the order of the terminals) and tree-bisection-reconnection swapping, storing ten trees per replication, was undertaken. The search was performed with all characters having equal weights and under collapsing rule 1 (Coddington and Scharff 1994), which collapses branches with ambiguous support. Increasing the number of replicates did not change the results. A second analysis was performed with similar settings, but using implied weights (Goloboff 1993, 1997). The weighting is made by means of a constant of concavity K that reduces the influence of homoplastic characters. Characters showing many extra steps in the most parsimonious trees are down-weighted in relation to characters that better fit those trees (Goloboff 1993). The search strategy included analyses with the constant of concavity set at different values ranging from strong to mild, seeking to explore how they influence the monophyletic groups obtained.

SYSTEMATIC PALAEOLOGY

Therapsida Broom, 1905

Cynodontia Owen, 1861

Epicyodontia Hopson and Kitching, 2001

Platycraniellus van Hoepen, 1917

Platycraniellus elegans (van Hoepen, 1916)

Text-figures 1–6

Holotype. TM 25, complete skull, with fragments of articulated lower jaw, a partial right humerus, a fragment tentatively identified as a scapular blade and other indeterminate osseous fragments attached to the skull.

Referred material. NMQR 1633, partial skull lacking the anterior portion of the snout and the left zygoma.

Diagnosis. A cynodont presenting a wide temporal region, c. 88 per cent with respect to the basal length of the skull (BL); the snout is short and proportionally similar to the temporal length. As in chiniquodontids, some galesaurids and some *Thrinaxodon* specimens, *P. elegans* has an angulation (c. 120 degrees) between the ventral edge of the maxillary zygomatic process and the anteroventral margin of the jugal. The osseous secondary palate is complete and extends to the penultimate postcanine. The crowns of the anterior upper postcanines are high and short mesiodistally, with a main cusp and a small posterior accessory cusp on the base of the crown.

Remarks. NMQR 1633 referred to *Platycraniellus elegans* because of its inferred short snout and a jugal that is extensively flared outward, intimating a wide temporal region. The preservation of the right zygoma is incomplete ventrally and the presence of the suborbital angulation cannot be confirmed. The osseous secondary palate in NMQR 1633 reaches the level of the third and fourth (penultimate) postcanines.

Geographical and geological provenance. The holotype and referred specimen were collected from Harrismith Commonage, Free State Province, from levels corresponding to the Harrismith Member of the Normandien Formation (Rubidge *et al.* 1995), which record a fauna biostratigraphically known as the *Lystrosaurus* AZ, Induan-early Olenekian in age (Groenewald and Kitching 1995).

DESCRIPTION

Skull

General preservation. The skull and lower jaw of TM 25 are in general well preserved, but severe damage caused by grinding during early preparation at the time of van Hoepen's initial description (Haughton 1924a) has, unfortunately, destroyed the anterior part of the mandible. On the right side only the lower postcanine roots remain visible, whereas the grinding process was even more destructive on the left side, where it also reached the upper dental row, destroying the crowns of the left upper dentition. In addition, some postcranial bones are attached to different parts of the cranium, notably the humerus, which covers a large portion of the basicranium.

NMQR 1633 is a poorly preserved partial skull that reveals some features of the basicranium not visible in the holotype. The specimen seems to have been prepared by acid. The snout is preserved anteriorly to the level of the canine in ventral view, whereas most of the dorsal bones of the snout are lacking and only a small posterior portion of both maxillae and complete lacrimals are preserved. The right zygomatic arch and the epipterygoid from both sides are also missing, but both prootics are present. In ventral view there is severe damage on the right side



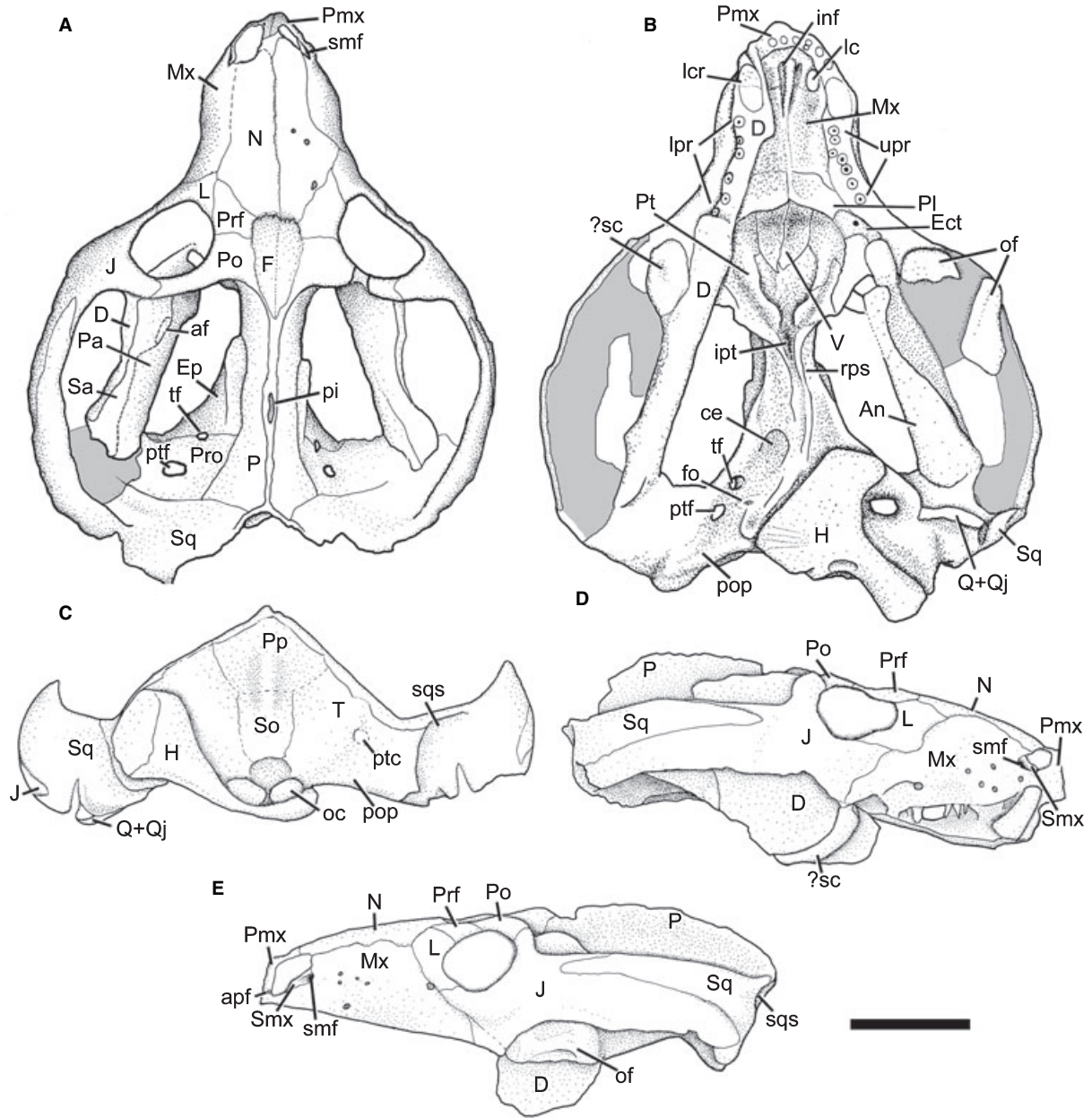
TEXT-FIG. 1. *Platycraniellus elegans* (TM 25). A, dorsal, B, ventral, C, occipital, D, right lateral, and E, left lateral views. Scale bars represent 2 cm.

of the secondary palate and most of the internal nasal openings. The basicranium is well preserved, and the right stapes and both quadrates are *in situ*. A partial left stapes, also *in situ*, was discovered after further preparation. The missing lower jaw seems to have been originally articulated to the skull, because there are remains of the lower postcanines preserved in the palate, medial to the upper teeth.

Cranial proportions. The holotype skull is 8.4 cm in BL (see measurements and key to abbreviations of measurements in Table 1). The cranial width is 88 per cent of the BL, representing what is proportionally the widest skull known for any non-mammaliaform cynodont (Text-figs 1A, 2A). The snout and the orbits are short (39 per cent and 17 per cent, respectively, of the BL), whereas the temporal region is notably long (40 per cent of

the BL). NMQR 1633 is smaller than the holotype, with an estimated BL of 6.5 cm (5.9 cm from the level of the canine to the occipital condyle).

Snout and orbits. The premaxilla features a well-developed ascending process, which is damaged dorsally and so does not make contact with the nasals (Text-figs 1A, 2A–B). There is a small opening directed anteriorly on the base of the ascending process of the left premaxilla (Text-fig. 2E). This foramen, termed anterior premaxillary foramen by Lillegraven and Krusat (1991), has also been reported for *Thrinaxodon* (Fourie 1974), *Progalesaurus* (Sidor and Smith 2004), *Chiniquodon* (Abdala 1996a) and the docodont *Haldanodon* (Lillegraven and Krusat 1991), and is likewise present in *Galesaurus* (NMQR 3340; BP/1/4602) and *Langbergia* (BP/1/5362). The intranasal process



TEXT-FIG. 2. Interpretative drawings of *Platyranellus elegans* (TM 25). A, dorsal, B, ventral, C, occipital, D, right lateral, and E, left lateral views. Scale bar represents 2 cm.

of the septomaxilla is present, but it seems less developed than in *Thrinaxodon*, whereas the short facial process encloses anterodorsally a small septomaxillary foramen and extends between the anterodorsal margin of the maxilla and the anterolateral margin of the nasal. The internasal and the right nasal-maxillary sutures are wide open, whereas the interfrontal suture is not visible. The nasal is almost twice as wide where it contacts the lacrimal and prefrontal bones than at its anterior margin (Text-fig. 2A). A series of small nutritive foramina appears close to the dental margin of the maxilla, whereas a small infraorbital foramen orientated anteriorly and ventrally is observed on the right side, at the level

of the sixth upper postcanine (Text-fig. 2D). This foramen, with the same orientation as in the holotype, is present on the maxillae of NMQR 1633, at the level of the second and third postcanines. The infraorbital foramen is remarkably smaller on the left side of NMQR 1633, where two additional foramina of the same size are placed more dorsally at the level of the third and fourth postcanines. These additional foramina are absent on the right side. The frontals in the holotype and NMQR 1633 are distinctive dorsally because they are depressed in relation to the remaining bones of the interorbital region. The zigzag suture between the frontal and the nasal is transverse.

The ovoid orbit is orientated mostly anteriorly and slightly dorsally and has a diameter slightly smaller than the interorbital width of the skull roof (Table 1). There are two lacrimal foramina on the posterior margin of the lacrimal bone. The ventral foramen is distinctly larger and seems to be connected with a foramen located between the lacrimal and the maxilla on the face, as in *Progalesaurus* and *Lumkuia* (Sidor and Smith 2004). The postorbital bar, formed by the postorbital dorsally and the jugal ventrally, is slender.

Zygoma and temporal region. The zygomatic arch is relatively robust, showing a similar height over its entire extent, and it is considerably flared laterally, producing one of the wider cynodont skulls. The ventral edge of the posterior portion of the maxilla presents an angle of *c.* 120 degrees in relation to the anteroventral margin of the jugal (Text-figs 1D–E, 2D–E). Angulations between these margins are also known in chiniquodontids (Abdala and Giannini 2002) and large galesaurids (Abdala and Damiani 2004). The zygomatic portion of the squamosal extends far anteriorly, reaching close to the base of the postorbital bar, as in *Thrinaxodon* (Parrington 1946, fig. 10), *Progalesaurus* (Sidor and Smith 2004, fig. 2) and *Chiniquodon* (Abdala 1996a). The anterior zygomatic portion of the squamosal demarcates a small dorsal and a well-developed ventral projection of the jugal (Text-fig. 2D–E). A division of the posterior projection of the jugal is present in *Lumkuia* (Hopson and Kitching 2001, fig. 2), *Procynosuchus* (Kemp 1979, fig. 3a), and *Galesaurus* (NMQR 1451, 3340), but is absent in *Thrinaxodon* (Parrington 1946, fig. 10) and *Progalesaurus* (Sidor and Smith 2004, fig. 2). The postorbital has a short posterior projection that extends over the parietals in the anterior portion of the sagittal crest. This projection is short and its posterior margin is undivided, and so is different from the forked margin described in *Progalesaurus* and other basal cynodonts (Sidor and Smith 2004). The sagittal crest

TABLE 1. Measurements of the skulls TM 25 and NMQR 860 (in cm). Percentages are related to the basal skull length (see Table 2).

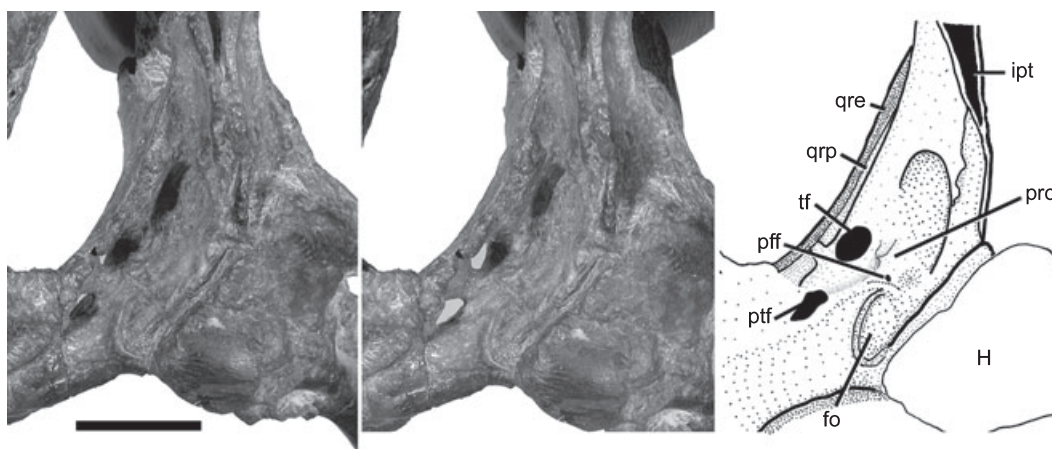
	TM 25	NMQR 860
Basal skull length (BL)	8.4	11.4
Middle dorsal length	7.8	10.8
Snout length (SL)	3.3 (39%)	4.8 (42%)
Orbital length (OL)	1.4 (17%)	2.2 (19%)
Temporal length (TL)	3.4 (40%)	4.6 (40%)
Interorbital width	1.9	2.9
Orbital diameter	1.5	2.0
Secondary palate length	2.8 (33%)	3.3 (29%)
Upper canine width	2.2	6.3
Upper postcanine series length	1.3	2.7
Maximum width of the skull	7.4 (88%)	9.7 (84%)
Maximum height of the zygomatic arch	1.6	2.0
Occipital plate height	2.6	3.6
Occipital plate base width	3.8	5.3
Basicranial girder width	0.7	1.1

begins immediately after the postorbital bar, and there is no plane surface on the dorsal skull roof anterior to the foramen parietal, as is observed in most galesaurid specimens. No interparietal suture can be observed on the crest, whereas an elongated pineal foramen is present in the middle of the sagittal crest.

Palate. The osseous secondary palate is complete, showing a short palatal process of the palatine (Text-figs 1B, 2B), which is remarkably wide at its posterior margin. The extent of the palate is almost the same as the snout length and reaches the penultimate postcanine. In NMQR 1633, the palate extends to the level of the third and fourth postcanines. A large incisive foramen, extending to the level of the posterior margin of the upper canine, is limited posteriorly by the maxilla (Text-fig. 2B). The paracanine fossa that accommodates the lower canine seems to be anteromedial to the upper canine. A small and roughly quadrangular ectopterygoid is present at the base of the pterygoid process (Text-fig. 2B). The pterygopalatine ridges of the internal choana converge posteromedially, ending in a well-developed projection orientated posteriorly and somewhat medially. The basicranial girder is slender with a small triangular interpterygoid vacuity at its anterior end (Text-fig. 2B). The quadrate ramus of the pterygoid is well extended posteriorly below the epipterygoid (Text-fig. 3) and contacts the quadrate.

Lateral wall of the skull and interorbital region. The epipterygoid is widely expanded anteroposteriorly. The trigeminal foramen is a large, round opening. The vascular groove on the lateral flange of the prootic, between the trigeminal and the pterygoparioccipital foramina, as described in *Thrinaxodon* (Rougier *et al.* 1992) and also observed in galesaurids (NMQR 1451), is not present in the holotype of *Platycraniellus*, but it is well developed in NMQR 1633. The suture between the dorsal lamina of the prootic and the epipterygoid is positioned above and anterior to the trigeminal foramen (Text-fig. 2A). A shallow external orbito-temporal groove is visible on the right side of the skull. The interorbital vacuity is well developed, with no trace of the orbitosphenoid dorsally. The frontal exhibits a long ventral process on the medial border of the orbit, but does not appear to make contact with the palatine.

Basicranium and cranio-mandibular joint. Most of the basicranium in TM 25 is covered by a fragment of humerus attached to the skull (Text-figs 1B, 2B), but the morphology of this region can be observed in NMQR 1633. Laterally, the suture between the prootic and the opisthotic in the fenestra ovalis is visible, and the anteroventral portion of the foramen seems to be formed by the basisphenoid (Text-fig. 3). Anterodorsal to the fenestra ovalis is a small primary facial foramen and a well-developed crest in the prootic separates that foramen from the ventral opening of the cavum epiptericum (Text-fig. 3). This crest is also visible in NMQR 1633. Ventral to the primary facial foramen is a marked depression in approximately the same place where Parrington (1946, fig. 3) illustrated the foramen for the abducens or palatine branch of the facial nerve in *Thrinaxodon*. However, the presence of a foramen in this depression could not be determined in TM 25. In NMQR 1633, the suture between

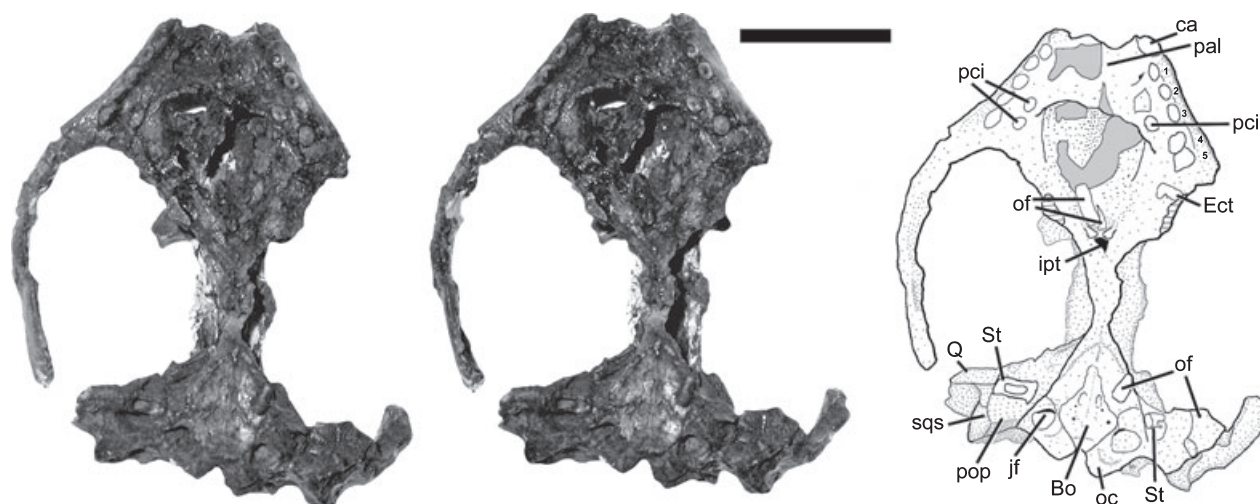


TEXT-FIG. 3. Stereopair of the basicranial region of *Platycraniellus elegans* (TM 25) in ventrolateral view and interpretative drawing. Scale bar represents 1 cm.

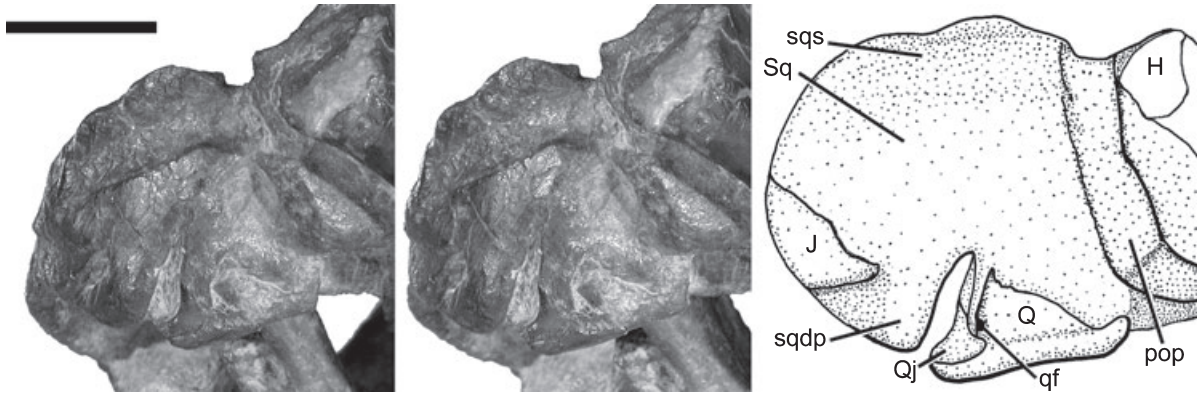
the basioccipital and the basisphenoid is clear, with an inverted V shape. There is no evidence of the carotid opening on the basisphenoid. The basioccipital has an extended anterior process and a pair of shallow fossae, which are positioned centrally and slightly anteriorly (Text-fig. 4). Two pairs of foramina are closely associated with the fossae, with the posterior in each pair distinctly larger than the anterior foramina. This pattern of foramina is not known in other cynodonts, but the presence of nutritive foramina in the basioccipital of *Procynosuchus* (Kemp 1979, fig. 2) suggests that those in NMQR 1633 may be the same, enlarged by acid preparation.

The quadrate and the quadratojugal of the left side are preserved *in situ* (Text-fig. 5). The quadrate contacts the quadrate ramus of the pterygoid, the lateral flange of the prootic and the squamosal. This condition is also present in basal cynodonts, including galesaurids and *Thrinaxodon* (Hopson and Barghusen 1986). The paroccipital process of the left side is located very close to the medial condyle of the quadrate trochlea, but there

seems to be no contact between them. The quadrate bears a cylindrical trochlea, with the medial condyle slightly more developed than the pointed lateral condyle (Text-fig. 5). Luo and Crompton (1994) described the quadrate lateral condyle of *Thrinaxodon* as cylindrical and more developed than the medial. A quadrate foramen is observed close to the lateral border of the bone in posterior view. The quadratojugal has a long vertical process between the squamosal notch and a short horizontal portion in contact ventrally with the lateral trochlear condyle of the quadrate. The vertical process is broken in the middle of its extension, and the horizontal portion of the bone is somewhat displaced from its original position. Restoration of this element would show a relationship between the quadrate and the quadratojugal similar to that of *Thrinaxodon* (Fourie 1974). The morphology and development of the quadrate and quadratojugal notches of the squamosal, and of the articulating flange of the squamosal, are also similar to the condition in *Thrinaxodon* and *Lumkuia* (Fourie 1974; Hopson and Kitching 2001). A bicurrate



TEXT-FIG. 4. Stereopair and interpretative drawing of NMQR 1633 in ventral view. Arabic numbers indicate left upper postcanines. Scale bar represents 2 cm.



TEXT-FIG. 5. Stereopair of the craniomandibular joint region of *Platycraniellus elegans* (TM 25) in posterior view and interpretative drawing. Scale bar represents 1 cm.

right stapes, in contact with the quadrate trochlea, is preserved *in situ* in NMQR 1633, showing the plate with a posteriorly directed process, and an anterior crus that is slightly more developed than the posterior (Text-fig. 4).

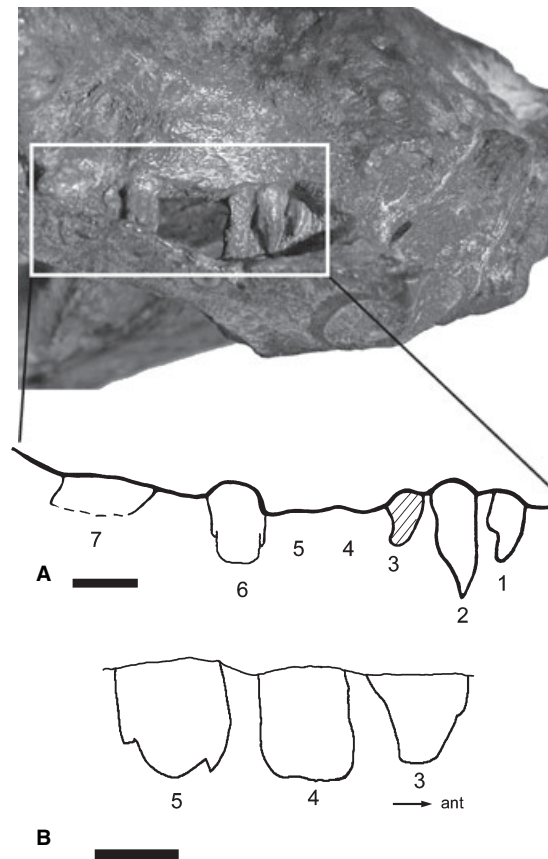
Occipital plate. The occipital plate is triangular in posterior view and only the sutures of the supraoccipital and, in part, the postparietal are visible (Text-figs 1C, 2C). A crest is present in the middle portion of the supraoccipital and the postparietal of the holotype, flanked laterally by two dorsoventrally elongated fossae, but it is absent in NMQR 1633. In the latter specimen, the suture between the right exoccipital and paroccipital process is visible, whereas the small post-temporal canal is completely encircled by the tabular. The ellipsoidal (wider than high) occipital condyles are separated by a notch. The distorted foramen magnum is also ellipsoidal in the holotype, and is slightly larger than the condyles.

Lower jaw. Only the posterior portions of the dentary and the postdentary bar remain (Text-figs 1A–B, 2A–B), whereas the anterior parts of both horizontal rami have been ground away. The mandibular rami are displaced from their original position and the postdentary bar does not articulate with the quadrate. The coronoid process is well developed and high. The lateral crest of the dentary, visible on the right side, is low, whereas the angle of the dentary appears to be slightly more prominent. In medial view, there is a well-developed adductor fossa, bounded by the surangular and the prearticular (Text-fig. 2A). The angular of the right side is well developed in lateral view and concave laterally. The strong base of the right reflected lamina is preserved.

Dentition

There are four incisors, one canine and six or seven postcanines in the upper dentition, which does not extend as far as the level of the orbits (Text-fig. 2B). A small diastema is present between the last incisor and the canine, whereas there is no diastema between the canine and the first postcanine. Much of the dentition was destroyed by grinding (see Text-fig. 2B) and most of the teeth are now represented only by their roots. The only crowns preserved are those of the right lower canine, the first, second, third, sixth and seventh right upper postcanines (Text-

fig. 6A), and the sixth right lower postcanine. The canine is smooth with some weak longitudinal striations, and is large in relation to the postcanines. The crowns of the anterior postcanines feature a high main anterior cusp, followed by a small posterior accessory cusp. This pattern, evident in the first and second postcanines, most closely resembles that of *Nanictosaurus*,



TEXT-FIG. 6. Postcanine dentition of *Platycraniellus elegans*. A, right upper postcanine series of TM 25. B, last three right upper postcanines of NMQR 1633. Arabic numbers indicate upper postcanines. Scale bars represent 2 mm.

TABLE 2. Measurements of the skull regions in *Galesaurus*, *Platycraniellus* and NMQR 860 (in cm). Basal skull length (BL), snout length (SL), orbital length (OL) and temporal length (TL). Percentages are related to basal skull length. The largest specimens of galesaurids were considered to compare with NMQR 860. Values in parentheses in NMQR 860 represent the corrected measure of the temporal length (TL) and the percentage of temporal length using the corrected temporal length (%TL).

Taxon	Specimen	BL	SL	%SL	OL	%OL	TL	%TL
<i>Galesaurus</i>	NMQR 1451	9.0	3.5	39	1.5	17	2.5	28
	AMNH 2223	10.0	4.1	41	1.6	16	3.6	36
	Average percentage			40		16.5		32
<i>Platycraniellus</i>	TM 25	8.4	3.3	39	1.4	17	3.4	40
	NMQR 860	11.4	4.8	42	2.2	19	4.6 (4.1)	40 (36)

especially RC 47 (van Heerden 1976, fig. 12; van Heerden and Rubidge 1990). The remaining crowns are incomplete. Five upper postcanines are present in NMQR 1633. The last right element shows a main cusp, and small anterior and posterior accessory cusps (Text-fig. 6B). Both the main and the posterior accessory cusps are blunt, whereas the anterior accessory cusp is more pointed. Although this tooth is not well preserved, it provides the only evidence of the lack of lingual cingular cusps in the upper postcanines of *Platycraniellus*.

Humerus

A major part of the diaphysis and the distal portion of the bone is preserved attached to the skull (Text-figs 1B–C, 2B–C), and hence a description of only the dorsal view of the element is possible. The deltopectoral crest appears well developed and forms an angle of c. 90 degrees with the long axis of the bone. The distal portion is wide, with the entepicondyle well expanded laterally, whereas the trochlea forms a triangular groove. Striations and scars indicating muscle attachment are visible on the two epicondyles. A large ectepicondylar foramen is present.

DISCUSSION

Taxonomic identity of NMQR 860

NMQR 860, a skull (Text-fig. 7) from the type locality that is larger than that of the holotype of *P. elegans*, was included in this species largely on the basis of skull proportions (Brink 1954a). Hopson and Kitching (1972), however, included this specimen in *Galesaurus planiceps*, which is also known from Harrismith Commonage (Kitching 1977). A comparison of NMQR 860 with both *P. elegans* and *G. planiceps* follows, in order to elucidate the taxonomic identity of this problematical specimen.

The holotype of *P. elegans* (TM 25) is the largest representative of this taxon known with a BL of 8.4 cm. *Galesaurus planiceps*, a common species in the Karoo, shows great variation in size, with the largest specimens (e.g. AMNH 2223; BP/1/5064) reaching a skull length of 10 cm (see Tables 2–3), closer to the BL of NMQR 860 (11.4 cm).

The skull proportions are similar in TM 25 and NMQR 860 (see Tables 1–2 for comparison of measurements),

featuring a wide temporal region: 88 per cent of BL in TM 25 and 84 per cent in NMQR 860. Wide temporal regions are also present in the trirachodontid *Sinognathus gracilis* (Young 1959; Sun 1988) and in some large galesaurid specimens (e.g. BP/1/5064), both showing c. 82 per cent. The equivalent lengths of the snout and the temporal region in NMQR 860 seem to be more similar to those of *P. elegans* (Table 2). This ratio is different for large specimens of *G. planiceps*, in which the snout is proportionally longer than the temporal region (Table 2). It should be mentioned, however, that the posterior portion of the sagittal crest is damaged (see Text-fig. 7A) and the posterior end of the temporal region appears to be displaced posteriorly. A corrected measurement for the temporal length (Table 2, in parentheses) brings the proportions of the snout and the temporal region closer to that observed in AMNH 2223, one of the larger specimens of *G. planiceps*.

TABLE 3. Relationship between basal skull length (BL) and the number of upper postcanines in *Galesaurus*, *Platycraniellus* and NMQR 860. Asterisk indicates estimation of the measurement. All observations by first-hand examination of the material except for the Walker Museum specimen from Rigney (1938). All the localities are situated in the Free State Province.

Specimen	BL (cm)	UP	Locality
<i>Galesaurus</i>			
Walker Mus.	6.2	7	Fairydale
NMP 581	6.5	9	Harrismith
RC 845	7.0	9	Fairydale
SAM-PK-K1119	7.2	8–9	Harrismith
TM 24	7.5*	9	Harrismith
UMCZ T819	8.3	9	Harrismith
BP/1/4602	8.6	?9	Fairydale
NMQR 1451	9.0	10	Bethulie
TM 83	9.0	8–?9	Harrismith
AMNH 2223	10.0	10	Harrismith
NMQR 3340	10.1	10	Dewetsdorp
BP/1/5064	10.4	10	Fairydale
NMQR 860	11.4	9	Harrismith
<i>Platycraniellus</i>			
TM 25	8.4	6–?7	Harrismith
NMQR 1633	6.5*	5	Harrismith

NMQR 860 exhibits a wide temporal roof extending from behind the postorbital bar to the parietal foramen (Text-fig. 7A), whereas in *P. elegans* the posterior projection of the postorbital strongly converges immediately after the postorbital bar (compare Text-fig. 2A and 7A). In this respect, NMQR 860 is clearly similar to *G. planiceps*.

The palate in NMQR 860 is peculiar (Text-fig. 7C). At first sight this specimen seems to have a complete osseous secondary palate, as in *P. elegans*. Close inspection of the palate shows that they differ in extent (Table 1), being longer in TM 25, where it extends nearly to the level of the last postcanine. The shortness of the palate in NMQR 860 and its extremely short palatine component resembles the condition in some galesaurid specimens (e.g. BP/1/5064), but on the other hand, AMNH 2223 shows a comparatively longer palate (Boonstra 1935, fig. 2), demonstrating individual variation in galesaurids. AMNH 2223 also shows the palatal plates of the maxillae and the palatines lying very close together. A slight deformation affecting the very close palatal projections of the maxilla and the palatine may have artificially produced the 'closed palate' condition observed in NMQR 860. The interpterygoid vacuity present in *P. elegans* is absent in NMQR 860. This difference may be ontogenetic, however, because Estes (1961) described interpterygoid vacuities in juveniles of *Thrinaxodon liorhinus*, whereas this structure is unknown in adult specimens.

An angulation (*c.* 120 degrees) between the ventral edge of the maxillary zygomatic process and the anteroventral margin of the jugal as observed in NMQR 860 (Text-fig. 7B) is also known in *Platycraniellus*, large galesaurid specimens (e.g. BP/1/5064; NMQR 1451, 3340), and in two *Thrinaxodon* specimens (BP/1/5208 and BMNH R 511). Consequently, the 'distinct angulation' (Hopson and Barghusen 1986; Hopson 1991) or an 'angulation of 110 degrees or more' (Abdala and Giannini 2002), between the ventral edge of the maxillary zygomatic process and the anteroventral margin of the jugal, previously considered diagnostic of chiniquodontid cynodonts, is a trait also present in basal cynodonts (Abdala 2003; Abdala and Damiani 2004).

Considering the lower jaw, the lateral crest of the dentary is a small projection in *P. elegans*, but appears as a well-developed structure in NMQR 860 (Text-fig. 7B). *Galesaurus planiceps* samples show variations in the lateral crest of the dentary, which is poorly developed in small specimens and even in NMQR 3340 (BL, 10.2 cm), but prominent in BP/1/5064 (BL, 10.4 cm).

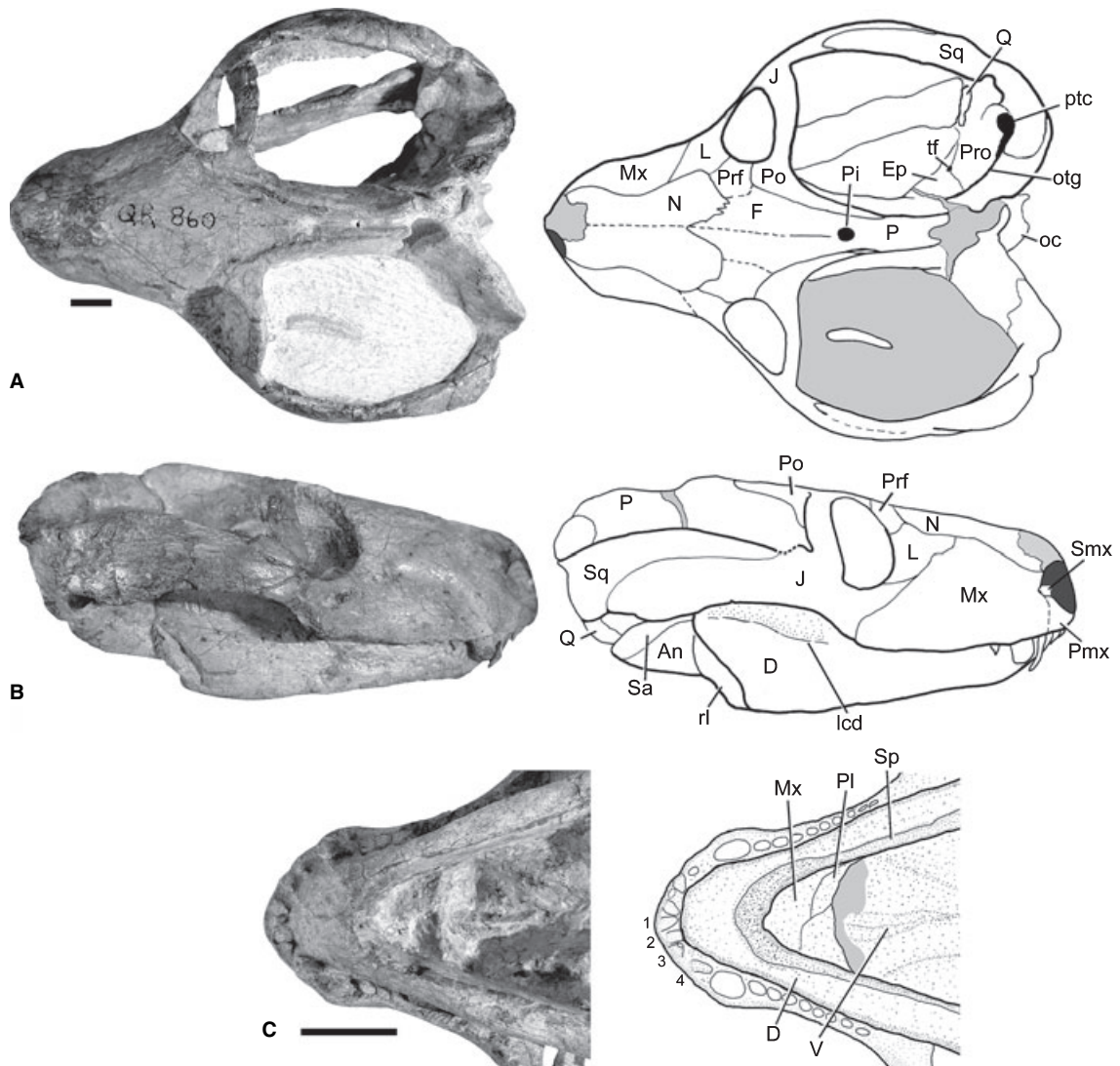
Nine left upper postcanines (three incompletely preserved teeth plus six alveoli with roots) and eight on the right (four incompletely preserved teeth plus four alveoli) were observed in NMQR 860. The preserved roots, more clearly visible on the left side, are circular in outline with

the exception of the last two, which are remarkably enlarged anteroposteriorly. The number of postcanines is very consistent in *G. planiceps*, which mostly possess either nine or ten teeth (see Table 3). In *P. elegans*, the number of postcanines is smaller (and more similar to the number usually present in *T. liorhinus*), whereas galesaurids of similar size exhibit more postcanine teeth (see Table 3). In this case the postcanine number of NMQR 860 seems to be more in accordance with that of *G. planiceps*. These teeth are poorly preserved in NMQR 860 and no single postcanine shows the overall tooth morphology. What can be compared of the postcanine crown patterns between *P. elegans* and NMQR 860 however, differs markedly. In *P. elegans* the postcanine crowns are relatively short mesiodistally, with a high main cusp, as opposed to the mesiodistally extended and apparently low crown inferred for NMQR 860. In addition, the crown of the last left lower postcanine is sufficiently preserved in NMQR 860 to suggest the presence of a backwardly curved main cusp and a posterior accessory cusp in the base of the crown, as in *Galesaurus* (Broom 1932b). This is in accordance with Brink's claim for the existence of indications of similar postcanine crown structures in NMQR 860 and those of *Glochinodontoides* and *Galesaurus* (Brink 1954a, p. 129).

The comparison developed here is hampered because of the poor preservation of NMQR 860, which causes uncertainty in the condition of the primary traits that are important for assessing its taxonomic identity. With this caveat in mind, it seems plausible that NMQR 860 represents the largest specimen of *G. planiceps* known to date.

Cladistic analysis of eutheriodonts

Five most parsimonious trees (MPTs) of 351 steps, a consistency index of 0.41 and a retention index of 0.75 resulted from the analysis using equal weighted characters. Therocephalians appear as a paraphyletic group with *Lycosuchus*, *Glanosuchus* and remaining 'Therocephalia' + Cynodontia forming a polytomy in the strict consensus tree (Text-fig. 8A). This basal polytomy is followed by a second polytomy composed of *Hofmeyria*, *Ictidosuchops*, *Moschorhinus*, *Bauria* and *Theriognathus* + Cynodontia. The majority rule consensus (Text-fig. 8B) shows a basal placement of *Lycosuchus* among 'therocephalians', and *Hofmeyria* placed as outgroup of *Ictidosuchops*, *Moschorhinus*, *Bauria* and *Theriognathus* + Cynodontia. Cynodonts are monophyletic, with *Procynosuchus* + *Dvinia* placed as the most basal clade, followed by a polytomy including *Cynosaurus*, the clade of *Galesaurus* + *Progalesaurus*, and a clade including the remaining cynodonts. *Platycraniellus* is placed as the immediate outgroup of Eucynodontia and *Thrinaxodon* as



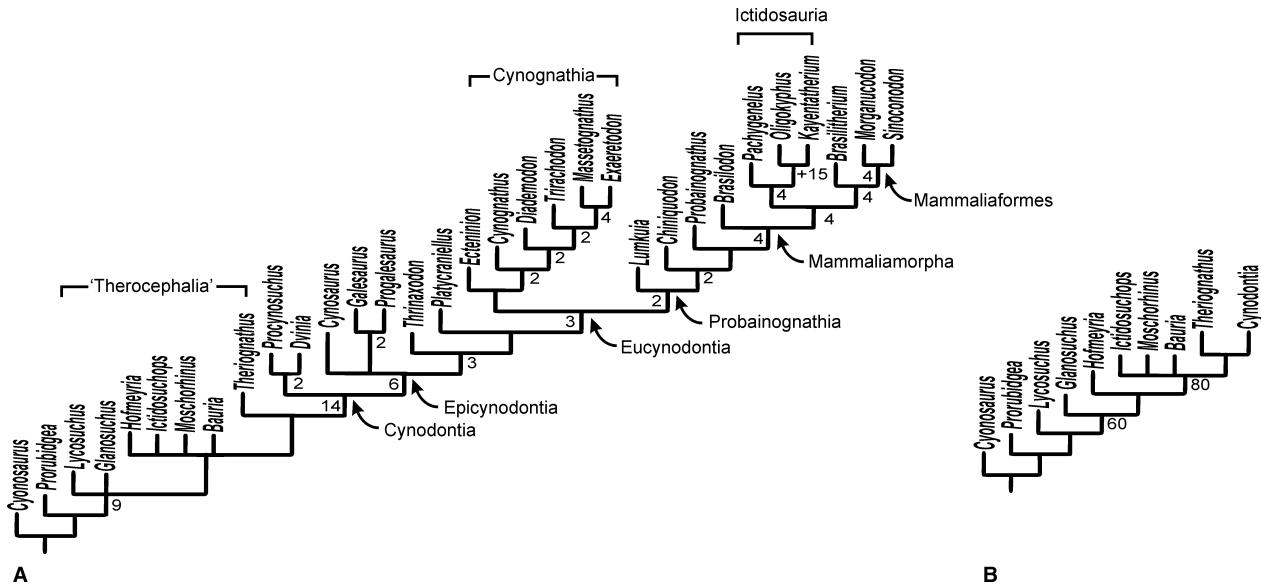
TEXT-FIG. 7. Specimen NMQR 860 in A, dorsal, B, right lateral, and C, palatal views. Grey shading in interpretative drawings is broken bone or matrix. Scale bar represents 2 cm.

their successive sister clade. Eucynodontia is composed of two main groups, Cynognathia and Probainognathia. Cynognathia has *Ecteninion* as the most basal taxon, followed by *Cynognathus* and the gomphodont cynodonts (Text-fig. 8). Probainognathia includes *Lumkuia* at the base, followed successively by *Chiniquodon* and *Probainognathus*. *Brasilodon* is placed at the base of the Mammalia-morpha, followed by a monophyletic group formed by *Pachygenelus* and tritylodontids (Text-fig. 8). Finally, *Brasilitherium* appears as the sister taxon of Mammalia-formes.

Text-figure 8A shows Bremer support values greater than 1. The best supported clades are Cynodontia, Tritylodontia (both with Bremer values above 10), and 'Therocephalia' + Cynodontia (with support of 9). Epi-cynodontia has a Bremer value of 6, and Mammalia-

formes, the clade of *Brasilitherium*, *Morganucodon* and *Sinoconodon*, and the clade of *Pachygenelus* and tritylodontids each have a support value of 4 (see Text-fig. 8A). Eucynodontia and the clade of *Thrinaxodon*, *Platycranielus* and Eucynodontia both have a support value of 3. Low support characterizes clades with 'therocephalian' taxa, Probainognathia and Cynognathia, and many clades within the last two groups (Text-fig. 8A).

The MPTs obtained from cladistic analyses under implied weights with different values of the constant of concavity do not differ significantly from the MPTs obtained from the analysis with equal weights. The number of MPTs obtained varied between one and two, depending on the different schemes of weighting. The placement of 'therocephalians' in the analyses under implied weights was similar to that present in the



TEXT-FIG. 8. A, strict consensus of five most parsimonious trees obtained from analysis with characters having equal weights. Values of Bremer support higher than 1 are indicated. B, majority rule consensus of the same analysis. Numbers indicate frequency of clades in the fundamental trees. Cynodontia in B has the same topology as in A.

majority-rule consensus of the analysis with characters having equal weight (Text-fig. 8B). Thus, *Lycosuchus* was placed as the most basal form of ‘Therocephalia’, followed by *Glanosuchus*, and then by *Hofmeyria*. Using the strongest scheme of weighting (i.e. until $K = 1$) the resultant MPT showed *Bauria* as sister taxon of cynodonts, followed by an outgroup formed by (*Moschorhinus* (*Ictidosuchops*, *Theriognathus*)). Differences in the topology of the MPTs under schemes of weight ranging with K values of 2 and higher were restricted to relationships between *Moschorhinus*, *Ictidosuchops* and *Bauria*. The placement of these taxa was highly variable and they appeared in all the possible combinations. In relation to cynodont relationships, a swapped placement between *Chiniquodon* and *Probainognathus*, with the latter appearing as more basal than the former, is obtained in weighted MPTs until $K = 25.3$. The swapped placement of these taxa is supported by three synapomorphies: 17 (osseous palate extended more than 45 per cent of the basal skull length), 19 (long palatal process of the palatine in relation to the palate length), and 45 (paroccipital process not placed at the base of the post-temporal fossa). Synapomorphies 17 and 19 have the lowest value of adjusted homoplasy in the analyses, resulting in MPTs in which *Probainognathus* is placed basal to *Chiniquodon* and remaining probainognathians (except for *Lumkuia*). Finally, with K values of 0.1–0.7 (i.e. with a very strong penalization of homoplastic characters), *Ectenion* and *Probainognathus* form a monophyletic group among Probainognathia.

Results from the analyses favoured a paraphyletic ‘Therocephalia’ with *Theriognathus* as the sister taxon of

Cynodontia. Four synapomorphies are shared by *Theriognathus* and Cynodontia in the equal weighted MPTs (see Appendix). This relationship differs from recent proposals that considered ‘Therocephalia’ as monophyletic (Hopson and Barghusen 1986; Hopson 1991; Rubidge and Sidor 2001), although in these cases, hypotheses were not based on a data matrix subjected to parsimony analysis. *Theriognathus* was also found as the sister taxon of cynodonts in a recent phylogeny by Botha *et al.* 2007). A close relationship between *Theriognathus* and cynodonts was first proposed by Kemp (1972a).

Cynodontia is supported by 16 synapomorphies, with *Procynosuchus* and *Dvinia* placed in a monophyletic group, characterized by four synapomorphies in four of the five MPTs, as its most basal representatives (but see Botha *et al.* 2007). A sister-group relationship between *Procynosuchus* and *Dvinia* was also recovered in the extensive phylogeny of Synapsida with ordered multistate characters by Sidor and Hopson (1998, pp. 257–258), and as one of the three MPTs by Hopson and Kitching (2001, p. 23), although it did not represent the hypothesis preferred by these authors. Galesauridae includes *Galesaurus* and *Progalesaurus* and is supported by two synapomorphies in the equally weighted MPTs (see Appendix). The placement of *Cynosaurus* is not fully resolved (see Text-fig. 8), and it is not possible to include this genus in Galesauridae as proposed by Sidor and Smith (2004). Nor is it possible to confirm the hypothesis of Botha *et al.* (2007) that *Cynosaurus* is the sister taxon of all remaining cynodonts, including the monophyletic group formed by *Galesaurus* and *Progalesaurus*. *Platytraniellus* is

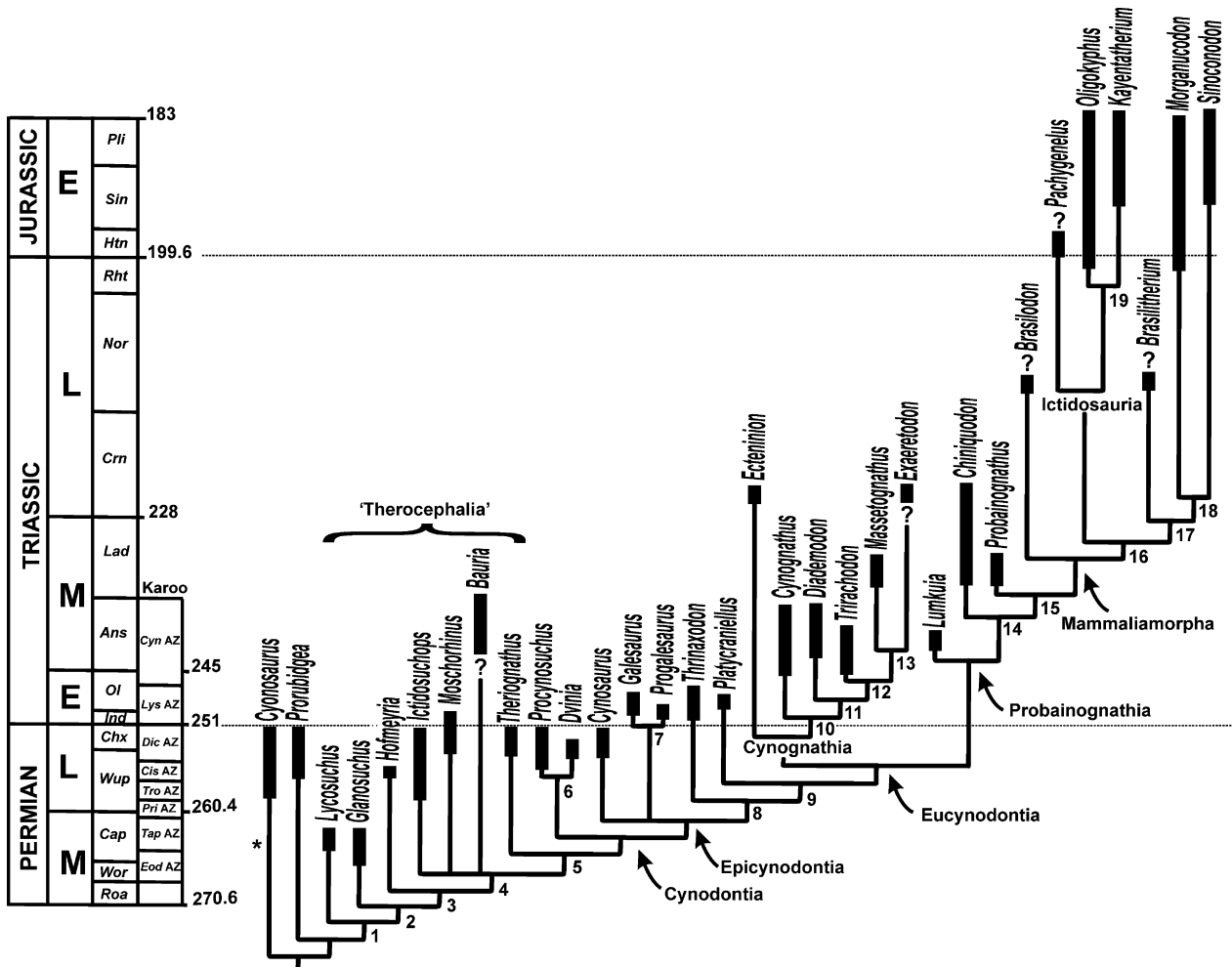
the sister group of Eucynodontia, with *Thrinaxodon* being placed as their successive outgroup. Only one synapomorphy supports the sister-group relationship of *Platycranialus* and Eucynodontia. These two taxa and *Thrinaxodon* formed a polytomy in Sidor and Smith's consensus tree (2004, fig. 7).

Five synapomorphies support the monophyly of Eucynodontia. The results presented here recognize a main dichotomy in Eucynodontia between Probainognathia and Cynognathia, a hypothesis proposed by Hopson and Kitching (2001) but with a composition different from that presented here (see below). The poor support of these two groups (both supported by three synapomorphies) shows that the relationships among eucynodonts are no better resolved than 10 years ago, when Martinez *et al.* (1996, p. 281) mentioned the plastic condition of their phylogeny between the basal nodes of Eucynodontia and Mammaliaforma. This is the first instance in which a sister-group relationship between *Pachygenelus* (a representative of Trithelodontidae) and Tritylodontidae is proposed in a cladistic framework. Seven synapomorphies support this relationship, previously proposed by Romer (1945, 1956), who included tritylodontids, *Trithelodon*, *Diarthrognathus* and Microcleptidae (= Haramiyidae) in Ictidosauria (see also Parrington 1947; Young 1947; Kühne 1956; Watson and Romer 1956). The placement of tritylodontids as more closely related to Mammaliaformes (i.e. in Probainognathia) than to Gomphodontia is in accordance with Kemp (1983), Rowe (1986, 1988, 1993), Wible (1991), Wible and Hopson (1993), Luo (1994), Abdala (1996a) and Martinez *et al.* (1996), but conflicts with Sues (1985a), Hopson and Barghusen (1986), Battail (1991), Hopson (1991, 1994), Hopson and Kitching (2001) and Bonaparte *et al.* (2005). The hypothesis presented here is consonant with that of Bonaparte *et al.* (2003, 2005) on the sister-group relationship of *Brasilitherium* and Mammaliaformes (supported by five synapomorphies), but does not confirm the monophyly of Brasilodontidae (i.e. *Brasilodon* + *Brasilitherium*). One of the main differences between these Brazilian genera is related to the promontorium. This structure is present in *Brasilitherium* (Bonaparte *et al.* 2005, fig. 11), but in *Brasilodon* the situation is unclear. The promontorium of the latter was described and figured by Bonaparte *et al.* (2003, p. 11, figs 3, 6), but the illustrations of the basicranium of *Brasilodon* are inconclusive with regard to the presence of the promontorium. Moreover, Bonaparte *et al.* (2003, p. 21) highlighted the absence of a promontorium in *Brasilodon* when comparing it with *Morganucodon*. Finally, the promontorium was scored as absent for *Brasilodon* in the data matrix presented by Bonaparte *et al.* (2005, character 57), a scoring that is followed in the analysis presented here.

The MPTs obtained from the cladistic analysis are mostly congruent with the first appearances of the taxa (Text-fig. 9). An initial Middle–Late Permian radiation is represented by 11 taxa, including two gorgonopsians, six ‘therocephalians’ and three cynodonts. The two gorgonopsians presented here are younger than the most basal ‘therocephalians’ (i.e. *Lycosuchus* and *Glanosuchus*), but the oldest known gorgonopsid (marked by an asterisk in Text-fig. 9) is roughly contemporaneous with the oldest ‘therocephalians’ (Sidor and Hopson 1998). *Moschorhinus* is the only taxon in the phylogeny crossing the Permian/Triassic extinction event. The other ‘Therocephalia’ known to cross the P/T boundary are the scaloposaurids *Ictidosuchoides* and *Tetracynodon* (Smith and Botha 2005). It should be mentioned, however, that the latter genus is represented by three small specimens (Broom and Robinson 1948; Sigogneau 1963; Damiani *et al.* 2004) that could eventually prove to be juveniles of another taxon (e.g. *Ictidosuchoides*). The Late Permian taxa *Dvinia* and *Procynosuchus* are the most basal cynodonts in this study. The oldest cynodont, however, is known from the *Tropidostoma* AZ of the Karoo, and is most likely early Late Permian (Botha *et al.* 2007).

A second radiation occurred in the Early Triassic and early Middle Triassic, and includes four cynodonts from the *Lystrosaurus* AZ and four cynodonts and one ‘therocephalian’ from the *Cynognathus* AZ. *Bauria* is the last ‘therocephalian’ and has been allied with the Early Triassic *Erciolacerta* (Hopson and Barghusen 1986), which was not included in this phylogeny; the latter genus may represent the temporal link between *Bauria* and the remaining ‘therocephalians’ (see Rubidge *et al.* 1995, fig. 3). The second radiation comprises the origin and first diversification in Gondwana of Gomphodontia, one of the more diverse groups of cynodonts (Abdala *et al.* 2006). The first record of Probainognathia is also represented at this time by the basal *Lumkuia* (Hopson and Kitching 2001). The radiation persisted through five cynodonts from the Ladinian to early Carnian of Argentina and Brazil. Three cynognathians, the carnivorous *Ecteninion* and two traversodontid gomphodonts *Massetognathus* and *Exaeretodon*, and two probainognathians, *Chiniquodon* and *Probainognathus*, are represented in the phylogeny at this age. The placement of *Ecteninion* at the base of Cynognathia represents a major incongruence between the phylogeny presented here and the first appearance date of a taxon included in the analysis (see Text-fig. 9): *Ecteninion* is early Carnian, whereas the first record of its sister group (i.e. *Cynognathus* + Gomphodontia) is late Olenekian.

The next phase is represented by *Brasilodon* and *Brasilitherium* from southern Brazil. These taxa were considered as early Norian by Rubert and Schultz (2004) and Martinelli *et al.* (2005), although a younger age cannot be



TEXT-FIG. 9. Majority rule consensus tree of the analysis with characters having equal weights plotted against the geological time scale (based on Gradstein and Ogg 2004). Key to biozones: *Eod* AZ, *Eodicynodon* Assemblage Zone (AZ); *Tap* AZ, *Tapinocephalus* AZ; *Pri* AZ, *Pristerognathus* AZ; *Tro* AZ, *Tropidostoma* AZ; *Cis* AZ, *Cistecephalus* AZ; *Dic* AZ, *Dicynodon* AZ; *Lys* AZ, *Lystrosaurus* AZ; *Cyn* AZ, *Cynognathus* AZ. Temporal extension of the assemblage zones based on Rubidge *et al.* (1995) and Cisneros *et al.* (2005). The geological time scale is portrayed to show the age of the taxa included in the analysis (see also Appendix), but not the inferred age of branch divergences. Some nodes are placed in the first appearance of the taxa in the fossil record. This is the case for nodes 13 (Traversodontidae), 18 (Mammaliaformes), 19 (Tritylodontidae) and Ictidosauria (based on the earliest record of Tritheledontidae). The asterisk indicates the earliest record of Gorgonopsia, the group including the taxon used to root the tree. For synapomorphies of the monophyletic groups, see Appendix.

completely disregarded (see Langer 2005). These contemporaneous Brazilian genera are not sister taxa in this phylogeny (contra Bonaparte *et al.* 2005): *Brasilodon* is the most basal Mammaliaomorpha, whereas *Brasilitherium* is the sister taxon of Mammaliaformes. This relationship indicates that *Brasilodon* is expected to appear earlier in the fossil record than *Brasilitherium*.

The last radiation in this phylogeny is represented by Rhaetian–Early Jurassic cynodonts, represented by two tritylodontids, the tritheledontid *Pachygenelus* and two mammaliaforms. Tritylodontids are first known in the Rhaetian (leaving aside the postcranial remains from the Argentinian Norian, attributed to cf. *Tritylodon* by Bona-

parte 1971), and were a diverse and cosmopolitan group by the Early Jurassic (Maisch *et al.* 2004; Kemp 2005). Tritheledontids are small cynodonts with their first records in the Norian of Argentina and Brazil and last records in the Lower Jurassic of South Africa and the United States (Shubin *et al.* 1991; Bonaparte *et al.* 2001). Recent phylogenies agree in recognizing Tritheledontidae as a monophyletic group (Martinelli *et al.* 2005; Sidor and Hancox 2006). The tritheledontid *Tritheledon*, only known by two partial maxillae with postcanines (Broom 1912; Houghton 1924b), was not included in these recent phylogenies. Gow (1980, p. 479) stated that the upper postcanines of *Tritheledon* were ‘essentially mirror images’

of the lower postcanines of *Diarthrognathus*. First-hand examination and comparison between South African tritheledontid postcanines show, however, that the buccolingually expanded upper postcanines of *Tritheledon* are notoriously divergent from the morphology observed in the other tritheledontids. Thus, the possibility remains that more complete materials of *Tritheledon* may prove that this taxon does not pertain to a monophyletic Tritheledontidae, as recognized by Martinelli *et al.* (2005) and Sidor and Hancox (2006). The earliest representative of Mammaliaformes is the enigmatic *Adelobasileus*, represented only by the posterior portion of the cranium, from early Carnian deposits in the United States (Lucas and Luo 1993; Kielan-Jaworowska *et al.* 2004). After that first record, an explosive radiation, mainly represented by isolated teeth, is recognized in Rhaetian–Early Jurassic faunas of continental Europe, the United Kingdom, China, India and the United States (Kielan-Jaworowska *et al.* 2004). The two mammaliaforms used in this phylogeny are part of this Rhaetian–Early Jurassic radiation.

A large temporal gap without representatives (Text-fig. 9) is particularly remarkable in the Late Carnian and in most of the long Norian Age. Unfortunately, the fossil record of therapsids for those particular ages is poor and fragmentary, with many taxa being represented only by isolated teeth, as in the Late Norian–Rhaetian European faunas (Godefroit and Battail 1997) or by incomplete or poorly preserved specimens from Late Carnian–Norian faunas of North America (e.g. *Arctotraversodon*, *Microcondon*; Sues *et al.* 1992; Sues 2001), Greenland (e.g. *Mitredon*; Shapiro and Jenkins 2001), South America (e.g. *Chalimimia*; pers. obs.) and South Africa (e.g. *Scalenodontoides*, *Elliotherium*; Gow and Hancox 1993; Sidor and Hancox 2006; pers. obs.).

CONCLUSIONS

As suggested by various authors (Hopson and Kitching 1972; Brink 1986; Battail 1991), *Platycraniellus elegans* is a valid species that is characterized by the wide temporal region of the skull and a short snout. Specimen NMQR 860, included in *P. elegans* by Brink (1954a) and in *Galesaurus planiceps* by Hopson and Kitching (1972), probably belongs to the latter. This identity is based on the overall morphology and size of the skull, the number of postcanine teeth and the inferred pattern of the postcanine dentition, among other features. Evidence from the palate is contradictory, because even though a closed secondary palate seems to be present in NMQR 860, it is extremely short, resembling the morphology of some specimens of *G. planiceps* with an incomplete osseous palate. Deformation of the palate may be the cause of this feature. The poor condition of NMQR 860 and the lack of preserva-

tion of important traits, however, hamper a confident taxonomic identification; the identity of NMQR 860 as *G. planiceps* therefore is tentative. Results of the phylogenetic analyses indicate that *Platycraniellus elegans* is the sister taxon of Eucynodontia, followed by *Thrinaxodon liorhinus* as their sister taxon. The MPTs indicate that Therocephalia is not a monophyletic group, in contrast to recent opinions of workers on therapsids. The whaitsiid *Theriognathus* is the sister taxon of Cynodontia, whereas the basal forms *Lycosuchus* and *Glanosuchus* form a basal polytomy with remaining ‘Therocephalia’ + Cynodontia. Two main clades are found between advanced cynodonts (eucynodonts): (1) Cynognathia, including the sectorial-toothed *Ecteninion* and *Cynognathus* and the gomphodont cynodonts *Diademodon*, *Trirachodon*, *Massetognathus* and *Exaeretodon*; (2) Probainognathia, including most sectorial-toothed eucynodonts (e.g. *Lumkuia*, *Probainognathus*, *Chiniquodon*), *Brasilodon*, tritylodontids, tritheledontids, *Brasilitherium* and mammaliaforms. Tritylodontids (*Oligokyphus* and *Kayentatherium*) and the tritheledontid *Pachygenelus* form a monophyletic group (i.e. Ictidosauria). Finally, as suggested by Bonaparte *et al.* (2005), *Brasilitherium* appears as the sister taxon of Mammaliaformes, but results of the analyses presented here do not corroborate the monophyly of brasilodontids (i.e. *Brasilodon* and *Brasilitherium*) proposed by these authors.

Acknowledgements. For granting access to the material studied, I thank H. Fourie (TM); B. de Klerk (AM); J. Botha and E. Butler (NMQR); M. Raath and B. Rubidge (BP); R. Smith and S. Kaal (SAM); D. Jennings (NMP); J. Neveling (CGP); J. van den Heever (US); J. E. Powell (PVL); J. F. Bonaparte (formerly MACN); A. B. Arcucci (formerly PULR); W. Sill and R. Martinez (PVSJ); M. C. Malabarba (MCP); C. L. Schultz (UFRGS); A. Liebau and F. Westphal (GPIT); P. Wellhofer (BSP); W.-D. Heinrich (MB); A. Milner and S. Chapman (BMNH); T. Kemp (OUMNH); J. Clack and R. Symonds (UMCZ); E. Gaffney (AMNH), and C. Schaff (MCZ). Funding was provided by the University of the Witwatersrand and the National Research Foundation, South Africa, through a postdoctoral fellowship. The Universidad Nacional de Tucumán (Argentina), DAAD (Deutscher Akademischer Austauschdienst), the Museum of Comparative Zoology, Harvard University, the American Museum of Natural History, PAST (Palaeontological Scientific Trust, Johannesburg), and the Royal Society of London provided grants that allowed study visits to palaeontological collections in Argentina, Brazil, South Africa, Germany, the United States and England. L. Backwell, T. Kemp, M. Raath and C. Snow made many suggestions on different versions of the text. J. Botha, T. Kemp and S. Modesto made many comments and suggestions that improved the final version. J. C. Cisneros drafted the components of Text-figure 2. Further preparation of TM 25 (holotype of *Platycraniellus elegans*) was generously permitted by H. Fourie and carried out by A. Nthaopa Ntheri.

REFERENCES

- ABDALA, F. 1996a. Los Chiniquodontoideos (Synapsida, Cynodontia) sudamericanos. Unpublished PhD thesis. Universidad Nacional de Tucumán, 381 pp.
- 1996b. Redescrición del cráneo y reconsideración de la validez de *Cynognathus minor* (Eucynodontia-Cynognathidae) del Triásico Inferior de Mendoza. *Ameghiniana*, **33**, 115–126.
- 2003. Galesaurid cynodonts from the Early Triassic of South Africa: another example of conflicting distribution of characters in non-mammalian cynodonts. *South African Journal of Science*, **99**, 95–96.
- and DAMIANI, R. 2004. Early development of the mammalian superficial masseter muscle in cynodonts. *Palaeontologia Africana*, **40**, 23–29.
- and GIANNINI, N. P. 2000. Gomphodont cynodonts of the Chañares Formation: the analysis of an ontogenetic sequence. *Journal of Vertebrate Paleontology*, **20**, 501–506.
- — 2002. Chiniquodontid cynodonts: systematic and morphometric considerations. *Palaeontology*, **45**, 1151–1170.
- and RIBEIRO, A. M. 2003. A new traversodontid cynodont from the Santa Maria Formation (Ladinian–Carnian) of southern Brazil, with a phylogenetic analysis of Gondwanan traversodontids. *Zoological Journal of the Linnean Society*, **139**, 529–545.
- — and SCHULTZ, C. L. 2001. A rich cynodont fauna of Santa Cruz do Sul, Santa Maria Formation (Middle–Late Triassic), southern Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **2001**, 669–687.
- BARBERENA, M. C. and DORNELLES, J. 2002. A new species of the Traversodontidae *Exaeretodon* from the Santa Maria Formation (Middle/Late Triassic) of southern Brazil. *Journal of Vertebrate Paleontology*, **22**, 313–325.
- NEVELING, J. and WELMAN, J. 2006. A new trirachodontid cynodont from the lower levels of the Burgersdorp Formation (Lower Triassic) of the Beaufort Group, South Africa and the cladistic relationships of Gondwanan gomphodonts. *Zoological Journal of the Linnean Society*, **147**, 383–413.
- ANDERSON, J. M. 1968. The confused state of classification within the family Procynosuchidae. *Palaeontologia Africana*, **11**, 77–84.
- BATTAIL, B. 1982. Essai de phylogénie des Cynodontes (Reptilia, Therapsida). *Geobios, Mémoire Spécial*, **6**, 157–167.
- 1983. La phylogénie des Cynodontes gomphodontes. *Acta Palaeontologica Polonica*, **28**, 19–30.
- 1991. Les cynodontes (Reptilia, Therapsida): une phylogénie. *Bulletin du Muséum National d'Histoire Naturelle, 4e Série*, **13**, 17–105.
- BONAPARTE, J. F. 1962. Descripción del cráneo y mandíbula de *Exaeretodon frenguelli*, Cabrera, y su comparación con *Diademodontidae*, *Tritylodontidae* y los cinodontes sudamericanos. *Publicaciones del Museo Municipal de Ciencias Naturales y Tradición. Mar del Plata*, **1**, 135–202.
- 1966. *Chiniquodon* Huene (Therapsida-Cynodontia) en el Triásico de Ischigualasto, Argentina. *Acta Geologica Lilloana*, **8**, 157–169.
- 1969. *Cynognathus minor* n. sp. (Therapsida-Cynodontia). Nueva evidencia de vinculación faunística afro-sudamericana a principios del Triásico. 273–281. In: *Gondwana Stratigraphy*. IUGS Symposium, Mar del Plata, 1967.
- 1971. Los tetrápodos del sector superior de la Formación Los Colorados, La Rioja, Argentina (Triásico Superior). I. Parte. *Opera Lilloana*, **22**, 1–183.
- FERIGOLO, J. and RIBEIRO, A. M. 2001. A primitive Late Triassic 'ictidosaur' from Rio Grande do Sul, Brazil. *Palaeontology*, **44**, 623–635.
- MARTINELLI, A. G. and SCHULTZ, C. L. 2005. New information on *Brasilodon* and *Brasilitherium* (Cynodontia, Probainognathia) from the Late Triassic of southern Brazil. *Revista Brasileira de Paleontologia*, **8**, 25–46.
- — and RUBERT, R. 2003. The sister group of mammals: small cynodonts from the Late Triassic of southern Brazil. *Revista Brasileira de Paleontologia*, **5**, 5–27.
- BOONSTRA, L. D. 1935. A note on the cynodont *Glochiodontoides gracilis* Houghton. *American Museum Novitates*, **782**, 1–6.
- 1938. On a South African mammal-like reptile, *Bauria cynops*. *Palaeobiologica*, **6**, 164–183.
- BOTHA, J., ABDALA, F. and SMITH, R. M. H. 2007. The oldest cynodont: new clues on the origin and diversification of the Cynodontia. *Zoological Journal of the Linnean Society*, **149**, 477–492.
- BRINK, A. S. 1954a. Note on a new *Platycraniellus* skull. *Navorsing van die Nasionale Museum*, **1**, 127–129.
- 1954b. *Thrinaxodon* and some other *Lystrosaurus* Zone cynodonts in the collection of the National Museum, Bloemfontein. *Navorsing van die Nasionale Museum*, **1**, 115–125.
- 1954c. On the Whatsiidae, a family of therocephalian mammal-like reptiles. *Transactions of the Royal Society of South Africa*, **34**, 43–59.
- 1955a. A study on the skeleton of *Diademodon*. *Palaeontologia Africana*, **3**, 3–39.
- 1955b. On the Cynognathidae. *Palaeontologia Africana*, **3**, 47–55.
- 1956. On *Aneugomphius ictidoceps* Broom and Robinson. *Palaeontologia Africana*, **4**, 97–115.
- 1959. Notes on some whatsiids and moschorhinids. *Palaeontologia Africana*, **6**, 23–49.
- 1963a. On *Bauria cynops* Broom. *Palaeontologia Africana*, **8**, 39–56.
- 1963b. A new skull of the procynosuchid cynodont *Leavachia duvenhagei* Broom. *Palaeontologia Africana*, **8**, 57–75.
- 1965a. A new large bauriamorph from the *Cynognathus*-Zone of South Africa. *Palaeontologia Africana*, **9**, 123–127.
- 1965b. On two new specimens of *Lystrosaurus*-Zone cynodonts. *Palaeontologia Africana*, **9**, 107–122.
- 1986. *Illustrated bibliographical catalogue of the Synapsida*. Handbook 10, Part 1. Department of Mineral and Energy Affairs, Pretoria, 35 pp.
- and KITCHING, J. W. 1951. On *Leavachia*, a procynosuchid cynodont from the Middle *Cistecephalus* Zone. *South African Journal of Science*, **47**, 342–347.
- BROILI, F. and SCHRÖDER, J. 1934. Zur Osteologie des Kopfes von *Cynognathus*. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematische-Naturwissenschaftliche, Abteilung*, 95–128.

- — 1935a. Beobachtungen an Wirbeltieren der Karrooformation XI. Über den schädel von *Cynidiognathus* Houghton. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematische-Naturwissenschaftliche, Abteilung*, **1935**, 199–222.
- — 1935b. Beobachtungen an Wirbeltieren der Karrooformation. IX. Über den Schädel von *Gomphognathus* Seeley. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematische-Naturwissenschaftliche, Abteilung*, **1935**, 115–182.
- — 1935c. Beobachtungen an Wirbeltieren der Karrooformation. X. Über die Bezahlung von *Trirachodon* Seeley. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematische-Naturwissenschaftliche, Abteilung*, **1935**, 189–198.
- BROOM, R. 1903. On an almost perfect skull of a new primitive theriodont (*Lycosuchus vanderrieti*). *Transactions of the South African Philosophical Society*, **14**, 197–205.
- 1904. On two new therocephalian reptiles (*Glanosuchus macrops* and *Pristerognathus baini*). *Transactions of the South African Philosophical Society*, **15**, 85–88.
- 1905. On the use of the term anomodont. *Records of the Albany Museum*, **1**, 266–269.
- 1911. On the structure of the skull in cynodont reptiles. *Proceedings of the Zoological Society*, **1911**, 893–925.
- 1912. On a new type of cynodont from the Stormberg. *Annals of the South African Museum*, **7**, 334–336.
- 1932a. *The mammal-like reptiles of South Africa and the origin of mammals*. H. F. & G. Witherby, London, 376 pp.
- 1932b. The cynodont genus *Galesaurus*. *Annals of the Natal Museum*, **7**, 61–66.
- 1935. On some new genera and species of Karroo fossil reptiles. *Annals of the Transvaal Museum*, **18**, 55–72.
- 1937a. On the palate, occiput and hind foot of *Bauria cynops* Broom. *American Museum Novitates*, **946**, 1–6.
- 1937b. A further contribution to our knowledge of the fossil reptiles of the Karroo. *Proceedings of the Zoological Society of London B*, **107**, 299–318.
- 1938. The origin of the cynodonts. *Annals of the Transvaal Museum*, **19**, 279–288.
- 1948. A contribution to our knowledge of the vertebrates of the Karroo Beds of South Africa. *Transactions of the Royal Society of Edinburgh*, **61**, 577–629.
- and ROBINSON, J. T. 1948. On some new types of small carnivorous mammal-like reptiles. 29–44. In DU TOIT, A. L. (ed.). *Robert Broom commemorative volume*. Royal Society of South Africa, Cape Town, 257 pp.
- CHATTERJEE, S. 1982. A new cynodont reptile from the Triassic of India. *Journal of Paleontology*, **56**, 203–214.
- CISNEROS, J. C., ABDALA, F. and MALABARBA, M. C. 2005. Pareiasaurids from the Rio do Rasto Formation: biostratigraphic implications for Permian faunas of the Paraná Basin. *Revista Brasileira de Paleontologia*, **8**, 13–24.
- CLARK, J. M. and HOPSON, J. A. 1985. Distinctive mammal-like reptile from Mexico and its bearing on the phylogeny of the Tritylodontidae. *Nature*, **315**, 398–400.
- COAD, B. W. 1977. On the nomenclature of the genus name *Tribolodon* (Osteichthyes and Reptilia). *Journal of Paleontology*, **51**, 1046–1047.
- CODDINGTON, J. and SCHARFF, N. 1994. Problems with zero-length branches. *Cladistics*, **10**, 415–423.
- COLBERT, E. H. and KITCHING, J. W. 1977. Triassic cynodont reptiles from Antarctica. *American Museum Novitates*, **2611**, 1–30.
- CROMPTON, A. W. 1955. A revision of the Scaloposauridae with special reference to kinetism in this family. *Navorsing van die Nasionale Museum*, **1**, 149–183.
- 1962. On the dentition and tooth replacement in two bauiamorph reptiles. *Annals of the South African Museum*, **46**, 231–255.
- 1963. Tooth replacement in the cynodont *Thrinaxodon liorhinus* Seeley. *Annals of the South African Museum*, **46**, 479–521.
- 1964. On the skull of *Oligokyphus*. *Bulletin of the British Museum (Natural History), Geology*, **9**, 69–82.
- 1972a. Postcanine occlusion in cynodonts and tritylodonts. *Bulletin of the British Museum (Natural History), Geology*, **21**, 29–71.
- 1972b. The evolution of the jaw articulation in cynodonts. 231–251. In JOYSEY, K. A. and KEMP, T. S. (eds). *Studies in vertebrate evolution*. Oliver and Boyd, Edinburgh, 284 pp.
- 1974. The dentitions and relationships of the southern African Triassic mammals, *Erythrotherium parringtoni* and *Megazostrodon rudnerae*. *Bulletin of the British Museum (Natural History), Geology*, **24**, 397–437.
- and HYLANDER, W. L. 1986. Changes in mandibular function following the acquisition of a dentary-squamosal jaw articulation. 263–282. In HOTTON, N. III, MACLEAN, P. D., ROTH, J. J. and ROTH, E. C. (eds). *The ecology and biology of mammal-like reptiles*. Smithsonian Institution Press, Washington, DC, 326 pp.
- and LUO, Z. 1993. Relationships of the Liassic mammals *Sinoconodon*, *Morganucodon oehleri*, and *Dinnetherium*. 30–44. In SZALAY, F. S., NOVACEK, M. J. and MCKENNA, M. C. (eds). *Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials*. Springer Verlag, New York, NY, 249 pp.
- and SUN, A.-L. 1985. Cranial structure and relationships of the Liassic mammal *Sinoconodon*. *Zoological Journal of the Linnean Society*, **85**, 99–119.
- DAMIANI, R., NEVELING, J., MODESTO, S. and YATES, A. 2004. Barendskraal, a diverse amniote locality from the *Lystrosaurus* Assemblage Zone, Early Triassic of South Africa. *Palaeontologia Africana*, **39**, 53–62. [dated 2003].
- DURAND, J. F. 1991. A revised description of the skull of *Moschorhinus* (Therapsida, Therocephalia). *Annals of the South African Museum*, **99**, 381–413.
- ESTES, R. 1961. Cranial anatomy of the cynodont reptile *Thrinaxodon liorhinus*. *Bulletin of the Museum of Comparative Zoology*, **125**, 165–180.
- FLYNN, J. J., PARRISH, J. M., RAKOTOSAMIMANANA, B., RANIVO HARIMANANA, L., SIMPSON, W. F. and WYSS, A. R. 2000. New traversodontids (Synapsida: Eucynodontia) from the Triassic of Madagascar. *Journal of Vertebrate Paleontology*, **20**, 422–427.
- FOURIE, S. 1963. Tooth replacement in the gomphodont cynodont *Diademodon*. *South African Journal of Science*, **59**, 211–213.

- 1974. The cranial morphology of *Thrinaxodon liorhinus* Seeley. *Annals of the South African Museum*, **65**, 337–400.
- GODEFROIT, P. and BATTAIL, B. 1997. Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern France). *Geodiversitas*, **19**, 567–631.
- GOLOBOFF, P. A. 1993. Estimating character weights during tree search. *Cladistics*, **9**, 83–91.
- 1997. Self-weighted optimization: tree searches and character state reconstructions under implied transformation costs. *Cladistics*, **13**, 225–245.
- FARRIS, J. and NIXON, K. 2003. TNT (Tree analysis using new technology): <http://www.zmuck.dk/public/phylogeny>.
- GOLUBEV, V. K. 2000. The faunal assemblages of Permian terrestrial vertebrates from eastern Europe. *Paleontological Journal*, **34** (Supplement 2), S211–S224.
- GOW, C. E. 1980. The dentitions of the Tritheledontidae (Therapsida: Cynodontia). *Proceedings of the Royal Society of London B*, **208**, 461–481.
- 1985. Dentitions of juvenile *Thrinaxodon* (Reptilia: Cynodontia) and the origin of mammalian diphyodonty. *Annals of the Geological Survey of South Africa*, **19**, 1–17.
- and HANCOX, P. J. 1993. First complete skull of the Late Triassic *Scalenodontoides* (Reptilia, Cynodontia) from southern Africa. 161–168. In LUCAS, S. G. and MORALES, M. (eds). *The nonmarine Triassic*. New Mexico Museum of Natural History and Science, Albuquerque, Bulletin, **3**, iv + 544 pp.
- GRADSTEIN, F. M. and OGG, J. G. 2004. Geologic Time Scale 2004 – why, how, and where next! *Lethaia*, **37**, 175–181.
- GRINE, F. E. 1977. Postcanine tooth function and jaw movement in the gomphodont cynodont *Diademodon* (Reptilia; Therapsida). *Palaeontologia Africana*, **20**, 123–135.
- GROENEWALD, G. H. and KITCHING, J. W. 1995. Biostratigraphy of the *Lystrosaurus* Assemblage Zone. 35–39. In RUBIDGE, B. S. (ed.). *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy, Biostratigraphic Series, **1**, 46 pp.
- HAMMER, W. R. 1995. New therapsids from the Upper Fremouw Formation (Triassic) of Antarctica. *Journal of Vertebrate Paleontology*, **15**, 105–112.
- HANCOX, P. J. 2000. The continental Triassic of South Africa. *Zentralblatt für Geologie und Paläontologie, Teil I, Heft 11–12*, **1998**, 1285–1324.
- HAUGHTON, S. H. 1918. Investigations in South African fossil reptiles and amphibians (Part 11). Some new carnivorous Therapsida, with notes upon the brain-case in certain species. *Annals of the South African Museum*, **12**, 175–215.
- 1924a. On Cynodontia from the middle Beaufort beds of Harrismith, Orange Free State. *Annals of the Transvaal Museum*, **11**, 74–92.
- 1924b. The fauna and stratigraphy of the Stormberg Series. *Annals of the South African Museum*, **12**, 323–497.
- HEERDEN, J. VAN 1972. Intraspecific variations and growth changes in the cynodont reptile *Thrinaxodon liorhinus*. *Researches of the National Museum*, **2**, 307–347.
- 1976. The cranial anatomy of *Nanictosaurus rubidgei* Broom and the classification of the cynodontia (Reptilia: Therapsida). *Navorsing van die Nasionale Museum*, **3**, 141–164.
- and RUBIDGE, B. 1990. The affinities of the early cynodont reptile *Nanictosaurus*. *Palaeontologia Africana*, **27**, 41–44.
- HEEVER, J. A. VAN DEN 1987. The comparative and functional cranial morphology of the early Therococephalia (Amniota: Therapsida). Unpublished PhD thesis, University of Stellenbosch, 567 pp.
- 1994. The cranial anatomy of the early Therococephalia (Amniota: Therapsida). *University of Stellenbosch, Annals*, **1**, 1–59.
- HOEPEN, E. C. N. VAN 1916. Preliminary notice of new reptiles of the Karoo Formation. *Annals of the Transvaal Museum*, **5** (Supplement 2), 1–2.
- 1917. Note on *Myriodon* and *Platycranium*. *Annals of the Transvaal Museum*, **5**, 217.
- HOPSON, J. A. 1971. Postcanine replacement in the gomphodont cynodont *Diademodon*. *Zoological Journal of the Linnean Society*, **50**, 1–21.
- 1984. Late Triassic traversodont cynodonts from Nova Scotia and southern Africa. *Palaeontologia Africana*, **25**, 181–201.
- 1991. Systematics of the nonmammalian Synapsida and implications for patterns of evolution in synapsids. 635–693. In SCHULTZE, H.-D. and TRUEB, L. (eds). *Origin of the higher groups of tetrapods: controversy and consensus*. Comstock Publishing Associates, Cornell University Press, Ithaca, NY, 724 pp.
- 1994. Synapsid evolution and the radiation of non-eutherian mammals. 190–219. In SPENCER, R. S. (ed.). *Major features of vertebrate evolution*. University of Tennessee Publications, Knoxville, TN, 270 pp.
- and BARGHUSEN, H. R. 1986. An analysis of therapsid relationships. 83–106. In HOTTON, N. III, MACLEAN, P. D., ROTH, J. J. and ROTH, E. C. (eds). *The ecology and biology of mammal-like reptiles*. Smithsonian Institution Press, Washington, DC, 326 pp.
- and KITCHING, J. W. 1972. A revised classification of cynodonts (Reptilia, Therapsida). *Palaeontologia Africana*, **14**, 71–85.
- — 2001. A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. *Bulletin of the Museum of Comparative Zoology*, **156**, 5–35.
- HUENE, F. R. VON 1950. Die Theriodontier der ostafrikanischen Ruhuhu-Gebietes in der Tübinger Sammlung. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **92**, 47–136.
- KEMP, T. S. 1972a. Whaitsiid therococephalia and the origin of cynodonts. *Philosophical Transactions of the Royal Society of London, Series B*, **264**, 1–54.
- 1972b. The jaw articulation and musculature of the whaitsiid Therococephalia. 213–230. In JOYSEY, K. A. and KEMP, T. S. (eds). *Studies in vertebrate evolution*. Oliver and Boyd, Edinburgh, 284 pp.
- 1979. The primitive cynodont *Procynosuchus*: functional anatomy of the skull and relationships. *Philosophical Transactions of the Royal Society of London, Series B*, **285**, 73–122.
- 1982. *Mammal-like reptiles and the origin of mammals*. Academic Press, London, 363 pp.
- 1983. The relationships of mammals. *Zoological Journal of the Linnean Society*, **77**, 353–384.

- 1988. Interrelationships of the Synapsida. 1–22. In BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods. Volume 2. Mammals*. Systematics Association, Special, Vol. 35B. Clarendon Press, Oxford, 329 pp.
- 2005. *The origin and evolution of mammals*. Oxford University Press, Oxford, 331 pp.
- KERMACK, D. M. 1982. A new tritylodontid from the Kayenta Formation of Arizona. *Zoological Journal of the Linnean Society*, 76, 1–17.
- KERMACK, K. A., MUSSET, F. and RIGNEY, H. W. 1973. The lower jaw of *Morganucodon*. *Zoological Journal of the Linnean Society*, 53, 87–175.
- — 1981. The skull of *Morganucodon*. *Zoological Journal of the Linnean Society*, 71, 1–158.
- KEYSER, A. W. 1973. A new vertebrate fauna from South West Africa. *Palaeontologia Africana*, 16, 1–15.
- KIELAN-JAWOROWSKA, Z., CIFELLI, R. L. and LUO, Z.-X. 2004. *Mammals from the age of dinosaurs: origin, evolution and structure*. Columbia University Press, New York, NY, 630 pp.
- KITCHING, J. W. 1977. The distribution of the Karoo vertebrate fauna. *Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Memoir*, 1, 1–131.
- 1995. Biostratigraphy of the *Dicynodon* Assemblage Zone. 29–34. In RUBIDGE, B. S. (ed.). *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy, Biostratigraphic Series, 1, 46 pp.
- KONJUKOVA, E. D. 1946. New data on *Permocynodon sushkini* Wood, the cynodont from the north Dwina fauna. *Comptes Rendus de l'Academie des Sciences de l'URSS*, 54, 527–530.
- KÜHNE, W. G. 1956. *The Liassic therapsid Oligokyphus*. Trustees of the British Museum (Natural History), London, 149 pp.
- LANGER, M. C. 2005. Studies on continental Late Triassic tetrapod biochronology. I. The type locality of *Saturnalia tupiniquim* and the faunal succession in south Brazil. *Journal of South American Earth Sciences*, 19, 205–218.
- LEWIS, G. E. 1986. *Nearctylodon broomi*, the first Nearctic tritylodont. 295–304. In HOTTON, N. III, MACLEAN, P. D., ROTH, J. J. and ROTH, E. C. (eds). *The ecology and biology of mammal-like reptiles*. Smithsonian Institution Press, Washington, DC, 326 pp.
- LILLEGRAVEN, J. A. and KRUSAT, G. 1991. Cranio-mandibular anatomy of *Haldanodon exspectatus* (Docodonta; Mammalia) from the Late Jurassic of Portugal and its implications to the evolution of mammalian characters. *Contributions to Geology, University of Wyoming*, 28, 39–138.
- LIPSCOMB, D. 1992. Parsimony, homology and the analysis of multistate characters. *Cladistics*, 8, 45–65.
- LUCAS, S. G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 143, 347–384.
- 2002. Tetrapods and the subdivision of Permian time. 479–491. In HILLS, L. V., HENDERSON, C. M. and BAMBER, E. W. (eds). *Carboniferous and Permian of the world*. Canadian Society of Petroleum Geologists, Memoir, 19, 947 pp.
- and HANCOX, P. J. 2001. Tetrapod-based correlation of the nonmarine Upper Triassic of southern Africa. *Albertiana*, 25, 5–9.
- and LUO, Z. 1993. *Adelobasileus* from the Upper Triassic of West Texas: the oldest mammal. *Journal of Vertebrate Paleontology*, 13, 309–334.
- LUO, Z. 1994. Sister-group relationships of mammals and transformations of diagnostic mammalian characters. 98–128. In FRASER, N. C. and SUES, H.-D. (eds). *In the shadow of the dinosaurs: early Mesozoic tetrapods*. Cambridge University Press, Cambridge, 435 pp.
- and CROMPTON, A. W. 1994. Transformation of the quadrate (incus) through the transition from non-mammalian cynodonts to mammals. *Journal of Vertebrate Paleontology*, 14, 341–374.
- and SUN, A. 1993. *Oligokyphus* (Cynodontia: Tritylodontidae) from the Lower Lufeng Formation (Lower Jurassic) of Yunnan, China. *Journal of Vertebrate Paleontology*, 13, 477–482.
- MAISCH, M. W., MATZKE, A. T. and SUN, G. 2004. A new tritylodontid from the Upper Jurassic Shishugou Formation of the Junggar Basin (Xinjiang, NW China). *Journal of Vertebrate Paleontology*, 24, 649–656.
- MARTINELLI, A. G., BONAPARTE, J. F., SCHULTZ, C. L. and RUBERT, R. 2005. A new tritheledontid (Therapsida, Eucynodontia) from the Late Triassic of Rio Grande do Sul (Brazil) and its phylogenetic relationships among carnivorous non-mammalian eucynodonts. *Ameghiniana*, 42, 191–208.
- MARTINEZ, R. N. and FORSTER, C. A. 1996. The skull of *Probesodon sanjuanensis*, sp. nov., from the Late Triassic Ischigualasto Formation of Argentina. *Journal of Vertebrate Paleontology*, 16, 285–291.
- MAY, C. L. and FORSTER, C. A. 1996. A new carnivorous cynodont from the Ischigualasto Formation (Late Triassic, Argentina), with comments on eucynodont phylogeny. *Journal of Vertebrate Paleontology*, 16, 271–284.
- MENDREZ, C. H. 1974. Etude du crane d'un jeune specimen de *Moschorhinus kitchingi* Broom, 1920 (?*Tigrisuchus simus* Owen, 1876), Therocephalia Pristerosauria Moschorhinidae d'Afrique australe. *Annals of the South African Museum*, 64, 71–115.
- 1975. Principales variations du palais chez les thérocéphales Sud-Africains (Pristerosauria et Scaloposauria) au cours du Permien Supérieur et du Trias Inférieur. *Problèmes Actuels de Paléontologie-Évolution des Vertébrés, Colloque International, CNRS*, 218, 379–408.
- MODESTO, S. P. and RYBCZYNSKI, N. 2000. The amniote faunas of the Russian Permian: implications for Late Permian terrestrial vertebrate biogeography. 17–34. In BENTON, M. J., KUROCHKIN, E. N., SHISHKIN, M. A. and UNWIN, D. M. (eds). *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, New York, 696 pp.
- MOREL, E. M., ARTABE, A. E., ZAVATTIERI, A. M. and BONAPARTE, J. F. 2001. Cronología del Sistema Triásico. 227–253. In ARTABE, A. E., MOREL, E. M. and ZAMUNER, A. B. (eds). *El Sistema Triásico en la Argentina*.

- Fundación Museo de La Plata 'Francisco Pascasio Moreno', La Plata, 358 pp.
- NEVELING, J. 2002. Biostratigraphic and sedimentological investigation of the contact between the *Lystrosaurus* and *Cynognathus* assemblage zones (Beaufort Group: Karoo Super-group). Unpublished PhD thesis, University of the Witwatersrand, Johannesburg, 232 pp.
- 2004. *Stratigraphic and sedimentological investigation of the contact between the Lystrosaurus and Cynognathus Assemblage Zones (Beaufort Group: Karoo Supergroup)*. Council for Geosciences, South Africa, Bulletin, **137**, 165 pp.
- OLSON, E. C. 1937. The cranial morphology of a new gorgonopsian. *Journal of Geology*, **45**, 511–524.
- 1944. Origin of mammals based upon cranial morphology of the therapsid suborders. *Geological Society of America, Special Paper*, **55**, 1–136.
- OWEN, R. 1861. *Palaeontology, or a systematic summary of extinct animals and their geological relations*. Second edition. Adam and Charles Black, Edinburgh, 463 pp.
- 1876. *Descriptive and illustrated catalogue of the fossil reptilia of South Africa in the collection of the British Museum*. London, 88 pp.
- PARRINGTON, F. R. 1934. On the cynodont genus *Galesaurus*, with a note on the functional significance of the changes in the evolution of the theriodont skull. *Annals and Magazine of Natural History*, **10**, 38–67.
- 1936. On the tooth-replacement in theriodont reptiles. *Philosophical Transactions of the Royal Society of London, Series B*, **226**, 121–142.
- 1946. On the cranial anatomy of cynodonts. *Proceedings of the Zoological Society of London*, **116**, 81–197.
- 1947. On a collection of Rhaetic mammalian teeth. *Proceedings of the Zoological Society of London*, **116**, 707–728.
- 1971. On the Upper Triassic mammals. *Philosophical Transactions of the Royal Society of London, Series B*, **261**, 231–272.
- PATTERSON, B. and OLSON, E. C. 1961. A triconodontid mammal from the Triassic of Yunnan. *International Colloquium on the evolution of mammals*. Koninklijke Vlaamse Academie voor Wetenschappen, Letteren en Schone Kunsten van België, Brussels, Part 1, pp. 129–191.
- RIGNEY, H. W. 1938. The morphology of the skull of a young *Galesaurus planiceps* and related forms. *Journal of Morphology*, **63**, 491–529.
- ROGERS, R. R., ARCUCCI, A. B., ABDALA, F., SERENO, P. C., FORSTER, C. A. and MAY, C. L. 2001. Paleoenvironment and taphonomy of the Chañares Formation tetrapod assemblage (Middle Triassic), north-western Argentina: spectacular preservation in volcanogenic concretions. *Palaeos*, **16**, 461–481.
- SWISHER, C. C. III, SERENO, P. C., MONETTA, A. M., FORSTER, C. A. and MARTÍNEZ, R. N. 1993. The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and $^{40}\text{Ar}/^{39}\text{Ar}$ dating of dinosaur origins. *Science*, **260**, 794–797.
- ROMER, A. S. 1945. *Vertebrate paleontology*. Second edition. University of Chicago Press, Chicago, IL, 687 pp.
- 1956. *Osteology of the Reptilia*. University of Chicago Press, Chicago, IL, 772 pp.
- 1967. The Chañares (Argentina) Triassic reptile fauna. III. Two new gomphodonts, *Massetognathus pascuali* and *Massetognathus terugii*. *Breviora*, **264**, 1–25.
- 1969a. The Brazilian cynodont reptiles *Belesodon* and *Chiniquodon*. *Breviora*, **332**, 1–16.
- 1969b. The Chañares (Argentina) Triassic reptile fauna. V. A new chiniquodontid cynodont, *Probelesodon lewisi*. Cynodont ancestry. *Breviora*, **333**, 1–24.
- 1970. The Chañares (Argentina) Triassic reptile fauna. VI. A chiniquodontid cynodont with an incipient squamosal-dentary jaw articulation. *Breviora*, **344**, 1–18.
- 1972. The Chañares (Argentina) Triassic reptile fauna. XVII. The Chañares gomphodonts. *Breviora*, **396**, 1–9.
- 1973. The Chañares (Argentina) triassic reptile fauna. XVIII. *Probelesodon minor*, a new species of carnivorous cynodont. Family Probainognathidae. *Breviora*, **401**, 1–4.
- ROUGIER, G. W., WIBLE, J. W. and HOPSON, J. A. 1992. Reconstruction of the cranial vessels in the Early Cretaceous mammal *Vincelestes neuquenianus*: implications for the evolution of the mammalian cranial vascular system. *Journal of Vertebrate Paleontology*, **12**, 188–216.
- ROWE, T. 1986. Osteological diagnosis of Mammalia, L. 1758, and its relationships to extinct Synapsida. Unpublished PhD thesis, University of California, 567 pp.
- 1988. Definition, diagnosis and origin of mammalia. *Journal of Vertebrate Paleontology*, **8**, 241–264.
- 1993. Phylogenetic systematics and the early history of mammals. 129–145. In SZALAY, F. S., NOVACEK, M. J. and MCKENNA, M. C. (eds). *Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials*. Springer Verlag, New York, NY, 249 pp.
- RUBERT, R. and SCHULTZ, C. L. 2004. Um novo horizonte de correlação para o Triássico Superior do Rio Grande do Sul. *Pesquisas em Geociências*, **31**, 71–88.
- RUBIDGE, B. S. 1995. Biostratigraphy of the *Eodicynodon* Assemblage Zone. 3–7. In RUBIDGE, B. S. (ed.). *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy, Biostratigraphic Series, **1**, 46 pp.
- 2005. Re-uniting lost continents – fossil reptiles from the ancient Karoo and their wanderlust. *South African Journal of Geology*, **108**, 135–172.
- and SIDOR, C. A. 2001. Evolutionary patterns among Permo-Triassic therapsids. *Annual Review of Ecology and Systematics*, **32**, 449–480.
- JOHNSON, M. R., KITCHING, J. W., SMITH, R. M. H., KEYSER, A. W. and GROENEWALD, G. H. 1995. An introduction to the biozonation of the Beaufort Group. 1–2. In RUBIDGE, B. S. (ed.). *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy, Biostratigraphic Series, **1**, 46 pp.
- SEELEY, H. G. 1894. Researches on the structure, organization, and classification of the fossil Reptilia. Part IX. Section 3. On *Diademodon*. *Philosophical Transactions of the Royal Society of London*, **185**, 1029–1041.
- 1895a. Researches on the structure, organization, and classification of the fossil Reptilia. Part IX. Section 4. On the Gomphodontia. *Philosophical Transactions of the Royal Society of London*, **186**, 1–57.

- 1895*b*. Researches on the structure, organization, and classification of the fossil Reptilia. Part IX. Section 5. On the skeleton in new cynodontia from the Karroo rocks. *Philosophical Transactions of the Royal Society of London*, **186**, 59–148.
- SHAPIRO, M. D. and JENKINS, F. A. 2001. A cynodont from the Upper Triassic of East Greenland: tooth replacement and double-rootedness. *Bulletin of the Museum of Comparative Zoology*, **156**, 49–58.
- SHUBIN, N. H., CROMPTON, A. W., SUES, H.-D. and OLSEN, P. E. 1991. New fossil evidence on the sister-group of mammals and early Mesozoic faunal distribution. *Science*, **251**, 1063–1065.
- SIDOR, C. A. and HANCOX, P. J. 2006. *Elliotherium kersteni*, a new tritheledontid from the Lower Elliot Formation (Upper Triassic) of South Africa. *Journal of Paleontology*, **80**, 333–342.
- and HOPSON, J. A. 1998. Ghost lineages and ‘mammalness’: assessing the temporal pattern of character acquisition in the Synapsida. *Paleobiology*, **24**, 254–273.
- and SMITH, R. M. H. 2004. A new galesaurid (Therapsida: Cynodontia) from the Lower Triassic of South Africa. *Palaeontology*, **47**, 535–556.
- SIGOGNEAU, D. 1963. Note sur une nouvelle espèce de Scaloposauridae. *Palaeontologia Africana*, **8**, 13–37.
- 1970. *Révision systématique des gorgonopsiens Sud-Africains*. Cahiers de Paléontologie, **1970**, xii + 416 pp., 93 pls.
- SIGOGNEAU-RUSSELL, D. 1989. Theriodontia I. 1–127. In WELLNHOFER, P. (ed.). *Handbuch der Paleoherpetologie, Teil 17B/I*. Gustav Fischer Verlag, Stuttgart.
- SIMPSON, G. G. 1928. *A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*. British Museum (Natural History), London, 215 pp.
- SMITH, R. M. H. and BOTHA, J. 2005. The recovery of terrestrial diversity in the South African Karoo Basin after the end-Permian extinction. *Comptes Rendus Palevol*, **4**, 555–568.
- and KEYSER, A. W. 1995*a*. Biostratigraphy of the *Tapinocephalus* Assemblage Zone. 8–12. In RUBIDGE, B. S. (ed.). *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy, Biostratigraphic Series, **1**, 46 pp.
- — 1995*b*. Biostratigraphy of the *Tropidostoma* Assemblage Zone. 18–22. In RUBIDGE, B. S. (ed.). *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy, Biostratigraphic Series, **1**, 46 pp.
- — 1995*c*. Biostratigraphy of the *Cistecephalus* Assemblage Zone. 23–28. In RUBIDGE, B. S. (ed.). *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. South African Committee for Stratigraphy, Biostratigraphic Series, **1**, 46 pp.
- and SWART, R. 2002. Changing fluvial environments and vertebrate taphonomy in response to climatic drying in a Mid-Triassic rift valley fill: the Omingonde Formation (Karoo Supergroup) of central Namibia. *Palaaios*, **17**, 249–267.
- SUES, H.-D. 1985*a*. The relationships of the Tritylodontidae (Synapsida). *Zoological Journal of the Linnean Society*, **85**, 205–217.
- 1985*b*. First record of the tritylodontid *Oligokyphus* (Synapsida) from the Lower Jurassic of western North America. *Journal of Vertebrate Paleontology*, **5**, 328–335.
- 1986. The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America. *Bulletin of the Museum of Comparative Zoology*, **151**, 217–268.
- 2001. On *Microconodon*, a Late Triassic cynodont from the Newark Supergroup of eastern North America. *Bulletin of the Museum of Comparative Zoology*, **156**, 37–48.
- and BOY, J. A. 1988. A procynosuchid cynodont from central Europe. *Nature*, **331**, 523–524.
- HOPSON, J. A. and SHUBIN, N. H. 1992. Affinities of ?*Scalenodontoides plemmyridon* Hopson, 1984 (Synapsida: Cynodontia) from the Upper Triassic of Nova Scotia. *Journal of Vertebrate Paleontology*, **12**, 168–171.
- SUN, A. 1988. Additional study on *Sinognathus gracilis* (Cynodontia; Reptilia). *Vertebrata Palasiatica*, **26**, 173–180.
- SUSHKIN, P. P. 1929. *Permocynodon*, a cynodont reptile from the Upper Permian of Russia. *Proceedings of the X International Congress of Zoology, Budapest*, pp. 804–808.
- TATARINOV, L. P. 1968. Morphology and systematics of the Northern Dvina cynodonts (Reptilia, Therapsida; Upper Permian). *Postilla*, **125**, 1–51.
- TEIXEIRA, A. M. S. 1982. Um novo cinodonte carnívoro (*Probesodon kitchingi*, sp. nov.) do Triássico do Rio Grande do Sul, Brasil. *Comunicações do Museu de Ciências PUCRS*, **24**, 1–31.
- WATSON, D. M. S. 1911. The skull of *Diademodon*, with notes on those of some other cynodonts. *Annals and Magazine of Natural History*, **8**, 293–330.
- 1913*a*. Further notes on the skull, brain, and organs of special sense of *Diademodon*. *Annals and Magazine of Natural History*, **8**, 12, 217–223.
- 1913*b*. On a new cynodont from the Stormberg. *Geological Magazine*, **5**, **10**, 145–148.
- 1914. Notes on some carnivorous therapsids. *Proceedings of the Zoological Society of London*, **1914**, 1021–1038.
- 1920. On the Cynodontia. *Annals and Magazine of Natural History*, **9**, **6**, 506–524.
- and ROMER, A. S. 1956. A classification of therapsid reptiles. *Bulletin of the Museum of Comparative Zoology*, **114**, 37–89.
- WIBLE, J. R. 1991. Origin of Mammalia: the craniodental evidence reexamined. *Journal of Vertebrate Paleontology*, **11**, 1–28.
- and HOPSON, J. A. 1993. Basicranial evidence for early mammal phylogeny. 45–62. In SZALAY, F. S., NOVACEK, M. J. and MCKENNA, M. C. (eds). *Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials*. Springer Verlag, New York, NY, 249 pp.
- WOPFNER, H. 2002. Tectonic and climatic events controlling deposition in Tanzanian Karoo basins. *Journal of African Earth Sciences*, **34**, 167–177.
- YOUNG, C.-C. 1947. Mammal-like reptiles from Lufeng, Yunnan, China. *Proceedings of the Zoological Society of London*, **117**, 537–597.
- 1959. Note on the first cynodont from the *Sinokannemeyeria*-faunas in Shansi, China. *Vertebrata Palasiatica*, **3**, 124–131.

APPENDIX

List of material examined, literature consulted, geological and biostratigraphical location and age for taxa included in the phylogenetic analysis

Asterisks indicate specimens stolen from the PULR

Bauria: BP/1/1180, 1685 (holotype of *Bauria robusta*), 3770, 4655; Watson (1914), Broom (1937a), Boonstra (1938), Crompton (1962), Brink (1963a, 1965a), Mendrez (1975). Burgersdorp Formation, Karoo Basin, South Africa, Subzone B of the *Cynognathus* Assemblage Zone [AZ] (Hancox 2000); early Anisian. Isolated teeth and a fragment of the posterior skull of Bauriidae are also known from the Subzone A of the *Cynognathus* AZ (pers. obs.), but it is not possible to assign this material confidently to *Bauria*.

Brasilitherium: Bonaparte *et al.* (2003, 2005). Caturrita Formation, Rio Grande do Sul, Brazil (Bonaparte *et al.* 2003; Martinelli *et al.* 2005); early Norian (Rubert and Schultz 2004; Martinelli *et al.* 2005), pre-Jurassic (Langer 2005).

Brasilodon: Bonaparte *et al.* (2003, 2005). Caturrita Formation, Rio Grande do Sul, Brazil (Bonaparte *et al.* 2003; Martinelli *et al.* 2005); early Norian (Rubert and Schultz 2004; Martinelli *et al.* 2005), pre-Jurassic (Langer 2005).

Chiniquodon: BMNH R8429; GPIT 40 (holotype of *Chiniquodon theotonicus*), 1050 (holotype of *Belesodon magnificus*); MCP PV1600 (holotype of *Probelesodon kitchingi*); PULR 12* (holotype of *Probelesodon minor*), 18* (holotype of *Probelesodon lewisi*), 100–102; PV 66T, 66Tg, 122T, 274, 275T; PVL 4167, 4444, 4448, 4674, 4675; MCZ 1533, 3035, 3614, 3615, 3776, 3777, 3779, 3781, 4002, 4020, 4100, 4296, 8823; PVSJ 411 (holotype of *Probelesodon sanjuanensis*). Bonaparte (1966), Romer (1969a, b, 1973), Crompton (1972b), Teixeira (1982), Abdala (1996a), Martinez and Forster (1996), Abdala and Giannini (2002). *Probelesodon* is considered a junior synonym of *Chiniquodon* following Abdala and Giannini (2002). Chañares and Ischigualasto formations, Ischigualasto-Villa Union Basin, Argentina; Santa Maria Formation, Paraná Basin, Brazil, *Dinodontosaurus* Biozone; early Ladinian–early Carnian (Abdala *et al.* 2001; Morel *et al.* 2001; Rogers *et al.* 2001; Langer 2005; but see Lucas 1998).

Cynognathus: AM 460 (holotype of *Cynognathus platyceps*), 2190, 3587 (described as ?*Cynognathus leptorhinus* by Seeley 1895b), 4202, 5800; AMNH R5538, R5641; BMNH R2571 (holotype of *Cynognathus crateronotus*), R2572, R3580; BP/1/1181, 2095, 3755, 4664; BSP 1934VIII₁, 1934VIII₂, 1934VIII₃, 1934VIII₆ (holotype of *Cynidiognathus merenskyi*); PVL 3859 (holotype of *Cynognathus minor*); NMQ R1227, R1444, SAM-PK-1056 (holotype of *Cynidiognathus broomi*), 6224 (holotype of *Cynidiognathus longiceps*), 6235, 11264, 11484. Seeley (1895b), Broili and Schröder (1934, 1935a), Brink (1955b), Bonaparte (1969), Abdala (1996b). Burgersdorp Formation, Karoo Basin, South Africa, Subzones A–C of the *Cynognathus* AZ (Hancox 2000); Omingonde Formation, Namibia (Smith and Swart 2002); Puesto Viejo Formation, Argentina (Bonaparte 1969); Fremouw Formation, Antarctica (Hammer 1995); late Olenekian–late Anisian (Hancox 2000).

Cynosaurus: AM 4947; BMHN R1718 (holotype of *Cynosuchus suppostus*); SAM-PK-4333 (holotype of *Cynosuchus whaitsi*); BP/1/3926, 4469. Owen (1876), Houghton (1918), Brink (1965b), van Heerden (1976); most of the Balfour Formation, Karoo Basin, South Africa, *Dicynodon* AZ (Kitching 1995); Brink (1965b) reported that the provenance of BP/1/3926 was from levels of the *Lystrosaurus* AZ (see also Sidor and Smith 2004), but Kitching (1977, p. 86) stated that this specimen unquestionably came from levels of the *Daptocephalus* Zone (= *Dicynodon* AZ); early to end of the Lopingian (Lucas 2002); late Wuchiapingian–Changhsingian (Cisneros *et al.* 2005); Changhsingian (Rubidge 2005).

Cynosaurus: BP/1/137, 735, 2109 (holotype of *Cyniscopoides broomi*), 2598, 2867; RC 51 (holotype of *Alopecorhynchus rubidgei*), 74 (holotype of *Cyniscops rubidgei*), 75 (holotype of *Cyniscops longiceps*); Olson (1937, 1944), Sigogneau (1970), Sigogneau-Russell (1989). Teekloof Formation and most of the Balfour Formation, Karoo Basin, South Africa, *Tropidostoma*, *Cistecephalus* and *Dicynodon* AZs (Kitching 1995; Smith and Keyser 1995b, c); late Guadalupian–Lopingian (Lucas 2002); middle Wuchiapingian–Changhsingian (Cisneros *et al.* 2005); Wuchiapingian–Changhsingian (Rubidge 2005).

Diademodon: AM 438, 458 (holotype of *Gomphognathus kannemeyeri*), 3753 (holotype of *Octagomphus woodi*); AMNH R5518; BMNH R2574, R2575, R2576–7 (holotype of *Gomphognathus polyphagus*), R2578, R3303 (holotype of *Diademodon mastacus*), R3304 (holotype of *Diademodon browni*), R3305 (holotype of *Microgomphodon oligocynus*), R3308, R3581 (holotype of *Microgomphodon eumerus*); R3587, R3588, R3724, R3765 (holotype of *Diademodon entomophonus*), R4092 (portion of the skull of the holotype of *Diademodon entomophoneus*), R9216; BP/1/1195, 2522, 3511, 3639 (holotype of *Diademodon rhodesiensis*), 3754, 3756–3758, 3769, 3771–3773, 3776 (holotype of *Cragievarus kitchingi*), 4647, 4669, 4677; BSP 1934VIII 14, 1934VIII 15, 1934VIII 16, 1934VIII 17 (holotype of *Gomphognathus grossarthi*), 1934VIII 18 (holotype of *Gomphognathus broomi*), 1934VIII 19 (holotype of *Gomphognathus haughtoni*), 1934VIII 20, 1936II 8 (holotype of *Sysphinctostoma smithi*) MB R1004; SAM-PK-3426, 4002, 5877, K-177, 5222, 5223, 5266, 5877; UMCZ T.430, T.436 (holotype of *Diademodon laticeps*), T.438, T.441, T.445, T.454, T.828, T.971. Seeley (1894, 1895a), Watson (1911, 1913a), Broili and Schröder (1935b), Brink (1955a), Fourie (1963), Hopson (1971), Crompton (1972b), Grine (1977). Burgersdorp Formation, Karoo Basin, South Africa, Subzones B–C of the *Cynognathus* AZ (Neveling 2004); Omingonde Formation, Namibia (Keyser 1973; Smith and Swart 2002); early–late Anisian (Hancox 2000; Neveling 2004).

Dvinia: UMZC T.299 (cast of the holotype of *Permocynodon sushkini*), T.1016 (cast of the holotype of *Dvinia prima*). Sushkin (1929), Konjukova (1946), Tatarinov (1968). Sokolki Subassemblage (lower Vyatskian Gorizont) (Golubev 2000; Modesto and Rychczynski 2000); late Wuchiapingian (Cisneros *et al.* 2005), Changhsingian (Rubidge 2005).

Ecteninion: PVSJ 422 (holotype of *Ecteninion lunensis*), 481, 693. Martinez *et al.* (1996). Ischigualasto Formation, Ischigualasto-Villa Union Basin, Argentina; early Carnian (Rogers *et al.* 1993; Abdala *et al.* 2001; Morel *et al.* 2001; Langer 2005; but see Lucas 1998).

Exaeretodon: MACN 18114, 18125; MCZ 111-64A, 33458M, 377-58M, 4074, 4468-4470, 4480, 4482, 4483, 4486, 4493, 4500, 4502, 4510, 4781; MLP 43-VII-14-2, 43-VII-14-3; MCP 1522 PV (holotype of *Exaeretodon riograndensis*), 2361 PV, 3843 PV; PVL 2056, 2079, 2082, 2083, 2094, 2473, 2554, 2565, 2750; PVSJ 157. Bonaparte (1962), Chatterjee (1982), Hopson (1984), Abdala *et al.* (2002). Ischigualasto Formation, Ischigualasto-Villa Union Basin, Argentina; Santa Maria Formation, Paraná Basin, Brazil, *Dinodontosaurus* (*Exaeretodon major*) and Rhynchosaur biozones (*Exaeretodon riograndensis*); Maleri Formation, India; the presence of *Exaeretodon* in the Ladinian of Brazil should be considered with caution, because the taxonomic identity of *E. major* is tentative (see Abdala *et al.* 2002); ?Ladinian-early Carnian (Rogers *et al.* 1993; Abdala *et al.* 2001; Morel *et al.* 2001; Langer 2005; but see Lucas 1998).

Galesaurus: AMNH R2223, R2227; BMNH R36220 (holotype of *Galesaurus planiceps*); BP/1/478 (holotype of *Notictosaurus trigonocephalus*), 4602, 4637, 5064; NMP 581; NMQ R860, R1451, R3340; RC 845; SAM-PK-K-1119, 9956; TM 24 (holotype of *Glochinodon dentidens*), 83 (holotype of *Glochinodontoides gracilis*); UMCZ T.819, T.823. Watson (1920), Broom (1932b), Parrington (1934), Boonstra (1935), Rigney (1938), Brink (1954b), Abdala (2003); upper portion of the Balfour Formation, and Katberg and Normandien formations, Karoo Basin, South Africa, *Lystrosaurus* AZ (Groenewald and Kitching 1995); Induan-Early Olenekian (Neveling 2004; Rubidge 2005).

Glanosuchus: CGP M796. Broom (1904), van den Heever (1987, 1994); Abrahamskraal Formation, Karoo Basin, South Africa, *Eodicynodon* and *Tapinocephalus* AZs (Rubidge 1995; Smith and Keyser 1995a); Wordian-early Capitanian (Cisneros *et al.* 2005); Wordian (Rubidge 2005).

Hofmeyria: TM 254 (holotype of *Hofmeyria atavus*), BP/1/1399, 4401, 4404. Broom (1935); Teekloof Formation, Karoo Basin, South Africa; *Hofmeyria* was not noted as part of the *Cistecephalus* AZ fauna by Smith and Keyser (1995c). Its inclusion in the *Cistecephalus* AZ is because specimens of this taxon seem always to have been recovered from below what Kitching (1977) called the 'Cistecephalus band', and is therefore probably part of the *Cistecephalus* AZ; middle Wuchiapingian (Cisneros *et al.* 2005); Wuchiapingian (Rubidge 2005).

Ictidosuchops: BP/1/218, 2125, 3155; RC 11 (holotype of *Ictidosuchoides intermedius*), 104, 106, 272. Crompton (1955); Teekloof Formation and most of the Balfour Formation, Karoo Basin, South Africa, *Tropidostoma*, *Cistecephalus* and *Dicynodon* AZs (Kitching 1995; Smith and Keyser 1995b, c); late Guadalupian-Lopingian (Lucas 2002); middle Wuchiapingian-Changhsingian (Cisneros *et al.* 2005); Wuchiapingian-Changhsingian (Rubidge 2005).

Kayentatherium: MCZ 8811, 8812. Kermack (1982), Clark and Hopson (1985), Lewis (1986), Sues (1986). Kayenta Formation, northern Arizona, USA; Sinemurian-Pliensbachian (Kielan-Jaworowska *et al.* 2004).

Lumkuia: BP/1/2669 (holotype of *Lumkuia fuzzi*). Hopson and Kitching (2001). Burgersdorp Formation, Karoo Basin, South Africa, Subzone B of the *Cynognathus* AZ (Hopson and Kitching 2001); early Anisian (Hancox 2000).

Lycosuchus: US D173 (holotype of *Lycosuchus vanderrieti*), CGP M793, CGP C60, BP/1/276, 499, 1100, 1768; Broom (1903); van den Heever (1987, 1994). Abrahamskraal Formation, Karoo Basin, South Africa, *Tapinocephalus* AZ (Smith and Keyser 1995a); Capitanian (Cisneros *et al.* 2005; Rubidge 2005).

Massetognathus: BMNH R8430; MCZ 3691, 3786, 3789, 3801, 3804, 3806, 3807, 4021, 4138, 4208, 4215, 4216, 4258, 4265, 4627; PULR 10 (holotype of *Massetognathus pascuali*), 11 (holotype of *Massetognathus major*), 13 (holotype of *Massetognathus teruggii*), without/number (holotype of *Megagomphodon oligodens*); PVL 3901-3904, 3906, 4613, 4726, 4727-4729. Romer (1967, 1972), Crompton (1972a, b); Abdala and Giannini (2000). Chañares Formation, Ischigualasto-Villa Union Basin, Argentina; Santa Maria Formation, Paraná Basin, Brazil, *Dinodontosaurus* Biozone; Ladinian (Abdala *et al.* 2001; Rogers *et al.* 2001).

Morganucodon: BMNH: many specimens described by Kermack *et al.* (1973, pp. 172-173; 1981, pp. 152-155). The collection of the BMNH also includes specimens formerly located in University College London. UMCZ: many specimens described by Parrington (1971). Kermack *et al.* (1973, 1981), Crompton (1974), Crompton and Luo (1993), Kielan-Jaworowska *et al.* (2004); Hallau, Switzerland; Saint-Nicolas-de-Port and Varangéville, France; Saint Bride's Island, Britain; Lower Lufeng Formation, Yunnan, China; Kayenta Formation, northern Arizona, USA; Rhaetian-Pliensbachian (Kielan-Jaworowska *et al.* 2004).

Moschorhinus: BP/1/, 1713 (holotype of *Moschorhinus natalensis*) 3983, 4227, TM 263 (holotype of *Moschorhinus minor*); RC 32 (holotype of *Moschorhinus esterhuyseni*). Mendrez (1974, 1975), Durand (1991); Balfour and Katberg formations, Karoo Basin, South Africa, *Dicynodon* and *Lystrosaurus* AZs (Groenewald and Kitching 1995; Kitching 1995); late Wuchiapingian-early Olenekian (Neveling 2004; Cisneros *et al.* 2005); Changhsingian-early Olenekian (Rubidge 2005).

Oligokyphus: BMNH: many specimens described by Kühne (1956) and Crompton (1964). Windsor Hill Quarry ('Mendip 14'), England (Kühne 1956); Rhaeto-Liassic bone bed, Baden-Württemberg, Germany (Simpson 1928); Kayenta Formation, northern Arizona, USA (Sues 1985b); Lower Lufeng Formation, Yunnan, China (Luo and Sun 1993); ?latest Norian-earliest Hettangian to Sinemurian-Pliensbachian (Sues 1985b; Kielan-Jaworowska *et al.* 2004).

Pachygenelus: BMNH R4091 (holotype of *Pachygenelus monus*); BP/1/4381, 4741, 4761, 5110, 5623, 5691, SAM-PK-K-1394.

Watson (1913*b*); Gow (1980); Shubin *et al.* (1991). Upper Elliot Formation, Karoo Basin, South Africa; McCoy Brook Formation, Nova Scotia, Canada; Early Jurassic (Liassic) (Shubin *et al.* 1991; Lucas and Hancox 2001; Kielan-Jaworowska *et al.* 2004).

Probainognathus: PULR 16*, 17* (holotype of *Probainognathus jenseni*); PVL 4169, 4445–4447, 4673, 4677, 4678, 4724, 4725; MCZ 4004, 4006, 4019, 4021, 4069, 4274–4280, 4283–4286, 4289, 4293, 4294. Romer (1970); Crompton (1972*b*); Crompton and Hylander (1986); Chañares Formation, Ischigualasto-Villa Union Basin, Argentina; Ladinian (Abdala *et al.* 2001; Rogers *et al.* 2001).

Procynosuchus: BP/1/226 (holotype of *Aelurodraco microps*), 591 (holotype of *Leavachia gracilis*), 1545, 1559, 2600, 3747, 3748, 5832; OUMNH TSK34; RC 5 (holotype of *Procynosuchus delaharpeae*), 12 (holotype of *Procynosuchus rubidgei*), 72 (holotype of *Galeophrys kitchingi*), 92 (holotype of *Leavachia duvenhagei*), 132; SAM-PK-K338, K8511; UMCZ T.810 (holotype of *Parathrinaxodon proops*). Broom (1937*b*, 1938, 1948), Brink and Kitching (1951), Brink (1963*b*), Anderson (1968), Kemp (1979); most of the Balfour Formation, Karoo Basin, South Africa, *Dicynodon* AZ (Kitching 1995); recent finds have shown the presence of *Procynosuchus* at the top of the *Cistecephalus* AZ (Botha *et al.* 2007); Madumabisa Mudstones, Luangwa Valley, Zambia (Kemp 1979); Kawinga Formation (= Usili Formation of Wopfner 2002), Ruhuhu Valley, Tanzania (Parrington 1936; von Huene 1950); lower Zechstein, West Germany (Sues and Boy 1988); early to end Lopingian (Lucas 2002); late Wuchiapingian–Changhsingian (Cisneros *et al.* 2005); Wuchiapingian–Changhsingian (Rubidge 2005).

Progalesaurus: SAM-PK-K-9954 (holotype of *Progalesaurus lootbergensis*). Sidor and Smith (2004); near the top of the Palingkloof Member of the Balfour Formation, Karoo Basin, South Africa, lowermost *Lystrosaurus* AZ (Sidor and Smith 2004); Induan (Neveling 2004; Rubidge 2005).

Prorubidgea: BP/1/813 (holotype of *Lycaenops alticeps*), 1566 (holotype of *Prorubidgea brinki*), 2190 (holotype of *Prorubidgea robusta*); RC 34 (holotype of *Prorubidgea maccabei*). Sigogneau (1970), Sigogneau-Russell (1989); Teekloof Formation and most of the Balfour Formation, Karoo Basin, South Africa, *Cistecephalus* and *Dicynodon* AZs (Kitching 1995; Smith and Keyser 1995*c*); late Guadalupian–Lopingian (Lucas 2002); middle Wuchiapingian–Changhsingian (Cisneros *et al.* 2005); Wuchiapingian–Changhsingian (Rubidge 2005).

Sinoconodon: Patterson and Olson (1961); Crompton and Sun (1985); Crompton and Luo (1993). Lower Lufeng Formation, Yunnan, China; Sinemurian (Kielan-Jaworowska *et al.* 2004).

Theriognathus: BP/1/100 (holotype of *Notosollasia longiceps*), 164, 182 (holotype of *Aneugomphius ictidoceps*), 717, 725, 785, 844, 4008, TM 264 (holotype of *Moschorhynchus latirostris*), 280 (holotype of *Notaelurops paucidens*); Brink (1954*c*, 1956, 1959); Kemp (1972*a, b*), Mendrez (1975); most of the Balfour Formation, Karoo Basin, South Africa, *Dicynodon* AZ (Kitching 1995); early to

end Lopingian (Lucas 2002); late Wuchiapingian–Changhsingian (Cisneros *et al.* 2005); Changhsingian (Rubidge 2005).

Thrinaxodon: AMNH R9563; BMNH R511 (holotype of *Thrinaxodon liorhinus*), R511a, R845, R1715 (holotype of *Nyctosaurus larvatus*), R3731, R5480; BP/1/472 (holotype of *Notictosaurus gracilis*), 1375, 1376, 4280, 5208, 5372; BSP 1934VIII 506; MCZ 8892; RC 107 (holotype of *Notictosaurus luckhoffi*); TM 80, 81, 1486 (holotype of *Micrictodon marionae*); NMQ R810 (?holotype of *Thrinaxodon putterilli*; see van Heerden 1972), R811, R812, R1533; SAM-PK-K-378, 380, 381, 1121, 1388, 1461, 1467, 1468, 1483, 1498, 1499, 3592, 10016, 10017; UMCZ T.811, T.813–T.817. Broom (1911), Watson (1920), Parrington (1936, 1946), Brink (1954*b*), Estes (1961), Crompton (1963), van Heerden (1972), Fourie (1974), Gow (1985); upper portion of the Balfour Formation, and Katberg and Normandien formations, Karoo Basin, South Africa, *Lystrosaurus* AZ (Groenewald and Kitching 1995); Lower Fremouw Formation, Antarctica (Colbert and Kitching 1977); Induan–Early Olenekian (Neveling 2004; Rubidge 2005).

Trirachodon: AM 434, 461 (holotype of *Trirachodon kannemeyeri*), BMNH R3350, R3306, R3307, R3579 (holotype of *Trirachodon berryi*), R3721 (holotype of *Trirachodon browni*), R3722; BP/1/4658, 5050; BSP 1934VIII 21–23; SAM-PK-5873 (holotype of *Trirachodon minor*), K-171, 4801, 7888, NMQ R122, R3251, R3255, R3256, R3268, R3280. Seeley (1895*a*), Broom (1911), Broili and Schröder (1935*c*), Crompton (1972*b*), Neveling (2002), Abdala *et al.* (2006). Burgersdorp Formation, Karoo Basin, South Africa, Subzone B of the *Cynognathus* AZ (Abdala *et al.* 2006); Omingonde Formation, Namibia (Keyser 1973). NMQR 3279 has a maxillary platform lateral to the postcanines indicating the presence of *T. berryi* in Subzone A (see Abdala *et al.* 2006); late Olenekian–early Anisian (Hancox 2000).

List of characters used in the cladistic analyses

The abbreviations after the character states indicate authors who have previously used the characters in data matrices that included non-mammaliaform cynodonts, and the corresponding number of the character: R, Rowe (1988); W, Wible (1991); LL, Lucas and Luo (1993); L, Luo (1994); M, Martinez *et al.* (1996); F, Flynn *et al.* (2000); HK, Hopson and Kitching (2001); A, Abdala and Ribeiro (2003); B, Bonaparte *et al.* (2003); SS, Sidor and Smith (2004); BO, Bonaparte *et al.* (2005); MA, Martinelli *et al.* (2005). Abbreviations in italic type indicate that the character or the character states defined by the author(s) differs from that provided here.

Multistate characters, in which the morphology represented in each state allowed for the recognition of adjacent states [e.g. zygomatic arch dorsoventral height; slender (0), moderately deep (1), very deep (2)], were coded as additives (Lipscomb 1992). A + indicates additive multistate characters. Codification of character 16 reflects differences in the osseous palate condition in *Bauria* and other taxa with partial or complete secondary palates. In this case the plesiomorphic state, absence of a secondary palate, is coded as 2; the extension of both maxillary and palatine processes of the palate, without contacting the processes from the opposite side, is coded as 1, and the complete osseous palate formed by the maxilla and palatine is coded as 0. The condition in *Bauria* in

which the palatines do not form part of the osseous palate is coded as 3. In making the character additive, the transformation from absence to a complete secondary palate, formed by the maxilla and the palatine, will have an intermediate state in which the palatal processes of both bones are extended to the middle, but do not form a complete palate (2 → 1 → 0). In contrast, the osseous palate in *Bauria* in which the palatines do not participate will require one step from the plesiomorphic state (2 → 3).

1. Extranasal process of the premaxilla: small (0), large but not contacting nasal (1), contacting nasal (2). *R2, W36, L82, M14* +
2. Septomaxilla facial process: long (0), short (1). *SS1*
3. Contact between nasal and lacrimal: absent (0), present (1). *HK2, SS2*
4. Prefrontal: present (0), absent (1). *R4, W1, M28, HK3, B22, BO30, MA25*
5. Frontal in orbital margin: included (0), excluded (1).
6. Postorbital bar: complete (0), incomplete (1), absent (2). *R7, W2, LL33, L55, M29, HK5, B40, BO31, MA50* +
7. Parietal/pineal foramen: present (0), absent (1). *R8, W12, LL34, L64, M31, HK7, A24, B24, BO34, MA28*
8. Postfrontal: present (0), absent (1). *HK4, SS3*
9. Posterior extension of parietal: anterior to or reaching the origin of the occipital crests (0), posterior to the origin of the occipital crests (1). *R10, W38, M36*
10. Contact between postorbital and squamosal: present (0), absent (1).
11. Snout in relation to temporal region: longer (0), subequal (1), shorter (2). +
12. Occipital crests: not confluent proximally (0), confluent (1).
13. Incisive foramen: absent (0), not closed (1), posteriorly closed by maxilla (2), completely enclosed by premaxilla (3). *M19, HK1, B21, BO27, MA24*
14. Paracanine fossa in relation to the upper canine: anterior (0), anteromedial (1), medial (2), posteromedial (3). *A6* +
15. Contact between vomer-maxilla in palate: absent (0), present (1), maxilla covers vomer (2).
16. Osseous secondary palate: complete, with contribution of palatine (0), maxillo-palatine extensions do not contact medially (1), absent (2), complete, without contribution of palatine (3). *HK12, HK13; SS11, SS12* +
17. Osseous palate extension: 45 per cent of skull length or less (0), more than 45 per cent of skull length (1).
18. Osseous palate posterior extent in relation to upper tooth row: anterior (0), at same level or posterior (1). *M23, L68, HK14, B26, BO36, MA30*
19. Palatal process of palatine in relation to palate length: short (0), long (1). *M22, HK40, B37, BO53, MA45*
20. Ectopterygoid: contacts maxilla (0), does not contact maxilla (1), absent (2). *HK9, SS15* +
21. Maxilla in margin of subtemporal fenestra: excluded (0), included (1). *R15, W14, L62, M16*
22. Palatal teeth: on pterygoid and palatine (0), on pterygoid only (1), absent (2). *HK16, SS14*
23. Maxillary platform lateral to dentition: absent (0), incipient in posterior portion of the teeth row (1); well developed (2). *M15, HK77, A23, BO15* +
24. Suborbital vacuity in palate: absent (0), present (1).
25. Interpterygoid vacuity in adults: present (0), absent (1). *M27, HK10, B25, BO35, MA29*
26. Boss/crest anterior to the interpterygoid vacuity: reduced or absent (0), well developed (1).
27. Carotid artery foramina in basisphenoid: present (0), absent (1). *R42, W50, LL14, L72, M45, HK26, B31, BO48, MA40*
28. Parasphenoid ala: long and borders fenestra ovalis (0); slightly reduced and excluded from fenestra ovalis (1); absent (2). *R40, W49, L74, M41* +
29. Parasphenoid ala: at same level as basicranium (0); ventrally expanded below basicranium (1). *?HK17, ?BO39, ?MA32*
30. Pterygoid quadrate ramus: present (0), absent (1). *M40, HK30, B34, BO52, SS20, MA43*
31. Quadrate rami of epipterygoid: absent (0), present but do not contact quadrate (1), present and contact quadrate (2). *LL23, M53*
32. Quadrate ramus of pterygoid/eipterygoid: at the same level as basioccipital (0), ventrally expanded below basioccipital (1). *R37, W46*
33. Paroccipital process: does not contact quadrate (0), contacts quadrate (1), crista parotica contacts quadrate (2). *R19, W41, M52, HK29*
34. Cavum epiptericum: open ventrally below trigeminal ganglion (0), partial prootic floor (1), complete prootic floor (2). *R49, W54, LL6, L43, M44*
35. Promontorium: absent (0), present (1). *R52, W6, LL1, L35, BO57*
36. Prootic canal: absent (0), present (1). *R50, W28, LL3, L45, MA49, BO58*
37. Prootic and opisthotic: separated (0), fused to form petrosal (1). *R51, W5, L34, BO56*
38. Internal auditory meatus: open (0), walled (1). *R53, W7, L39, M47, HK36, B36*
39. Hyoid muscle fossa in paroccipital process: absent (0), present and incipient (1), present and well developed (2). *R55, W56, LL7, L40, M59, MA48, BO61*
40. Tuberculum sphenoccipital: present (0), absent (1).
41. Fenestra rotunda and jugular foramen: confluent (0), separated (1). *R60, W29, LL10, L42, M46, HK42, B39, BO60*
42. Jugular foramen: faces posteriorly (0), ventrally (1). *SS30*
43. Occipital condyle: single (0), double (1). *HK37*
44. Paroccipital process: undifferentiated (0), differentiated into mastoid and quadrate processes (1), differentiated into anterior and posterior processes (2). *BO66* +
45. Paroccipital process in base of posttemporal fossa: present (0), absent (1). *HK24, SS16*
46. Posttemporal fossa large axis in relation to foramen magnum diameter: of same size or slightly smaller (0), notably smaller (1).
47. Stapes: perforated (0), unperforated (1).
48. Lateral crest of dentary: absent (0), incipient (1), well developed (2), strongly projected (3). +
49. Masseteric fossa in dentary: absent (0), fossa high on coronoid process (1), fossa extends to angle of dentary (2). *HK45, SS36* +
50. Base of coronoid process extension in lateral view: relatively narrow (0), moderately expanded anteroposteriorly (1), very expanded anteroposteriorly (2). +

51. Location of coronoid process in temporal fossa: lateral (0), in the middle (1). SS33
52. Mediolateral thickening of anterior margin of coronoid process: absent (0), present (1). HK50
53. Longitudinal depression in lateral side of the dentary: absent (0), present (1).
54. Foramen on external surface of lower jaw between dentary and angular: absent (0), present (1). SS41
55. Angle of dentary: anterior to postorbital bar (0), at same level or slightly posterior (1), well to posterior (2). +
56. Position of dentary/surangular dorsal contact: closer to post-orbital bar (0), midway (1), closer to jaw joint (2). HK48, SS40 +
57. Reflected lamina of angular: corrugated plate (0), smooth plate with slight depressions (1), hook-like laminae (2), thin projection (3). HK52, SS44 +
58. Squamosal articulation for lower jaw: absent (0), narrow and medially directed (1), wide glenoid cavity ventrally directed (2). L26, B19, BO37, MA22 +
59. Craniomandibular articulation: quadrate/articular (0), main quadrate/articular, secondary surangular/squamosal (1), quadrate/articular by an extensive reduction of surangular (2), main dentary/squamosal (3). R66, R67, W9, L23, L24, M60, HK25, B30, SS19, BO26, MA39
60. Craniomandibular articulation: at same height as postcanine line (0), higher than postcanine line (1). L25
61. Quadrate notch in squamosal: absent (0), present (1). ?HK31
62. Mandibular symphysis: unfused (0), fused (1). R68, W10, L19, M68, HK44, B17, SS34, BO21, MA21
63. Contact between frontal and palatine in interorbital wall: absent (0), present (1). R6, W37, L56, L60, M24, M30, HK23, B29, BO46, MA38
64. Frontal-epipterygoid contact: absent (0), present (1). R39, W48, L61, HK35, SS24
65. Parietal region: at same level as remaining skull profile (0), high (1). SS7
66. Trigeminal exit: between prootic incisure and epipterygoid (0), via foramen between epipterygoid and prootic (1), via two foramina (2). M48, HK28, B33, BO51, SS27, MA42 +
67. Epipterygoid ascending process: rodlike (0), moderately expanded (1), greatly expanded (2). HK32, SS22 +
68. Lateral flange of prootic: absent (0), present (1). HK34, SS28
69. Zygomatic arch dorsoventral height: slender (0), moderately deep (1), very deep (2). R16, W40, L54, M39, HK18, SS5, BO40, MA33 +
70. Infraorbital process: absent (0), suborbital angulation between maxilla and jugal (1), descendant process of jugal (2). M18, HK21, HK41, A25, B38, BO29, BO44, MA36, MA46 +
71. Inferior margin of jugal in the zygoma: poorly developed longitudinally not reaching posterior border of zygoma (0), well developed longitudinally and low (1), well developed and high (2). L28, HK20, A26, BO43
72. Posterior extension of squamosal dorsal to squamosal sulcus: absent (0), incipient (1), well developed (2).
73. Latero-posterior exposure of squamosal on zygoma: without or with incipient depression (0); with deep squamosal sulcus (1). M55, HK22, B28, SS18, BO45, MA37 +
74. Temporal fossa: widest in the middle (0), same width throughout (1), widest posteriorly (2). HK39, BO42, MA44
75. V-shape notch separating lambdoidal crest from zygoma: absent (0), incipient (1), deep (2). HK43, SS17, BO55
76. Upper tooth series extension: anterior to orbit (0), below orbit (1).
77. Upper incisors: more than four (0), four (1), fewer than four (2). R81, W63, ?L5, M1, HK53, B3, A1, SS45, BO3, MA3 +
78. Lower incisors: four or more (0), three (1), fewer than three (2). M2, HK54, B4, SS46, BO4, MA4 +
79. Incisors: all small (0), some or all enlarged (1). HK56, A2, B5, B6, BO5, MA5, MA6, MA7
80. Incisor cutting margins: serrated (0), smoothly ridged (1), denticulated (2). HK55, SS47
81. Incisor occlusion: teeth relatively evenly placed and sized (0), first lower incisor enlarged and fits into a gap between first upper incisors (1). M3
82. Incisor/canine diastema: present (0), absent (1). A3
83. Pre-canine maxillary teeth: absent (0), present (1). SS48
84. Upper canine: large (0), reduced (1), absent (2). L6, HK57, A4 +
85. Lower canine: large (0), reduced (1), absent (2). L6, HK58, A5 +
86. Canine serrations: present (0), absent (1). HK59, SS49
87. Axis of posterior part of maxillary tooth row: directed lateral to subtemporal fossa (0), directed toward centre of fossa (1), directed toward medial rim of fossa and curved (2), directed toward medial rim of fossa and parallel (3). R80, M12, HK78, B13, MA17, MA20, BO14, BO16, BO17 +
88. Postcanine occlusion: absent (0), unilateral without forming a consistent pattern between upper and lower teeth (1), precise unilateral occlusion (2), tooth-to-tooth contact because of widened postcanines (3). R84, R86, W33, L1, L14, M8, B1, BO1, MA1
89. Postcanines: undifferentiated (0), differentiated into premolariforms and molariforms (1). R87, W34, L8
90. Upper postcanine morphology: conical, simple (0), sectorial without or with incipient cingulum broadening the crown (1), sectorial with a well-developed lingual cingulum (2), bucco-lingually expanded [including multicuspidate with their cusps aligned in series] (3). L13, M5, HK60, HK62, A7, SS51, SS55, BO13 +
91. Posterior postcanines with strongly curved main cusp: absent (0), present (1). SS52
92. Upper postcanine buccal cingulum: absent (0), present (1). R85, HK61, B9, BO7, MA10
93. Transverse crest in upper postcanines: absent (0), present with two cusps (1), present with three or more cusps (2). HK63, A11
94. Lingual cingulum in lower postcanines: absent (0), small (1), well developed (2). L12, B11, B12, BO9, BO10, SS56 +
95. Lower postcanine roots: single (0), divided (1). R88, W65, L9, M7, B8, BO6, MA9
96. Upper postcanine roots: single (0), divided and longitudinally aligned (1), multiple roots (2). R88, W66, L9, M7, B8, BO6, MA9, L9

Data matrix
Polymorphic states are enclosed in brackets []; ?, unknown; ~, inapplicable.

CYNOSAURUS	00000 000-0	00010	2---0	00000	00110 10100	00000 00000	00000 00000	00000 00000	00010	00000	00010	00000	00000	00100	00000 00000 00000	0
PROURIDEA	00000 000-0	00010	2---0	00000	00110 00000	00000 00000	00000 00000	00000 00000	00010	00000	00010	00000	00000	00700	00000 00000 00000	0
LYCOSUCHUS	00000 00011	01010	2---0	11110	00000 10000	00000 00010	00000 00010	00000 00010	00000	00011	00000	10000	00000	01000	00000 01000 00000	0
GLANOSUCHUS	00000 00011	01010	2---0	01010	00000 10000	00000 00010	00000 00010	00000 00010	00000	00010	00000	00000	00000	01100	00000 00000 00000	0
HOPEWYIA	00001 00[01]11	01010	2---0	01010	10000 00100	00000 00010	00000 00010	00000 00010	00000	00010	00000	00000	00000	00701	00100 00000 00000	0
ICTIDOSUCHOPS	00000 [01]0111	01011	2---0	02010	10000 10100	00000 00010	00000 00010	00000 00010	00000	00010	00000	00000	00000	00001	01100 00000 00000	0
THERIOGNATHUS	00000 00111	01011	2---0	02-00	10000 10100	00000 00010	00000 00010	00000 00010	00000	00010	00000	10000	00000	02100	1[01]020	-
MOSCHORHINUS	10000 00111	01010	2---0	02010	10010 10100	00000 00010	00000 00010	00000 00010	00000	00010	00000	00000	00000	00100	10000 00000 00000	0
BAURIA	00000 11111	012[01]2	30000	[01]2210	10000 00100	00000 00100	00000 00100	00000 00100	00000	00100	00000	00000	00000	01111	00000 11300 00000	0
CYNOSAURUS	01101 00111	01110	10000	02001	-0000 10000	00000 10000	00000 10000	00000 10000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
PROCYNOSUCHUS	00101 00111	01110	10001	02000	00000 10000	00000 10000	00000 10000	00000 10000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
DVINIA	01010 00101	01110	10000	02000	00000 10000	00000 10000	00000 10000	00000 10000	00000	00010	00000	00000	00000	00000	00000 00000 00000	?
GALESIAURUS	01101 00111	[01]1110	10000	02001	-0000 10000	00000 10000	00000 10000	00000 10000	00000	00010	00000	00000	00000	00000	00000 00000 00000	?
PROGALESIAURUS	01101 00111	01000	10000	02001	-0000 10000	00000 10000	00000 10000	00000 10000	00000	00010	00000	00000	00000	00000	00000 00000 00000	?
THRINAXODON	01101 00111	01212	00001	02001	-0000 10000	00000 10000	00000 10000	00000 10000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
PLATYCRANIPELLUS	01101 00101	11212	00000	12000	00000 00100	00000 00100	00000 00100	00000 00100	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
CYNOSGNATHUS	10101 00110	01212	00001	02001	-1101 20000	00000 20000	00000 20000	00000 20000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
DIADEMODON	00101 00111	01212	00000	02001	-1100 20000	00000 20000	00000 20000	00000 20000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
TRIRACHODON	11101 01011[01]1	11212	00001	02201	-1101 20000	00000 20000	00000 20000	00000 20000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
MASSETOGNATHUS	01101 01111	21322	00002	02201	-1101 10000	00000 10000	00000 10000	00000 10000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
EXAMERTODON	00101 01111	11332	0101]002	12201	-1101 10010	00000 10010	00000 10010	00000 10010	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
CHINQUODON	11101 01111	11312	01112	12001	-1001 20000	00000 20000	00000 20000	00000 20000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
LUMKUIA	00101 01111	11212	00102	12000	10010 10000	00000 10000	00000 10000	00000 10000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
ECTENINON	00101 01111	01000	00000	02001	-1101 20010	00000 20010	00000 20010	00000 20010	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
PROBRATINGNATHUS	01101 01101	11312	00102	02101	-0101 20000	00000 20000	00000 20000	00000 20000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
PACHYGENIUS	20111- 2111-	11312	01112	12100	00101 20000	00000 20000	00000 20000	00000 20000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
BRASILIODON	00111- 2111-	01000	00000	02001	00000 00000	00000 00000	00000 00000	00000 00000	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
BRASILITHERIUM	00111- 2111-	01000	00000	02000	102-1 00101	00000 00101	00000 00101	00000 00101	00000	00010	00000	00000	00000	00000	00000 00000 00000	0
OLLIGORYTHUS	00111- 2011-	013-2	00000	12200	00000 00000	00000 00000	00000 00000	00000 00000	00000	00010	00000	00000	00000	00000	00000 00000 00000	2
KALIENTATHERIUM	10111- 2111-	013-2	01012	12201	-1111 01210	00000 01210	00000 01210	00000 01210	00000	00010	00000	00000	00000	00000	00000 00000 00000	2
MORGANUCODON	00111- 2111-	01000	00000	12001	-0201 10211	00000 10211	00000 10211	00000 10211	00000	00010	00000	00000	00000	00000	00000 00000 00000	1
STENOUCODON	00111- 2111-	01012	01112	12001	-0201 10011	00000 10011	00000 10011	00000 10011	00000	00010	00000	00000	00000	00000	00000 00000 00000	1

Synapomorphies

Listed synapomorphies are common to the five MPTs, with exception of nodes 2, 3 and 4, which are only present in the majority rule consensus (see Text-fig. 9).

Node 1: 'THEROCEPHALIA' + CYNODONTIA (all trees): 10(1), 12(1), 22(0 → 1), 24(1), 28(1 → 0), 29(0), 44(0 → 1), 54(1), 67(0 → 1), 69(1 → 0).

Node 2 (three trees): 68(1).

Node 3 (four trees): 26(1), 80(0 → 1).

Node 4 (four trees): 22(1 → 2), 86(1); (three trees): 82(1).

Node 5: *THERIOGNATHUS* + CYNODONTIA (all trees): 24(0), 55(0 → 1), 61(1), 67(1 → 2).

CYNODONTIA (all trees): 3(1), 5(1), 13(0 → 1), 16(2 → 1), 33(1 → 0), 40(1), 43(1), 44(1 → 0), 49(0 → 1), 50(0 → 1), 51(1), 57(0 → 1), 66 (0 → 1), 74(2 → 0); (some trees): 42(1), 56(0 → 1).

EPICYNODONTIA (all trees): 2(1), 25(1), 48(0 → 1), 49(1 → 2), 50(1 → 2), 69(0 → 1), 77(0 → 1), 82(0).

Node 6: PROCYNOSUCHIDAE (all trees): 65(1), 78(1 → 0), 83(1); (some trees): 90(1 → 2).

Node 7: GALESURIDAE (all trees): 70(0 → 1), 91(1).

Node 8 (all trees): 13(1 → 2), 15(0 → 2), 16(1 → 0), 54(0), 57(1 → 2).

Node 9 (all trees): 56(1 → 2).

EUCYNODONTIA (all trees): 28(0 → 1), 30(1), 58(0 → 1), 59(0 → 1), 91(1).

CYNOGNATHIA (all trees): 2(0), 27(1), 86(0).

Node 10: *CYNOGNATHUS* + GOMPHODONTIA (all trees): 48(1 → 2), 69(1 → 2), 70(0 → 2), 72(1 → 2), 73(1), 74(0 → 2), 80(1 → 0).

Node 11: GOMPHODONTIA (all trees): 71(1 → 2), 76(1), 87(0 → 1), 88(0 → 3), 90(1 → 3), 93(0 → 1).

Node 12: *TRIRACHODON* + TRAVERSODONTIDAE (all trees): 11(0 → 1), 23(0 → 2), 74(2 → 1).

Node 13: TRAVERSODONTIDAE (all trees): 13(2 → 3), 14(1 → 2), 20(1 → 2), 31(2 → 1), 82(1), 85(0 → 1), 86(1), 87(1 → 2), 91(0).

Node 14 (all trees): 13(2 → 3), 36(1), 63(1).

PROBAINOGNATHIA (all trees): 18(1), 20(1 → 2), 76(1).

Node 15 (all trees): 23(0 → 1), 87(0 → 1), 90(1 → 2), 91(0).

ICTIDOSAURIA (all trees): 1(0 → 1), 36(0), 58(12 → 0), 77(1 → 2), 79(1), 81(1), 87(1 → 3).

Node 16 (all trees): 37(1), 48(1 → 3), 85(0 → 1), 94(1 → 2).

MAMMALIAMORPHA (all trees): 4(1), 6(0 → 2), 44(0 → 2), 52(1), 62(0), 69(1 → 0), 92(1).

Node 17: *BRASILITHERIUM* + MAMMALIAFORMES (all trees): 11(1 → 0), 23(1 → 0), 28(1 → 2), 35(1), 78(1 → 0).

Node 19: TRITYLODONTIDAE (all trees): 23(1 → 2), 29(1), 33(0 → 2), 34(0 → 1), 60(1), 61(0), 65(1), 69(0 → 2), 71(1 → 2), 72(1 → 2), 73(1), 84(1 → 2), 85(1 → 2), 88(0 → 3), 90(2 → 3), 95(1), 96(0 → 2).

Node 18: MAMMALIAFORMES (all trees): 34(0 → 1), 67(2 → 1), 95(1), 96(0 → 1).