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TOOTH REPLACEMENT PATTERNS IN EUTHERIODONTIA (SYNAPSIDA, THERAPSIDA) FROM THE SOUTH AFRICAN KAROO SUPERGROUP

by

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Thesis

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I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

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Luke Allan Norton

24th day of April 2020 in Johannesburg, South Africa

ABSTRACT

This is the first comprehensive study, using micro-computed tomography, of eutheriodont tooth replacement patterns through ontogeny in therocephalians (*Lycosuchus* and *Bauria*) and cynodonts (*Cynosaurus* and *Galesaurus*). Comparison of tooth replacement patterns of the incisors, canines and postcanines revealed that this varied the most in the postcanines, followed by the canines. The incisor replacement pattern is conservative, with all four taxa exhibiting alternating replacement. Lycosuchidae retain the basal synapsid condition of two maxillary canine loci, whereas *Bauria* and the epicynodonts *Cynosaurus* and *Galesaurus* have only a single maxillary canine. Maxillary canine replacement occurred several times through ontogeny in the two epicynodonts with cessation of canine replacement coinciding with attainment of skeletal maturity. This differs from the condition previously reported for the epicynodont *Thrinaxodon*, in which canine replacement continued well into adulthood. In contrast, there is no evidence of canine replacement in *Bauria*.

Alternating postcanine replacement occurs in *Lycosuchus*, *Cynosaurus*, and *Galesaurus*, with the pattern of *Cynosaurus* more closely resembling that previously described in *Thrinaxodon*. In *Cynosaurus*, replacement waves move along the jaw from front-to-back in multiples of two in the mandible, and three in the maxilla. It is hypothesised that the first maxillary postcanine locus became dormant after two replacements, causing a distal shift in the postcanine series. Conversely, *Galesaurus*, does not exhibit cessation of replacement and the first

maxillary postcanine is replaced even in the largest specimens. Additional teeth are added distally to the postcanine series in *Galesaurus*, such that larger specimens have more postcanine teeth. Only one *Bauria* specimen manifests postcanine replacement, suggesting that reduction in replacement activity is an adaptation to maintain precise occlusion. As each of the study taxa exhibit different replacement patterns, especially with regard to the postcanines, this study highlights a previously unrecognised diversity in tooth replacement patterns amongst the Eutheriodontia.

"Because of their hardness the teeth are the most generally and perfectly preserved of all fossilized organs; hence they are the especial guides and friends of the palæontologist in his peculiar field of work from imperfect evidence."

—H.F. Osborn (1907), *Evolution of Mammalian Molar Teeth*, p. 1

"In paleontology, increasing knowledge leads to triumphant loss of clarity."

—A.S. Romer (1961), *Synapsid Evolution and Dentition*, p. 33

In memory of my grandmother,

Cynthia Harriet Briedenham

5 January 1938 – 9 October 2014

my son,

Michael Tomas Norton

13 May 2017 – 1 July 2017

and my father,

Anthony George Norton

23 November 1955 – 19 November 2019

M E M E N T O M O R I

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ABBREVIATIONS

Institutional Abbreviations

AM	Albany Museum, Grahamstown, South Africa
AMNH	American Museum of Natural History, New York, USA
BP	Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa
CGS	Council for Geosciences, Pretoria, South Africa
FMNH	Field Museum of Natural History, Chicago, USA
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
MB	Museum für Naturkunde, Berlin, Germany
MCP	Museo de Ciências e Tecnología, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil
NHMUK	The Natural History Museum, London, United Kingdom
NMP	Natal Museum, Pietermaritzburg, South Africa
NMQR	National Museum, Bloemfontein, South Africa
PIN	Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia
RC	Rubidge Collection, Wellwood, Graaff-Reinet, South Africa
SAM	Iziko: South African Museum, Cape Town, South Africa
TM	Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa

UA	University of Antananarivo, Antananarivo, Madagascar
UMZC	Museum of Zoology, University of Cambridge, United Kingdom
US	University of Stellenbosch, Stellenbosch, South Africa

Anatomical Abbreviations

APL	anteroposterior length
BSL	basal skull length
SL	snout length

THESIS LAYOUT

This thesis is presented as a series of four research papers that were prepared by the author while registered for the degree of Doctor of Philosophy. The four research papers (chapters 3–4) are preceded by an Introduction (Chapter 1) and Materials and methods (Chapter 2). Chapter 7 is a synthesis of the accomplishments of this study, and Chapter 8 is a compilation of all the references cited in the thesis.

List of papers produced for the Ph.D.

Norton L.A., Abdala, F., Rubidge, B.S. and Botha, J. (in prep.) Re-evaluation of tooth replacement patterns of the Lycosuchidae (Therapsida, Therocephalia) using micro-computed tomography. Intended for submission to *Acta Palaeontologica Polonica*.

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Norton L.A., Abdala, F., Rubidge, B.S. and Botha, J. (in prep.) Tooth replacement patterns in the Early Triassic epicynodont *Galesaurus planiceps* (Therapsida, Cynodontia). Intended for submission to *PLOS One*.

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Other papers published during Ph.D. registration

Benoit, J., **Norton, L.A.**, Manger, P.R., and Rubidge, B.S. (2017) Reappraisal of the envenoming capacity in *Euchambersia mirabilis* (Therapsida, Therocephalia) using μCT-scanning techniques. *PLOS One*, 12 (2): e0172047. https://doi.org/10.1371/journal.pone.0172047.

Benoit, J., Manger, P.R., **Norton, L.A.**, Fernandez, V., and Rubidge, B.S. (2017) Synchrotron scanning reveals the palaeoneurology of the head-butting *Moschops capensis* (Therapsida, Dinocephalia). *PeerJ*, 5: e3496. https://doi.org/10.7717/peerj.3496.

1 INTRODUCTION

Teeth are hardened structures in the mouth associated with feeding. Such structures have arisen several times in the fossil record, and are found in various invertebrate and vertebrate clades. Most amniotes have teeth, however, there are exceptions in each of the major groups, e.g., pangolins and modern birds, which have secondarily lost their teeth. Of those groups within the Amniota that do have teeth, most of them will replace their teeth at least once during the course of their lifetime. Dyce *et al.* (1996) described tooth eruption as being a complicated process involving a number of factors namely: root growth, bone growth, pulpal proliferation, tissue pressure, and periodontal traction. The relative importance of each of these factors is disputed, but Dyce *et al.* (1996) consider periodontal traction as likely to be the most significant.

Reif's (1978) model of the formation of teeth in an embryonic shark shows first the initiation of the even-numbered, and then the odd-numbered tooth positions of the upper jaw. The pattern reverses in the lower jaws, but alternate positions are established in both (Smith and Coates, 2001). Reif (1978: 109) suggested that this pattern of initiation "automatically leads to an arrangement of the teeth in tooth families [vertical rows] as well as in diagonal rows."

To understand the types of tooth replacement patterns that occurred in extinct taxa, it is useful to understand the different types of tooth replacement patterns observed in modern taxa. There are two major types of replacement seen in the sauropsid lineage and the mammalian lineage.

The shared primitive condition (symplesiomorphic) of alternate replacement can be traced back to osteolepid fishes and labyrinthodont amphibians (Watson, 1926), e.g., *Eryops* (Sawin, 1941), from the Late Carboniferous to early Permian (~310–295 Ma) (Vaughn, 1958). In Sawin (1941: pls 2–5, fig. 4), the cranium of *Eryops* is illustrated to show empty alveoli situated between functional teeth. Thus, the condition of alternating tooth replacement in tetrapods is both shared and widespread amongst the lineages (Parrington, 1936a; Edmund, 1960; Osborn, 1975; Berkowitz, 2000; Berkowitz and Shellis, 2017).

For a comprehensive, if not outdated, account of the dentition of the lower vertebrates, including, but not limited to the Chondrichthyes, Osteichthyes, Amphibia, Diapsida,[1] and Mammalia, the work of Peyer (1968) should be consulted. Although Dr Peyer may himself have not been aware of the work on therapsid tooth replacement by Crompton (1962, 1963) and Fourie (1963), his successor Dr Zangerl certainly was—these papers, as well as Hopson's (1964) study on therapsid tooth replacement are cited on p. 215. Despite this, only a short account of the tooth replacement in the non-mammalian Synapsida is offered

[1] The Reptilia and Aves. In this work, a brief account of the non-mammalian Synapsida is also included within the Reptilia.

(Peyer, 1968: 170–177), mostly recounting the work on the "Pelycosauria" by Romer and Price (1940) and Romer (1945, 1961). In a recent synopsis of the tooth attachment and replacement patterns in amniotes (Bertin *et al.*, 2018), the Therapsida were apparently glossed-over in a similar manner, with some of the earliest (e.g., Parrington, 1936a, 1936b), as well as most-recent (e.g., Abdala *et al.*, 2013) works being omitted.

The synapsid lineage diverged from amniote vertebrates over 300 Ma ago, during the late Carboniferous (Pennsylvanian) of the Palaeozoic (Kielan-Jaworowska *et al.*, 2004). The earliest synapsids—or "pelycosaur-grade" synapsids— thrived during the late Pennsylvanian through to the middle Permian (Kemp, 1982; Carroll, 1988; Hopson, 1994; Botha-Brink and Modesto, 2007; Modesto *et al.*, 2011). Therapsida first appear in the fossil record from the middle Permian, and soon after split into several stem groups to dominate the terrestrial biota (Kielan-Jaworowska *et al.*, 2004). This rapid radiation has led some authors, e.g., Kemp (2009), to surmise that the various lineages within the Therapsida may have arisen simultaneously, and thus formed a polytomy. The only exception is Kemp's recognition of the Eutheriodontia being a monophyletic clade comprising the Therocephalia and Cynodontia.

Polyphyodonty, or the capacity for continuous tooth renewal, is displayed in most non-mammalian vertebrates. However, this capacity to continuously replace teeth has been lost in the evolutionary history of most mammals. Exceptions include members of the genus *Manatee* (Domning, 1983, 1987; Finch, 1990), and the

Australian rock wallabies (Domning, 1983), which continuously replace their teeth throughout life. Additionally, elephants can replace their teeth up to six times (Sikes, 1971), and humans up to two times (Fahy, 2010).

Most sauropsid taxa are polyphyodont, meaning that they replace their dentition several times, throughout their lifespan. In contrast, most mammals have only two sets of teeth, and are thus diphyodont. Some mammal lineages (toothed whales and rodents) have reduced the number of sets of teeth even further to only a single generation, and are thus monophyodont. The reduction in regenerative capability of the teeth has been linked to a trade-off between tooth number, and tooth complexity and size (Jernvall and Thesleff, 2012). In addition to reducing the number of tooth generations produced in mammals, many representatives of the group also show a differentiation of the teeth into different types based upon their morphologies, i.e., incisor, canine, premolar, and molar. Not all these tooth varieties are replaced. By definition, true molars typically erupt later than the other tooth types, and are part of the second dental succession, having no deciduous tooth to replace in the tooth family.

It is thought that differences in tooth replacement patterns may be as a result of different growth patterns between reptiles and mammals. Reptiles tend to grow slowly, at irregular rates dependent on the availability of food. Placental mammals are much larger at birth in comparison, and grow rapidly to adult size (Gow, 1985a). Thus reptile populations are often comprised of individuals spanning a broad spectrum of sizes, where distinguishing between juveniles and adults can be

quite difficult. Individuals within mammalian populations tend to be much more easily distinguishable into juvenile and adult 'classes' (Gow, 1985b). In addition, mammalian teeth are also implanted in the bones of the skull via roots, i.e., they are thecodont (Peyer, 1968; Dyce *et al.*, 1996).

Four eutheriodont taxa were chosen for inclusion in this study. The Permian Lycosuchidae and Triassic therocephalian *Bauria* are included in order to test for changes in tooth replacement patterns through the phylogeny of Therocephalia. It is hypothesised that the Lycosuchidae would present the basal condition of alternating tooth replacement, whereas *Bauria* would have a different, more derived, pattern of tooth replacement. Furthermore, the 'derived' pattern of tooth replacement in at least the postcanines of *Bauria* is hypothesised to resemble the sequential pattern of postcanines observed in the gomphodont cynodonts. The Permian epicynodont *Cynosaurus* and the Triassic *Galesaurus* were included in order to test for possible changes in tooth replacement patterns related to changes in postcanine morphology. The broader implications of this study, is that it is the starting point of testing the phylogenetic relationship between Therocephalia and Cynodontia using non-morphological characters.

1.1 Synapsida

The first mammal-like reptiles from Russia were described by Kutorga (1838), with Owen (1844) later describing several specimens from South Africa. However, the name Therapsida was not introduced until Broom (1905a) proposed the term. The Therapsida are considered to be the ancestors of mammals. This

lineage is particularly well represented in the rocks of the Karoo Supergroup, where a time expansive (Carboniferous–Jurassic) sedimentary record chronicles the evolutionary history of the Therapsida, and the acquisition of mammalian characters in remarkable detail (Rubidge and Sidor, 2001). Whereas the cranial morphology of many therapsid taxa has been described in some detail, relatively little has been written depicting tooth succession and replacement in this group.

The first observation of possible tooth replacement in a non-mammalian synapsid was made by Broom (1903a), when describing *Lycosuchus vanderrieti*, who compared the condition of the double canine to that observed in the cynodont *?Cynognathus leptorhinus* (= *Cynognathus crateronotus*). Broom considered that this condition was only temporary in the cynognathid, and more permanent in *L. vanderrieti*. In the same paper, Broom noted a similar condition in the holotype of *Trirachodon kannemeyeri*, where the replacing canine was located mesial to the old canine root.

A decade later, Broom (1913a) recognised that the differentiation of cynodont dentition was likely because cynodonts were closely related to modern mammals, as opposed to the two arriving at a similar condition through convergent evolution. The additional shared characters of the cranium listed by Broom at the end of this paper provide additional support for this idea.

Broom (1913a) provided a summary of what was known at the time regarding tooth replacement in the Therapsida. No references were provided in this short

paper, but it is assumed that all examples were described by Broom himself in his various contributions to the knowledge of Karoo palaeontology.

It is considered by many, e.g., Kermack (1956), that the alternate method of tooth replacement present in Sauropsida is the primitive pattern of tooth replacement within the Amniota, and that at some stage in the evolutionary history of mammals, the mode of tooth replacement changed. Edmund (1960) demonstrated how a 'mammalian-grade' of tooth replacement could be derived from the 'reptilian-grade' through the reduction of the total dentition to only two *Zahnreihen* (German for tooth row); the first comprising the deciduous teeth (incisors, canines, and premolars) and molars, with the second comprising the permanent teeth (incisors, canines and premolars). Molars therefore represent the delayed eruption of elements from the first *Zahnreihen*.

Osborn (1907) provided a comprehensive account of the transition of postcanine types from reptilian to cusped-molars for mammals of the Triassic, Jurassic, Cretaceous, and Early Eocene. In this work, Osborn (1907) recognised four types of molar morphology:

(1) Haplodont—simple, recurved crown
(2) Protodont—single main cusp with lateral denticles
(3) Tuberculate—crown in 'basin-shaped' with a raised border
(4) Multituberculate—cusps arranged in regular, parallel rows

No such survey of the material has been undertaken for the Theriodontia, and more specifically the Eutheriodontia of the Permian and Early Triassic. This is perhaps due to the preconceived notion that these animals had simple conical teeth of the 'reptilian' grade (e.g., Owen's [1860: 60] original description of the postcanine teeth of *Galesaurus* as conical), and as such replaced them in the same manner as modern reptiles (sauropsids).

1.2 Basal synapsids ("Pelycosauria")

Based on the similarity in the arrangement of the reflected lamina of the angular in sphenacodont pelycosaurs, and in members of the Therapsida, as well as the onset of heterodonty, Romer and Price (1940) and Romer (1961) concluded that the sphenacodont pelycosaurs were a good representation of the expected ancestor to early therapsids. This close phylogenetic relationship between the Sphenacodontidae and Therapsida has been supported by the recent cladistic analysis of Benson (2012).

The dentition in the paraphyletic "Pelycosauria" is only slightly modified from the primitive tetrapod condition of simple conical structures (Reisz, 1986), and do not have accessory cusps or complex crown morphologies (Romer, 1961). Marginal teeth are always present as a single row in the premaxilla, maxilla, and dentary, and in several taxa (e.g., *Edaphosaurus*) large numbers of well-developed palatal teeth are also present (see Romer, 1961: figs 5 and 6). Coronoid teeth are also known to be present in *Edaphosaurus*, *Casea*, and possibly *Dimetrodon* (Williston, 1914: fig. 13; but see Romer, 1961).

Implantation of the marginal teeth in pelycosaurs is subthecodont (Romer, 1956) or protothecodont (Romer, 1961) resulting in a high dental lamina on the labial side, and lower dental lamina on the lingual side (Reisz, 1986). In addition, thin partitions of spongy bone occur between successive tooth sockets (Romer, 1961). Teeth of the premaxilla are often well developed, and are comparable to the incisors of mammals (Romer, 1961). The number of teeth in the maxillary series varies from 9 to 45, with a reduction in numbers of posterior ('postcanine') teeth associated with the development of large caniniform teeth (Romer, 1961). Most ophiacodonts and sphenacodonts have a pair of maxillary teeth that are alternatively replaced, and are thus potentially identifiable as canines (Romer, 1961)

Romer and Price (1940) demonstrated that the replacement process in "pelycosaurs" consisted of alternating replacement of the odd- and even-numbered teeth along the tooth margin. According to Reisz (1986), the rates of replacement between the various pelycosaur groups varied considerably. The Ophiacodontidae likely replaced their teeth frequently, suggested by the presence of many immature teeth and gaps in the tooth rows. It appears that tooth replacement was less frequent in the Varanopidae and Sphenacodontidae, with little evidence of tooth replacement amongst the Edaphosauridae (Reisz, 1986).

1.3 Therapsida

It had been suggested, as early as the 1960s (Romer, 1961), that the Therapsida may have had a polyphyletic origin. The most recent supporter of the polyphyletic

origin of Therapsida was Kemp (2009). While there have been some studies on the tooth replacement patterns of the Dinocephalia (Boonstra, 1962; Norton *et al.*, 2009) and the Anomodontia (Cisneros *et al.*, 2011, 2015), these groups are not included within the scope of this literature review. This is partly due to the fact that the dentition of anomodonts is considered as not being homologous to the caniniform dentition of the Theriodontia (Froebisch, 2005).

Instead, this literature review will focus on the three remaining 'carnivorous' groups. Similarly, the phylogenetic relationship of the Gorgonopsia to the Eutheriodontia (Therocephalia and Cynodontia) remains uncertain. Rubidge and Sidor (2001: fig. 3) advocated a sister group relationship between Gorgonopsia and Eutheriodontia, whereas a subsequent cladistic analysis by Huttenlocker (2009: fig 3) has recovered Anomodontia as the sister group to Eutheriodontia. These two views agree that the Gorgonopsia are basal to the Eutheriodontia, with the current majority view supporting Rubidge and Sidor (2001) (see also Kemp, 2005: 78–80).

1.4 Gorgonopsia

In the Gorgonopsia the postcanines still comprise a simple, recurved cone. In some instances serrations are present on the mesial, distal, or both surfaces of the tooth. In an investigation of the tooth replacement of the Gorgonopsia, Kermack (1956) was one of the first to use X-rays for this purpose in the Therapsida. This study found that all the teeth were replaced at least once, meaning that no teeth were analogous to the molars of modern mammals. Incisors were replaced at least

twice, and the upper canines were replaced up to three times, indicating that the mammalian condition of diphyodonty had not yet evolved.

With the exception of the upper canines, there was no functional distichial (or alternating) replacement of teeth. Instead, each tooth was immediately replaced by a tooth from the same tooth family, which erupted lingually to the functional tooth. The only sign of functional distichial replacement was the tendency of functional canines to fall into two alternating groups. For example, Kermack (1956) observed two alveoli in each maxilla for the canines, while only one functional canine was present on each side of the upper jaw. Kermack (1956) suggested that the canines were borne alternately by each pair of alveoli, implying a total of four canine tooth groups in the upper jaw, two in each maxilla, which worked alternatively to replace the functional canine.

Kermack (1956) observed that erosion of the tooth took place at the enamel-dentine junction (EDJ), resulting in the crown being shed, while the root was retained within the alveolus before being resorbed and replaced by spongy bone. The functional canine was born in the mesial alveolus, and the distal alveolus contained a ‘plug’ of spongy bone and a root in the process of resorption. It was suggested that after a certain time in the animal’s life, tooth replacement stopped, with the ‘permanent’ maxillary canine always being socketed in the mesial alveolus. This reduction in tooth replacement to a finite number of replacement generations was considered analogous with mammals (Kermack, 1956).

Eriphostoma was originally considered a therocephalian (Broom, 1932a: fig. 16F), and later thought by some to be undiagnosable to family level (e.g., Boonstra, 1935); however, the only known specimen (AMNH FARB 5524) has more recently been redescribed as a gorgonopsian (Kammerer, 2011, 2014; Kammerer *et al.*, 2015). Specimen AMNH FARB 5524 has four or five small incisors, two long pointed canines of about equal length, and two small pointed postcanines. Alternating, or distichial replacement of the canines is a derived condition, such that at any one time at least one functional tooth remained (Kermack, 1956; Sigogneau-Russell, 1989). Sigogneau-Russell (1989) wrote that the number of replacements would have been limited and fixed, allowing for the teeth of adults to be more firmly set in the jaws, likely due to the mineralisation of the periodontal ligament.

1.5 Eutheriodontia

It is within the Eutheriodontia (Therocephalia, Cynodontia, and their descendents) that significant differentiation in the morphologies of the postcanine teeth takes place. The majority of early therocephalians (e.g., Lycosuchidae and Pristerognathidae) have postcanines of the simple 'reptilian' type (Huttenlocker, 2009). More derived therocephalians, such as *Bauria*, have buccolingually expanded, gomphodont postcanine teeth. In contrast, even the earliest cynodonts from the fossil-record have a postcanine dentition with complex, multi-cusped morphologies (Botha *et al.*, 2007). These range in shape from the bicuspid "lobster-claws" of *Galesaurus*, to multicusped sectorial teeth of *Thrinaxodon* and

Cynosaurus, to the mammal-like postcanines of *Cynognathus*, *Trirachodon*, and the tritylodontids.

1.5.1 Therocephalia

Therocephalia (Figure 1) appear early in the fossil record, along with some of the other earliest representatives of therapsid faunas, in deposits of the *Eodicynodon* Assemblage Zone (AZ) of South Africa (Rubidge, 1995). The Therocephalia are one of only three synapsid lineages to survive the end-Permian mass extinction event, and their evolutionary record continues through to the Middle Triassic *Cynognathus* AZ (Rubidge, 1995; Sidor, 2001; Huttenlocker, 2009).

Van den Heever (1994) briefly commented on canine replacement in *Lycosuchus*. Previous studies had recognised the Lycosuchidae as a distinct group within the Therocephalia, based upon the presence of two functional canines in each maxilla (Broom, 1932a; Haughton and Brink, 1954). However, van den Heever (1980) considered the condition of the double canine to reflect the process of replacement, and that for a short time, the animal had both the functional and replacement canines present in the same alveolus.

Broom (1903a: 205) postulated that both canines in *Lycosuchus* could be functional at the same time, due to the replacing (mesial) canine being "peculiarly specialised," as though it were to have been used for a different function. The conclusion that the different teeth were differentiated may have been incorrect,

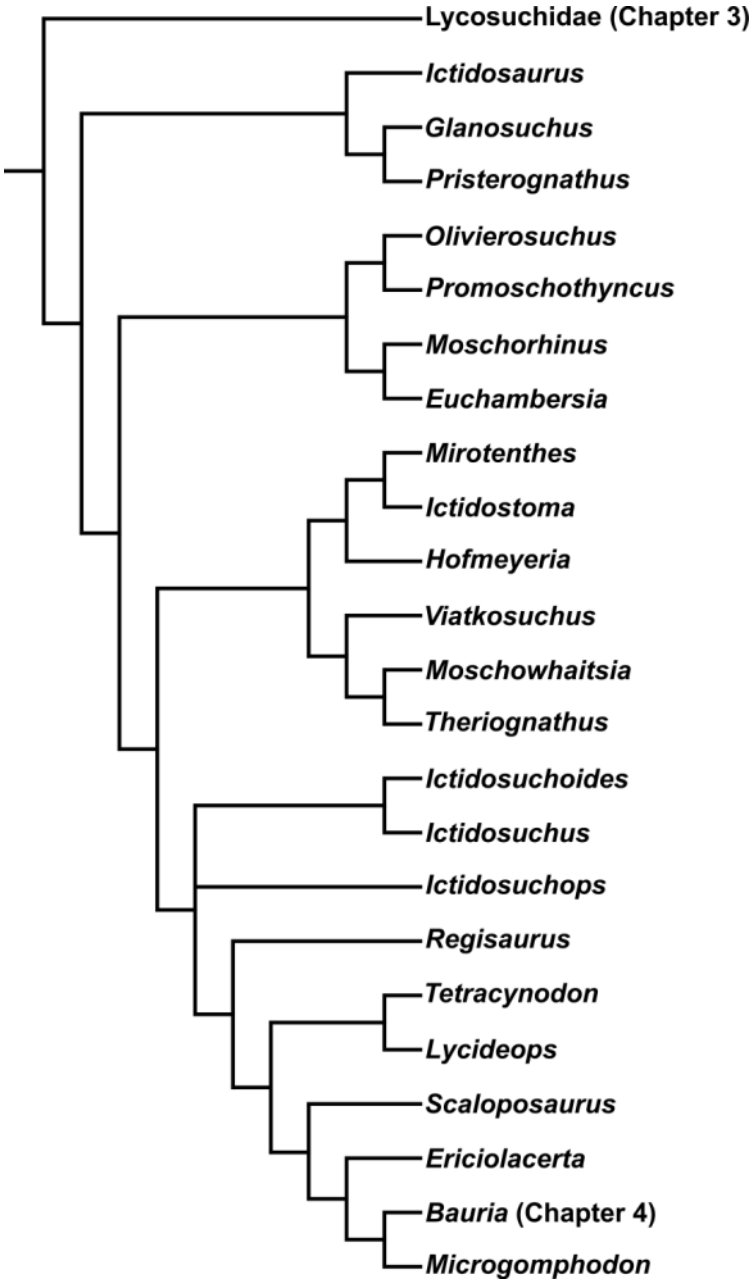

Figure 1. Cladogram showing the hypothesised relationships between the Therocephalia. Redrawn after Huttenlocker (2009; Fig.3, 2014: fig. S1).

and the differences in serrations may instead have been due to physical wearing of the mesial serrations of the older, functional canines.

The earliest occurring eutheriodont for which postcanine crown occlusion is described was *Ericiolacerta* (Watson, 1931; Crompton, 1962). Watson (1931) demonstrated that the type of tooth replacement in this taxon was of the reptilian type, due to a replacement tooth being present directly under a broken erupted tooth. Parrington (1936b) suggested that although this type of replacement occurred in *Ericiolacerta*, it did not exclude the possibility that the derived bauriamorphs may have had a mode of tooth replacement more similar to that of the gomphodont cynodonts.

Bauria is one of the last occurring therocephalian taxa (Kemp, 2005), and is found in Lower-Middle Triassic *Cynognathus* Assemblage Zone deposits (Kitching, 1995). *Bauria* is remarkable due to its apparent convergence in tooth structure with that of the contemporaneously occurring gomphodont cynodont *Diademodon* (Kemp, 2005). The postcanine teeth are transversely widened, allowing for the upper and lower dentitions to meet in true, direct occlusion (Kemp, 2005). The crowns consist of a large labial cusp, and a row of smaller lingual cusps. The teeth intermesh in a manner that allows for the mesial edge of the upper tooth to shear with the distal edge of the corresponding lower tooth, resulting in a cutting action.

Whereas some Therocephalia adapted a postcanine dentition similar in morphology to that seen in the later gomphodont cynodonts, some genera have

reduced the number of postcanine teeth, and in some cases even lost the postcanine teeth in the maxilla (e.g., *Euchambersia*[2]), dentary (e.g., *Mirotenthes*), or both (e.g., *Theriognathus*).

1.5.2 Cynodontia

The Cynodontia appear later in the fossil record than the Therocephalia, with the oldest fossils being found in the early–late Permian *Tropidostoma* AZ (Botha *et al.*, 2007; Botha-Brink and Abdala, 2008). During the late Permian and Triassic the cynodonts underwent a rapid diversification, with members of the group eventually giving rise to mammals (Rubidge and Sidor, 2001) (Figure 2). The dentition of all cynodonts has reached a state of heterodonty (i.e., incisors, canine, and postcanine teeth) that is comparable to the mammalian pattern (Kemp, 2005).

Tatarinov (1968) offered the first description of the lower "molars" of *Dvinia prima*. Sushkin (1928, 1929) had previously offered brief descriptions of "*Permocynodon*." The only specimens belonging to *Permocynodon* were redescribed by Tatarinov (1968), who synonymised *Dvinia* and *Permocynodon*, placing them in the newly created subfamily Dviniidae, within the Procynosuchia (*sensu* Brink, 1963a, 1963b).

[2] The lower jaw of *Euchambersia* is not known.

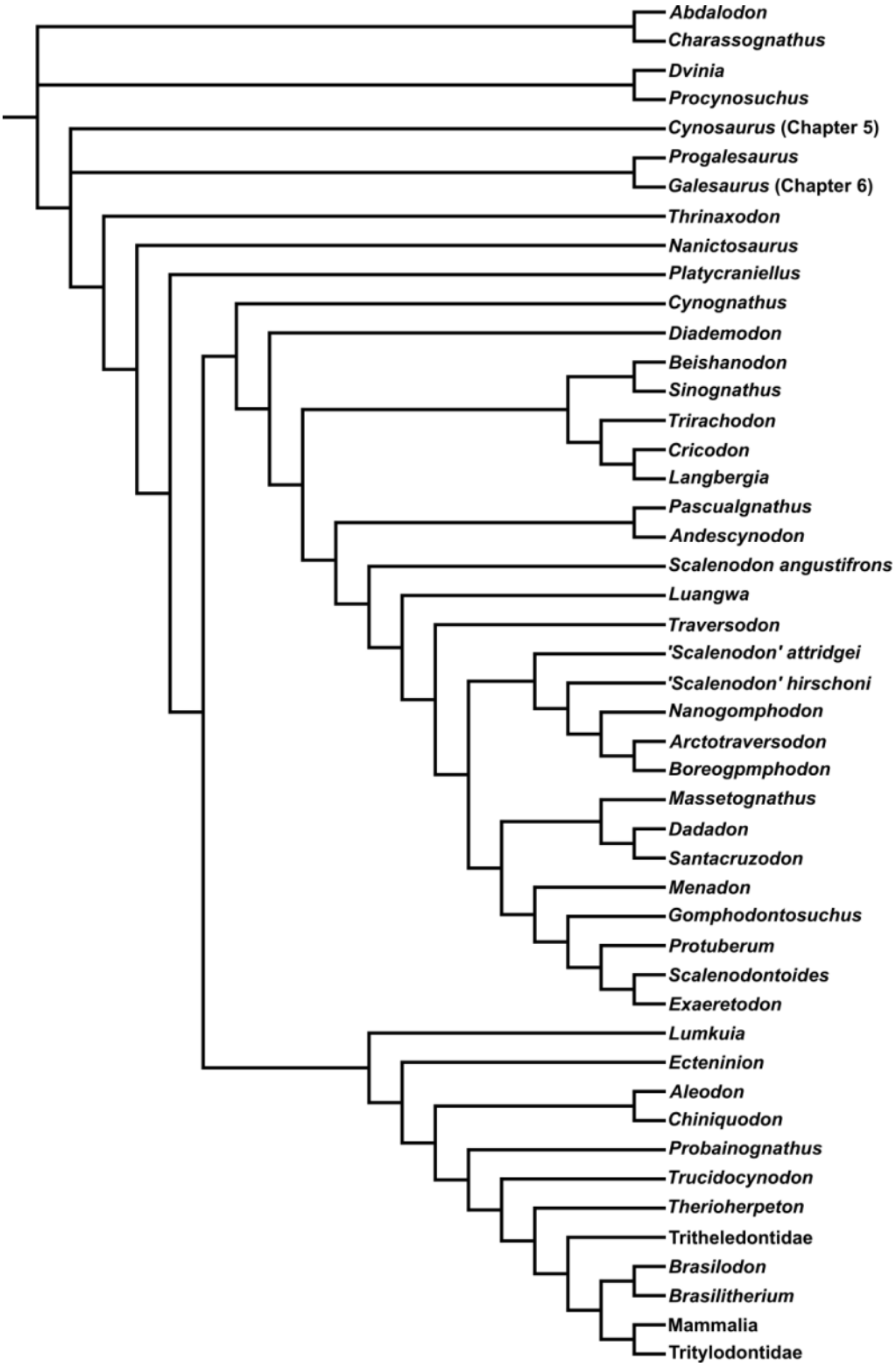

Figure 2. Cladogram showing the hypothesised relationships between the Cynodontia. Redrawn after Ruta *et al*. (2013: fig. 1) and Van Den Brandt and Abdala (2018: fig. 11).

Despite being a late Permian cynodont, *Dvinia* displays some derived features, such as differentiation of the postcanine dentition into 'premolars' and 'molars,' a well-developed bony secondary palate, and gomphodont dentition with numerous accessory cusps. The postcanine dentition of *Dvinia* did not occlude as in the Triassic cynodonts, instead the maxillary postcanine teeth passed labial to the mandibular series during jaw adduction (Tatarinov, 1968).

Hopson and Kitching (1972) synonymised many of the early basal cynodont genera with *Procynosuchus*. This genus possesses a number of incisiform teeth borne on the maxillae (Kemp, 2005) that are sometimes referred to as precanine teeth. Broom (1937a: fig 14, 1938: figs 2 and 5) illustrated the snout of *Procynosuchus* as having replacement maxillary canines medial to the alveolus of the functional canine.

The postcanine dentition of *Procynosuchus* is differentiated into five anterior premolariform teeth (each with a slightly recurved mesial cusp, and a slight swelling on the distal side of the tooth), followed by a series of eight more complex molariform teeth (Kemp, 2005). Kemp, (1979) states that the type of tooth replacement can be described as alternate, as is seen in *Thrinaxodon*.

Probably the most well studied therapsid, *Thrinaxodon* has been the subject of several studies into the origin of the mammalian dental condition, as early as 1936 by Parrington. This genus is known from South Africa and Antarctica (Colbert,

1982), and is structurally on the same grade as *Galesaurus*, i.e., intermediate between *Procynosuchus* and epicynodonts (Kemp, 2005).

Brink (1955a) described a particularly small specimen of *Thrinaxodon*, and mentioned a discussion with A.W. Crompton about the type of tooth replacement that would have occurred in the animal. It was decided that the mammalian grade of diphyodonty had not yet evolved, but it was postulated that an animal like *Diademodon*, with its more complex postcanine teeth might have already evolved the mammalian condition of diphyodonty. The most recent study on the tooth replacement patterns of *Thrinaxodon* was undertaken by Abdala *et al.* (2013).

The work of Abdala *et al.* (2013) was the first study of the tooth replacement patterns in *Thrinaxodon* using micro-computed tomography (μCT). Although Hopson (1964) and Gow (1985b) recognised replacement of the incisors, they were unable to comment on the pattern of replacement. Abdala *et al.* (2013), on the other hand, described an alternating pattern of replacement in both the upper and lower incisors. Additionally, Abdala *et al.* (2013) noted that the rate of replacement of the incisors increased through ontogeny, with larger specimens having replacement teeth associated with nearly all of the incisors. In contrast, it was shown that the rate of replacement of the canines was higher in juveniles. Abdala *et al.* (2013) also confirmed the observations of previous researchers that replacing maxillary canines erupted mesial to the functional tooth, whereas replacement mandibular canines erupted distal to the functional tooth. Although Fourie (1964) and Gow (1985b) identified a juvenile *Thrinaxodon* which showed

a replacement maxillary canine erupting distal to the functional tooth, this arrangement was not observed in any of the μCT-scanned specimens (Abdala *et al.*, 2013).

Alternating replacement of the postcanines is well documented in *Thrinaxodon* (Parrington, 1936b; Crompton, 1963; Osborn and Crompton, 1973; Gow, 1985b), with the distal migration of the series through ontogeny first proposed by Crompton (1963). Abdala *et al.* (2013) confirmed such a migration of the postcanines in both the maxillary and mandibular series. Cessation of replacement was as the result of the canine invading the postcanine alveolus, leading to the resorption of the postcanine roots. Finally, Abdala *et al.* (2013) concluded that replacement continued through ontogeny to the final stages of life.

In the more derived cynodont *Diademodon*, the postcanines engaged in precise tooth-to-tooth occlusion during jaw adduction, leading researchers to believe they had adopted a herbivorous diet (Kemp, 2005). Despite this shift to a herbivorous lifestyle, large canines are still present.

Broom (1913a) offered the first evidence of tooth replacement in the incisors and 'molars' in *Diademodon*, and the dentition of *Diademodon* has since received much attention, e.g., Fourie (1963), Fourie (1964), Ziegler (1969), Hopson (1971), and Osborn (1974).

Brink (1955b, 1956, 1977) and Crompton (1955) demonstrated that postcanine replacement in *Diademodon* occurred from front to back. Similar front-to-back waves of tooth eruption have also been described in the postcanines of derived gomphodonts (Patterson and Olson, 1961) and tritylodonts (Kühne, 1956). In these examples, however, there is no evidence for replacement of the distal-most teeth, indicating the addition of teeth to the postcanine series with increasing age. Such addition of postcanines, which do not have a deciduous precursor, may represent an early stage in the development of mammalian diphyodonty. Gomphodont cynodonts and tritylodontids were the only non-mammalian synapsids to have reduced the number of postcanine replacement generations (Crompton, 1955; Kühne, 1956).

Gow (1994) described a specimen of *Diarthrognathus* (BP/1/4884) consisting of a fragmentary lower jaw, which showed signs of tooth replacement. The fragment preserves a series of nine postcanine teeth, of which the first is a partially erupted replacement tooth. The fifth tooth shows signs of partial resorption of the root, and a partially erupted replacing tooth is visible beneath the erupted tooth.

Gow (1994) described the presence of crypts along the groove for the dental lamina, and suggests the addition of teeth to the distal margin of the postcanine series. He also described how the postcanine teeth of *Diarthrognathus* changed orientation within the dentary ramus after eruption, a condition that does not occur in the sister taxon, *Pachygenelus*.

2 MATERIALS AND METHODS

2.1 Material

Several specimens belonging to several eutheriodont taxa were μCT-scanned during the course of this study. Taxa were selected such that an ontogenetic sequence could be represented in the sample. These are listed in Table 1. For a more comprehensive list of specimens included for gross anatomical observations, consult the relevant chapters.

Table 1. Specimens of Eutheriodontia μCT-scanned for this study. Specimens arranged according to increasing basal skull length (BSL) or snout length (SL) if the skull is incomplete.

Taxon	Specimen	BSL (mm)	SL (mm)
Lycosuchidae (*n* = 2) (Chapter 3)	US D173	232	114
	CGS C60	—	119
Bauria (*n* = 4) (Chapter 4)	BP/1/2837	—	—
	BP/1/4678	—	—
	BP/1/1180	114	47
	BP/1/1685	132	72
Cynosaurus (*n* = 5) (Chapter 5)	BP/1/1563	49	16
	BP/1/4469	56	22
	SAM-PK-K10694	—	34
	AM 4947	—	~35
	BP/1/3926	115	45
Galesaurus (*n* = 8) (Chapter 6)	RC 845	69	—
	BP/1/4714	81	—
	BP/1/4602	88	—
	NMQR 135	94	—
	NMQR 3542	102	—
	BP/1/5064	103	—
	SAM-PK-K10468	105	—
	NMQR 860	114	—

2.2 Micro-computed tomography scanning

All specimens listed in Table 1 were scanned using a Nikon metrology XTH 225/320 LC dual source industrial CT system at the Wits Microfocus X-ray CT Facility (Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa). For detailed parameters used during the scanning experiments, consult the relevant chapters.

2.3 Segmentation workflow

Three dimensional rendering and segmentation of the volume data were performed using VGStudio MAX (Volume Graphics, Heidelberg, Germany). Replacement teeth were recognisable due to the presence of mineralised tissue and are therefore considered as being at least in an advanced bell stage (Luckett, 1993). It is during middle–late bell stages that tooth crown morphology is determined due to apposition and mineralisation of dentine and enamel (Avery and Chiego, 2006). For all samples, teeth were segmented as separate material from the surrounding bone and matrix. Due to low contrast between tooth and bone in several specimens, segmentation was performed manually using the ‘polygon lasso’ or ‘polyline’ tool. When there was sufficient contrast, segmentation was performed using the semiautomatic 3-D ‘region-growing’ tool. Images were exported from VGStudio MAX in TIFF format with the custom image size set between 3 500–4 000 pixels wide.

2.4 Photography

Specimens were photographed using a Canon EOS 450D, with either a Canon EF-S 15–85 mm *f*/3.5–5.6 IS USM or a Canon EF-S 60 mm *f*/2.8 USM lens attached, depending on the size of the specimen/feature to be photographed. A vertical camera stand or tripod was used, and image stabilisation was switched off. In order to prevent "camera shake," a remote cable shutter release was used.

2.5 Figure preparation

Figures were created using GNU Image Manipulation Program (GIMP) 2.8.22 for the handling of raster images (photographs and images exported from VGStudio MAX), and Inkscape 0.92 for vector images (line drawings) and the labelling of figures. Figures included in chapters intended for submission for publication (i.e., Chapters 3–4) were prepared according to the guidelines laid out by the respective journal's instructions to authors.

2.5.1 Symbols and colours

Symbols used in scatter plots were chosen based on the suggestions of Krzywinski and Wong (2013). Symbols were chosen such that interference in legibility due to overlapping of data points could be minimised. The reliance on colour was also minimised where possible, ensuring that information would remain discernible even if reproduced in greyscale.

The use of colours to differentiate between features in 3-D renderings of specimens was also minimised. Colours were chosen, after consulting Wong

(2011), such that figures would be colour-deficient friendly. Samples of the colours used, and how they appear to respective colour-deficient readers appear below (Figure 3).

Colour figures were checked for legibility using the "Preview Mode" in Scribus 1.4.7, which allows for the simulated colour perception of the three types of colour-deficiency illustrated in Figure 3.

Original	Colour name	RGB (0–255)	CMYK (%)	Simulation		
				Protan	Deuter	Tritan
	Blue	0,114, 177	100, 50, 0, 0			
	Vermilion	212, 94, 0	0, 80, 100, 0			
	Sky blue	86, 180, 233	80, 0, 0, 0			
	Bluish green	0, 158, 115	97, 0, 75, 0			
	Yellow	240, 228, 66	10, 5, 90, 0			
	Orange	230, 159, 0	0, 50, 100, 0			
	Reddish purple	204, 121, 167	10, 70, 0, 0			
	Black	0, 0, 0	0, 0, 0, 100			

Figure 3. Colours used in this thesis, optimised for colour-blind individuals. Simulation of the approximate hues perceived by individuals with impaired colour vision. The top two rows represent colours used in this work, whereas the remaining five colours represent possible alternatives. Abbreviations: Protan, protanopia (red-green); Deuter, deuteranopia (red-green); Tritan, tritanopia (blue-yellow). Modified from Okabe and Ito (2008: fig. 16) and Wong (2011: fig. 2).

2.6 Terminology

2.6.1 Tooth types

The taxa described in this body of work are heterodontous, i.e., the dentition of different parts of the jaw are morphologically distinguished from one another. This is perhaps best demonstrated in mammals, in which the dentition can be differentiated into incisors (I/i), canines (C/c), premolars and molars. Due to there being no analogues to true molars in the sample, all dentition distal to the canine(s) are termed postcanines (PC/pc). The abbreviation PC/pc is preferred to avoid possible confusion with mammalian premolars. This work follows an adapted terminology of Smith and Dodson (2003) as follows:

- I*n*, C*n*, PC*n* for referring to dentition of the upper jaw, and
- i*n*, c*n*, pc*n* when referring to the dentition of the lower jaw,

where '*n*' indicates the tooth position. If both upper and lower dentitions are denoted in a single formula, then the uppers will be written to the left of a virgule (/) and the lowers to the right, e.g., I5/4, C2/1, PC3/5.

2.6.2 Orientation

Smith and Dodson (2003) demonstrated that until recently there was no agreed standard terminology for describing dentition in vertebrate palaeontology. The proposed terms are those used by Edmund (1960). Edmund (1969) preferred the terms mesial and distal over alternatives such as anterior and posterior, due to the curved nature of the dental arcades (Figure 4). These terms are further defined below:

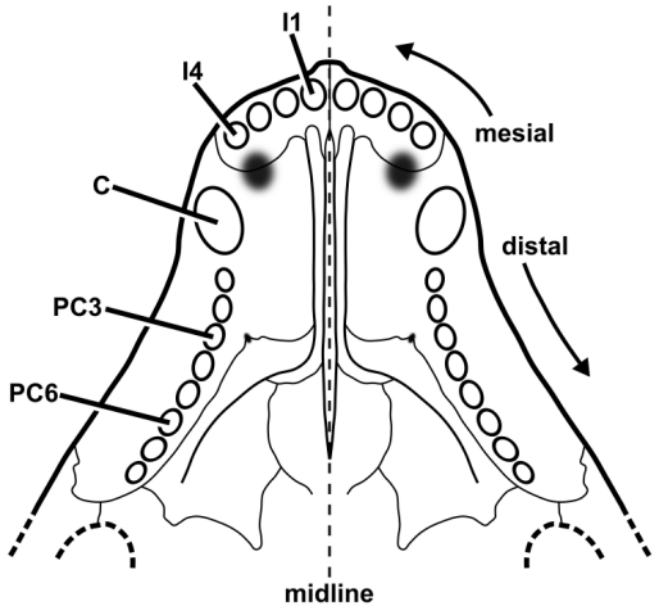

Figure 4. Schematic diagram of the dental arcades of *Cynosaurus suppostus* in ventral view, depicting the dental notation and terminology used in this work. Abbreviations: C, maxillary canine; I, premaxillary incisor; PC, maxillary postcanine. Redrawn from Brink (1986), with annotations after Peyer (1968: fig. 10) and Dyce *et al.* (1996).

Mesial	surface of tooth facing along the tooth row towards the premaxillary/dentary symphysis
Distal	surface of tooth facing along the tooth row away from the premaxillary/dentary symphysis
Occlusal	grinding or biting surface(s) of a tooth
Labial	surface of the tooth facing away from the buccal cavity, i.e., towards the lips or cheeks
Lingual	surface of the tooth facing towards the buccal cavity, i.e., towards the tongue

2.6.3 Number of tooth replacement generations

Smith (1958) described several types of tooth replacement patterns, illustrating them in his figure 5:

Polyphyodont	continual replacement of teeth through ontogeny (e.g., most non-mammalian vertebrates)
Oligophyodont	several sets of deciduous teeth, followed by a complete set of permanent teeth (e.g., some crocodilians and several families of lizard)
Fully diphyodont	one complete set of deciduous teeth, replaced by one complete set of permanent teeth (e.g., basal mammals)
Hemidiphyodont	one partial set of deciduous teeth, replaced by a complete set of permanent teeth, resulting in addition of teeth to distal margin of series through ontogeny (e.g., most eutherians)
Fully monophyodont	only a single set of permanent dentition (e.g., toothed whales)

3 RE-EVALUATION OF TOOTH REPLACEMENT PATTERNS OF THE LYCOSUCHIDAE (THERAPSIDA, THEROCEPHALIA) USING MICRO-COMPUTED TOMOGRAPHY

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3.1 Abstract

The Lycosuchidae represent the earliest-diverging family within Therocephalia from the middle Permian of South Africa. One of the most recognisable features of the group is the presence of two large maxillary canines. This condition has in the past been used either to diagnose the family, or to indicate that the Lycosuchidae represents an unnatural grouping of individuals undergoing replacement of the maxillary canine. Study of tooth replacement using micro-computed tomography scanning revealed that the incisors, canines, and postcanines underwent alternating replacement. Additionally, it was discovered that each of the prominent maxillary canines was replaced independently. It is proposed that the Lycosuchidae had two active maxillary canine tooth families that functioned simultaneously, such that a new replacement canine erupted in each locus alternately. Thus, instead of the functional canine alternating between the left and right side, as proposed by previous researchers, results of this study support the hypothesis that each maxilla bore a functional canine simultaneously, and that the functional tooth instead alternated between the mesial and distal canine locus.

3.2 Introduction

The early Therocephalia of the middle Permian of South Africa possibly represent one of the least studied therapsid groups. This is exacerbated by the fact that much of the therocephalian material from the *Tapinocephalus* Assemblage Zone (TAZ) is poorly preserved, distorted, almost always incomplete, and often encased in hard matrix (van den Heever, 1987).

Therocephalians from the *Eodicynodon* and *Tapinocephalus* assemblage zones are the oldest in the world (Abdala *et al.*, 2008), with the estimated age of the TAZ being older than ~260 Ma (Rubidge *et al.*, 2013; Day *et al.*, 2015). No therocephalians are known from the middle Permian deposits of China (Liu and Abdala, 2017), and only a single species (*Porosteognathus efremovi*) has been described from the middle Permian Isheevo locality of Russia (Vjuschkov, 1955; Ivakhnenko, 2011), which correlates with the TAZ of the South African Karoo (Benton *et al.*, 2012). In contrast, a rich record of dinocephalians, anomodonts and parareptiles are known from the middle Permian rocks of China and Russia (Li, 2001; Ivakhnenko, 2003).

Recently, a new taxon of basal therocephalian (*Gorynychus masyutinae*) has been described from the Kotelnich locality of Russia (Kammerer and Masyutin, 2018). The Kotelnich rocks, attributed to the middle or upper Permian, are roughly equivalent in age to the *Pristerognathus* AZ of South Africa (Tatarinov, 2000; Benton *et al.*, 2012), although, based on comparisons of anomodont taxa, the *Tropidostoma* AZ may also be a contender (Kurkin, 2011). Thus, the early

therocephalian fauna from the Karoo of South Africa records an important period of evolution of the basal Eutheriodontia that at present has not been recovered in similarly aged deposits from other parts of the world.

Several basal therocephalian taxa (Table 2) have been established based on descriptions of poorly preserved, fragmentary specimens (see Abdala *et al.* [2014a: fig. 1]). This has lead to a complex taxonomy of the group where the relationships between families, as well as the relationship of Therocephalia to other members of Therapsida is not well resolved (Boonstra, 1972; Kemp, 1982; van den Heever, 1994). Previous phylogenetic work on the Eutheriodontia has yielded two hypotheses regarding the interrelationships of the Therocephalia. A paraphyletic Therocephalia with regards to the Cynodontia, originally proposed by Kemp (1972) is supported by Abdala (2007), Botha *et al.* (2007), and Abdala *et al.* (2008). In these analyses, the basal therocephalian families Lycosuchidae and Scylacosauridae, as well as the whaitsiid *Theriognathus* were placed outside of the core therocephalian group, Eutherocephalia. More recent phylogenetic analyses (e.g., Huttenlocker [2009, 2014], Huttenlocker *et al.* [2011], Sigurdsen *et al.* [2012], Huttenlocker and Smith [2017], and Liu and Abdala [2017, 2019]), which have included a larger sample of therocephalian taxa, recovered a monophyletic Therocephalia, as has been advocated in the past by several authors (Hopson and Barghusen, 1986; Hopson, 1991; van den Heever, 1994; Rubidge and Sidor, 2001). These authors all agree that the Lycosuchidae represent one of the most basal therocephalian groups.

Table 2. List of specimens attributed to the Lycosuchidae after the taxonomic revisions of van den Heever (1987) and Abdala *et al.* (2014a). Adapted from Abdala *et al.* (2014a: tables 1 and 2).

Specimen	Identification		
	Original	**van den Heever (1987)**	**Abdala *et al.* (2014a)**
US D173	*Lycosuchus vanderrieti* (Broom, 1903a)	valid	valid
SAM-PK-632	*Scymnosaurus ferox*	Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*
SAM-PK-633	*Lycosuchus mackayi* (Broom, 1903b)	Therapsida *incertae sedis*	Gorgonopsia *incertae sedis*
SAM-PK-1079	*Hyaenasuchus whaitsi* (Broom, 1908a)	*Lycosuchus vanderrieti*	Lycosuchidae *incertae sedis*
SAM-PK-1076		Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*
AMNH FARB 5543	*Trochosuchus major*[a] (Broom, 1915a)	Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*
SAM-PK-2756	*Trochosaurus intermedius*	Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*
TM 275	*Trochorhinus vanhoepeni* (Broom, 1936a)	Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*
SAM-PK-9005	*Scymnosaurus major*	Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*
SAM-PK-12185	*Zinnosaurus paucidens*	*Lycosuchus vanderrieti*	Lycosuchidae *incertae sedis*
SAM-PK-3430	*Scymnosaurus ferox*	Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*
SAM-PK-9084[b]	*Scymnosaurus ferox*	Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*
SAM-PK-10556	*Scymnosaurus major*	Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*
SAM-PK-8999	*Scymnosaurus* sp.	Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*
SAM-PK-11961	*Scymnosaurus* sp.	Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*

[a] Abdala *et al.* (2014a: table 1) give original name as *Trochosaurus major*.

[b] Used by Huttenlocker (2014: appendix S3) as a voucher specimen for *Lycosuchus*

Table 2. List of specimens attributed to the Lycosuchidae after the taxonomic revisions of van den Heever (1987) and Abdala *et al.* (2014a) (Continued).

Specimen	Identification		
	Original	**van den Heever (1987)**	**Abdala *et al.* (2014a)**
NHMUK R5747[c]	*Trochosaurus major*[d]	Lycosuchidae *incertae sedis*	Lycosuchidae *incertae sedis*
NHMUK PV OR 49422	*Simorhinella baini* (Broom, 1915b)	—	valid
CGS M793	—	*Lycosuchus vanderrieti*	*Lycosuchus vanderrieti*
CGS C60	—	*Lycosuchus keyseri*	Lycosuchidae *incertae sedis*
—[e]	*Trochosaurus dirus* (Broom, 1936b)	*nomen dubium*	—
BP/1/5592[f]	—	—	*Simorhinella baini*
CGS MJF68	—	—	*Lycosuchus vanderrieti*
BP/1/7162	—	—	*Lycosuchus vanderrieti*
MB.R.995	—	—	*Lycosuchus vanderrieti*
SAM-PK-751	—	—	Lycosuchidae *incertae sedis*
CGS RMS1013	—	—	Lycosuchidae *incertae sedis*
CGS RMS990	—	—	Lycosuchidae *incertae sedis*
FMNH 1707	—	—	Lycosuchidae *incertae sedis*
CGS RMS888	—	—	Lycosuchidae *incertae sedis*
SAM-PK-11936	—	—	Lycosuchidae *incertae sedis*
CGS MJF21	—	—	Lycosuchidae *incertae sedis*
CGS RMS869	—	—	Lycosuchidae *incertae sedis*

[c] Tooth replacement described Kermack (1956)

[d] *Trochosuchus* referred to *Trochosaurus* by Broom (1932a)

[e] Holotype lost (van den Heever, 1987: 491)

[f] Adult specimen described by Abdala *et al.* (2014a)

The Lycosuchidae are one of two therocephalian families that occur in the TAZ of the main Karoo Basin, South Africa, the other being the Scylacosauridae (van den Heever, 1994; Abdala *et al.*, 2014a). The Lycosuchidae comprises two genera, *Lycosuchus* and *Simorhinella*. It was previously thought that *Lycosuchus* was restricted to the TAZ (Smith and Keyser, 1995a; Abdala *et al.*, 2008; Smith *et al.*, 2011), but recent work has shown that its stratigraphic range extends upwards, well into the overlying *Pristerognathus* Assemblage Zone (Kammerer, 2009; Day, 2013; Abdala *et al.*, 2014a). Fossils belonging to *Lycosuchus* have been recovered from the uppermost Abrahamskraal Formation, and the Poortjie Member of the Teekloof Formation of the TAZ (Day, 2013).

Several authors have in the past considered the presence of two large 'functional' canines in each maxilla as a diagnostic character of the Lycosuchidae (Broom, 1932a; Haughton and Brink, 1954), which comprised the genera *Hyaenasuchus*, *Lycosuchus*, *Trochorhinus*, and *Trochosaurus*. Van den Heever (1980), however, disputed the validity of the family, and tested his hypothesis in a detailed study of the mode of replacement of the maxillary canines. He concluded that specimens bearing two maxillary canines represented members of the Pristerognathidae that were undergoing replacement of the canine at the time of death. He further suggested that the Lycosuchidae represented an unnatural grouping, and proposed that the name be invalidated (van den Heever, 1980).

Later, van den Heever (1987, 1994) resurrected the Lycosuchidae as a monotypic family, placing the other early therocephalian families in the Scylacosauridae.

Previously, 12 nominal taxa were recognised in the Lycosuchidae (Haughton and Brink, 1954) (Table 2), but van den Heever (1987) reduced this number to two genera, *Lycosuchus* and *Simorhinella*, and regarded most of the previously described material as Lycosuchidae *incertae sedis*. Most recently, Abdala *et al.* (2014a) described an adult specimen of *Simorhinella baini*, and referred a large number of previously undescribed specimens to the family Lycosuchidae. Until the palates of these specimens are prepared, it is not possible to determine their generic assignment with certainty, and they are considered Lycosuchidae *incertae sedis*.

The first investigation into the tooth replacement patterns of basal theriodonts was undertaken by Parrington (1936a). However, these were based on very fragmentary material, and the taxonomic identification of these specimens remains uncertain. Of particular interest is Parrington's figure 2, which shows a transverse section through the upper dentition of a theriodont. Parrington (1936a: 113) tentatively identified the specimen (Figure 5) as a therocephalian. However, in a private communication with Kermack (1956: 125), Parrington later mused that the specimen may just as well represent a gorgonopsian. In Parrington's (1936a) figure, the cross-sections of five canines are labelled in each maxilla, and seemingly represent two distinct canine families; with the teeth labelled B, C and E representing a mesial tooth family, and A and D representing a distal tooth family. Without a proper taxonomic identification for the specimen in question, the significance of this arrangement of the replacing canines was apparently

overlooked in subsequent studies on the tooth replacement of the basal theriodonts.

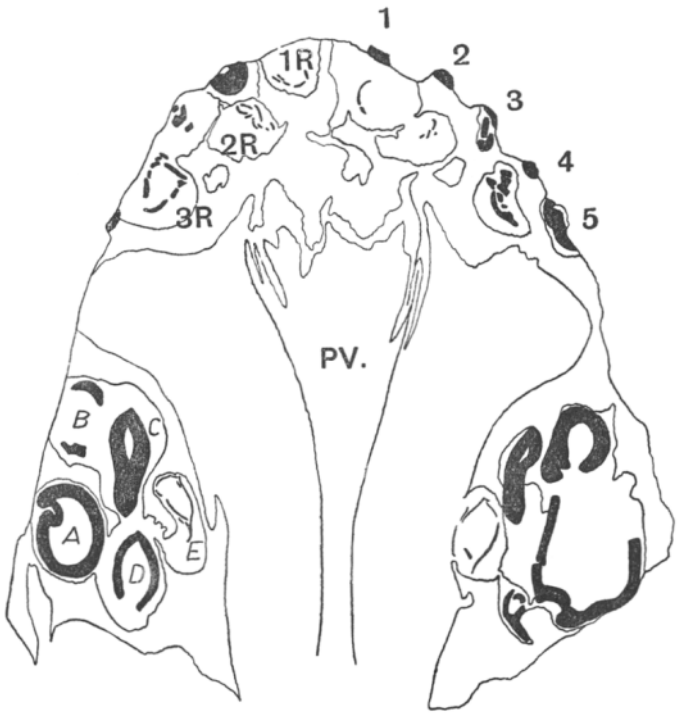

Figure 5. Section through the palate of an unknown theriodont.
1–5, incisors of left premaxilla; 1R–3R, replacement incisors of the right premaxilla; A–E, maxillary canine teeth labelled in order of increasing size, PV., "prevomers." Reproduced from Parrington (1936a: fig. 2).

Previous studies on the tooth replacement of the Lycosuchidae have focused primarily on the canines. Kermack (1956) studied several specimens (mostly from the NHMUK) that had been previously sectioned, were fragmentary in nature, or were specifically prepared for the study using acid preparation. The taxonomic identifications of the therocephalian specimens have been updated following van den Heever (1987) and Huttenlocker and Abdala (2015) (Table 3).

Table 3. Therocephalian specimens included in the study by Kermack (1956) with updated identifications.

Specimen	Alt. no.[a]	Current identification	Kermack's (1956) Identification	Preparation technique	PC count (MX/mn)
NHMUK PV R 5747		Lycosuchidae *incertae sedis* (van den Heever, 1987)	*Trochosaurus major* (Broom, 1932a)	Fragmentary with acid treatment according to van den Heever (1987)	3/? (2?/5)
NHMUK PV R 2581		*Pristerognathus polyodon*	*Pristerognathus polyodon* (Seeley, 1894)	Acid	4/3 (8/7)
NHMUK PV R 15958	Watson's no. "R393"	Scylacosauridae (cf. *Glanosuchus*) (Huttenlocker, pers. comm., 2018)	*Pristerognathus polyodon*	Acid	2?/3? (5/7)
NHMUK PV R 4097		Scylacosauridae *incertae sedis* (van den Heever, 1987)	*Cynariognathus platyrhinus* (Boonstra, 1934)	Sectioned by Boonstra, (1934: fig. 1)	6/– (?/8)
NHMUK PV R5699		*Theriognathus microps* (Huttenlocker and Abdala, 2015)	*Notosollasia laticeps* (Broom 1925)	Fragmentary	—[b]
UMZC T.904	Parrington's no. "100"	*Theriognathus microps* (Huttenlocker and Abdala, 2015)	*Whaitsia* sp.	Acid	—[b]

[a] Alternative numbers used by Kermack (1956).

[b] *Theriognathus microps* does not have postcanine dentition (Huttenlocker, 2009; Huttenlocker and Abdala, 2015).

Several of these specimens had been previously figured by Boonstra (1934). Kermack (1956: 100) also employed the "usual medical techniques" to create radiographs of several gorgonopsian specimens and a single therocephalian specimen (NHMUK PV R 15958), however, only images of the latter were published (pl. 8, fig. 24a [note that figure labels are swapped in the captions of Kermack (1956)]). This was the first published study demonstrating the use of X-rays for the study of tooth replacement in theriodonts. More recently, Abdala *et al.* (2008) demonstrated the usefulness of medical CT-scanning to differentiate between canine and precanine dentition of the scylacosaurid *Ictidosaurus* (NMQR 2910).

It is beyond the scope of this study to disentangle the complex taxonomic histories of the basal Therocephalia (see van den Heever [1987] for detailed descriptions of the numerous taxonomic revisions of the families of the TAZ Therocephalia). The aim of this research is rather to gain an understanding of the tooth replacement patterns of the group, such that they may be incorporated as characters in future phylogenetic analyses. Determining the pattern of tooth replacement in the basal Therocephalia is in important step towards understanding how the tooth replacement patterns of more derived therocephalians (e.g., *Bauria*) may have evolved to become better suited towards herbivory. This chapter follows the taxonomy of the Lycosuchidae according to Abdala *et al.* (2014a).

Due to the fragmentary nature of many basal therocephalian specimens, as well as the small number of lycosuchid specimens positively identified to genus/species

level (*Lycosuchus n* = 5, *Simorhinella n* = 2) (Table 2), the results will also be discussed at the family level as a means to complement the results, and to facilitate comparison with other taxa.

3.3 Materials and methods

Day (2013) mentions six specimens belonging to *Lycosuchus*, whereas Abdala *et al.* (2014a) identified five specimens belonging to *Lycosuchus vanderrieti* (Table 4). Due to the fragmentary preservation and unprepared nature of several specimens, only two specimens were suitable for scanning purposes. Additional specimens of the Lycosuchidae were studied through first-hand observation, and historical accounts were consulted for specimens that were not available for this study.

Table 4. Specimens attributed to *Lycosuchus* by Abdala *et al.* (2014a). Adapted from Abdala *et al.* (2014a: tables 5 and 6).

Specimen	BSL (mm)	SL (mm)	Incisors	Canines (L/R)	PC
CGS MJF68	220	212	5	1/1	3
US D173	232	114	5	C1/R?	3
CGS M793	~275	—	—	C1/1	2
BP/1/7162	298	149	5	C2/C1	?3
MB.R.995	—	~195	5	C2/C2	2

Abbreviations: BSL, basal skull length; L, left; PC, maxillary postcanine count; R, right; C1, mesial canine replacing the distal canine; C2, distal canine replacing the mesial canine; R?, replacement occurring but cannot determine which tooth is the new element; SL, snout length.

3.3.1 US D173

The holotype of *Lycosuchus vanderrieti* (Broom, 1903a), comprises a complete skull measuring 232 mm in length, with a tightly occluded mandible. This well preserved specimen was previously prepared using an 11% solution of formic acid (van den Heever, 1980).

3.3.2 CGS C60

Named *Lycosuchus keyseri* by van den Heever (1987), Abdala *et al.* (2014a) have subsequently considered specimen CGS C60 as Lycosuchidae *incertae sedis* (Table 2). It comprises an almost complete anterior skull with an associated lower jaw. Despite being broken into several fragments, this specimen is one of very few lycosuchids to preserve the complete dentition. The specimen has been previously prepared mechanically (van den Heever, 1980). Only fragments preserving teeth were scanned, and each fragment was scanned separately (Table 5).

Table 5. Parameters used for the µCT-scanning of Lycosuchidae specimens.

Specimen	Material	Tube voltage (kV)	Tube current (µA)	Frame rate (fps)
US D173	Snout	135	200	0.5
CGS C60	Left maxilla	100	200	0.25
	Right maxilla	130	200	1
	Left dentary	105	140	1
	Right dentary	130	200	1

3.4 Results

3.4.1 Lycosuchidae tooth morphology

3.4.1.1 Incisors

The incisor crowns bear lateral ridges on the mesial and distal margins. These may become worn in the functional teeth, but are clearly visible in the unworn crowns of unerupted replacement teeth. The crown is similar in length to the root.

3.4.1.2 Canines

The crowns of the canine teeth are labiolingually flattened, and bear serrations on the mesial and distal surfaces. In comparison, the canine roots are more rounded in cross section, and the ridges are absent. The root of the maxillary canine is slightly longer than the crown, and extends high into the maxilla. The mandibular canines are smaller and more gracile than the maxillary canines. A single canine is preserved in each dentary, and their laterally compressed crowns bear serrations on the mesial and distal edges.

3.4.1.3 Postcanines

The postcanines are simple conical, labiolingually compressed teeth, reduced in both size (relative to the anterior dentition) and number (in comparison to other therocephalians). The postcanine teeth show evidence for serrations on the distal edges.

3.4.2 Tooth replacement

Evidence of tooth replacement was recorded in both µCT-scanned specimens of Lycosuchidae. Both specimens allowed an evaluation of the replacement activity for the preserved dental complement of the same individual. Replacement teeth for all tooth types are situated lingual to the erupted tooth. The following sections describe the states of replacement of the teeth (i.e., presence of replacement teeth, developmental condition of roots, etc.) for the two µCT-scanned lycosuchid specimens.

3.4.3 US D173 (BSL 232 mm, SL 114 mm)

3.4.3.1 Incisors

Based on preserved teeth and empty alveoli (Figure 6A, B), there is evidence for five incisors in each premaxilla. In the left premaxilla, I2, I4, and I5 are represented by functional teeth. The root apices of the functional teeth are closed, indicating that they were fully developed. Replacement teeth with mineralised tissue are situated lingual to the alveoli of I1, I2, I3, and I4. The crown of the replacing I1 is visible in the alveolus. The crown of I3 is broken, but a root showing partial resorption by the associated replacement tooth remains in the alveolus. The replacements of I1 and I3 have nearly fully formed crowns, whereas those of I2 and I4 are little more than crypts with mineralised tooth germs. The right premaxilla preserves functional teeth in the I1, I2, I4, and I5 loci, and replacement teeth are visible lingual to the functional I2 and I4 (Figure 7). The I3 was still erupting at the time of death. The tooth has an open root, and the tooth walls are thinner than those of the neighbouring functional teeth.

Three incisors are preserved in each dentary (Figure 6C, D). Functional teeth are present in i2 and i3 on the left, and i1 and i2 on the right. Large replacement teeth are associated with each i1, with the replacement on the left being slightly more developed. Developing crowns of replacement teeth were also developing lingual to each i3, with that on the right being more developed. Remnant roots of exfoliated teeth are situated at the left i1 and right i3.

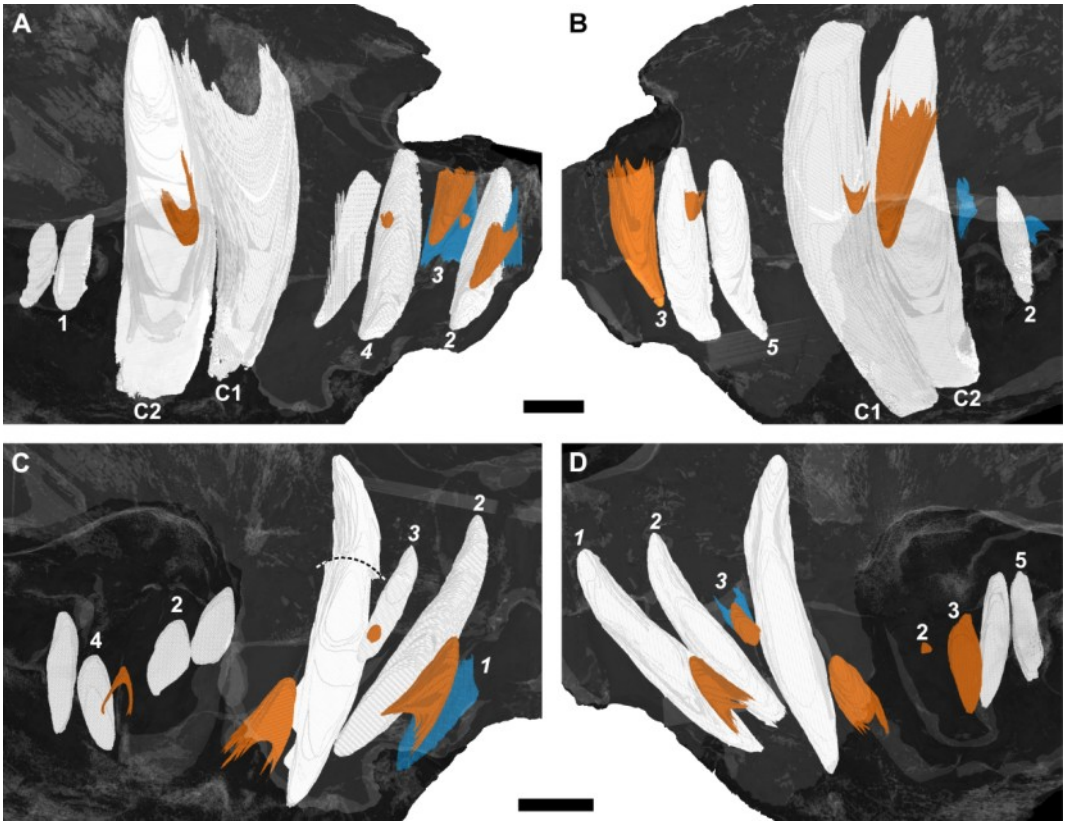

Figure 6. Three-dimensional rendering of the tooth rows of *Lycosuchus vanderrieti* (US D173) in medial view.
A, upper left; B, upper right; C lower left; D, lower right. Replacement teeth in orange, old remnant roots in blue. Dashed line indicates a break in crown the of the left mandibular canine. Abbreviations: C1, mesial maxillary canine; C2, distal maxillary canine. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bars equal 10 mm.

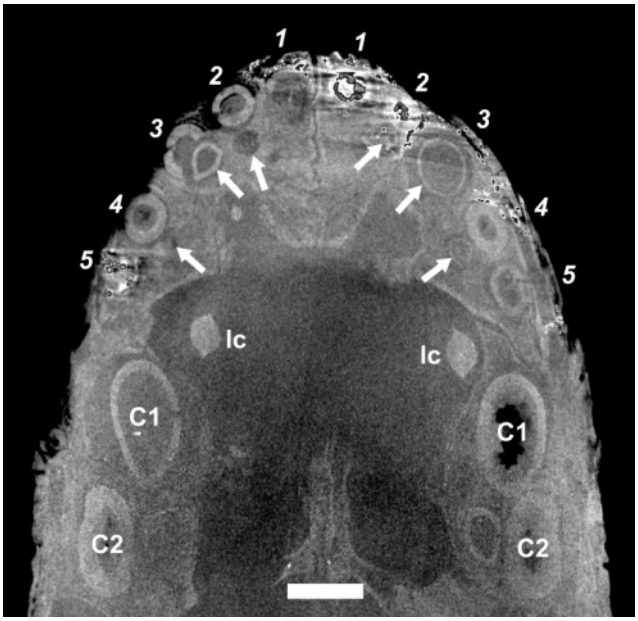

Figure 7. Virtual Transverse cross-section through the premaxilla of *Lycosuchus vanderrieti* (US D173).

Note the bright spots associated with the left I5 and right I1, I2, and I4, resulting from metallic inclusions in the specimen. Abbreviations: C1, mesial maxillary canine; C2, distal maxillary canine; lc, mandibular canine. Arrows indicate replacement incisors. Arabic numerals indicate incisor positions. Scale bar equals 10 mm.

3.4.3.2 Canines

Two large canines are preserved in each maxilla. On the left (Figure 6A), the distal canine (C2) is considered the functional tooth, as it is larger and has a closed root. The mesial tooth (C1) has an open root, and was still in the process of erupting. A replacement tooth was developing lingual to C2. Both canines of the right maxilla are of similar size and development (Figure 6B). The mesial canine has a root that is more fully developed than that of the left, but the root apex does not appear to be fully closed. In comparison, the root of the distal canine is

completely closed, indicating that it is the more mature of the two canines, however both C1 and C2 could be considered to represent functional teeth. Replacement teeth are developing lingual to each of the erupted canines, with the distal replacement being larger. A single functional canine is preserved in each dentary (Figure 6C, D). A developing crown of a replacement mandibular canine is located distal to each functional canine, with a similar degree of development on both sides.

3.4.3.3 Postcanines

A series of three postcanine teeth is preserved in each maxilla. The first tooth is the largest, with the remaining teeth becoming successively smaller. There are no observable signs of replacement activity. A series containing five teeth is present in the left dentary. The crown comprises approximately one-third of the total length of the tooth, and is slightly recurved. A replacement tooth is developing lingual to pc3. The replacing pc3 is in the same plane as pc1 in occlusal view, whereas the remaining teeth of the series (pc2, pc4, pc5) lie in a single, more labial plane. There is insufficient contrast in the right dentary to accurately determine the state and number of elements of the right postcanine series. However, the larger replacement is interpreted as the developing pc3, based on comparison to the left replacement pc3 and position relative the mandibular canine.

3.4.4 CGS C60 (SL 119 mm)

3.4.4.1 Incisors

Due to the fragmentary nature of this specimen, the first pair of incisors are lost, such that only four incisors are preserved in each premaxilla. In the left premaxilla, small replacement teeth are visible lingual to the functional I2 and I4 (Figure 8A). The crowns of the I3 and I5 are almost perfectly preserved, whereas the crowns of the I1 and I3 have been lost. It is not certain if the stage of replacement is responsible for this condition. In the right premaxilla (Figure 8B), functional teeth are present at I2, I3, and I5, whereas I4 is represented by an alveolus filled in with bone. A large developing crown is present lingual to the empty alveolus at I4. There are three incisors in each dentary. In both hemimandibles the first two teeth are considerably larger than the i3. Replacements are present lingual to each i2, with the left replacement being larger than that of the right.

3.4.4.2 Canines

Two canine loci are visible in the left maxilla. The mesial locus contains a large functional tooth, whereas the distal locus has been partially refilled by spongy bone. Large replacement teeth are associated with both loci, with the distal replacement being much larger than the mesial replacement (Figure 8A). A similar condition is present in the right maxilla (Figure 8B). The crown of the distal replacement tooth is of similar size to that of the functional canine, and is partially erupted. The bone surrounding the alveolus of the exfoliated distal canine has undergone sufficient remodelling, such that it is almost indistinguishable from

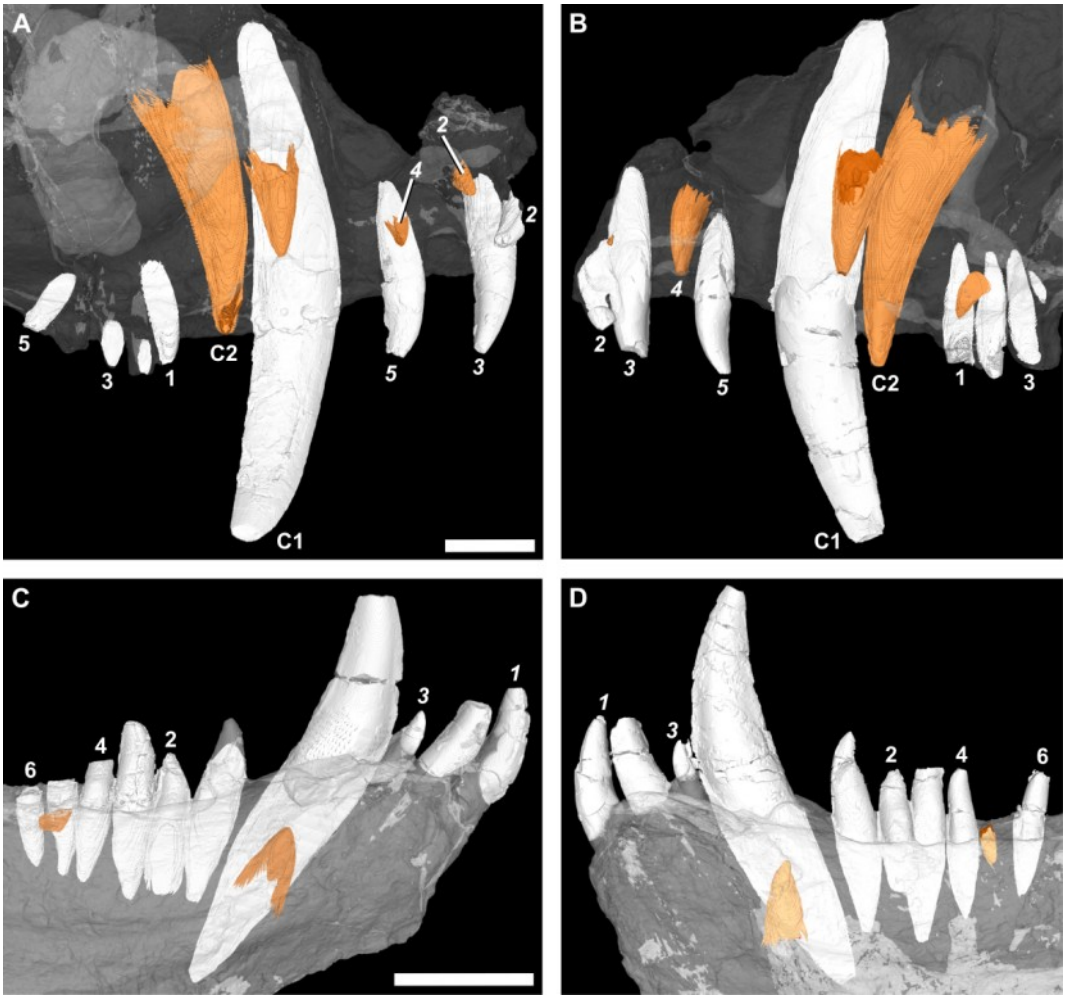

Figure 8. Three-dimensional rendering of the tooth rows of Lycosuchidae *incertae sedis* (CGS C60, = "*Lycosuchus keyseri*") in medial view.
A, upper left; B, upper right; C lower left; D, lower right. Abbreviations: C1, mesial maxillary canine; C2, distal maxillary canine. Replacement teeth in orange. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bars equal 20 mm.

the surrounding bony tissue. The mesial replacement crown is not yet in contact with the root of the functional crown, but it does appear as though resorption of the root had begun. Both dentaries bear a large functional canine (Figure 8C, D). A developing crown of a replacement canine is present lingual to the functional

tooth on both sides. These replacements are of similar size and developmental state in both sides.

3.4.4.3 Postcanines

Five postcanines are present in the left maxillary series. A replacement germ is positioned between the erupted PC3 and PC4. The first functional element (PC1) is positioned more lingual than the remaining teeth of the series, such that it lies in a similar plane to the replacement tooth (Figure 8A). It appears that there are only four postcanine teeth preserved in the right maxilla, with the distal-most element being represented by only a fragment of the root apex. A large replacement crown is associated with the first element.

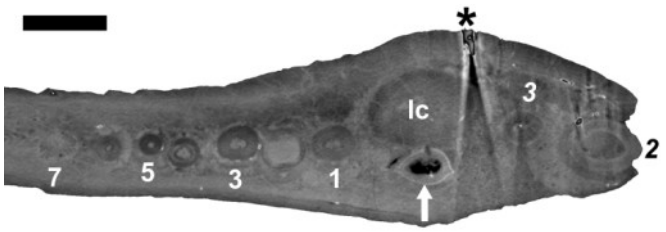

Figure 9. Virtual transverse section through the left dentary of Lycosuchidae *incertae sedis* (CGS C60, = "*Lycosuchus keyseri*").
Note that the odd-numbered postcanines lie in a plane more labial than the even-numbered postcanines. Abbreviation: lc, mandibular canine. Arrow indicates replacement mandibular canine. Arabic numerals indicate postcanine and incisor (italicised) positions. Asterisk (*) indicates artefact due to beam hardening. Scale bar equals 10 mm.

Six postcanine teeth are preserved in the left dentary (Figure 8C), with possible evidence for an empty alveolus in the position of pc7 (Figure 9). A replacement tooth was in the process of erupting lingual to the pc5. The even-numbered postcanines are situated more lingual than the odd-numbered teeth of the series, and are thus likely to still be in the process of erupting, and/or migrating to their final positions. A small partially resorbed root of a shed tooth is preserved labial to the functional pc2. As in the left, there is evidence for seven postcanine loci in the right dentary. The degree of development and positioning of the preserved teeth closely resemble that already described for the left dentary. One notable difference is that the functional tooth at pc5 of the right dentary had already been shed and a replacement tooth was developing.

3.4.5 Survey of Lycosuchidae from the literature

To complement the observations from the μCT-scanned specimens, previous descriptions were examined and first-hand observations of available specimens assigned to the Lycosuchidae were undertaken. *Lycosuchus* is considered first, followed by *Simorhinella*, and finally the numerous specimens attributed to Lycosuchidae *incertae sedis* by Abdala *et al.* (2014a).

3.4.5.1 *Lycosuchus vanderrieti* (CGS M793)

Due to weathering of the skull, van den Heever (1987) noted that the number of incisors could not be determined, but that serrations were present on all of the preserved teeth. The distal margins of both postcanine series are damaged, however, evidence for at least two teeth are preserved in each maxilla. Van den

Heever (1987: fig. 9) illustrated two maxillary canines on the left, with Abdala *et al.* (2014a) later interpreting the mesial canine as the replacement tooth.

3.4.5.2 *Simorhinella baini*

There are two specimens formally described as *Simorhinella baini*, NHMUK PV R49422 and BP/1/5592. Broom (1915b: 164) stated that the type of *Simorhinella* was "specially remarkable for the shortness and breadth of the snout and for the small size of the teeth," and reported the presence of four incisors, two canines, and three postcanines in each half of the upper buccal cavity. Broom (1915b: 164) further described NHMUK PV R49422 as "a young animal in which there is clear evidence of dental succession." Broom did not elaborate further on this statement, nor is any replacement activity indicated in his figure 1.

Abdala *et al.* (2014a: 1146) described two canines "positioned side by side" in the right maxilla of an adult specimen of *Simorhinella* (BP/1/5592), and interpreted the laterally positioned canine as a replacement. In the left maxilla, the more common arrangement of the replacement tooth lying mesial to the functional tooth is reported. The arrangement of one side of the canine dentition being at a more advanced stage of development has also been recorded in the Gorgonopsia (Kermack, 1956), as well as some basal Cynodontia (Abdala *et al.*, 2013) (see also Chapter 6). No replacement activity was reported in the incisors or postcanines.

3.4.5.3 Lycosuchidae *incertae sedis*

Several specimens showing double canines have previously been attributed to the Lycosuchidae (for a complete list of specimens see Table 2). Observations of those specimens that are now considered to be at least Lycosuchidae *incertae sedis* are presented. Specimens are treated in size order from shortest to longest snout length.

"*Trochosuchus acutus*" (SAM-PK-1076)—In his initial description, Broom (1908a) compared the small specimen (SL 101 mm) to *Aelurosaurus*. Broom described five incisors, two canines, and four postcanines. He described the first canine as being of similar size to the incisors, but laterally compressed and having distinct mesial and distal edges. It is likely that these teeth were still in the process of erupting, whereas the larger distal canines were functional. Two postcanines are preserved, with alveoli for an additional two. Broom regarded the first alveolus to be no longer functional.

"*Trochosuchus major*" (AMNH FARB 5543)—In his discussion of the canine teeth, Broom (1915a) writes of the possibility of one of the canines representing the replacement of the other. He later added, from observations of other therocephalians that the distal canine was in some instances replaced independently of the mesial canine. Broom also commented on the presence of roots for both canines in several taxa, coming to the conclusion that both canine loci held functional teeth, and were replaced indefinitely. No maxillary postcanines are preserved, but there are three mandibular postcanines.

"*Zinnosaurus paucidens*" (SAM-PK-12185)—Boonstra (1964) provided a very superficial description of the skull, instead focussing his attention on the description of the associated postcranial elements. Boonstra described the specimen as having a single maxillary canine, however, Abdala *et al.* (2014a) interpreted the left mesial canine as replacing the distal one, suggesting that two loci are represented in the specimen.

"*Lycosuchus mackayi*" (SAM-PK-633)—Described by Broom (1903b), the specimen consists of a badly weathered maxilla with some fragmentary skull elements in association. The maxilla preserves two large canines and a single postcanine. The similar dental formula lead Broom to believe that SAM-PK-633 belonged to *Lycosuchus*, but due to its greater size, he considered the specimen to be of a different species. Broom also concluded that the animal was a juvenile, possibly due to the distal canine having been in the process of erupting.

"*Trochosaurus intermedius*" (SAM-PK-2756)—Haughton (1915) wrote that both maxillary canines were large and functional, with C2 being slightly larger. A cross section of the snout revealed a smaller replacement tooth lingual to C1. Haughton commented that this specimen shared several characters with *Lycosuchus* and *Trochosuchus*, leading him to create a new species for this 'intermediate' specimen.

"*Hyaenasuchus whaitsi*" (SAM-PK-1079)—Broom (1908a) recognised that this specimen resembled *Lycosuchus vanderrieti*, but assigned it to a new taxon based

on the different dental formula. SAM-PK-1079 has an upper dentition comprising six incisors, two canines, and four postcanines. He interpreted the distal maxillary canine of the left side as being the more recently erupted tooth of the functional pair. In contrast, van den Heever (1980, 1987) considered the distal canine as a replacement tooth, as opposed to both teeth being functional. Abdala *et al.* (2014a: table 6) erroneously gave the canine count as a single element per side.

"*Scymnosaurus ferox*" (SAM-PK-632)—Described by Broom (1903b), the specimen consists of a partial snout ~180 mm in length. Broom described five incisors in the premaxilla, and a large canine followed by three postcanines in the maxilla. The crowns of the incisors are poorly preserved, but from the cross sections, Broom described a prominent distal edge and a more insipient mesial edge. Replacement teeth associated with the I1, I2, and I3 were documented. Broom described an old root preserved labial to the root of the left functional canine. Distal to the functional canine are the remains of the roots of a second canine, the pulp cavity of which is filled with spongy bone. No replacement activity was described for the postcanine dentition.

"*Symnosaurus*" *incertae sedis*—In his treatment of the pristerognathid Therocephalia from the *Tapinocephalus* AZ, Boonstra (1954) referred several fragmentary specimens to *Scymnognathus*, designating them *incertae sedis*. These include SAM-PK-8999, SAM-PK-11459, SAM-PK-11833, SAM-PK-11961, and SAM-PK-9126. Several of these have subsequently been designated Lycosuchidae *incertae sedis* by Abdala *et al.* (2014a: table 1).

"*Trochosaurus major*" (NHMUK R5747)—Boonstra (1934: 228, fig. 9) mentioned "definite evidence that the molars [= postcanines] as well as the canines and incisors are replaced," but did not show replacement of the incisors in his figure. Kermack (1956) described the condition of replacement in the incisors of the left premaxilla, noting that the I2 was only half erupted, and a replacement lingual tooth is lingual to the I5.

Boonstra (1934: fig. 9) shows replacement canines associated with both the mesial and distal canines in the right maxilla, and illustrates a similar condition in the left maxilla using dotted outlines of two replacement canines. Kermack's schematic representation (fig. 11a) agrees with that of Boonstra. The mesial functional canine was still in the process of eruption. Kermack (1956: fig. 11a) illustrated the presence of two replacement canines in the right maxilla. The state of development of the replacement canines in the left maxilla is not known.

3.5 Discussion

3.5.1 Tooth morphology and number

3.5.1.1 Incisors

According to van den Heever (1994) the number of upper incisors in the Lycosuchidae is always five. The observations in this study, as well as those of Abdala *et al.* (2014a), show that the fragmentary specimen CGS C60 has only four incisors preserved in each premaxilla. Due to the poor preservation of the anterior region of the snout, it is likely that the first pair of teeth have been lost. The juvenile specimen of *Simorhinella baini* (NHMUK PV OR 49422) also has

four upper incisors, whereas the adult specimen (BP/1/5592) has the typical five upper incisors.

The dentary holds three incisors. The first two teeth are considerably larger than the third, which is situated more lingual, giving the impression that it was still in the process of erupting. The closed root morphology of the i3, however shows that the tooth was already fully developed. In the upper incisors it appears that the roots of erupting teeth only fully close once the tooth has migrated to its functional position. Thus, it is likely that the lingual positioning of the i3 in the dental arcade is its final, 'functional' position.

3.5.1.2 Canines

The maxillary canines in lycosuchids are massive, laterally compressed teeth, bearing serrations on the mesial and distal edges. It has been demonstrated that serrations may be a character from a shared common ancestor (Brink and Reisz, 2014), and are not a novel adaptation to the Lycosuchidae.

The most well known feature of Lycosuchidae is the frequent occurrence of double canines in the maxilla. This has been considered a diagnostic character (e.g., Haughton and Brink, 1954), as well as being used to show that the Lycosuchidae represent "pristerognathid therocephalians" undergoing tooth replacement (van den Heever, 1980). Nonetheless, in the sample of 20 specimens attributed to the Lycosuchidae, 11 show double canines in either a single maxilla or both maxillae (Abdala *et al.*, 2014a).

3.5.1.3 Postcanines

Abdala *et al.* (2014a) gave the number of maxillary postcanine teeth in US D173 and CGS C60 as three. The results in this study show that there were at least four teeth in the right maxilla, and five teeth in left maxilla of CGS C60. The teeth are conical and slightly recurved, bearing serrations on the mesial edges. There are six postcanines preserved in each dentary of CGS C60, with evidence for a developing pc7 in the right dentary, and an empty alveolus distal to pc6 in the left dentary. In comparison, each dentary of US D173 shows evidence for only five postcanines.

3.5.2 Tooth replacement

3.5.2.1 Incisors

Broom's (1903a) original description of US D173, mentions that the first right upper incisor (I1) is smaller than the I2. Broom pointed out that the right I3 has been shed, and that the crown of a replacement tooth was erupting. A similar condition is seen on the left side, but the root of the shed I3 is retained. For both sides, the I5 is described as being smaller than the I4, a condition attributed to the recent replacement of the I5 in each premaxilla. Broom inadvertently described an alternating pattern of replacement in the upper incisors of the specimen. Although Kermack's (1956) figure 11b shows an alternating pattern of replacement in at least the lower incisors of "*Trochosaurus*," he did not refer to it as such.

The results here confirm that an alternating pattern of replacement is present in the upper incisors of *Lycosuchus* as formerly proposed by Kermack (1956: fig. 11b).

Furthermore, it appears that two waves move along the series at the same time, one replacing the odd numbered teeth, and the second the even numbered teeth. Due to the limited sample size, no clear pattern of replacement could be determined for the lower incisors. Despite no observable replacement incisors in the dentaries of CGS C60, both dentaries of US D173 (Figure 6C, D) preserve replacement teeth lingual to i1 and i3. Therefore, an alternating pattern of replacement likely occurred in the mandibular incisors.

3.5.2.2 Canines

Previous studies on *Lycosuchus* have concluded that one maxillary canine replaces the other, such that only one tooth per side is functional at a time. The results here instead confirm the presence of two families of canine teeth, which are active simultaneously, and replace independently and alternately from one another. This pattern was first illustrated by Parrington (1936a) for an unknown theriodont, and later described in several basal theriodonts by Kermack (1956). This arrangement means that instead of distichial replacement occurring between the left and right maxillary canines of an individual as proposed by Kermack (1956), replacement activity would have alternated between the mesial and distal canine locus within each maxilla. Therefore, unlike the basal cynodonts that almost uniformly show the replacement maxillary canine erupting mesial to the functional canine (Abdala *et al.*, 2013), in the Lycosuchidae, the erupting canine may have been positioned in either the mesial or distal locus of the maxilla. The position of the erupting canine relative to the functional tooth is possibly related to the ontogenetic stage of the individual.

Data presented by Abdala *et al.* (2014a: tables 5 and 6) shows that 55% of specimens attributed to Lycosuchidae (n = 20) were undergoing canine replacement at the time of death. This percentage rises considerably to 75% when dealing with specimens definitively identified as *Lycosuchus vanderrieti* (n = 5). This number can be broken up as follows: 62.5% of Lycosuchidae specimens with a BSL ~200–234 mm (n = 8), have the mesial canine erupting, 100% specimens with a BSL of ~237 mm (n = 2) show the eruption of the distal canine, and 50% specimens with a BSL greater than ~275 mm (n = 8) indicate eruption of the mesial canine. Specimens with a BSL longer than ~300 mm tended to show no signs of replacement activity, and have only a single canine present in each maxilla. This suggests either a cessation of replacement of the canines, or the rate of development/mineralisation of the replacement tooth has slowed to such an extent that the tooth does not fully form, nor erupt while the animal was still alive. A similar alternating pattern of eruption of the maxillary canine between a mesial (e.g., BP/1/512) and distal (e.g., BP/1/870) alveolus is observed in the whaitsiid therocephalian, *Theriognathus* (Norton, personal observation).

In three of the smallest specimens of the cynodont *Thrinaxodon* (BSL ~30–42 mm), replacement maxillary canines were erupting distal to the functional tooth (Abdala *et al.*, 2013). In contrast, replacement canines were erupting mesial to the functional maxillary canine in all five of the μCT-scanned specimens of *Thrinaxodon* (BSL 37–87 mm) of Abdala *et al.* (2013). No replacement of the maxillary canines distal to the functional tooth was observed in studies of *Cynosaurus* (Chapter 5) and *Galesaurus* (Chapter 6).

Kermack (1956) noted in the largest gorgonopsian and therocephalian specimens studied, that the erupting maxillary canine tended to occupy the mesial locus. From this evidence he hypothesised that the last maxillary canine to erupt during the animal's life occupied the mesial locus, and suggested a cessation of replacement of the canines. It has not yet been determined if this is true cessation, i.e., there are no signs of development of replacement teeth associated with either alveolus (with possible changes in canine root morphology) as seen in *Cynosaurus* (Chapter 5) and *Galesaurus* (Chapter 6), or if there is merely a perceived cessation. This may be due to the development of the replacing tooth having slowed to such an extent that the last replacement does not erupt prior to the animal's death (i.e., if the animal were to live indefinitely, replacement would continue indefinitely, with no finite number of tooth replacement generations). A similar arrangement of distichial replacement of the maxillary canines appears to be present in *Theriognathus* (Huttenlocker and Abdala, 2015) (Norton, personal observation).

3.5.2.3 Postcanines

Only the right maxillary series of CGS C60 shows evidence of replacement activity. The PC1 is interpreted as still erupting, due to its lingual positioning relative to the other elements of the series. The replacement tooth located between the functional PC3 and PC4 lies in the same plane as the erupting PC1. If this tooth represents a replacement PC3, then it may be considered that an alternating pattern of replacement of the maxillary postcanines occurred.

In contrast, replacement activity of the postcanines is observable in the left and right dentary of both US D173 and CGS C60. A pattern of alternating replacement is easier to elucidate for the mandibles, as the even- and odd-numbered elements lie in two different planes (Figure 9).

3.5.3 Double canines as the ancestral condition

The earliest synapsids to show regionalised differentiation of the dentition into distinct caniniforms are the sphenacodont "pelycosaurs" (Edmund, 1960). In taxa such as *Dimetrodon*, there are two caniniform teeth in the maxilla. Edmund (1960) noted that occasionally both maxillary caniniforms appeared to be functional, but the usual case was that one tooth was functional while the other was undergoing replacement. Boonstra (1962) also described the replacement of the paired maxillary caniniform teeth in the sphenacodont pelycosaurs as having been replaced alternately.

There are two known taxa that occur in "Olson's Gap" during which time it is likely the Therapsida evolved from a pelycosaur-like ancestor. These are *Tetraceratops insignis* (Matthew, 1908) and *Raranimus dashankouensis* (Liu *et al.*, 2009).

Although fragmentary, the only specimen of *Raranimus* (IVPP V 15424) clearly shows the presence of two maxillary canines (Liu *et al.*, 2009: figs 1 and 2). If *Raranimus*, or at least a taxon of similar grade, represents the common ancestor to Therapsida (or at least the Theriodontia if an alternative polytomic tree, *sensu*

Kemp [2009, 2011], is adopted), then it may be assumed that the earliest Theriodonts would have retained the condition of two maxillary canines. This is precisely the condition observed in the Gorgonopsia (Kermack, 1956; Sigogneau-Russell, 1989) and basal Therocephalia. Since the condition of double canines was seemingly inherited, it is likely that the pattern in which they were replaced was also inherited from these ancestors to theriodonts. Thus, the condition of two canine tooth families occurring simultaneously, and replacing alternately most likely represents the basal condition for the Theriodontia. An alternate hypothesis is that the double maxillary canines in the Lycosuchidae represents an evolutionary reversal.

Kermack (1956) writes of the distichial replacement between mesial and distal canine alveoli in basal Therocephalia and Gorgonopsia. The phylogenetic relationship between the Gorgonopsia and Therocephalia is not fully agreed upon (see for example Kemp [2009, 2011]), with both taxa first appearing in the *Eodicynodon* Assemblage Zone of the Karoo (Rubidge, 1995). Thus, it is likely that neither group gave rise to the other and that the two groups evolved independently either from a biarmosuchian grade ancestor, or a basal therapsid similar to *Tetraceratops*/*Raranimus*. This retention of the primitive condition is not unexpected, as Lycosuchidae are almost universally accepted as the most basal therocephalian radiation.

3.5.4 Prevalence of double canines in early therocephalians

Van den Heever (1980: 122) noted in the collections of the SAM at least 112 specimens of early therocephalian crania and cranial fragments for which the canines could be observed. Of these, 14 possess double canines in either one or both maxillae. This equates to 12.5% of the early therocephalian specimens having double canines. This low occurrence of double-canines led van den Heever (1980) to conclude that the period during which two maxillary canines were present was relatively short lived.

However, when looking at specimens attributed to Lycosuchidae (n = 20) and *Lycosuchus* (n = 5) by Abdala *et al.* (2014a), the proportion of specimens with double canines rises to 60% and 80% respectively. This suggests that the Lycosuchidae may have retained the ancestral condition of the sphenacodont "pelycosaurs" in which two functional caniniform teeth are present simultaneously (Romer and Price, 1940).

In order to better understand van den Heever's (1980) conclusions, perhaps his definition of early Therocephalia needs to be examined. Fortunately, by looking at the taxa included in his other works (van den Heever, 1987, 1994), one may gain a better idea of what he intended.

Van den Heever (1994: 3) expresses that his definition of the early Therocephalia is equivalent to the Pristerognathidae of that time. Although the Pristerognathidae are an invalidated family (van den Heever, 1994: 50), van den Heever's (1994)

figure 28 implies that the group included all taxa outside of Eutherocephalia. The most recent phylogenetic work on the early Therocephalia by Liu and Abdala (2019), results in this group including the following South African taxa: *Alopecodon*, *Ictidosaurus*, *Pardosuchus*, *Scylacosaurus*, *Glanosuchus*, *Pristerognathus*, and *Lycosuchus*.

In addition to the Lycosuchidae already described, evidence for multiple canines were described for the following South African taxa: *Alopecodon* (Broom, 1908a), *Ictidosaurus* (Broom, 1903b), *Pardosuchus* (Broom, 1908a), *Scylacosaurus* (Broom, 1903b, 1903c) (Figure 10). However, many of the elements described by Broom as the first canine, were done based on them being housed in the maxilla. It is now more common for these teeth to be considered as precanines. There is evidence of remnant roots of a previous canine distal to the functional canine in *Ictidosaurus* (Broom, 1903b; Abdala *et al.*, 2008), and *Scylacosaurus* (Broom, 1903c). The dentition of the "better-known" therocephalian genera were tabulated by Broom (1908b: 371–372), which was later reproduced by van den Heever (1987: 40) (Figure 10).

3.5.5 Function of the double canines

Van den Heever (1980: 122–123) is correct in his observations that the retention of two "bulky" canine teeth would have hindered the animal's ability to hunt/feed; the close proximity of the crowns would likely have obscured the serrations, and the two teeth together would have been less efficient at penetrating prey items than a single tooth would have been. However, this assumes that the elongated

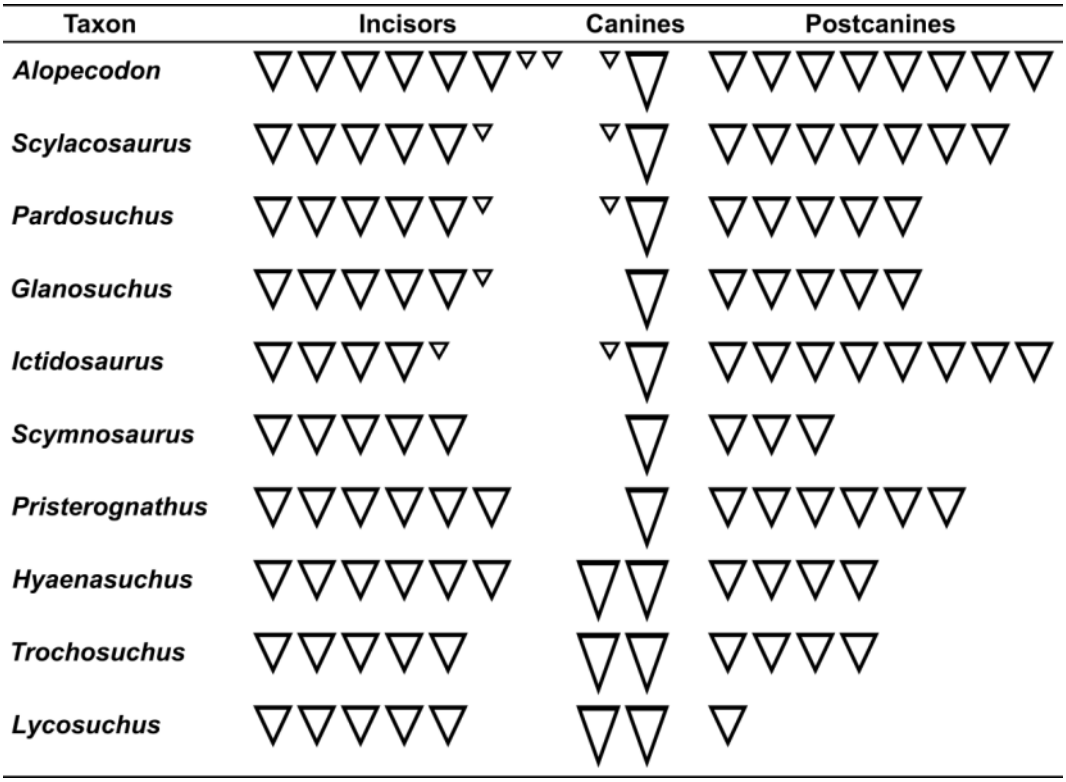

Figure 10. Dental formulae of the early Therocephalia according to Broom (1908b: 371–372) and van den Heever (1987: 40).
Alignment of canines follows that of Broom. Teeth not to scale.

canines of *Lycosuchus* were for the capture, subdual, and processing of prey items. It has been shown that the short-snouted robust skulls of the Gorgonopsia were comparatively better suited for taking down the large prey that were around at the time (Jenkins, 1998; Jenkins *et al.*, 2002). It has also been demonstrated that there was an evolutionary arms race taking place between the predator and prey of the middle–late Permian, with predators becoming larger and taxa such as pareiasaurs increasing the size and density of their protective osteoderms (Lee, 1997). There was also a turn-over of ecological roles around this time, with the gorgonopsians growing larger in size, and the once dominant Therocephalia

decreasing in size, and subsequently filling new ecological niches as is evident by the possible adoption of insectivorous, omnivorous and possibly herbivorous lifestyles in various lineages (Kemp, 2005; Smith *et al.*, 2011; Huttenlocker, 2014).

The origin of serrated (ziphodont) dentition likely evolved independently in the sphenacodont pelycosaurs and Therapsida (Brink and Reisz, 2014). Canine serrations may have been more important for younger/smaller individuals, but as animals grew larger they may have relied on them less. Thus, lycosuchids may have depended less on their enlarged canines for the acquisition of food, than van den Heever (1980) thought. Nevertheless, if these enlarged teeth were not related to feeding, then what could their purpose have been? A few hypotheses as to the alternative purpose/function of these enlarged teeth are presented.

3.5.5.1 Structural reinforcement

It has been proposed by van den Heever (1980) that functionality of the two canines of the maxilla would have been compromised due to the close proximity of the cutting edges of the teeth. However, if the main task of these teeth is not related to feeding, then there is no need for the cutting surfaces to be exposed. Instead, it is proposed that due to the lateral flattening of the teeth, the two did indeed function as a unit to reinforce one another against external forces, and that the presence of serrations on the distal and mesial edges are retained from an ancestral trait.

3.5.5.2 Sexual display

Cranial structures for intraspecific display have been described in the therocephalian *Choerosaurus* (Benoit *et al.*, 2016a), and the enlarged canine teeth of the anomodont *Tiarajudens* have also been hypothesised as a means to deter attack from other species, or used for intraspecific display or combat (Cisneros *et al.*, 2011, 2015).

Could the presence of two large canines in each maxilla be an adaptation to display 'fitness,' as opposed to serving a role in feeding? The teeth are somewhat laterally compressed, which means they may not have been as resistant to external physical stresses as the cylindrical sabre-like canines of the Gorgonopsia. However, their function in sexual display cannot be ruled out.

3.6 Conclusion

The present study of two µCT-scanned specimens of Lycosuchidae (US D173 and CGS C60) shows that an alternating pattern of tooth replacement was present in all the incisors, canines, and postcanines. From the comparison of these two specimens, as well as descriptions from historical accounts, the dental formula of Lycosuchidae is established as I5/3, C2/1, PC 3/5.

Of the five specimens attributed to *Lycosuchus vanderrieti* by Abdala *et al.* (2014a), only CGS MJF68 has a single functional canine in each maxilla. However, another specimen (CGS M793) has double canines in the left maxilla, and a single canine in the right. This lends evidence to the hypothesis that the two

canines were present for a prolonged period of time, and may even have both been functional simultaneously.

If there was a high degree of pre- and post-eruption migration of the large maxillary canines, then one would expect there to be evidence for the erosion of the roots in one functional canine tooth by the other. This is not observed in the sample, and instead resorption of the functional maxillary canine roots is associated with the development of replacement teeth lingual to each functional tooth. This pattern of resorption of the roots in the maxillary canines by the replacement teeth, as well as the similar developmental stages of the replacement canines of the maxilla suggest there are two maxillary canine tooth families. Furthermore, this suggests that the condition of having two functional canines was the predominant condition in *Lycosuchus*, and not a short-lived/temporary condition associated with replacement as proposed by van den Heever (1980). This is further supported by the high number of lycosuchid specimens that have been described with two maxillary canines (Table 4). Instead, it is suggested that the condition of having only one functional canine in each maxilla is a short-lived condition in the Lycosuchidae, with the replacing tooth erupting soon after exfoliation of the old tooth.

This suggests that rather than being hypercarnivores, the Lycosuchidae may have been opportunistic scavengers; the enlarged serrated canines being inherited from a basal theriodont ancestor, rather than a novel adaptation for capturing and subduing prey. Alternatively, the double canines may have been a means of

reinforcing the tooth against impact forces from taking down large prey items such as pareiasaurs or tapinocephalid dinocephalians, or perhaps even played a role in sexual display.

4 DENTAL REPLACEMENT IN THE MIDDLE TRIASSIC THEROCEPHALIAN *BAURIA CYNOPS* BROOM, 1909

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4.1 Abstract

Four specimens representing several ontogenetic stages of *Bauria cynops* were scanned using micro-computed tomographic techniques. The postcanine dentition has expanded complex crown morphology for processing plant material. The results showed very limited replacement of the incisor and postcanine dentition in *Bauria*, and no evidence of replacement of the canines. This is in contrast to the condition described for the Gorgonopsia and other Therocephalia, where replacement ceases first in the postcanines, followed by the canines, and lastly the incisors. *Bauria* exhibits less replacement activity than was previously hypothesised. This peculiar situation may be connected with an increase in the amount of mastication taking place, and the limited tooth replacement would have ensured constant occlusion of the postcanine dentition. The pattern of tooth replacement in *Bauria* is more similar to that of traversodontid cynodonts, than to that of non-baurioid Therocephalia. This is a clear instance of convergence, in which similar trends of change in a molar pattern (i.e., buccolingual expansion of the crown) are coupled to similar replacement cycles.

4.2 Introduction

When Broom (1909) described the first specimen of *Bauria* (SAM-PK-1333) he considered it to be a new basal cynodont. He noted that the specimen had an incomplete postorbital bar, leading him to describe the specimen as having an "extremely mammal-like appearance" (p. 272). In addition to this 'mammalian' character, Broom (1909: 272) erroneously described the postcanine teeth as being "simple conical molars, as in most Therocephalians." Furthermore, Broom remarked that the posterior extension of the dentary towards the jaw articulation was intermediate to the conditions seen in Therocephalia and Cynodontia. Despite the misinterpretation of the postcanine tooth morphology, Broom identified *Bauria* as a more basal taxon of Cynodontia than any other known at the time (Broom, 1909), and later erected the family Bauridae [sic] to distinguish the specimen from other known Theriodontia (Broom, 1911b). Broom (1913b: 346) later described the "grinding teeth" as simple little pegs, and compared them to those of an armadillo. More recent studies have shown the postcanine dentition of *Bauria* to have buccolingually expanded crowns (Crompton, 1962).

There have been several descriptive papers on *Bauria*, many of these dealing with poorly preserved or incompletely prepared material. Brink (1963c) offered a summary of the work undertaken on *Bauria*, and Abdala, Jashashvili, *et al.* (2014) provided a more recent historical review. Abdala, Jashashvili, *et al.* (2014) consider the following taxa to be junior synonyms of *Bauria cynops*: *Aelurosuchus browni* (Broom, 1906), *Baurioides watsoni* (Broom, 1925),

Microhelodon eumerus (Seeley, 1895), *Sesamodontoides pauli* (Broom, 1950), and *Bauria robusta* (Brink, 1965b).

Boonstra (1938) demonstrated that replacement teeth in *Bauria* lay lingual to the functional postcanines in both the maxilla and dentary. Crompton (1962) gave the tooth replacement pattern of *Bauria* as alternating. Although there are now 15 specimens attributed to *Bauria cynops*, Crompton's (1962) work remains the only formal description on the tooth replacement in the species. This lack of study on tooth replacement in *Bauria* is most likely due to most skulls having the lower jaw preserved in tight occlusion (e.g., BP/1/1180, BP/1/3770). It is thus not surprising that the only specimen that has had the lower jaw removed, SAM-PK-1333, is also the only specimen for which tooth replacement has been described (Crompton, 1962).

The relatively large sample size from which to select specimens, as well as the apparent ontogenetic sequence represented in the sample, makes *Bauria* a good candidate for the study of the tooth replacement using non-invasive techniques such as μCT-scanning. Additionally, *Bauria* represents one of the most derived Therocephalia (Figure 1), and has a postcanine dentition that approaches the morphological complexity of the gomphodont cynodonts. Any changes in the pattern of tooth replacement in *Bauria* from that of basal therocephalians (e.g., Lycosuchidae, Chapter 3) may contribute to the broader understanding of the evolution of the Therocephalia to occupy a multitude of dietary niches.

4.3 Materials and methods

Eight of the 15 specimens attributed to *Bauria cynops* were examined for the current study (Table 6). Four of these specimens, representing a presumed juvenile (BP/1/4678), subadults (BP/1/1180 and BP/1/2837), and an adult (BP/1/1685) were analysed using μCT (Table 7). An isolated dentary attributed to *Bauria* (BP/1/2523) had been serially sectioned by A.H. LeBlanc for a study on the periodontal tissues of mammal ancestors (LeBlanc *et al.*, 2016, 2018). Observations of the dentition of a ninth specimen, BP/1/1679, were added from the accounts of Brink (1963c), Mendrez (1975), and the unpublished notes, photographs and drawings of the late Dr Mendrez-Carroll.

4.3.1 Micro-computed tomography scanned specimens

Four specimens of *Bauria cynops*, representing an ontogenetic series were analysed using μCT (Table 7). The basal skull length (BSL) of this sample ranges from ~70 mm (BP/1/2837) to ~132 mm (BP/1/1685).

Due to differing physical dimensions, states of preparation, and chemical compositions of the specimens, the scan parameters were adjusted to obtain the best results for each specimen (Table 7). In order to reduce artefacts due to beam-hardening, a 1.2 mm copper or 1.8 mm aluminium filter was used (Abel *et al.*, 2012).

Table 6. Specimens of *Bauria cynops* included in the study.

Specimen	Alternate Coll. No.	BSL (mm)	Maxillary postcanine counts		Synonyms/Authority
			Brink (1963c)	Abdala *et al.* (2014b)	
BP/1/2837[a]		—	—	—	Abdala *et al.* (2014b)
BP/1/4678 [a]		—	—	—	Abdala *et al.* (2014b)
SAM-PK-5875		92	—	8–9?	*Aelurosuchus browni* Broom (1906), Abdala *et al.* (2014b)
BP/1/1180 [a]	BP M 317	114	9/10	At least 9	Brink and Kitching (1953), Crompton (1955), Brink (1963c)
BP/1/3770	BP M358[b]	117	9/10	9	Brink (1963c)
SAM-PK-1333		122[b]	10	10/11	Broom (1909)
BP/1/1679[c]	BP M 230[d]	124[e]	9/10	—	Brink (1963c)
BP/1/2523	BP M321	?	?/11	—	Brink (1963c)
BP/1/1685 [a]		132[f]	—	11	*Bauria robusta* Brink (1965b), Abdala *et al.* (2014b)

[a] Specimen μCT-scanned.

[b] Collection number given as 'M358' in Brink (1963c) and 'M338' in Brink (1986).

[c] Specimen lost.

[d] Collection number given as 'M230' in Brink (1963c) and 'M320' in Brink (1986).

[e] Estimate from Brink (1963c: table on p. 42).

[f] Estimate from Abdala *et al.* (2014b: table 13.3).

Table 7. Parameters used for micro-computed tomography scanning of *Bauria cynops* specimens.

Specimen	Material	Tube current (µA)	Projections
BP/1/2837	complete skull[a]	170	2000
BP/1/4678[b]	snout fragment	170	2000
	jaw fragment	140	3142
BP/1/1180	complete skull	240	3142
BP/1/1685	partial skull	165	3142

All specimens were scanned with a tube voltage of 140 kV.

[a] Sagitally sectioned, with both parts scanned simultaneously

[b] Fragmentary, only fragments identified with teeth were scanned

4.4 Results

4.4.1 Tooth numbers and morphology

Due to the conservative nature of the dentition—with regard to the relative lack of variation in both number of teeth and tooth crown morphology across the sampled ontogenetic series—of *Bauria*, the reporting of the results for the incisors and canines are grouped together under the heading "Anterior dentition."

4.4.1.1 Anterior dentition

There are four teeth comprising the incisor series of the premaxilla and mandible. The incisors are recurved points, with the upper incisors being almost as large as the maxillary canine. The i4 is considerably smaller than the three preceding incisors, and in BP/1/1180 the crowns of both i4 are broken, such that only the roots remain. A single canine is present in each quadrant of the buccal cavity. The canines are reduced in size when compared to other therocephalians (e.g.,

Lycosuchus), but are still slightly larger than the incisors. There do not appear to be striations on any of the incisors or canines.

4.4.1.2 Postcanine dentition

The number of postcanines range from 8–10 teeth in the maxilla, and 10–12 teeth in the dentary (Table 8). The buccolingually expanded postcanine dentition of *Bauria* are spaced apart from one another. The first postcanine tooth of the maxillary series of BP/1/1180 is not buccolingually expanded in transverse section, instead having a more circular perimeter. This 'simplification' of the crown morphology of the PC1 to appear more caniniform is reminiscent of the condition described in the PC1 of *Galesaurus* (Chapter 6).

The intermaxillary space between postcanine series is narrower than that of the mandible, such that the maxillary postcanines occlude with the lingual surface of the mandibular postcanines. The labial crown of the mandibular postcanines is elevated above that of the lingual surface.

Table 8. Observed dental formulae in µCT-scanned specimens of *Bauria cynops*.

Specimen	BSL (mm)	Incisors Pmx (Mn)	Canines Mx (mn)	Postcanines Mx (Mn)
BP/1/2837	—	4 (4)	1 (1)	10 (12)
BP/1/4678	—	4 (4)	1 (1)	10 (11)
BP/1/1180	114	4 (4)	1 (1)	8/9 (11/10)
BP/1/1685	132[a]	4 (4)	1 (1)	9/10 (11/10)

Abbreviations: BSL, basal skull length; Mn, mandibular; Mx, maxillary; Pmx, premaxillary.

[a] Brink (1965b) estimated the BSL as 164 mm.

4.4.2 Tooth replacement

Due to the considerable reduction in replacement activity in the dentition of *Bauria cynops* in comparison to the other taxa of this study (Chapters 3, 5, and 6), each specimen will not be treated individually as in previous chapters. Instead, instances of replacement observed for each tooth group are reported collectively.

4.4.2.1 Incisors

Of the µCT-scanned *Bauria* specimens, the subadult BP/1/1180 is the only specimen to show evidence of replacement of the incisors. The left upper I2 is smaller in diameter than either of the neighbouring teeth, and is thus likely to have still been in the process of eruption at the time of death. A very small structure (< 1 mm in diameter) is visible lingual to the left upper I4 (Figure 11). Given its location relative to the functional I4, this structure is likely representative of the developing germ of the replacement I4. Neither of these features are present in the right premaxilla. The left I1 and I3 and right I3 of BP/1/1180 appear to have open roots (Figure 12A, B), suggesting an alternating pattern of replacement.

4.4.2.2 Canines

There was no evidence for the replacement of either the maxillary or mandibular canines in any of the four µCT-scanned specimens of *Bauria cynops*. The roots of the maxillary canines (Figure 12A, B) and possibly the left mandibular canine (Figure 12C) appear to be open. The matches the condition of open-rooted canines previously reported in adult specimens of *Cynosaurus* (Chapter 5) and *Galesaurus* (Chapter 6).

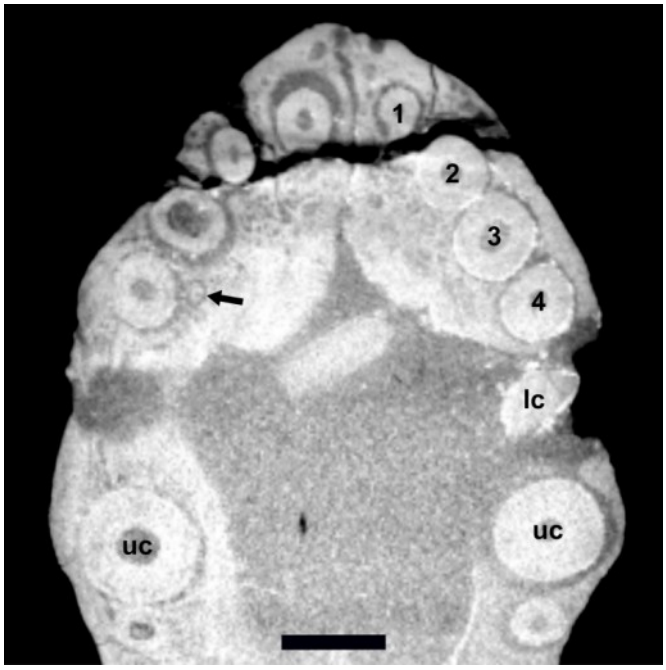

Figure 11. Virtual Transverse cross-section through the premaxilla of *Bauria cynops* (BP/1/1180).
Abbreviations: lc, mandibular canine; uc, maxillary canine. Arrow indicates the replacement developing lingual to the left I4. Arabic numerals indicate incisor positions. Scale bar equals 5 mm.

4.4.2.3 Postcanines

Apart from the subadult BP/1/1180 none of the specimens studied show evidence of postcanine replacement. Eight postcanines are preserved in each maxilla of BP/1/1180, and the only evidence of replacement activity is at the right PC3, where the remnant roots from an exfoliated crown are preserved. Ten postcanines are preserved in each dentary of BP/1/1180. In the left, pc3 shows signs of replacement, whereas on the right no replacement is evident. There appears to be a resorption pit of a developing pc11 distal to the pc10 of both mandibular postcanine series.

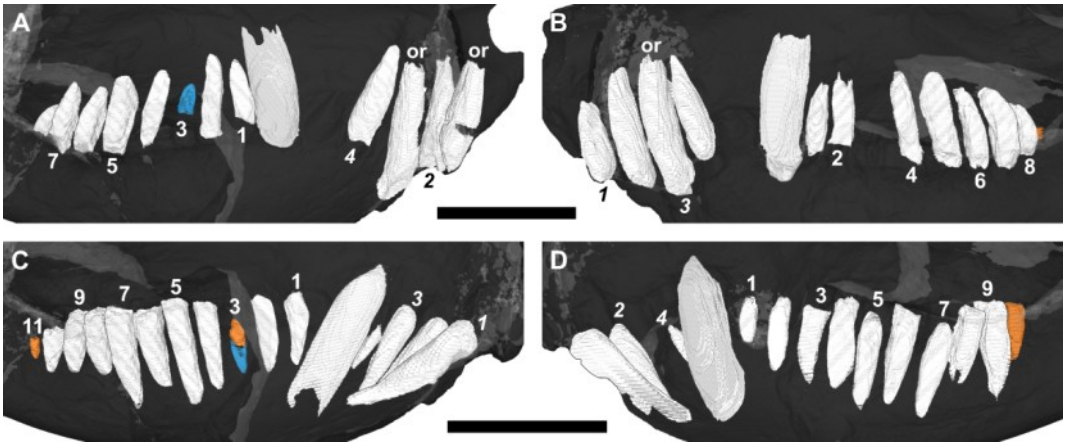

Figure 12. Three-dimensional rendering of the tooth rows of *Bauria cynops* (BP/1/1180) in medial view.

A, upper left; B, upper right; C, lower left; D. lower right. Replacement teeth in orange, old remnant roots in blue. Abbreviation: or, open root. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bar equals 20 mm.

4.5 Discussion

4.5.1 Tooth morphology

This section compares the crown morphology of the dentition of *Bauria cynops* to those of other members of the Bauriidae (*sensu* Huttenlocker [2014]).

4.5.1.1 Anterior dentition

The incisors of *Bauria* do not bear any serrations, which is hypothesised to have been the derived morphology for Therocephalia (Huttenlocker *et al.*, 2015; Brocklehurst, 2019). In addition, the canines are considerably reduced in size, such that they are of similar size to the incisors (Brink, 1963c). Both of these adaptations suggest a shift away from a primarily carnivorous diet.

The upper incisors of *Microgomphodon* are smooth and conical, progressively increasing in size distally. Lower incisors are large and procumbent, and decrease in size distally. The anterior dentition of *Microgomphodon* lacks serrations (Abdala, Jashashvili, *et al.*, 2014). Similar to *Bauria*, the canines of *Microgomphodon* are reduced in size, with a robust base. Abdala *et al.*, (2014b) demonstrated through the application of 3-D geometric morphometrics, that the maxillary canine of *Microgomphodon* is more strongly recurved than that of *Bauria* (at least for the two specimens modelled). Much like *Microgomphodon*, the maxillary canine of the Chinese bauriid *Traversodontoides* is directed anteriorly (see Young, 1974: plate II, fig. 2).

The maxillary canine of the Russian *Antecosuchus* is short and recurved. Unlike the canines of *Microgomphodon* and *Bauria*, the canine tooth bears several well-developed longitudinal facets (Ivakhnenko, 2011).

4.5.1.2 Postcanines

The postcanine roots of *Microgomphodon* (SAM-PK-5865) were described as being long with a large pulp cavity (Broom, 1905b). The crowns are short, and well enamelled. The crowns are worn, such that Broom (1905b) suggested that some degree of antero-posterior movement of the jaw was possible during mastication. Given the pronounced arc of the postcanine dentition, particularly in *Bauria*, an antero-posterior movement does not seem likely, and instead the teeth would have been worn due to the rotational movement of the curved mandible during adduction of the mandible (Brink, 1963c). Broom (1905b) described the

postcanine teeth of SAM-PK-5866 (= *Microgomphodon*) as resembling those of SAM-PK-5865, but lacking the thickened ridge of enamel at the base of the crown. All postcanines in another specimen of *Microgomphodon* (SAM-PK-10160) are of similar size, with the exception of the distal-most tooth in the mandibular series, which is reduced in size (Abdala *et al.*, 2014b).

Ivakhnenko (2011) describes the postcanine dentition of *Antecosuchus* as being similar in morphology to that of *Bauria*. Similarly, Ivakhnenko (2011) wrote that the dentition of *Antecosuchus* resembles that of the Chinese *Traversodontoides* (in structure, number and relative sizes of the teeth), and the Brazilian *Gomphodontosuchus* (in position and number, and general shape of the mandible). *Antecosuchus* was described as a traversodontid cynodont (Tatarinov, 1973), due to the postcanine crown morphologies. Later, Battail and Surkov (2000) proposed that *Antecosuchus* instead belonged within the Bauriidae. (Ivakhnenko, 2011) noted that the positions and number of teeth, as well as the general shape of the mandible of *Gomphodontosuchus* closely resemble that of *Antecosuchus*.

Ivakhnenko (2011) notes the similar dental structure of *Antecosuchus* to *Traversodontoides*, with regard to the presence of the diastema, number and relative sizes of teeth, and proportions of the upper jaw. Sun (1981) described the postcanine dentition of *Traversodontoides* as having transversely widened crowns that are in close contact. The teeth also show signs of wear in the form of facets on the occlusal surfaces.

The postcanine dentition of the Chinese bauriid, *Nothogomphodon* has sectorial morphology (Liu and Abdala, 2015), resembling the morphology of the basal cynodonts (e.g., *Galesaurus*). This is the only evidence of such postcanine morphology evolving in the Therocephalia (Liu and Abdala, 2015). Whereas the postcanines of the South African bauriids (*Bauria* and *Microgomphodon*) are buccolingually expanded, the postcanines of *Nothogomphodon* are labiolingually flattened. This represents a considerable amount of variation in the crown morphologies of the postcanine dentition in bauriids. This in turn, may be attributed to adaptations towards slightly different dietary niches.

The widely spaced postcanine teeth suggest that *Bauria* was less reliant on precise occlusion during the processing of food, and more reliant on a 'hammer-like' pounding action of the postcanines together. Further possible evidence pointing to this nature of chewing is seen in the robust corpus of the dentary (cf. the lower jaw of elephants in van der Merwe *et al.* [1995]), which may have allowed for stronger muscle attachment, or potentially had a shock-absorbing affect. Alternatively, this lateral expansion of the dentary corpus may have served no additional function, instead having as a means to house the buccolingually expanded postcanine dentition.

4.5.2 Dental formula

4.5.2.1 Incisors

There has been discussion in past descriptions of the number of incisors in *Bauria* being variable. From the results of the μCT scans, it is evident that the number of

incisors is four in both the premaxilla and dentary. Broom (1909) described the four upper incisors and maxillary canines as being of a moderate-size, lacking serrations, and being round in transverse section.

Brink and Kitching (1953b), Crompton (1962) and Brink (1963c), however, differ from Broom's (1909) observations for the lower dentition, instead giving the formula for the lower dentition as i3.c1.pc11. This discrepancy in the number of mandibular incisors was attributed by Crompton (1962) as being due to the possible damage, and subsequent displacement of the crown of the fourth upper incisor in the holotype (SAM-PK-1333). Results show that all four of the µCT-scanned specimens have four mandibular incisors.

Brink (1963c) describes the fourth upper incisors of BP/1/3770 to be smaller than the other incisor teeth. In both sides of BP/1/1180, the crown of the i4 is broken, which may have lead to Brink (1963c) not seeing the i4 during his assessment of *Bauria*. Broom (1950) counted four incisors in the dentary of "*Sesamodontoides pauli*" (RC 114), which has been synonymised with *Bauria cynops* (Abdala *et al.*, 2014b).

4.5.2.2 Canines

Like most non-lycosuchid therocephalians (see Chapter 3), *Bauria* has a single canine family in the maxilla and dentary.

4.5.2.3 Postcanines

Broom (1909) recorded 10 conical postcanine teeth distal to the canine. Broom also gives the postcanine count for the dentary as 10; thus the dental formula for *Bauria* according to Broom was; I4/4, C1/1, PC 10/10. The same formula for the upper dentition was observed by Boonstra (1938), Brink and Kitching (1953b), and Crompton (1962).

Brink (1986) gave the general dental formula for *Bauria cynops* as; I4/3, C1/1, PC12/12. Broom (1950) also counted only eight postcanines in the maxilla and mandible of "*Sesamondontoides pauli*" (RC 114).

In addition to the perceived larger size of BP/1/1685, Brink (1965b) suggested that the presence of 11 maxillary postcanine teeth also be used as a diagnostic character to distinguish *Bauria robusta* from *Bauria cynops*, which he considered to have only nine maxillary postcanine teeth.

4.5.3 Tooth replacement

The apparent sequential addition of teeth to the distal margin of the mandibular postcanine series in BP/1/1180 (Figure 12), suggests that without the loss of the mesial-most tooth, the number of teeth in the postcanine series should increase through ontogeny. However, the number of postcanine presented in Table 8, indicates that the number of teeth in both the maxillary and mandibular postcanine series remains relatively constant through ontogeny.

Apart from the works by Crompton (1962) on *Ericiolacerta* and *Bauria*, and Mendrez-Carroll (1979) on *Scaloposaurus*, there is not much literature on the tooth replacement of Bauriamorpha. Although a therocephalian, a discussion on the replacement of the postcanine dentition of *Bauria cynops* would be incomplete without a comparison to the tooth replacement patterns of postcanine dentition of the gomphodont cynodonts.

This comparison is important because of the convergent morphology of the postcanine teeth of the Bauriidae and gomphodont cynodonts. The similarities in the postcanine dentition, and extent of this convergence, is made even more prominent when taking into consideration that several bauriamorph taxa (e.g., *Antecosuchus ochevi*, "*Neotrirachodon*" *expectatus*, "*Scalenodon*" *boreus*, and *Traversodontoides wangwuensis*) have at some stage been considered as traversodontid cynodonts (Young, 1974; Hopson, 1985; Tatarinov, 1988, 2002; Battail and Surkov, 2000; Gao *et al.*, 2010; Sues and Hopson, 2010).

The Gomphodontia are a diverse clade of mostly Triassic Cynodontia, and are readily characterised by the buccolingually expanded postcanine dentition that exhibit precise tooth-to-tooth occlusion (Crompton, 1972; Reisz and Sues, 2000). This section will focus on summarising the reported instances of tooth replacement in the Traversodontidae.

The absence of tooth replacement activity in *Bauria* is unusual, and may possibly be explained by the relatively small sample size ($n = 4$) of μCT-scanned specimens. However, studies on the tooth replacement patterns of Lycosuchidae

(*n* = 2) (Chapter 3), *Cynosaurus* (*n* = 5) (Chapter 5), and *Thrinaxodon* (*n* = 5) (Abdala *et al.*, 2013) have also used small samples, with tooth replacement activity recorded in the incisors (10 specimens), canines (11 specimens), and postcanines (all 12 specimens) in a majority of the specimens studied. If it were not for the damage to the anterior region and absence of the mandibles in some specimens, it is almost certain that evidence for the replacement of the incisors would have also been recorded in all specimens. Furthermore, the largest specimen of *Cynosaurus* to be µCT-scanned (BP/1/3926, BSL 115 mm) is likely to have achieved maturity, and thus ceased replacement of the canines (see Chapters 5 and 6 for more detail).

Even with the addition of observations from non-scanned specimens (SAM-PK-1333 and AMNH FARB 5622), and LeBlanc's (2016: fig. 4.18E) report of a single instance of retained roots adjacent to a functional postcanine in BP/1/2523, only four of the seven specimens of *Bauria* show limited signs of tooth replacement.

Interestingly, Hopson (1964) hypothesised that in the Theriodontia replacement ceased in the postcanine dentition first, followed by the senescence of replacement of the canines, and finally the incisors. However, recent work on the tooth replacement of the basal cynodonts *Cynosaurus* (Chapter 5) and *Galesaurus* (Chapter 6) have shown a cessation of replacement of the canines with the attainment of maturity, with the continued replacement of postcanines, and to a lesser extent incisors, in the largest specimens scanned. The presence of

replacement activity in the incisors and postcanines of BP/1/1180, with no replacement associated with the canines matches these observations in cynodonts.

4.5.3.1 Incisors

Replacement of the anterior dentition (incisors and canines) has been documented in several therocephalian taxa. Given that alternating replacement of the incisors is reported in the more basal Gorgonopsia (Kermack, 1956), the maxillary incisors of *Lycosuchus* (Chapter 3), and more derived cynodonts (Abdala *et al.*, 2013) (Chapters 5 and 6), it is inferred through the use of phylogenetic bracketing that if replacement of the incisors took place in *Bauria*, it would have occurred in an alternating fashion. The evidence for replacement of the left I2 and I4 of BP/1/1180 support this. In BP/1/3770 (BSL 117 mm), both I4s are considerably smaller than the other incisors of the specimen, suggesting that these teeth had not yet fully erupted.

The near lack of replacement activity observed in the incisors of *Bauria* is surprising as there are numerous reports of replacement of the incisors in gomphodont cynodonts. An erupting replacement I2 is preserved in the left premaxilla of *Dadadon* (FMNH PR 2232) (Ranivoharimanana *et al.*, 2011). In *Scalenodon angustifrons* there is evidence for the frequent replacement of the incisors and canines (Crompton, 1955, 1958). A replacement I2 is also known in *Mandagomphodon* (NMHUK R8577) (Hopson, 2014: fig. 14.1). This suggests that the reduction in replacement of the incisors of *Bauria* is not necessarily related to a change from primarily carnivorous to omnivorous/herbivorous diet.

4.5.3.2 Canines

No replacement was recorded in any of the μCT-scanned specimens of *Bauria*, nor in any of the additional specimens examined in this study. Broom (1950: fig. 2B) described and illustrated two canines in the left dentary of the closely allied *Microgomphodon* (RC 114), hypothesising that one was a replacement.

There is evidence for the frequent replacement of the canines in basal theriodonts (e.g., Kermack [1956]), as well as the basal cynodonts (see Chapters 5 and 6 for overviews). Parrington (1936a: fig. 2) illustrated multiple replacement generations associated with the maxillary canines of an unknown theriodont, most likely representative of a basal therocephalian.

A specimen of the baurioid, *Ictidosuchops* (BP/1/3155) shows a replacing maxillary canine tooth erupting mesial to the functional canine. This is the same condition described for several cynodonts (Abdala *et al.*, 2013) (Chapters 5 and 6), and also observed in a non-baurioid therocephalian of similar skull length, *Hofmeyria* (BP/1/4401).

Ivakhnenko (2011: 1112) describes a very small alveolus that is fused to the distal margin of the alveolus of the functional canine of the holotype of *Antecosuchus ochevi* (PIN no. 1579/53), suggesting that it may be a "rudimentary alveolus of a replacement canine." Furthermore, in a referred specimen (PIN no. 2865/596), Ivakhnenko (2011) describes an open-rooted maxillary canine. These are currently

the only two examples of evidence for the replacement of the canines in the Bauriidae.

For *Thrinaxodon*, replacement of the canines was observed in adult specimens, and was present in every specimen that was μCT-scanned (Abdala *et al.*, 2013). In contrast, *Cynosaurus* (Chapter 5) and *Galesaurus* (Chapter 6) showed a halt in replacement of the canines in specimens considered to have reached adult size. The canine teeth of these adult specimens are open-rooted. It was previously thought that amongst therapsids only the caniniform tusks of Dicynodontia were open-rooted (Jinnah and Rubidge, 2007) however it has been previously hypothesised that open rooted canines may have occurred in some cynodont taxa (Liu and Powell, 2009; Liu and Sues, 2010).

Fourie (1963) reported replacement maxillary canines erupting both mesial and distal to the functional canine in *Diademodon*. Of interest is his report of a mandibular canine erupting mesial to the functional tooth in a sectioned specimen of *Diademodon*.

Continued growth of the canine is hypothesised for the traversodontid cynodont *Andescynodon* (Liu and Powell, 2009). *Luangwa sudamericana* (MCP 3167 PV) was described as having erupting maxillary canines (Abdala and Sa-Teixeira, 2004). The right maxillary canine of *Dadadon* (FMNH PR 2232) was described as partially erupted, whereas the left was considered to be fully erupted (Ranivoharimanana *et al.*, 2011).

A second skull (FMNH PR 2444) was referred to *Menadon* (Kammerer *et al.*, 2008). The teeth of this specimen are not preserved, however, the empty alveoli closely match the pattern and arrangement of the holotype (UA-10601). Based on the alveolar morphology, Kammerer *et al.* (2008) concluded that the fifth tooth in the series was the canine, and that the interpretation of replacement in the holotype by Flynn *et al.* (2000) was incorrect. Kammerer *et al.* (2008) favoured the interpretation of the fourth tooth representing the I4 with a caniniform morphology.

It is thus apparent from the diversity of taxa shown to exhibit canine replacement, as well as the apparent frequent replacement (at least in subadults of certain taxa) of the canines, that the lack of evidence for replacement of the canines in *Bauria* is of some significance. Again, due to evidence of replacement in the herbivorous traversodontids, it cannot be attributed to change in diet.

4.5.3.3 Postcanines

Broom (1909), in the original description of *Bauria* (SAM-PK-1333), did not mention tooth replacement activity. This is most likely due to the incomplete preparation of the specimen at the time, as Broom figured the lower jaw in articulation. It was only later that the palate of *Bauria* was described by Boonstra (1938) and Broom (1937b). Broom (1937b: 1) described "remains of teeth of an earlier set that have been replaced," associated with PC1 and PC2.

In *Scaloposaurus* (NHMUK PV R 1723) there is evidence of replacement of the left pc7, whereas Mendrez-Carroll's (1979) figure 16 also shows that pc9 and pc11 may have still been erupting.

Waves of replacement moving along the jaw from front to back, have been described in some derived gomphodonts (Patterson and Olson, 1961), and tritylodontids (Kühne, 1956). In these cases there is no evidence for the replacement of teeth, instead new teeth erupt posterior to the distal margin of the postcanine series, resulting in the sequential addition of teeth to the postcanine series through ontogeny (Abdala *et al.*, 2002, 2013). Such addition of postcanines to the end of the series, which do not have a deciduous precursor, may represent an early stage in the development of mammalian diphyodonty.

Gomphodont cynodonts and tritylodontids were originally thought to be the only non-mammalian synapsids to have reduced the number of postcanine replacement generations Crompton (1955) and Kühne (1956). However, it has recently been proposed that a reduction in the number of replacement generations per tooth locus can be observed as early as the basal epicynodont, *Cynosaurus* (Chapter 5).

Ranivoharimanana *et al.* (2011) found that additional postcanines (PC11) were in the process of eruption in *Dadadon* (UA-10606), and are poorly exposed. The left maxillary postcanine series has an extra tooth present mesially. Ranivoharimanana *et al.* (2011) interpreted the corresponding tooth of the right maxilla to have been lost, and the alveolus filled with bone prior to the animal's death. The distal-most

tooth (PC10) of both maxillae is unworn and only partially erupted. Similarly, the distal-most tooth (pc11) of the dentary in UA-10608 is also partially erupted.

Replacement of the postcanines in *Scalenodon angustifrons* is recorded from only the distal region of the series (Crompton, 1955). During growth, teeth were added to the distal margin of the postcanine series, and were lost from the mesial margin. Similar observations have been made for the tritylodontid *Oligokyphus* (Kühne, 1956). Thus, it has been suggested that the origin of the mammalian pattern of tooth replacement must have arisen exclusively in the sister-taxon to Tritylodontidae, the Mammaliaformes.

Martinelli (2010) noted that there was little evidence for tooth replacement in *Pascualgnathus*, most likely due the small sample size ($n = 4$). Two specimens of different cranial length showed the same number of teeth in the maxillary postcanine series, with the distal-most element described as "semi-erupted" (Martinelli, 2010: 633).

4.5.4 Reduced tooth replacement rates in Therocephalia

As already noted, the scarcity of evidence for tooth replacement activity in the specimens of *Bauria* included in the study is quite remarkable. To date the only other known therocephalian that shows such a reduction in the replacement activity is the highly specialised *Euchambersia* (Benoit *et al.*, 2017). Replacement activity in the dentition of *Bauria cynops* may have been reduced as a means of maintaining tooth-on-tooth occlusion of the buccolingually expanded postcanines.

Similar reductions in replacement activity are recorded in the gomphodont cynodonts, which have a postcanine dentition of comparable morphological complexity. Interestingly, it has recently been demonstrated that *Bauria* and basal members of the Cynognathia, (represented by the non-gomphodont *Cynognathus* and gomphodont *Diademodon*) had similar mechanisms of tooth attachment to the jaw as mammals (LeBlanc, 2016; LeBlanc *et al.*, 2018). This apparent convergence towards the mammalian condition of gomphosis may be attributed to the evolution towards a herbivorous diet.

Martinelli (2010) noted an increase in the number of teeth in the maxillary postcanine series of *Scalenodon* and *Massetognathus*, and a reduction in the number of teeth in *Exaeretodon* during ontogeny, and concluded a fixed/consistent number of postcanine teeth in *Pascualgnathus*. Similar reduction/stable postcanine count during ontogeny has been described for *Thrinaxodon* (Abdala *et al.*, 2013). In contrast, it has been demonstrated for the closely related *Cynosaurus* (Van den Brandt and Abdala, 2018) (Chapter 5) and *Galesaurus* (Chapter 6) that the number of teeth in the maxillary and mandibular postcanine series increased during ontogeny.

Reduction in replacement rates of the dentition, and the postcanines in particular, may be as a result of the shift away from a carnivorous diet. Changes in the morphology of the dentition support this transition from a carnivorous to omnivorous, and potentially herbivorous diet (Brocklehurst, 2019). These include

the loss of serrations on the incisors, reduction in canine size, and the buccolingual expansion of the postcanine dentition.

Less frequent replacement of the dentition would have allowed for more precise dental occlusion, and evidence for "shifting" of the dentition to facilitate continued precise occlusion despite the continued growth of the animal has been demonstrated via histological examinations of *Bauria* (LeBlanc, 2016). Similarly, the relative robustness of the dentary corpus in *Bauria* suggests an adaptation for stronger muscle attachment, possibly associated with the processing/mastication of tougher food items, such as fibrous plant matter.

Interestingly, Reisz (1986) also reported little evidence of tooth replacement in the herbivorous edaphosaurid pelycosaurs. Thus, a reduction in replacement may be related to a change in diet from carnivory/omnivory to one of herbivory. This may be as a result of the precise occlusion of the postcanine dentition of *Bauria* such that the crushing surfaces of the upper and lower teeth interact.

However, such a process does not take place in *Edaphosaurus*. Instead food processing is facilitated by the expanded plates of the palate and corresponding surfaces of the lower jaw, which are covered in small denticles (Kemp, 1982). The postcanines in *Edaphosaurus* possess cutting edges, and likely functioned solely in the cropping of plant material (Modesto, 1995; Reisz and Sues, 2000), and not in its actual mastication.

4.6 Conclusion

The almost complete lack of replacement activity in the sample of μCT-scanned specimens of *Bauria cynops* is not anticipated. This is especially true for the canines, which show frequent and continued replacement even in the herbivorous gomphodont cynodonts.

Reduced replacement activity in the postcanine regions of *Bauria* may be related to the precision occlusion between the crowns of the upper and lower series during mastication. However, this does not account for the lack of replacement in the anterior dentition in the sample.

Replacement of the incisors likely took place in an alternating fashion, occurring at least once during the animal's lifetime. The mode of tooth replacement of the postcanines in *Bauria* resembles that of gomphodont cynodonts, with replacement taking place in the middle of the postcanine series, as well as the sequential addition of teeth to the distal margin of the postcanine series. *Bauria* indicates a convergence, in both postcanine crown morphology and replacement patterns, with the condition of the gomphodont cynodonts.

5 TOOTH REPLACEMENT IN THE NON-MAMMALIAN CYNODONT *CYNOSAURUS SUPPOSTUS* FROM THE LATE PERMIAN OF SOUTH AFRICA

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5.1 Abstract

Five specimens of the late Permian cynodont *Cynosaurus suppostus*, representing an ontogenetic growth series, were scanned using micro-computed tomographic techniques to determine tooth replacement patterns. Due to the small sample size, and damage to the rostrum in several specimens, replacement patterns of the incisors could not be accurately determined in this study. Replacement of the canines ceases at a basal skull length of approximately 88 mm, with the last generation of mandibular canines having open root apices. An alternating pattern of replacement is described for the maxillary and mandibular postcanine series. Cessation of replacement in the first postcanine locus (PC1) is synchronised with the eruption of the replacement tooth in the third locus (PC3). Postcanine replacement waves move along the maxilla in multiples of three, in contrast to the mandible where replacement appears to pass along the jaw in multiples of two. With the cessation of replacement at PC1, the postcanine series moves distally. This pattern provides possible evidence for a finite number of replacements occurring at the active PC1. There appear to have been two replacement cycles per postcanine locus in *Cynosaurus*, with the first PC1 locus becoming dormant at a basal skull length of approximately 56 mm. This is a lower number of total replacements per postcanine locus than previously estimated for the closely related Early Triassic cynodont, *Thrinaxodon liorhinus*.

5.2 Introduction

Cynosaurus suppostus (Owen, 1876) is a small to medium-sized (basal skull length of 49–122 mm) non-mammalian cynodont from late Permian deposits of the Beaufort Group of the Main Karoo Basin, Republic of South Africa. After *Procynosuchus*, it is the second most abundant late Permian (Lopingian) cynodont (Botha *et al.*, 2007; Botha-Brink and Abdala, 2008; Van den Brandt and Abdala, 2018), and has been recovered from both the *Cistecephalus* and *Daptocephalus* assemblage zones (Smith and Keyser, 1995b; Viglietti *et al.*, 2016; Van den Brandt and Abdala, 2018). Anatomically the skull of *Cynosaurus* is similar to that of the Early Triassic cynodonts *Progalesaurus* and *Galesaurus*, with all three taxa having an open osseous palate (Hopson and Barghusen, 1986; Sidor and Smith, 2004; Abdala and Allinson, 2005; Jasinoski and Abdala, 2017a). The tricuspid postcanine dentition of *Cynosaurus* is, however, more similar in morphology to the multicusped postcanine dentition of *Thrinaxodon* than the bicuspid dentition of *Galesaurus*. Ivakhnenko (2012: 201–202) categorised the postcanine dentition of *Thrinaxodon* as Type 2, having "[a]ccessory cusps expand anteriorly and posteriorly onto the lingual surface; however, they are merely projections at the base of the main cusp rather than form a continuous cingulum," whereas he considered *Cynosaurus*, together with *Progalesaurus* and *Galesaurus* to possess Type 3, postcanines "without a cingulum." In contrast, Abdala *et al.* (2013: 1422) considered the presence of a lingual cingulum as a feature of the dentition of *Thrinaxodon*, describing two types, "the most simple is composed of cingular cusps that do not form a collar around the tooth, and the more complex have a collar formed by a series of cingular cusps." Postcanines with a 'collared

cingulum' have only been described from the lower jaw of *Thrinaxodon*. Van den Brandt and Abdala (2018: 216) described the crown morphology of the postcanine teeth of *Cynosaurus* as "smooth, with no cingular or cingular cusps present." This description agrees with the observations of Ivakhnenko (2012).

5.2.1 Taxa synonymised with *Cynosaurus*, *sensu* Owen (1876)

Cynosaurus was first described by Owen (1876), but was assigned the name *Cynosuchus suppostus*. A new generic name, *Cynosaurus*, was proposed for the taxon by Schmidt (1927), as *Cynosuchus* was preoccupied for a subgenus of alligator (Gray, 1862). *Cynosuchus* (Gray, 1862) has subsequently become a junior synonym of *Jacare* (Gray, 1844), which is in turn a junior synonym of *Caiman* (de Spix, 1825) (Mook and Mook, 1940). As such the generic name *Cynosuchus* is available for the specimen (NHMUK PV R 1718) originally described by Owen (1876). However, it is suggested that the generic name *Cynosaurus* be preserved due to its familiarity in the literature.

The nine specimens currently assigned to *Cynosaurus* (Van den Brandt and Abdala, 2018), have had a convoluted taxonomic history, with several instances of 'lumping and splitting.' Here a brief overview of the taxonomy, with a special focus on the tooth morphology and replacement, is provided.

Lydekker (1890) referred a right dentary (NHMUK PV OR 49404) to '*Cynosuchus*' *suppostus*. This specimen was later described as a new species, *Cyniscodon lydekkeri* by Broom (1915b). More recent examination of the material

has, however, shown it to be a gorgonopsian (Sigogneau, 1970; Sigogneau-Russell, 1989; Kammerer, 2014).

In 1918, a second species of *Cynosuchus* was described by Haughton (1918) as *Cynosuchus whaitsi.* Haughton (1918: 197) erected the new species for SAM-PK-4333, based on the "imperfect nature" of the holotype of *Cynosuchus suppostus* (NHMUK PV R 1718) and the premise that the "type species is somewhat indeterminable." Haughton's *Cynosuchus whaitsi* shared the dental formula of I4/3, C1/1, PC8/8 with *Cynosuchus suppostus* (contra Lydekker [1890] and Broom [1915b] who gave postcanine counts of seven maxillary and seven mandibular teeth).

Broom (1931) reassigned *Cynosuchus whaitsi* to the genus *Cynosuchoides*, creating the new combination *Cynosuchoides whaitsi*. Broom's diagnosis was based primarily on his interpretation of Haughton's specimen having seven postcanine teeth, whereas that of Owen had eight. Broom (1932a) later noted that the cusp morphologies of the two specimens differed, with Haughton's type having tricuspid postcanines, and Owen's type having bicuspid postcanines. Brink (1965a) attributed an additional specimen (BP/1/3926) to *Cynosuchoides*. Although BP/1/3926 has nine maxillary postcanine teeth, Brink attributed this difference to ontogeny and argued that there were no definite features to differentiate BP/1/3926 from Haughton's type.

Hopson and Kitching (1972) synonymised the genera *Cynosuchoides*, *Nanictosaurus*, *Mygalesuchus*, and *Baurocynodon* with *Cynosaurus*. The specimens of *Mygalesuchus*, *Baurocynodon*, and *Nanictosaurus* were considered to represent juveniles of *Cynosaurus suppostus*. Despite this proposed synonymisation, some researchers (e.g., van Heerden, 1976; van Heerden and Rubidge, 1990) continued to recognise *Nanictosaurus* as a valid taxon. Additionally, van Heerden and Rubidge (1990) synonymised *Nanictosaurus robustus* and *Nanictosaurus rubidgei* with *Nanictosaurus kitchingi*, considering this species to be the most closely related form to the well-known Early Triassic cynodont *Thrinaxodon liorhinus*. This was supported in subsequent phylogenetic analyses by Botha *et al.* (2007), Botha-Brink and Abdala (2008), Ruta *et al.* (2013), Kammerer (2016), and Van den Brandt and Abdala (2018).

Brink (1986) also concluded that there was too much variation between the specimens attributed to *Mygalesuchus*, *Nanictosaurus*, and *Baurocynodon* to warrant them being included as juveniles of *Cynosaurus*. He suggested that *Baurocynodon* remain a distinct genus, and considered that *Mygalesuchus* and the three species of *Nanictosaurus* (*N. kitchingi*, *N. robustus*, *N. rubidgei*) were referred to *Cynosaurus* in error by Hopson and Kitching (1972). Brink (1986) further considered *Cynosaurus suppostus* as the only valid species of *Cynosaurus*.

More recent works have also recognised *Nanictosaurus* as a distinct and valid taxon (Botha *et al.*, 2007; Botha-Brink and Abdala, 2008; Botha-Brink *et al.*, 2011; Ruta *et al.*, 2013; Kammerer, 2016). Sidor and Smith (2004), on the other

hand, considered the specimens of *Nanictosaurus* to represent juvenile specimens of *Cynosaurus*, and therefore did not include them in their cladistic analyses. Ivakhnenko (2012) agreed with Hopson and Kitching (1972) in the synonymisation of *Cynosuchoides*, *Nanictosaurus*, *Mygalesuchus*, and *Baurocynodon* with *Cynosaurus*.

5.2.2 Tooth replacement in *Cynosaurus suppostus*

There have been no previous studies dedicated to the tooth replacement of *Cynosaurus*. In contrast, a great deal of work has been undertaken on the closely related Early Triassic cynodont *Thrinaxodon* (Abdala *et al.*, 2013). The earliest observation of tooth replacement in *Cynosaurus* comes from Haughton (1918), who noted that the postcanine teeth of the right maxilla of SAM-PK-4333 were not of the same age. Although Haughton (1918) did not describe it as such, his observation of the PC2 and PC4 of the right maxilla being more immature than the other teeth in the series suggests an alternating pattern of tooth replacement.

Broom (1932a) gave a brief account of evidence for tooth replacement in the holotype of *Cynosaurus suppostus* (NHMUK PV R 1718), mentioning the third incisor and second postcanine (no sides given) as being younger teeth. Broom (1932a: 267) also noted that the fourth postcanine of each maxilla was "developing."

Most recently, in their cladistic analysis of the Cynodontia, Ruta *et al.* (2013: datasets S2 and S3) gave the postcanine replacement pattern in adult *Cynosaurus*

as alternating. Ruta *et al.* (2013: electronic supplementary material) cited Brink (1965a) as the source of this information, however, Brink did not mention tooth replacement in this publication. Descriptions of several of the specimens showing signs of tooth replacement (e.g., BP/1/1563) have remained unpublished until recently, with the most recent descriptions of the dentition coming from Van den Brandt and Abdala (2018).

The present study, using micro-computed tomography (μCT), is the most detailed study yet undertaken with regard to tooth replacement in *Cynosaurus*. The taxonomy of Brink (1986) is followed, and therefore, *Mygalesuchus* and *Nanictosaurus* are not considered to be synonymous with *Cynosaurus*. Two additional specimens attributed to *Cynosaurus suppostus* by Botha-Brink and Abdala (2008) and Van den Brandt and Abdala (2018), AM 4947 and BP/1/4469, are also included in the study (Table 9). As *Cynosaurus* occurs earlier in the stratigraphic record than both *Galesaurus* and *Thrinaxodon* (Van den Brandt and Abdala, 2018), *Cynosaurus* likely represents a good analogue of the hypothesised shared common ancestor of the two Early Triassic epicynodonts.

5.3 Materials and methods

At present, there are six positively identified specimens of *Cynosaurus suppostus* that are adequately prepared for studies of the dentition (Table 9). These represent a presumed ontogenetic growth series based on basal skull length (BSL), which ranges from approximately 50 mm (BP/1/1563) to 115 mm (BP/1/3926). Due to the small sample size and the incomplete preservation of two specimens, the snout

length (SL) was also recorded as a means to complement the BSL measurements (Table 9). All specimens with known collection localities included in the study are from the Daggaboersnek, Barberskrans, Elandsberg, or lower Palingkloof members of the Balfour Formation, which correspond to the *Daptocephalus* Assemblage Zone (Viglietti *et al.*, 2016).

Three specimens (BP/1/1563, BP/1/3926, and SAM-PK-4333) do not have associated mandibles, and none of the crowns of the functional teeth are preserved. The mandible is preserved in tight occlusion in two specimens (BP/1/4469 and AM 4947), and only the labial surfaces of the upper dentition is visible. Prior to the application of scanning technology, SAM-PK-K10694 was the only specimen of *Cynosaurus* for which the lower dentition was suitably exposed for description. Recent advancements in three-dimensional (3-D) scanning techniques have allowed for studies of the dentition of therapsid fossils to be undertaken *in silico* (Norton *et al.*, 2009; Abdala *et al.*, 2013; Benoit *et al.*, 2017). This means that permanent damage to material in order to study internal morphology, as was common practice in the past (e.g., Rigney, 1938; Brink, 1961; Boonstra, 1962; Hopson,1964; Fourie, 1974) is no longer necessary. Furthermore, this has allowed for increased sample sizes in such studies, as well as the inclusion of holotype material (e.g., Benoit *et al.*, 2017). Micro-computed tomography scanning (μCT) of selected specimens allowed for unerupted replacement teeth, functional teeth, and partially resorbed roots of shed teeth to be easily distinguished. This facilitated descriptions of the crown morphologies and patterns of replacement for the entire dental complement.

Table 9. Specimens of *Cynosaurus suppostus* examined for this study, listed in increasing size.

Specimen	Synonyms/Authority	BSL (mm)	SL (mm)	Ontogenetic Stage	Mx PC (L/R)	Mn pc (L/R)
BP/1/1563	Van den Brandt and Abdala (2018)	49	16	Juvenile	7?/7?	—
BP/1/4469	Botha-Brink and Abdala (2008)	56	22	Juvenile	6/7	8/9
SAM-PK-K10694	Van den Brandt and Abdala (2018)	88.36[a]	34	Subadult	8/8	9?/7?
AM 4947	Botha-Brink and Abdala (2008)	90.91[a]	~35	Subadult	9/9	10/9
BP/1/3926	*Cynosuchoides whaitsi* Brink (1965a)	115	45	Adult	10/9	—
SAM-PK-4333	*Cynosuchus whaitsi* Haughton (1918), *Cynosuchoides whaitsi* Broom (1931, 1932a)	122	46	Adult	8/8	—

Ontogenetic stages based on Benoit *et al.* (2015) and Van den Brandt and Abdala (2018). Abbreviations: BSL, basal skull length; Mn pc, mandibular postcanines; Mx PC, maxillary postcanines; SL, snout length. A question mark (?) indicates that the posterior region of the maxilla is damaged, and that additional postcanines may have been present distal to the last preserved tooth of the series.

[a] Estimated values derived from the methods described in Chapter 5.3.2.

5.3.1 Micro-computed tomography scanned specimens

Five specimens of *Cynosaurus suppostus* comprising an ontogenetic growth series were μCT-scanned. Ontogenetic stages were based on the classifications of Benoit *et al.* (2015) and Van den Brandt and Abdala (2018), with the sample including presumed juveniles, BP/1/1563 (scanned with an isotropic voxel size of 29.11 μm) and BP/1/4469 (34.16 μm); subadults, SAM-PK-10694 (47.58 μm) and AM 4947 (70.77 μm); and an adult, BP/1/3926 (47.58 μm). Complete scanning parameters used for the experiments are presented in Table 10.

Table 10. Parameters used for micro-computed tomography scanning of *Cynosaurus suppostus* specimens.

Specimen	Voxel size (μm)	Tube voltage (kV)	Tube current (μA)	Proj.	Filter
AM 4947	70.77	150	75	2268	1.2 mm Cu
BP/1/1563	29.11	90	39	1989	1.8 mm Al
BP/1/3926	47.58 [a]	150	75	3142	1.2 mm Cu
BP/1/4469	34.16	80	64	3048	1.8 mm Al
SAM-PK-K10694	47.58	150	75	2886	1.2 mm Cu

All specimens were scanned at a frame rate of 0.5 frames per second.

Abbreviations: Al, aluminium; Cu, copper; Proj., projections.

[a] The reported voxel size of 0.0708 mm for BP/1/3926 by Benoit *et al.* (2015: online resource 1), Benoit *et al.* (2016b), and Benoit *et al.* (2016c) is incorrect. The authors instead gave the voxel size for AM 4947 (K. Jakata, pers. comm., 2018).

5.3.2 Estimation of basal skull length for fragmentary specimens

Two medium-sized specimens (BP/1/4469 and SAM-PK-10694) are represented by fragmentary snouts, such that a basal skull length (BSL) could not be recorded.

In order to better facilitate comparison with the more complete specimens in the sample, , estimated BSL measurements for the two incomplete specimens were calculated using the following methods.

5.3.2.1 Ordinary least squares regression

The known BSL and snout length (SL) measurements for the *Cynosaurus* sample were plotted on the X- and Y-axis of a Cartesian coordinate system respectively (Figure 13). Ordinary least square (OLS) regression models for both 'x on Y' and 'y on X' were calculated such that the uncertainty, or error, for measurements of both the BSL and SL could be minimised independently. These two asymmetric regression models also form the limits of the possible values for BSL, which would be estimated through the use of symmetrical regression models, such as reduced major axis (Kermack and Haldane, 1950). For clarity, only the RMA straight line is represented in Figure 13, but the equations of the OLS regression lines are as follows (see also Table 11);

$$\text{x on Y equation: } y = 0.4064x - 2.4972 \qquad (1)$$

$$\text{y on X equation: } y = 0.4026x - 2.1732 \qquad (2)$$

5.3.2.2 Reduced major axis regression

In order to minimise the error in the measurements of the BSL and SL in the sample simultaneously, reduced major axis (RMA) regression analysis was used to fit a straight line to the data (Kermack and Haldane, 1950). Advantages of using RMA over ordinary least squares (OLS) is that the equation for the RMA straight line is symmetrical, allowing for either variable (BSL or SL) to be

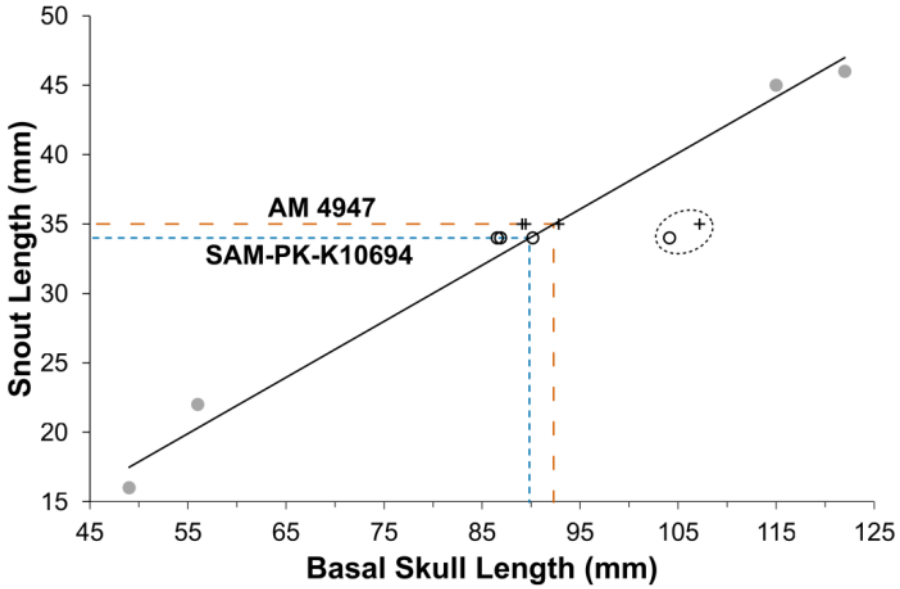

Figure 13. Estimates of the basal skull length for damaged specimens of *Cynosaurus suppostus*.
Complete specimens (●), BSL estimates calculated using R_{BSL} for SAM-PK-K10694 (+) and AM 4947 (○), BSL estimates calculated using RMA for SAM-PK-K10694 (blue dotted line) and AM 4947 (orange dashed line), straight line calculated using reduced major axis model (solid line), and outliers (grey dotted circle).

identified as the 'independent variable.' The straight line produced from RMA also represents the geometric mean of the two possible straight lines produced by OLS techniques, depending on which variable is treated as the independent variable (x on Y vs. y on X regression). Smith (2009) discusses three sources of error in biological data, namely measurement technique, sampling variation and intrinsic natural variation in the data. Measurements of fossils may introduce error from a fourth possible source, variation due to taphonomic distortion. The equation of the RMA straight line is as follows:

$$y = 0.4045x - 2.3348 \qquad (3)$$

Table 11. Estimated basal skull length calculated from the regression models.

Regression model	Slope	Y-intercept	Estimated BSL (mm)	
			SAM-PK-K10694	AM 4947
OLS: x on Y	0.4064	-2.4972	89.81	92.27
OLS: y on X	0.4026	-2.1732	89.85	92.33
RMA[a]	0.4045	-2.3348	89.83	92.30

Abbreviations: BSL, basal skull length; OLS, ordinary least squares; RMA, reduced major axis.

[a] Note that the values calculated from the equation from the RMA are the average of the BSL values calculated from the two OLS models.

5.3.2.3 Ratio of snout length to basal skull length

To complement the estimates from the RMA regression the ratio of the SL relative to the to BSL for each of the complete specimens was calculated (Table 12);

$$R_{BSL} = \frac{SL}{BSL} \quad (4)$$

Each of the four calculated R_{BSL} values were then substituted into the equation;

$$BSL_i = \frac{SL_i^*}{R_{BSL}} \quad (5)$$

Where SL_i^* is the measured SL for each of the two specimens for which BSL was estimated. Four BSL values were calculated for each fragmentary specimen (Table 12). The calculated ratio per complete specimen was substituted into the equation (5) with the measured SL values for damaged specimens.

Estimated BSL values generated in this manner ranged from 86.55–104.13 mm (average: 91.93 mm) for SAM-PK-K10694, and 89.09–107.19 mm (average: 94.64 mm) for AM 4947. Additional estimated BSL values calculated using the average of the calculated R_{BSL} values (0.3719), as well as the R_{BSL} calculated from the ratio between the average SL and BSL measurements (0.3860), produce estimated BSLs for each specimen that fall within the range calculated from the method above.

Table 12. Calculation of estimated basal skull length from the ratio of basal skull length to snout length.

Specimen	BSL (mm)	SL (mm)	R_{BSL}	Estimated BSL (mm)	
				SAM-PK-K10694	AM 4947
BP/1/1563	49	16	0.3265	104.13	107.19
BP/1/4469	56	22	0.3929	86.55	89.09
BP/1/3926	115	45	0.3913	86.89	89.44
SAM-PK-4333	122	46	0.3770	90.17	92.33

Abbreviations: BSL, basal skull length; SL, snout length.

5.3.2.4 Comparison of estimated values

Checking for outliers—The estimated BSL values based on the R_{BSL} for BP/1/1563 are higher than anticipated, possibly due to the proportionally shorter snout. This is expected in juvenile specimens, and as such, these values likely represent an overestimate of the BSL. These values were deemed outliers based on the 1.5 × interquartile range (IQR) rule, and were excluded from the derivation of the average BSL value for each specimen.

Calculating an average—For the final step, an average BSL was calculated for each specimen. Additionally, the estimates from the OLS regression were also removed, as the RMA already represents the average of these two values. The final average BSL value calculated for each specimen reported in the main text was derived as follows: (3 × R_{BSL} values + RMA value)/4. Final averages of the estimated BSL values are as follows: SAM-PK-K10694 (88.36 mm) and AM 4947 (90.91 mm).

5.4 Results

5.4.1 Tooth morphology

5.4.1.1 Incisors

Cynosaurus suppostus has four upper and three lower incisors. There is one deviation to this pattern, the right premaxilla of SAM-PK-K10694 contains five incisors (Figure 14). It is uncertain in this specimen which of these elements is the supernumerary tooth, nor whether the retention is the result of delayed exfoliation of the crown due to the incomplete resorption of the root, or pathology. The anterior snout is not preserved in BP/1/1563 and AM 4947, and the incisor crowns are not preserved in BP/1/3926. Incisor crowns are recurved cones with fine striations visible on the distal edges (e.g., BP/1/4469 and SAM-PK-K10694).

Due to the mandible being preserved in tight occlusion (e.g., BP/1/4469, NHMUK PV R 1718), a complete lack of an associated mandible (e.g., BP/1/1563, BP/1/3926, SAM-PK-4333), or damage to the dentary (e.g., SAM-PK-K10694,

AM 4947), the crown morphology of the lower incisors of *Cynosaurus* has not previously been described.

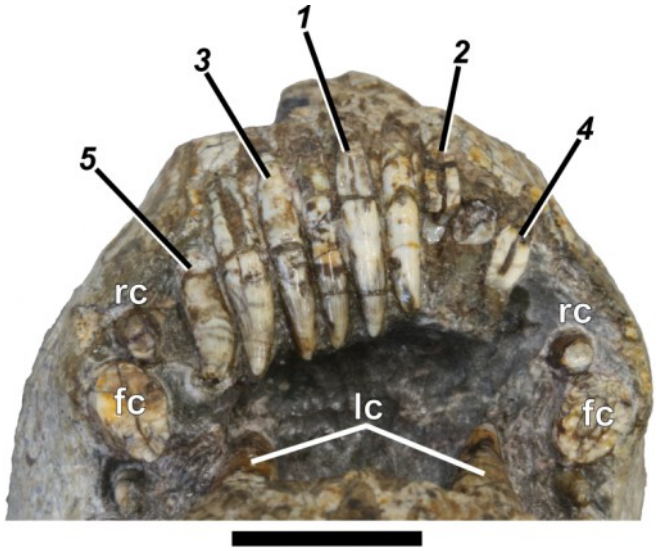

Figure 14. Ventral view of the anterior dentition of a subadult *Cynosaurus suppostus* (SAM-PK-K10694).
Note the presence of an additional incisor in the right premaxilla (left of figure), and erupted crowns of the replacement maxillary canines mesial to the functional canines. Arabic numerals indicate incisor positions. Abbreviations: fc, functional maxillary canine; lc, mandibular canine; rc, replacement maxillary canine. Scale bar equals 10 mm.

The three lower incisors have conical crowns that are slightly recurved. Striations on the crowns were not visible in the tomograms of BP/1/4469. The lower incisors are more slender than the uppers, with the laterally compressed root being approximately twice the length of the crown. Although the crowns of the mandibular incisors are arranged in an arc, the root apex of the third incisor is

positioned more medial (almost caudal) to that of the second incisor (Figure 15). This peculiar arrangement has led earlier researchers (e.g., Van den Brandt and Abdala, 2018) to record the number of mandibular incisors in SAM-PK-K10694 as two.

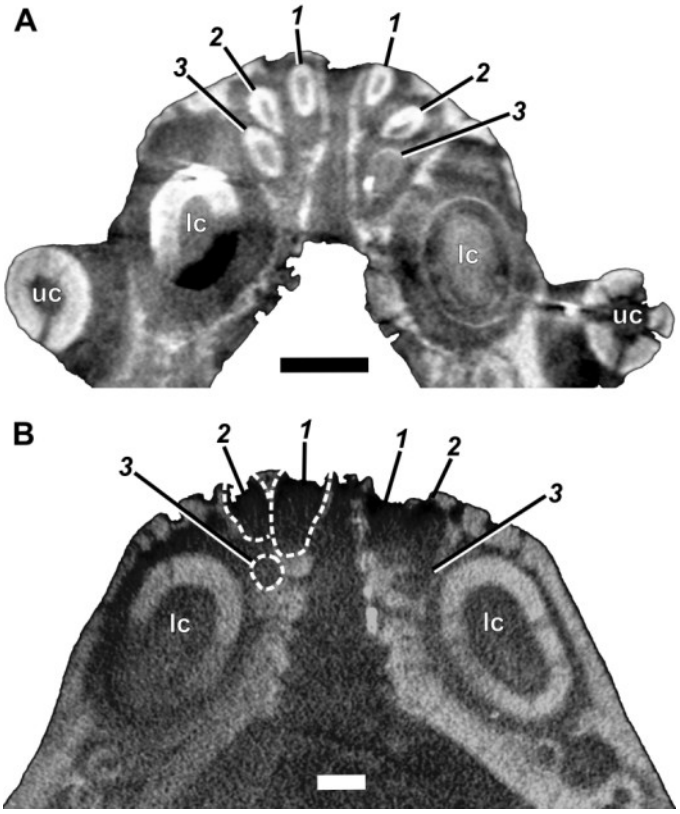

Figure 15. Virtual transverse cross-sections through the dentaries of A, juvenile (BP/1/4469) and B, subadult (SAM-PK-K10694) *Cynosaurus suppostus*. Abbreviations: lc, mandibular canine; uc, maxillary canine. Arabic numerals and dashed lines indicate incisor positions. Scale bar equals 2 mm.

5.4.1.2 Canines

A single functional canine is present in each maxilla. Both maxillary and mandibular canines bear longitudinal furrows that extend the length of the crown. Similar ornamentations have been reported for the canine teeth in the Early Triassic cynodonts *Galesaurus* and *Progalesaurus* (Sidor and Smith, 2004).

5.4.1.3 Postcanines

The first two postcanines of the maxillary series are bicuspid, whereas the remaining four–eight teeth are tricuspid. A general trend for the increase in number of postcanine teeth with ontogenetic development is demonstrated by the five μCT-scanned specimens, with a subsequent decrease in tooth number in the largest specimen. The smallest specimen (BP/1/1563) has seven functional maxillary postcanine teeth, and the largest specimen (SAM-PK-4333) has eight (Table 9). Ten postcanines are preserved in the left maxilla of AM 4947, whereas nine are preserved in the left maxilla.

Only three of the scanned specimens have an associated mandible. Here too an increase in the number of postcanine teeth is recorded through ontogeny (Table 9). The smallest mandible (BP/1/4469) has nine postcanine teeth preserved, whereas the largest mandible (AM 4947) has 10. Reduced anterior and posterior accessory cusps are present on the first tooth of the mandibular postcanine series. These cusps become more defined as one moves distally along the postcanine series.

5.4.2 Tooth replacement

Evidence of tooth replacement, such as the presence of resorption pits, was observed in the gross osteological examination of specimens, but was more accurately surveyed from the μCT data. Replacement teeth for the incisors and postcanines are situated lingual to the functional tooth. In several of the specimens, evidence for the eruption of the replacement maxillary canines is evident.

The following section describes the state of replacement of the teeth (i.e., presence of replacement teeth, developmental condition of roots, etc.) for the five μCT-scanned specimens of *Cynosaurus suppostus*. These scans enabled evaluation of the replacement activity in the full dentition of the same individual in three specimens, and the maxillary dentition in two specimens (Table 9). Replacement variables, such as the presence of replacement teeth and condition of the roots of the functional teeth are described for five specimens of *Cynosaurus*, listed in increasing ontogenetic age.

5.4.3 BP/1/1563 (BSL 49 mm)

This specimen comprises a complete skull without lower jaw. The anterior snout and zygomatic arches are damaged, and none of the functional tooth crowns are preserved.

5.4.3.1 Incisors

No incisors are preserved in BP/1/1563 (Figure 16).

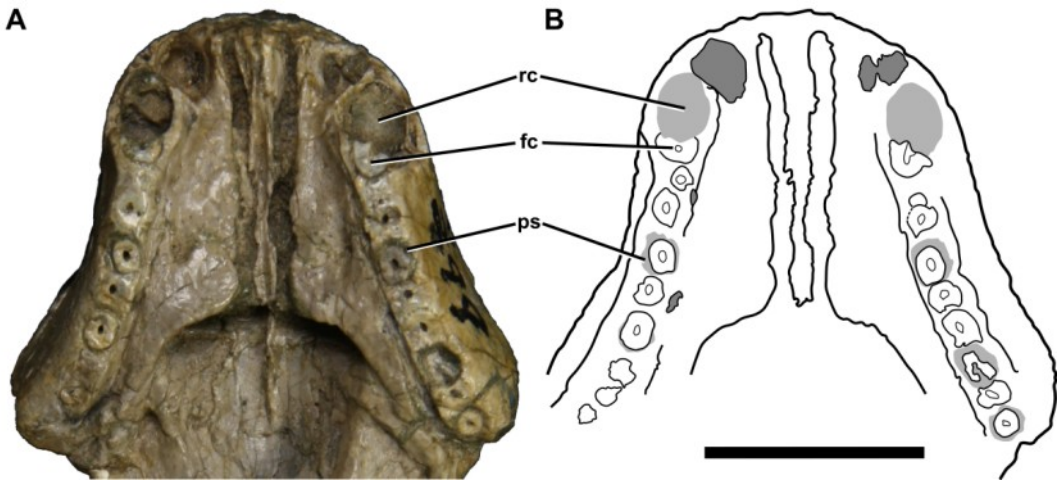

Figure 16. Ventral view of the dentition of a juvenile *Cynosaurus suppostus* (BP/1/1563).

A, photograph; B, interpretive drawing. Abbreviations: fc, functional maxillary canine; ps, periodontal space; rc, alveolus of replacement maxillary canine. Scale bar equals 10 mm.

5.4.3.2 Canines

The maxillary canines were in the process of being replaced when the animal died, such that a functional canine and alveolus of the replacement tooth are present on each side. Both functional canines are broken at the neck, and the mesial edge shows signs of resorption by the replacing tooth (Figure 17A, B). A large alveolus, interpreted as that of the replacement canine, is present mesial to the old preserved root of each functional canine (Figure 16 and Figure 17). It is proposed that the replacing canines had fallen out, due to the alveoli not yet having closed sufficiently around the tooth to hold it in place post mortem. An endocast of the right canine root is discernible from the surrounding bone/matrix (Figure 17B). The preserved root of the right functional canine has undergone

more resorption than that of the left, suggesting that the right tooth is at a slightly more advanced developmental stage.

5.4.3.3 Postcanines

Seven functional postcanines are preserved in each maxilla (Figure 17). The crowns of all postcanine teeth are broken at the level of the alveolar margin. In ventral view, a space is visible between the tooth and the bone surrounding PC2, PC5 and PC7 in the left maxilla, and PC2 and PC4 in the right maxilla (Figure 16). This suggests that these teeth had erupted more recently, or were still in the process of erupting, and that the bone had not yet reformed to hold the tooth firmly in place. In addition to the functional teeth, a partially resorbed root is preserved mesial to the erupted PC1 of each maxilla. This tooth (PCX) represents a tooth locus for which replacement has ceased, resulting in the caudal shift of the postcanine series. The root of PC2 in each maxilla is more elongated than those of the other teeth in the series.

In the left maxilla, replacement crypts are situated between PC3 and PC4 and lingual to PC6, and in the right maxilla there is a crypt associated with PC3 and a partially mineralised crown associated with PC5. All the replacement germs are in an early developmental stage, as only the tip of the crown apex has been mineralised. The PC7 in each maxilla is positioned more lingual than the other teeth of the postcanine series in occlusal view, suggesting that it was the last tooth to be added to the series, and may still have been in the process of erupting.

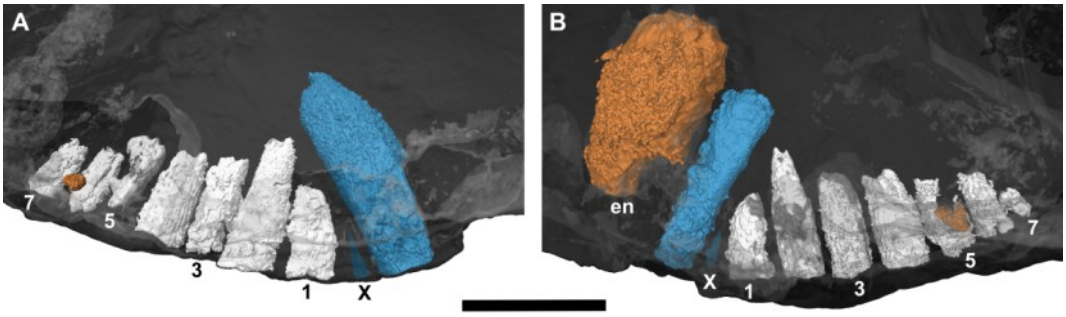

Figure 17. Three-dimensional rendering of the maxillary tooth rows of a juvenile *Cynosaurus suppostus* (BP/1/1563) in medial view.
A, upper left; B, upper right. Replacement teeth in orange, old remnant roots in blue. Abbreviations: en, endocast of right replacement canine root; X, dormant position of a shed PC1. Arabic numerals indicate postcanine positions. Scale bar equals 5 mm.

5.4.4 BP/1/4469 (BSL 56 mm)

This specimen comprises an almost complete skull, with lower jaw preserved in tight occlusion.

5.4.4.1 Incisors

Four incisors are preserved in each premaxilla. On the left (Figure 18A), a replacement tooth is associated with I3, and on the right (Figure 18B) replacements are associated with I2 and I4. Three incisors are preserved in each dentary. In the left dentary (Figure 18C) replacement teeth are associated with i1 and i2. In the right dentary (Figure 18D) a single replacement tooth is evident lingual to i3. The roots of both the functional i2 and i3 appear to have undergone some etching by this replacement tooth.

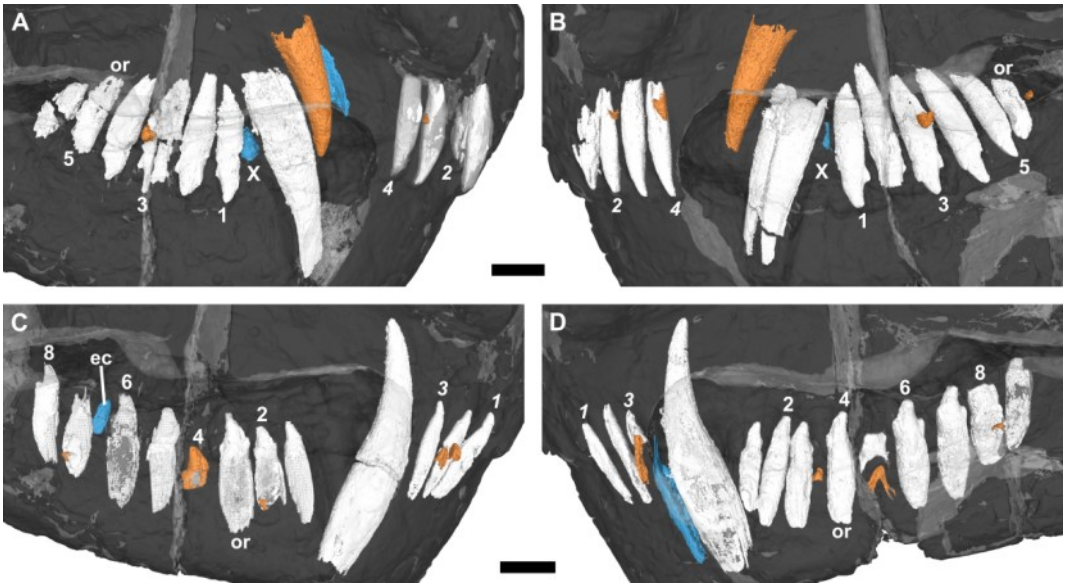

Figure 18. Three-dimensional rendering of the tooth rows of a juvenile *Cynosaurus suppostus* (BP/1/4469) in medial view.
A, upper left; B, upper right; C, lower left; D, lower right. Replacement teeth in orange, old remnant roots in blue. Abbreviations: ec, exfoliated crown; or, open root; X, dormant position of a shed PC1. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bars equal 5 mm.

5.4.4.2 Canines

Prominent replacement canines are visible mesial to the functional canines in both maxillae (Figure 18A, B). In addition to the replacing tooth, a remnant root of a previously shed canine is identifiable in the left maxilla, mesial to both the replacement canine and functional canine (Figure 18A). There is no evidence for the development of a replacement canine in either hemimandible (Figure 18C, D). A remnant root is preserved mesial to the functional canine in the right dentary. The roots of both the maxillary and mandibular canines are open.

5.4.4.3 Postcanines

Six functional postcanines are preserved in each maxilla (Figure 18A, B). The crowns of PC1–PC6 were visible prior to μCT scanning, but the presence of a retained root (PCX) mesial to the first erupted tooth became apparent only after μCT scanning the specimen. In both sides, there is no apparent replacement associated with the PCX locus. Additionally, in the right maxilla a germ is present on the distal end of the postcanine series. Both the left and right PC3 have an associated replacement of similar development, suggesting some synchronicity in the replacement activity between the two maxillae.

Eight functional postcanines are preserved in the left dentary, and nine in the right. There is no retained root (pcX) mesial to the postcanine series of either dentary. In the left dentary (Figure 18C), replacement teeth are associated with pc2, pc4, and pc7, with a crypt associated with pc6. A small tooth is preserved between pc6 and pc7. Due to its considerably smaller size, it is interpreted as the retained crown of a tooth about to have been exfoliated, as opposed to a functional tooth. In the right dentary (Figure 18D), replacement teeth are associated with pc3, pc5, and pc8.

5.4.5 SAM-PK-K10694 (SL 34 mm)

This specimen consists of an incomplete antorbital snout with an associated partial lower jaw.

5.4.5.1 Incisors

The left premaxilla manifests the normal condition of four incisors (Figure 19A), whereas the right maxilla preserves an additional erupted tooth (Figure 14 and Figure 19B). It is unclear which of the five incisors represents the supernumerary element, as all the roots are at a similar developmental stage, and none of them show signs of resorption. Replacement teeth are associated with the left I1 and right I3. The incisor region of both dentaries is damaged such that no teeth are preserved. From the alveoli (Figure 15B), it is evident that three lower incisors are present in each dentary.

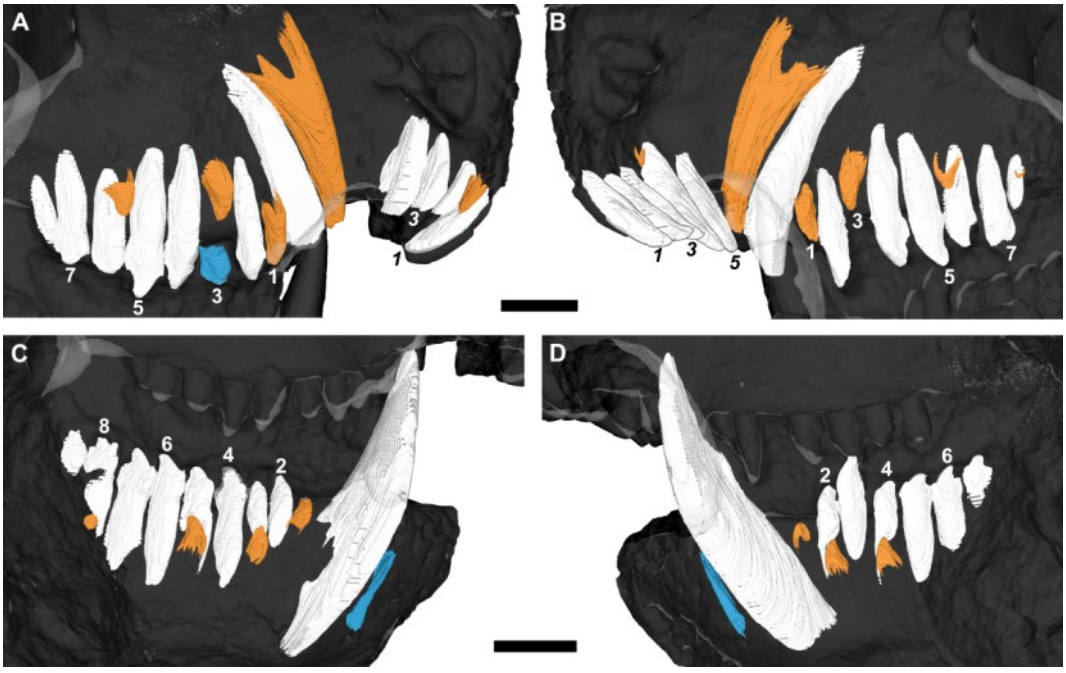

Figure 19. Three-dimensional rendering of the tooth rows of a subadult *Cynosaurus suppostus* (SAM-PK-K10694) in medial view.
A, upper left; B, upper right; C, lower left; D, lower right. Replacement teeth in orange, old remnant roots in blue. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bars equal 10 mm.

5.4.5.2 Canines

Large replacement canines are present mesial to the functional canine in both maxillae (Figure 19A, B). The retained roots of the functional maxillary canines are closed, whereas the roots of the replacing teeth are open. No replacement canines are evident in the lower jaw, however remnant roots from a previously shed canine tooth are preserved mesial to the functional canine on each side (Figure 19C, D). Both mandibular canines have open roots.

5.4.5.3 Postcanines

Eight postcanines are present in each maxilla. On the left (Figure 19A), replacement teeth are associated with PC3, PC6, and PC8. A similar condition is seen in the right maxilla, except that the functional PC3 has already been exfoliated (Figure 19B). There is insufficient space mesial to either PC1 to have held a PCX.

The lower postcanine series are incomplete, because the dentaries are broken posterior to pc9 on the left, and pc7 on the right side (Figure 19C, D). Replacement teeth are present lingual to the functional pc3, pc5 and pc8 in the left dentary. The left pc1 was still in the process of erupting, and has open roots. Similarly, in the right dentary, the pc1 position preserves an unerupted replacement tooth. Replacement teeth of similar developmental stages are associated with pc2 and pc4 in the right dentary.

5.4.6 AM 4947 (SL ~35 mm)

This specimen comprises an incomplete antorbital snout with a partial lower jaw in tight occlusion.

5.4.6.1 Incisors

The snout of AM 4947 is damaged such that most of the incisors are absent, or are represented by fragmentary roots. There is no evidence of replacement activity.

5.4.6.2 Canines

Large functional canines, with open roots, are preserved in each maxilla (Figure 20A, B). The crown of the left is weathered, but the root indicates that it would have been of similar size to the right canine. Remnant roots of previously shed canines are preserved distal to each maxillary canine. In contrast to the functional canines, the roots of these teeth have a closed root apex. A single canine is present in each dentary and there are no signs of either developing replacement teeth, or retained roots (Figure 20C, D).

5.4.6.3 Postcanines

Nine postcanine teeth are present in each maxilla (Figure 20A, B), and replacement teeth are associated with the positions PC1, PC3, and PC5.

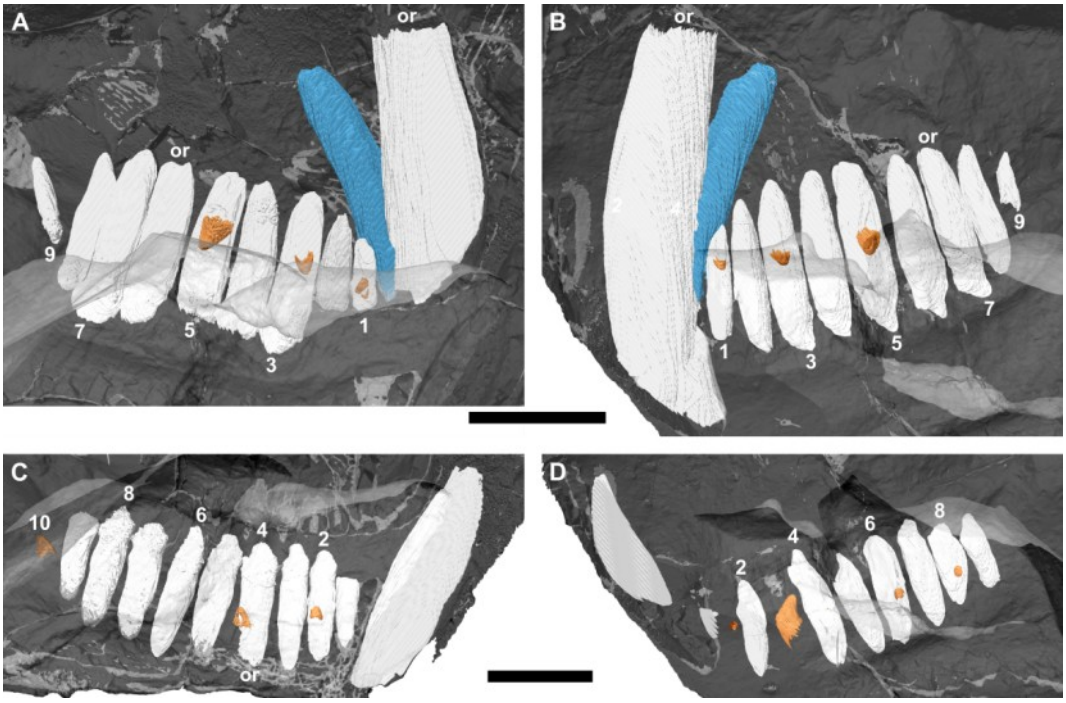

Figure 20. Three-dimensional rendering of the tooth rows of a subadult *Cynosaurus suppostus* (AM 4947) in medial view.
A, upper left; B, upper right; C, lower left; D, lower right. Replacement teeth in orange, old remnant roots in blue. Abbreviation: or, open roots. Arabic numerals indicate postcanine position. Scale bar equals 10 mm.

Each dentary preserves nine functional postcanine teeth (Figure 20C, D). A tenth tooth was developing distal to the pc9 of the left dentary. Replacement teeth are associated with pc2 and pc4 in the left (Figure 20C), and pc2, pc6, and pc8 in the right (Figure 20D). A crypt is present lingual to pc4 in the right dentary, such that each of the even-numbered loci show signs of replacement activity. In addition, the right pc3 was in the process of erupting.

5.4.7 BP/1/3926 (BSL 115 mm)

This specimen comprises a skull without a mandible. The right postorbital and both zygomatic arches are damaged.

5.4.7.1 Incisors

Four incisors are present in each premaxilla. There are no signs of replacement activity on the left (Figure 21A), but a single replacement germ is evident lingual to the right functional I2 (Figure 21B). In addition, an old root is preserved labial to the functional right I3.

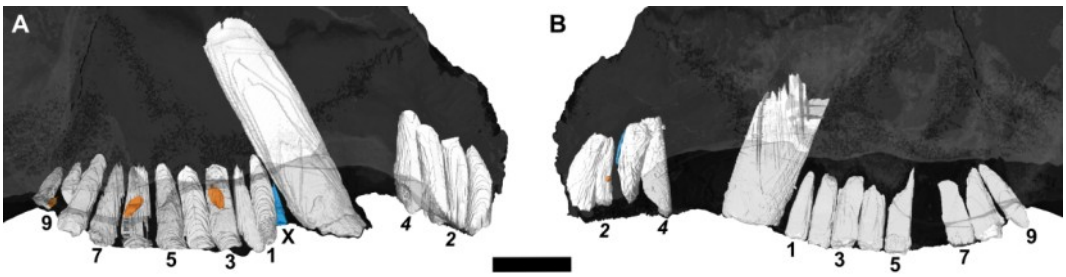

Figure 21. Three-dimensional rendering of the maxillary tooth rows of an adult *Cynosaurus suppostus* (BP/1/3926) in medial view.
A, upper left; B, upper right. Replacement teeth in orange, old remnant roots in blue. Abbreviation: X, dormant position of a shed PC1. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bar equals 10 mm.

5.4.7.2 Canines

Prominent canines are preserved in each maxilla. Both are broken at, or just above, the level of the alveolar margin. The roots of the left maxillary canine are

closed (Figure 21A). Due to poor contrast, the extent of development of the right maxillary canine could not be determined (Figure 21B). No replacement activity is associated with either canine tooth.

5.4.7.3 Postcanines

Ten functional postcanine teeth are present in the left maxilla (Figure 21A). The crown of PC9 is not preserved, and the tooth was not visible prior to µCT-scanning of the specimen. A remnant root is preserved mesial to the first erupted tooth. Replacement teeth were forming lingually to PC3, PC6, and PC9. The right maxilla (Figure 21B), shows evidence for nine postcanine teeth, with the sixth locus represented by an empty alveolus. There is no remnant root present mesial to the first erupted tooth. There is less replacement activity visible in the right maxilla, with only a single replacement germ present in association with the empty sixth locus.

5.4.8 SAM-PK-4333 (BSL 122 mm)

This specimen, the largest of the sample, comprises an obliquely compressed skull with damaged postorbital and zygomatic arches. There is no mandible preserved, and all tooth crowns are broken. The specimen was not µCT-scanned, and the following is a report of the observations made from first-hand examination of the specimen.

5.4.8.1 Incisors

No evidence for the replacement activity of the incisors is visible. A small, partial pit is present lingual to the left I2, which is interpreted as the incisiform foramen, and not a structure related to tooth replacement.

5.4.8.2 Canines

No evidence of replacement activity of the canines is visible.

5.4.8.3 Postcanines

In the left maxilla (Figure 22A), PC2 and PC4 have alveoli that lie lower on the tooth, such that the neck of the tooth is partially exposed on the lingual surface. These teeth, as well as PC6 and PC8, lie lingual to the odd-numbered teeth of the series. Resorption pits indicative of replacement activity are evident lingual to PC1, PC3, PC5, and PC8.

Due to compression, the lingual view of the right maxilla is not accessible. Eight postcanine teeth are visible (Figure 22B). The periodontal space surrounding PC2, PC4 and PC7 is wider than that of the neighbouring teeth. The small crown of PC 8 lies lingual to the other teeth of the postcanine row, and was likely still in the process of erupting.

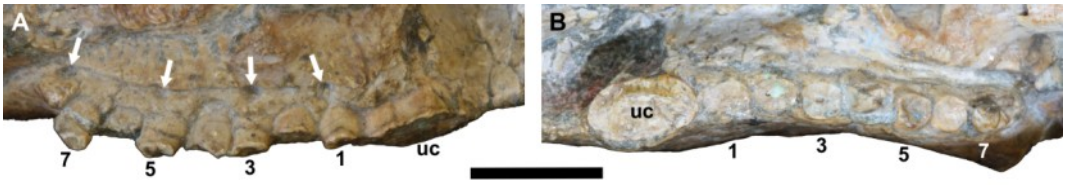

Figure 22. Postcanine dentition of an adult specimen of *Cynosaurus suppostus* (SAM-PK-4333).

A, left maxilla in medial view; B, right maxilla in occlusal view. Abbreviation: uc, maxillary canine. Arrows indicate pits associated with replacement activity. Arabic numerals indicate postcanine positions Scale bar equals 10 mm.

5.5 Discussion

5.5.1 Tooth morphologies and number

5.5.1.1 Anterior dentition

The basal cynodont dental formula of four upper and three lower incisors (Broom, 1932a; Hopson and Barghusen, 1986; Hopson and Kitching, 2001; Abdala, 2007) is observed in the majority of specimens assigned to *Cynosaurus suppostus*. The upper incisors of all specimens are evenly spaced along the premaxilla from the midline to the maxilla. A supernumerary tooth is present in the right premaxilla of SAM-PK-K10694. Wood and Wood (1933) offered four mechanisms that may result in the occurrence of a supernumerary tooth: (1) mechanical splitting of the tooth germ; (2) retention of a deciduous tooth; (3) production of a new tooth through mutation; and (4) reversion to an ancestral condition. Since several groups of basal theriodonts have five or more upper incisors (Kemp, 1982; van den Heever, 1994; Liu *et al.*, 2009), it is plausible that the extra tooth may have arisen by any of these four means.

A supernumerary incisor has been described in the right premaxilla of *Abdalodon* (SAM-PK-K10138) (Botha-Brink and Abdala, 2008; Kammerer, 2016). Botha-Brink and Abdala (2008) described this fifth incisor as erupting, and Kammerer (2016) further speculated that the extra tooth was a replacement I4 and not a true fifth incisor. This suggests that the presence of a supernumerary incisor distal to the I4 may have been a common occurrence during the process of tooth replacement in basal cynodonts.

This study revealed that the lower incisors are evenly spaced at the level that the crowns protrude from the dentary, but the roots are more tightly packed. In the large specimen (SAM-PK-K10694) the lower incisors are broken at the level of the alveolar margin. The alveolus of the i3 is situated lingual to the tooth row (Figure 15), such that Van den Brandt and Abdala (2018) interpreted the specimen to have had only two lower incisors. The misalignment of the mandibular incisor roots may be due to pathology, or morphological variation. Interestingly, similar crowding of the lower incisor roots has been observed in adult specimens of *Galesaurus* (see Chapter 6), suggesting that the condition is related to ontogeny.

A single functional canine is present in the maxillae of all five specimens, and a single mandibular canine is present in the dentary. The maxillary canine is buccolingually compressed. The tapering crown is relatively long and gracile, with distinct striations that run apically along the length of the crown.

The root apex morphologies of both the maxillary and mandibular canines vary with ontogenetic growth. Functional canines with open roots are present in both maxillary and mandibular of BP/1/4469 (Figure 18). However, it is likely that the maxillary canines were still in the process of developing. In contrast, the partially resorbed roots of the functional maxillary canines of SAM-PK-K10694 appear to have had a more closed morphology (Figure 19A, B). Unlike the maxillary canines, the mandibular canines of SAM-PK-K10694 were open-rooted (Figure 19C, D). The old remnant in the maxilla of AM 4947 show very clearly a closed morphology, whereas the larger functional teeth have wide open roots (Figure 20A, B). The roots of the maxillary canines of BP/1/3926 appear to be more developed than those of AM 4947, but it is not possible to determine whether these roots were fully closed (Figure 21).

5.5.1.2 Postcanines

Brink (1986) described the postcanine teeth of *Cynosaurus suppostus* as having a moderately developed lingual cingulum, in contrast to Kemp (1982) who considered that no cingulum was present. Botha-Brink and Abdala (2008: 3) described the postcanines of *Cynosaurus* as being simple, ovoid, and lacking a cingulum. Later, Botha-Brink and Abdala (2008: 4) wrote that the postcanines have a posterior accessory cusp, and even a second posterior accessory cusp in the distal-most postcanines of the series. The anterior accessory cusp was described as "barely visible" (Botha-Brink and Abdala, 2008: 4). The tricuspid nature of the distal elements of the postcanine series (from PC3 posteriorly) resembles the postcanine teeth of *Thrinaxodon liorhinus* (Abdala *et al.*, 2013). This change in

morphology is likely due to the replacing tooth having a more simple crown morphology, a condition observed in *Thrinaxodon* (Abdala *et al.*, 2013) and *Galesaurus* (Chapter 6).

In BP/1/4469 the first three postcanines of the lower jaw are closely packed, whereas the remaining five/six teeth of the series are more evenly spaced. These first three teeth are concealed laterally by the maxillary canine. This close packing of the mesial lower postcanines is not evident in the postcanine series of the much larger specimens SAM-PK-K10694 and AM 4947.

5.5.2 Reduction in size of the ultimate maxillary postcanine

Size reduction of the distal-most element of the maxillary postcanine series is recorded in a juvenile (BP/1/1563) and two subadult specimens (SAM-PK-K10694 and AM 4947) of *Cynosaurus suppostus*. In SAM-PK-K10694 (Figure 19A, B), the ultimate postcanine (PC8) is of comparable size and crown morphology to the erupting PC1. In contrast, the ultimate maxillary postcanines of BP/1/1563 (PC7, Figure 17B) and AM 4947 (PC9, Figure 20A, B) are smaller than their respective PC1s. This phenomenon has been previously described in other cynodont taxa including *Thrinaxodon* (Abdala *et al.*, 2013), *Probainognathus* (Abdala, 1996) and *Bonacynodon* (Martinelli *et al.*, 2016).

Osborn and Crompton (1973) interpreted this reduction in size and crown morphology of the mesial and distal postcanines of the series in *Thrinaxodon* as an indication of the cessation of replacement at these loci. It is interpreted that the

distal-most element of the postcanine series represents the first tooth to erupt at that locus, and is thus of a younger generation than the other functional teeth. Of the five μCT-scanned specimens, the development of a replacement tooth associated with the last tooth in the series was only observed in the left and right maxillae of SAM-PK-K10694 (Figure 19A, B), indicating that replacement did occur in the distal-most elements of the postcanine series.

5.5.3 Tooth replacement

In *Cynosaurus*, replacement teeth are always positioned lingual to the functional tooth. As the new tooth develops, it moves labially, etching at, and causing the resorption of the root of the functional tooth. Once the root of the functional tooth has been sufficiently eroded through this process, the crown is shed (Wu *et al.*, 2013).

5.5.3.1 Incisors

The pattern of replacement in both the upper and lower incisors is typical of the alternating pattern described for the epicynodonts *Thrinaxodon* (Abdala *et al.*, 2013) and *Galesaurus* (Chapter 6). There are more replacements present in the premaxilla of the juvenile (BP/1/4469) than in the subadult (SAM-PK-K10694), suggesting a higher rate of replacement in younger individuals. As previously discussed, the cause of the presence of a supernumerary incisor in the right premaxilla of SAM-PK-K10694 is uncertain. However, as there is a replacement associated with the left I1 (Figure 19A), it is possible that the first or second incisor in the right premaxilla may represent a replacement that has pushed its

way passed the functional tooth, and erupted while the previous element was still implanted in the jaw. Alternatively, the developing germ of the replacement tooth may have split during development, such that the functional I1 was replaced by two teeth. Supernumerary 'canine' teeth present in Dicynodontia have been attributed to both pathology (Froebisch, 2005; Jinnah and Rubidge, 2007), as well as genetic mutation (Fröbisch and Reisz, 2008), whereas the supernumerary incisor of *Abdalodon* has been attributed to the retention of a functional tooth (Botha-Brink and Abdala, 2008; Kammerer, 2016).

5.5.3.2 Canines

Specimen BP/1/1563, which has the smallest BSL, and is considered a juvenile individual, shows clear evidence for canine replacement, with the presence of a large alveolus mesial to each functional canine (Figure 16). It also has remnant roots associated with both maxillary canines, suggesting that the functional teeth were not the first canines of the individual. Van den Brandt and Abdala (2018) interpreted the distal canines as being the replacing tooth. In contrast, here it is interpreted that the mesial tooth was the replacing element, based on the resorption of the mesial margin of the distal tooth (Figure 17). It is likely that the replacing tooth has been lost, as the alveolar margin had not yet closed sufficiently around the developing tooth to hold it in place post mortem (Parrington, 1936b; Romer and Price, 1940; Colbert and Kitching, 1981). In both *Thrinaxodon* (Abdala *et al.*, 2013) and *Galesaurus* (Chapter 6) the more common condition is for the replacement maxillary canine to erupt mesial to the functional tooth.

Specimen BP/1/4469 preserves both a replacement canine and the remnant roots of an old canine mesial to the functional maxillary canine (Figure 18A), whereas in AM 4947 the remnant roots are positioned distal to the functional canine (Figure 20A, B). The presence of both the old remnant root and the replacing tooth mesial to the functional tooth could suggest that *Cynosaurus* had two tooth families alternately occupying the canine locus (Figure 18A). Abdala *et al.* (2013) made similar observations relating to the preservation of remnant roots both mesial and distal to the functional canine in several juvenile specimens of *Thrinaxodon*, however, none of the µCT-scanned specimens included in their study showed replacement of the maxillary canine distal to the functional canine. They suggested that the arrangement of both the erupting tooth and remnant roots preserved mesial to the functional tooth may have come about through the subsequent migration of the erupting tooth, as there were insufficient specimens supporting the presence of two alternating tooth families associated with each canine locus. Osborn and Crompton (1973) suggested a similar hypothesis for the migration of the maxillary canines in *Thrinaxodon*. None of the specimens in the present study sample show any indication of the replacement maxillary canine erupting distal to the functional tooth. Thus, the condition of two canine families alternately occupying a single locus remains limited to the Gorgonopsia and Therocephalia (Kermack, 1956; van den Heever, 1980, 1994) (see Chapter 3).

Replacement of the upper canines, with no evidence for the development of replacement mandibular canines, is observed in the juvenile BP/1/4469 (BSL 56 mm) and subadult SAM-PK-K10694 (SL 34 mm). The same state of replacement

has been documented in subadult specimens of the Early Triassic cynodont *Galesaurus* (Chapter 6), as well as an adult specimen of *Thrinaxodon* (BP/1/5905, BSL 87 mm) (Abdala *et al.*, 2013). Both BP/1/4469 (Figure 18C, D) and SAM-PK-K10694 (Figure 19C, D) have remnant roots of a shed canine mesial to the functional canine of the mandible. This region of the lower jaw is damaged in AM 4947, and no remnant roots are identifiable (Figure 20C, D).

The smallest µCT-scanned specimen of *Galesaurus* (RC 845, BSL 69 mm), showed that the mandibular canines are replaced before those of the maxilla (Chapter 6). Since the lower jaw is not preserved for the smallest specimen of *Cynosaurus*, no comparisons can be made.

As in *Galesaurus* (Chapter 6), no replacement of the maxillary and mandibular canines is evident in the larger specimens of *Cynosaurus* (e.g., AM 4947 and BP/1/3926), suggesting a cessation of canine replacement at a SL of ~35 mm (see Table 9). This is in contrast to the situation in *Thrinaxodon* for which Abdala *et al.* (2013) demonstrated that the canines were replaced well into adulthood. The lack of replacement of the maxillary and mandibular canines in the intermediate sized *Cynosaurus* specimen AM 4947 (SL ~35 mm) may indicate that it had already reached skeletal maturity, as in *Galesaurus* where the cessation of replacement of the canines coincides with the attainment of adulthood (Chapter 6). Of interest is that the similarly-sized SAM-PK-K10694 (SL 34 mm) shows replacement of the maxillary canines, and not those of the mandible. This suggests that by a SL of 34 mm the last replacement generation of mandibular canines had

already erupted, and the replacing canines of the maxilla were to be the last replacement generation in the animal. As such, the maxillary and mandibular canines may have the same number of replacement generations, with the lower canines erupting first as seen in *Thrinaxodon* (Abdala *et al.*, 2013) and *Galesaurus* (Chapter 6). The noticeable difference in developmental stages of the canines of the two similarly sized subadult specimens may also be attributed to individual variation.

From the estimates of the BSL for SAM-PK-K10694 and AM 4947 (Table 11 and Table 12), it appears that the last generation of maxillary canines developed in individuals with a BSL of 86.55–92.33 mm. These values closely match the BSL of ~90 mm for which the similarly sized *Galesaurus* (BSL 62–114 mm) is estimated to have reached adulthood based on studies of the cranium (Jasinoski and Abdala, 2017a), postcrania (Butler *et al.*, 2019), and dental replacement (Chapter 6).

5.5.3.3 Postcanines

Replacement of the postcanine teeth of *Cynosaurus* occurs in an alternating pattern (Figure 23). The data suggest that the mesial-most tooth of the maxillary series is not replaced throughout the lifespan of the animal. Instead, the expanded root diameter of the replacing canine invades the alveolus of PC1, resulting in the distal shift in the postcanine series. A similar situation has previously been described for *Thrinaxodon* (Abdala *et al.*, 2013). Due to the limited material, no

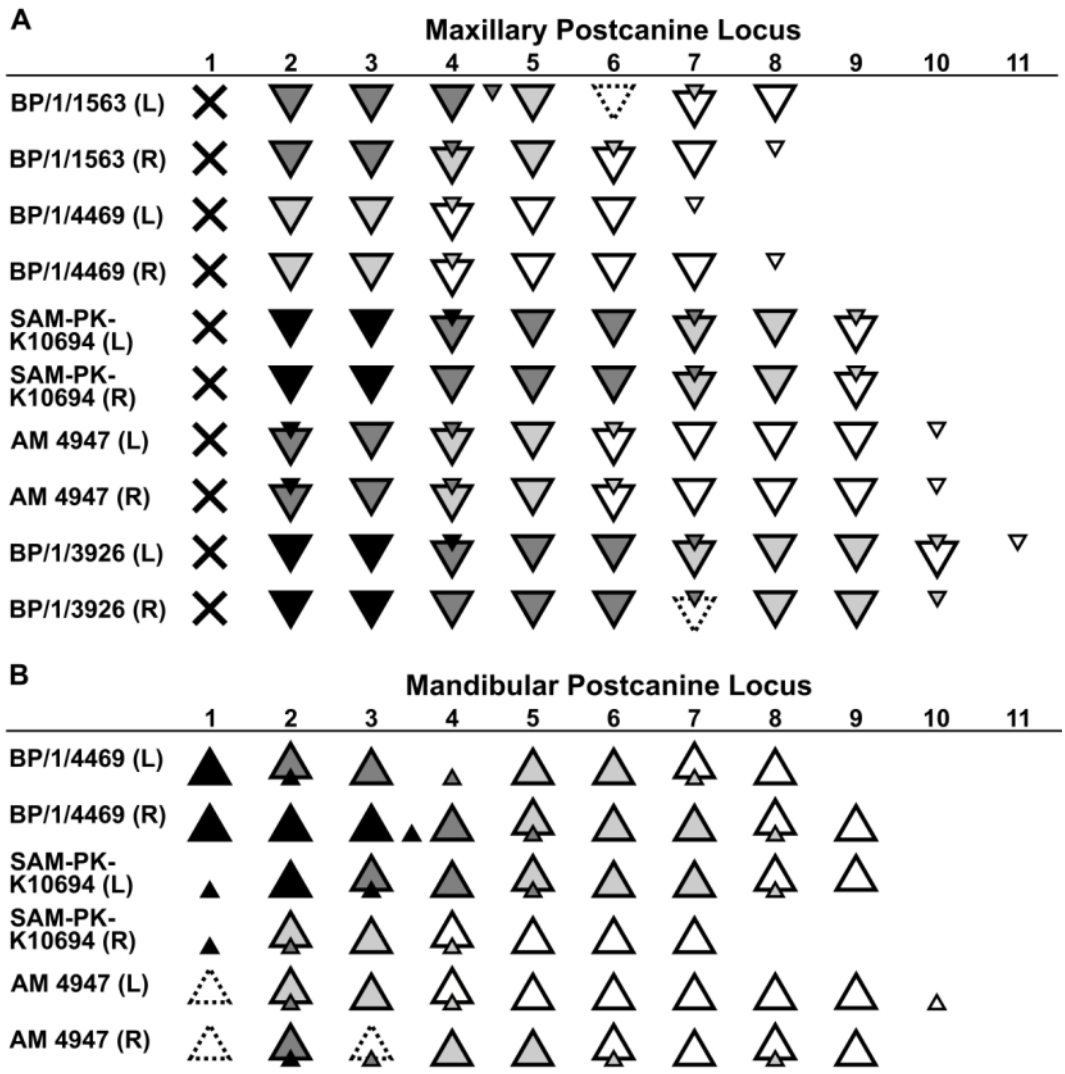

Figure 23. Schematic diagram of the observed tooth replacement in μCT-scanned specimens of *Cynosaurus suppostus*.

A, maxillary postcanine series; B, mandibular postcanine series. Replacement teeth are indicated by small triangles, functional teeth by large triangles. Dashed outlines indicate the functional tooth has been exfoliated. The 'X' represents the hypothesised presence of a dormant alveolus, based on the model described in the text. Shading is used to differentiate between different tooth generations, with darker tones representing later replacement waves, and does not indicate/imply similar tooth age between different individuals. Not to scale.

such deduction could be made for the mandibular postcanine series of *Cynosaurus*.

In all the scanned specimens, the third maxillary postcanine locus always has an associated replacement tooth. This suggests that the timing of the development of the replacement tooth coincides with the exfoliation of the tooth in the first position (X). Whereas development of the replacement teeth at the 'PC1' site does eventually cease, there is evidence that at least one replacement cycle may have taken place at the newly formed PC1 locus. A model showing the hypothesised development and replacement of the maxillary postcanine series (Figure 24), allows replacement to occur at each locus up to three times, before the active PC1 position is encroached upon by the expanding canine alveolus. In several specimens an alternating pattern for which tooth loci (e.g., PC3, PC6, and PC9) are being replaced in multiples of three are observed. A model to explain this condition, which additionally allows for the loss of the first maxillary postcanine (Figure 24), shows that it is possible that each maxillary postcanine locus has three tooth generations. Due to the small number of specimens with a preserved mandible, no such model is proposed for the mandibular postcanines. However, since the mandibular series seems to be replaced in multiples of two (i.e., pc2, pc4, pc6) it could be assumed to exhibit a similar condition to that reported for *Thrinaxodon* (Abdala *et al.*, 2013). However, from actual observations the three larger specimens, SAM-PK-K10694, AM 4947, and BP/1/3926 tend to support the presence of four replacement waves moving along the maxilla concurrently.

The presence of a replacement tooth associated with the PC1 in AM 4947 suggests that the locus remains active for at least one replacement cycle before it becomes a dormant locus (X).

In SAM-PKK10694, it is likely that the previous PCX was entirely resorbed by the expanding alveolus of the functional canine. Thus the current PC1s probably represent the last generation to occupy the position before the locus became dormant.

In the right maxilla of SAM-PK-4333 the periodontal space surrounding PC2, PC4 and PC7 is wider than that of the neighbouring teeth, suggesting that PC2, PC4 and PC7 may be younger than adjacent teeth, and therefore of different replacement waves.

The model of tooth replacement observed in the postcanines of *Cynosaurus* corresponds with Edmund's (1960, 1962) Zahnreihe theory, whereby teeth are replaced in successive waves that move through the jaw in a back to front direction.

5.5.4 Postcanine replacement model

A working model of replacement of the maxillary postcanines in *Cynosaurus suppostus* is proposed (Figure 24), based on observations of the states of tooth replacement from the five µCT-scanned specimens. In Figure 24, developmental stages 1–6 represent hypothetical juvenile conditions that are currently not

preserved in the *Cynosaurus* fossil record. A new tooth is added to the distal margin of the postcanine series in each stage at a constant rate through ontogeny. From observations of a replacement developing at the third locus coinciding with the first locus becoming dormant in two μCT-scanned specimens (BP/1/4469 and BP/1/3926), it is estimated that the first wave of replacement would be initiated at developmental stage 4. The second replacement wave would be initiated at developmental stage 7.

From the model (Figure 24), it appears that BP/1/1563 (the smallest known specimen of *Cynosaurus*), which corresponds approximately to developmental stage 6/7, had already replaced the tooth at PC1 at least once. The presence of seven postcanines in the series, and evidence for two replacement waves suggests that the tooth at PC1 has been replaced twice, and that the current PC1 is the last tooth to fill that position before the locus becomes dormant, as in BP/1/4469.

According to the model, BP/1/4469 represents a condition intermediate to developmental stages 9 and 10, whereby the tooth at PC1 has yet to be exfoliated. Based on this assumption, the postcanine series of SAM-PK-K10694 and AM 4947 are shifted to the right by at least one locus in the model. AM 4947 shows three replacement waves, suggesting a possible fourth replacement generation at PC1. The model suggests that in *Cynosaurus* the first tooth of the postcanine series was replaced at least once prior to the locus becoming dormant, and that the following tooth had likely been replaced at least twice before becoming the new

active PC1. This suggests a minimum of three replacement generations at each maxillary postcanine locus.

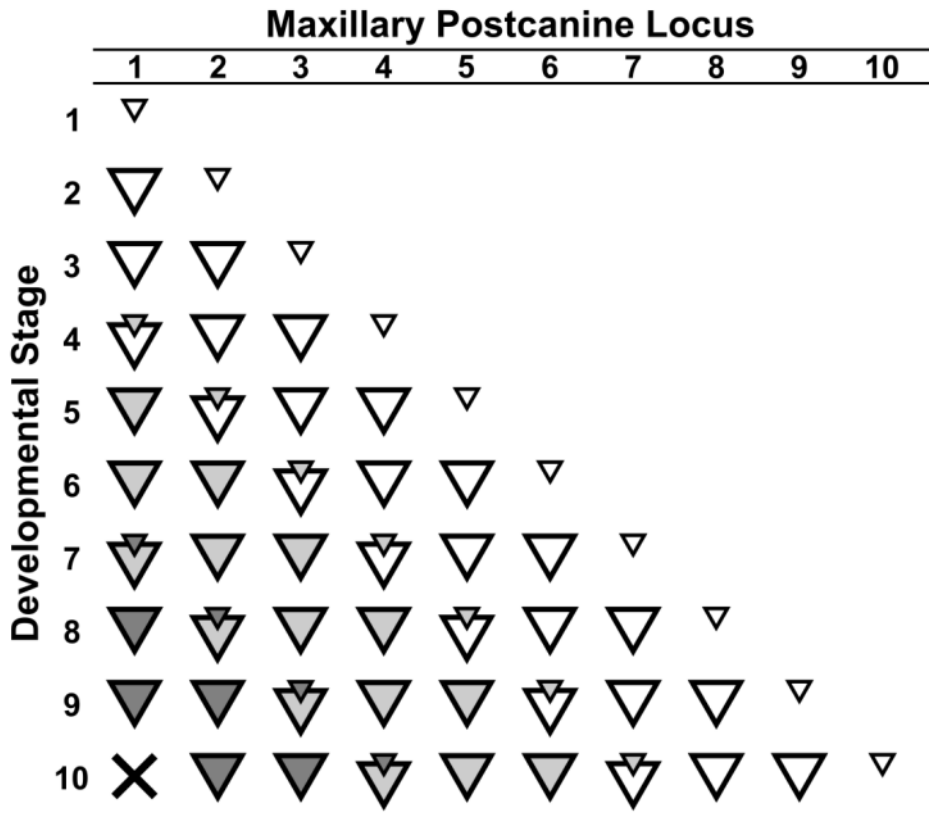

Figure 24. Model of hypothetical tooth states through ontogeny in the maxilla of *Cynosaurus suppostus*.
Replacement teeth are indicated by small triangles, functional teeth by large triangles. The 'X' represents an alveolus that has become dormant. Shading is used to differentiate between different tooth generations, with darker tones representing later replacement waves. Not to scale.

One of the shortcomings of the proposed model is that it does not take into account any changes to the rate at which replacement teeth developed, either as a

result of ontogeny or individual variation. As such, the model cannot account for a decrease in the number of postcanines as seen in the largest specimen in this study (SAM-PK-4333).

Abdala *et al.* (2013) offered the first estimates of the number of replacement cycles in the postcanines of *Thrinaxodon*. These were calculated based on the relative size increase of the replacing tooth crown relative to the crown of the functional tooth. This percentage increase was then used to calculate the number of replacement generations required to move from the tooth size in the smallest specimen (BP/1/5372) to that of the largest specimen (BP/1/5905). From their calculations, the maxillary postcanines were estimated to be replaced between 3–14 times, whereas the mandibular postcanines were replaced 3–6 times.

The estimate of 3–6 replacements for the mandibular series is in line with that proposed here for the number of replacements in *Cynosaurus*. However, the estimate for the maxillary series of *Thrinaxodon* is likely inaccurate, due to the fact that the percentage increase of the anteroposterior length (APL) of the postcanine crowns was calculated using measurements from the mandibular series. This equation also assumes that the teeth increase in size with each successive replacement at the same ratio. Furthermore, comparison of the crown measurements of the subadult specimens, BP/1/7199 and TM 180, which both have a BSL of 75 mm, shows that there is some variation in the crown size (Abdala *et al.*, 2013: fig. 15), particularly for the mandibular postcanine series. All of this makes estimating the number of tooth replacement cycles based solely

on percentage increase of associated replacement teeth relatively inaccurate. However, given the small sample size (n = 5) of scanned specimens of *Thrinaxodon*, this method offers the best mathematical estimate we have to date for calculating the number of replacement generations.

5.5.5 Inclusion of tooth replacement patterns in phylogenetic analyses

Recent studies of the phylogenetic relationships of the Cynodontia recover *Cynosaurus* as the basal-most member of the Epicynodontia (Botha *et al.*, 2007; Ruta *et al.*, 2013). Slight variations of this position show *Cynosaurus* to be included in the Galesauridae (Sidor and Smith, 2004), as well as *Cynosaurus* and the Galesauridae (represented by *Progalesaurus* and *Galesaurus*) forming a polytomy at the base of the Epicynodontia (Abdala, 2007). Importantly, Botha *et al.* (2007) and Ruta *et al.* (2013) consider *Nanictosaurus* to be a valid taxon and include it in their matrices, whereas Abdala (2007) and Sidor and Smith (2004) have excluded the genus.

The phylogenetic study by Ruta *et al.* (2013) is comprehensive, and included more characters related to tooth morphology than previous studies (Table 13). Of interest was the inclusion of character 130 “postcanine replacement pattern in adult” in their analysis (Ruta *et al.*, 2013: datasets S2, S3). Although the character has been used in several previous cladistic analyses (e.g., Hopson and Kitching, 2001; Martinelli *et al.*, 2005; Sidor and Hancox, 2006; Martinelli and Rougier, 2007; Liu and Olsen, 2010), none of these studies have included *Cynosaurus*. There are also several discrepancies between the coding for postcanine

Table 13. Comparison of the number of taxa and characters used in the phylogenetic analyses that have included *Cynosaurus suppostus*.

Reference	Taxa		Characters			
	Total	**Non-mammalian cynodont**	**Total**	**Cranial**	**Dental**	**Postcranial**
Sidor and Smith (2004)	12	10	56	44	12 (21.43%)	0
Abdala (2007)	32	23	96	75	21 (21.88%)	0
Botha *et al.* (2007)[a]	18	10	59	47	12 (20.34%)	0
Ruta *et al.* (2013)	54	52	150	95	35 (23.33%)	20
Kammerer (2016)[a]	13	11	62	49	13 (20.97%)	0
Van den Brandt and Abdala (2018)[a]	14	12	52	41	11 (21.15%)	0

[a] The character matrix of Van den Brandt and Abdala (2018) is based on that of Kammerer (2016), which is in turn based on Botha *et al.* (2007).

replacement by Ruta *et al.* (2013), and the types of postcanine replacement patterns offered by Abdala *et al.* (2013), particularly for the more derived cynodonts.

With the recent contributions on the tooth replacement of *Thrinaxodon* (Abdala *et al.*, 2013) and *Galesaurus* (Chapter 6) adding new information regarding the modes of replacement of the incisors and canines, it may be pertinent to include characters related to the patterns of tooth replacement in future cladistic analyses.

The tricuspid postcanine morphology of *Cynosaurus* is less derived than the multicusped postcanine morphology of *Thrinaxodon*, and may represent an evolutionary precursor. The patterns of tooth replacement described here for *Cynosaurus* also closely match those previously described for *Thrinaxodon* (Abdala *et al.*, 2013). Thus, the more simplified postcanine crown morphology, and similar tooth replacement patterns make *Cynosaurus* a good analogue to the ancestor of *Thrinaxodon*.

5.6 Conclusion

The replacement patterns of the dentition of the late Permian *Cynosaurus* is similar to that of the Early Triassic *Thrinaxodon.* Noteworthy deviations from *Thrinaxodon* include the cessation of replacement of the canines in adults, as observed in *Galesaurus* (Chapter 6), and the pattern of replacement in the maxillary postcanine series. In *Thrinaxodon*, waves of replacement move along the maxilla such that every second postcanine has an associated replacement,

whereas in *Cynosaurus*, these waves pass in multiples of three, such that replacement activity is present at every third locus. As in *Thrinaxodon*, there is a cessation of replacement in the first maxillary postcanine locus (PC1), resulting in the maxillary postcanine series shifting distally with increased skull size. Furthermore, all scanned specimens showed replacement activity associated with the third maxillary postcanine (PC3). Thus, it appears that the eruption of PC3 coincides with the exfoliation of the last element of the PC1 tooth family. Based on these observations, a model of the tooth replacement states through ontogeny was generated. From this model it is predicted the PC1 was replaced at least twice before becoming dormant, and that at least two replacement waves passed along the maxilla simultaneously.

6 TOOTH REPLACEMENT PATTERNS IN THE EARLY TRIASSIC EPICYNODONT *GALESAURUS PLANICEPS* (THERAPSIDA, CYNODONTIA)

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6.1 Abstract

Sixteen specimens of the Early Triassic cynodont *Galesaurus planiceps* (including eight that were scanned using micro-computed tomography) representing different ontogenetic stages were assembled to study the dental replacement in the species. *In silico* examination of the canines revealed that no replacement took place in specimens with a skull length longer than ~90 mm, suggesting that *Galesaurus* had a finite number of replacement cycles in the canine dentition. Additionally, the functional canine root morphology of these larger specimens showed a tendency to be open-rooted, a condition not previously documented in Theriodontia. An alternating pattern of tooth replacement was documented in the maxillary and mandibular postcanine series. Both postcanine series increased in tooth number as the skull lengthened, with the mandibular postcanine series containing more teeth than the maxillary series. In the maxilla, the first postcanine is consistently the smallest tooth, showing a proportional reduction in size as skull length increased. Evidence of developing teeth mesial to the postcanine series is preserved in the largest specimen. This suggests that in *Galesaurus* the first postcanine locus remains active for a longer period of development than in *Thrinaxodon*, and may contribute to the lengthening of the postcanine series through ontogeny. There are considerable differences between *Galesaurus* and *Thrinaxodon* relating to the replacement and development of their teeth. In *Galesaurus*, replacement of the canine ceases with the attainment of skeletal maturity, whereas in *Thrinaxodon*, replacement of the canines continue into adulthood.

6.2 Introduction

Galesaurus planiceps (Owen, 1860) is a small non-mammaliaform cynodont with a maximum known skull length of 114 mm. It was the first cynodont to be described and evidence of the heterodonty in this taxon later led to the establishment of the Cynodontia in order to differentiate the genus from other fossil 'reptiles' recovered from South Africa (Owen, 1861).

Remains of *Galesaurus* are known exclusively from the Lower Triassic *Lystrosaurus* Assemblage Zone (LAZ) of the South African Main Karoo Basin (Groenewald and Kitching, 1995). The first appearance of the genus in the stratigraphic record is approximately 22 m above the Permian–Triassic Boundary (PTB), in the upper Palingkloof Member of the Balfour Formation, Beaufort Group (Groenewald and Kitching, 1995; Botha and Smith, 2006). The appearance of the taxon close to the PTB suggests that *Galesaurus*, or at least a ghost lineage of the Galesauridae, survived the end-Permian mass extinction (EPME) (Smith and Ward, 2001; Sidor and Smith, 2004; Ruta *et al.*, 2013; Huttenlocker, 2014).

Galesaurus occurred contemporaneously with the closely allied taxon, *Thrinaxodon liorhinus* (Groenewald and Kitching, 1995; Ruta *et al.*, 2013), but its stratigraphic range is more constrained (Botha *et al.*, 2007), with the last occurrence of *Galesaurus* approximately 85 m above the PTB within the lower Katberg Formation (Groenewald and Kitching, 1995; Botha and Smith, 2006). In contrast, the range of *Thrinaxodon* extends to the top of the Katberg Formation (Botha and Smith, 2006). Despite its short stratigraphic range, *Galesaurus* is the

second most abundant cynodont (after *Thrinaxodon*) recovered from the LAZ (Abdala and Ribeiro, 2010; Smith *et al.*, 2011), with over 30 specimens attributed to the genus (Jasinoski and Abdala, 2017a).

Galesaurus has a general cranial morphology reminiscent of *Thrinaxodon* but, as in the more basal *Procynosuchus*, the osseous secondary palate in *Galesaurus* has a wide cleft between the maxillary and palatine processes (Kemp, 1979; Hopson and Barghusen, 1986). In contrast, the cleft in *Thrinaxodon* is relatively narrow with the palatal plates nearly in contact (Jasinoski *et al.*, 2015). Interestingly, *Galesaurus* also presents characters only recognised in some members of the more derived Eucynodontia (Kemp, 2005). These include an angulation between the ventral edge of the maxillary zygomatic process and the anteroventral margin of the jugal, and a well-projected posterodorsal portion of the zygomatic process of the squamosal (Abdala, 2003).

Despite the close morphological and hypothesised behavioural (Abdala *et al.*, 2006; Butler, 2009; Fernandez *et al.*, 2013) affinities between *Galesaurus* and *Thrinaxodon*, which even resulted in the first specimens of *Thrinaxodon* to be erroneously identified as *Galesaurus* (Owen, 1886; Seeley, 1889, 1894), the former has received comparatively little research interest. This is likely due to the fact that *Thrinaxodon* has been traditionally considered as a hypothetical model ancestor to the Mammalia (Crompton and Jenkins, 1968; Hopson and Crompton, 1969; Hopson and Barghusen, 1986). An important feature for this key placement was that the postcanine morphology of *Thrinaxodon* resembles that of the early

mammal *Morganucodon* (Crompton and Jenkins, 1973; Luo *et al.*, 2004) (= Mammaliaformes [Rowe, 1988; McKenna and Bell, 1997; Luo *et al.*, 2001; Kielan-Jaworowska *et al.*, 2004; Luo, 2007; Zhou *et al.*, 2013]). The relative abundance of *Thrinaxodon* has indeed also contributed to its detailed study, which includes a large body of literature focusing on the tooth replacement pattern (Parrington, 1936b; Crompton, 1963; Hopson, 1964; Osborn and Crompton, 1973; Gow, 1985b; Abdala *et al.*, 2013). Only the Middle Triassic gomphodont cynodont *Diademodon* has undergone a comparable amount of research on tooth replacement (Fourie, 1963, 1964; Ziegler, 1969; Hopson, 1971; Osborn, 1974). In contrast, no dedicated studies on the tooth replacement patterns of *Galesaurus* have been published.

Owen (1860) described the postcanine dentition of *Galesaurus* as being simple-crowned and of equal size. Van Hoepen (1916) later described a new taxon, *Glochinodon detinens*, as having a morphologically unique postcanine dentition, where the teeth are bicuspid, with a large anterior cone, reflected posteriorly over a smaller posterior cusp. Watson (1920) redescribed the holotype of *Galesaurus*. Watson's account of the dentition mostly agreed with Owen's original description, but he added that the postcanines were laterally compressed, such that they are oval in cross-section, with the maximum length being in the anteroposterior direction. Watson (1920) also noted that there is no evidence of tooth replacement in the holotype. Broom (1932b) later examined the material of *Galesaurus* and *Glochinodon* and noticed a similar bicuspid morphology in impressions of postcanine crowns of *Galesaurus*. This shared postcanine

morphology lead to the synonymisation of the two genera (Broom, 1932a, 1932b). Parrington (1934) also provided a brief description of the dentition of *Galesaurus*, but did not add much more detail regarding the postcanine dentition. He concluded that the maxillary postcanine series contained fewer teeth than the mandibular series, contradicting Broom's (1932a) notion that the two series had an equal number of elements. Parrington (1934) also documented the presence of replacement incisors in the dentaries.

Glochinodontoides gracilis (Haughton, 1924) was described as having postcanine teeth of the same peculiar morphology as *Glochinodon*, but they were smaller in size. The postcanine series was also considered to be shorter than that of *Glochinodon*, with the teeth being more widely spaced. A second specimen attributed to *Glochinodontoides* was described as having postcanine teeth with a less curved anterior cusp than *Galesaurus* (Brink, 1954). *Glochinodon* and *Glochinodontoides* were later considered to be synonymous with *Galesaurus* (Broom, 1932a, 1932b; Brink, 1954; Hopson and Kitching, 1972). Additionally, it was noted by Hopson and Kitching (1972: 73–74) that "small, immature specimens have usually been referred to the genus *Galesaurus*, [and] large, mature specimens to *Glochinodontoides*." Determining the tooth replacement patterns in *Galesaurus*, and comparison to that observed in the previously studied cynodont *Thrinaxodon* (Abdala *et al*., 2013) may help to ascertain the tooth replacement patterns of the basal-most cynodonts.

Due to increased effort in the collection of fossils stratigraphically close to the PTB (e.g., fieldwork undertaken by R.M.H. Smith and J. Botha), the number of *Galesaurus* specimens in museum collections has increased during the last 10 years, generating a multitude of studies inspecting the taxon from different perspectives. The most recent significant research on the biology of *Galesaurus*, have been studies of the postcranial skeleton and paleohistology (Butler, 2009; Butler *et al.*, 2019), ontogeny of the cranium (Jasinoski and Abdala, 2017a), evidence for parental care (Jasinoski and Abdala, 2017b), and the tooth attachment system (LeBlanc *et al.*, 2018). In addition, Pusch *et al.* (2019) recently described the internal cranial anatomy of a single specimen of *Galesaurus* (AMNH FARB 2227).

Due to the mandible being preserved in tight occlusion in most specimens of *Galesaurus*, in the past, only the labial surfaces of the upper dentition were accessible for study. By µCT-scanning selected specimens, it was possible to describe the entire dental complement for the first time. The µCT data also allowed for *in silico* observation of tooth replacement patterns as unerupted replacement teeth, functional teeth, and partially resorbed roots of shed teeth were easily distinguishable.

This paper presents a detailed analysis of the tooth replacement of *Galesaurus*, and a comparison with the tooth replacement patterns of *Thrinaxodon liorhinus* from previous studies (Parrington, 1936b; Crompton, 1963; Osborn and Crompton, 1973; Gow, 1985b; Abdala *et al.*, 2013). Micro-computed tomography

scanning of an ontogenetic series facilitated a comprehensive examination of the tooth replacement in upper and lower dental series comprising specimens of different sizes. This study provides the first comparison of tooth replacement patterns between two contemporaneous non-mammalian cynodonts. This assessment is of particular interest as it offers a comparison of biological processes, as opposed to simply a comparison of anatomical and morphological characters of the two genera.

6.3 Materials and methods

There are currently more than 30 specimens attributed to *Galesaurus planiceps*. Seventeen of these specimens are sufficiently prepared such that the dentition may be studied (Table 14). These specimens represent a presumed ontogenetic growth series based on the basal skull length (BSL), which ranges from 62 mm (FMNH PR 1774) to 114 mm (NMQR 860).

6.3.1 Micro-computed tomography scanned specimens

Eight specimens of *Galesaurus planiceps*, representing an ontogenetic series consisting of subadult (BSL 69–88 mm) and adult (BSL >90 mm)specimens (Jasinoski and Abdala, 2017a), were analysed using μCT (Table 15). The basal skull length (BSL) of this sample ranges from 69 mm (RC 845) to 114 mm (NMQR 860).

Table 14. Specimens of *Galesaurus planiceps* included in this study, listed in increasing size.

Specimen	BSL (mm)	Ontogenetic stage	Postcanine count (L/R)	
			Maxilla	Mandible
FMNH PR 1774[a]	62	Juvenile	7/7	9/9
NMP 581	64	Juvenile	9/9	10?/–
RC 845[b]	69	Subadult	10/9	11/11
SAM-PK-K1119	72	Subadult	8/9	9/?
SAM-PK-K9956	73	Subadult	–/9	–
NMQR 655	~75	Subadult	8/?	–
AMNH FARB 2227	79	Subadult	10/10	?/11
BP/1/4714[b]	81	Subadult	11/12?	12/13
BP/1/4602[b]	88	Subadult	10/10	11/12?
BP/1/3892[c]	90	Adult	9/9	–
NMQR 1451	90	Adult	10/10?	–
NMQR 135[b]	94	Adult	9/9?	–
NMQR 3340	~102	Adult	10/10	–
NMQR 3542[b]	102	Adult	11/11	14/12
BP/1/5064[b]	103	Adult	11/11	14/13
SAM-PK-K10468[b]	105	Adult	9/9	9/10
NMQR 860[b]	114	Adult	12/10	13/12?

Ontogenetic stages based on Jasinoski and Abdala (2017a). Abbreviations: BSL, basal skull length; L, left; R, right. A dash (–) indicates that the maxilla/mandible is not preserved or that the mandible is preserved in tight occlusion; a question mark (?) represents an uncertain count due to partial damage/obstruction of the maxilla/hemimandible.

[a] Specimen serially sectioned, information from Rigney (1938)

[b] Specimen µCT-scanned

[c] Specimen missing from collection, information from Brink (1965a)

Table 15. Parameters used for µCT-scanning of *Galesaurus planiceps* specimens.

Specimen	Voxel size (µm)	Tube voltage (kV)	Tube current (µA)	Frame rate (fps)
RC 845	42.60	140	250	2
BP/1/4714	68.56	115	135	0.5
BP/1/4602	66.72	130	185	1
NMQR 135	58.80	190	210	1
NMQR 3542	80.00	110	150	1
BP/1/5064	66.04	170	95	1
SAM-PK-K10468	71.30	120	120	1
NMQR 860	74.10	210	300	1

Due to differing physical dimensions, states of preparation, and chemical compositions of the specimens, the scan parameters were adjusted to obtain the best results for each specimen at 4000 projections (Table 15). In order to reduce beam-hardening artefacts, a 1.2 mm copper or 1.8 mm aluminium filter was used (Abel *et al.*, 2012). The resulting scans ranged in isotropic voxel sizes from 42.6 µm (RC 845) to 80 µm (NMQR 3542).

6.3.2 Standardisation/normalisation of basal skull length measurements

In order to better facilitate the comparison between the BSL of the three epicynonodonts *Thrinaxodon* (BSL ~30–96 mm), *Cynosaurus* (BSL 49–122 mm), and *Galesaurus* (BSL 62–114 mm), the measurements were recalculated using feature scaling/unity-based normalisation.

$$x' = \frac{BSL_i - BSL_{\min}}{BSL_{\max} - BSL_{\min}} \qquad (6)$$

In the equation, BSL_i represents the original value, BSL_{min} represents the smallest and BSL_{max} the largest BSL values in the range. Feature scaling was chosen as it allows for the recalculation of the ranges, such that the data occupy ranges from zero to one, without affecting the mean and standard deviation of the sample.

6.4 Results

6.4.1 Tooth numbers and morphology

6.4.1.1 Incisors

Galesaurus planiceps has four upper and three lower incisors. Upper incisor morphology is simple with a distally directed cusp. Both upper and lower incisors

usually have a broad base and taper gradually towards the crown apex. In some instances, the mandibular incisors also show tapering towards the root apex. Mandibular incisors tend to have a slight procumbent orientation (e.g., BP/1/4602 and BP/1/5064), and the third mandibular incisor (i3) has a straighter, more dorsal orientation (e.g., RC 845, Figure 25).

6.4.1.2 Canines

The canine is a single functional tooth, with a broad, conical morphology. The crowns of both the upper and lower canines are similar in shape, although the latter is slightly more slender. The orientation of the lower canines is almost vertical, whereas the uppers have a slight rostral inclination. The μCT-scanned specimens showed both maxillary (e.g., NMQR 135) and mandibular canines to have prominent lateral ridges (e.g., RC 845 and BP/1/4602).

6.4.1.3 Postcanines

Postcanine morphology of *Galesaurus* is unique in the Epicynodontia. The teeth of both the upper and lower jaw are mesiodistally elongated and bear two cusps. Crown morphology of the upper and lower postcanines is the same. The mesial cusp is larger and curves distally over the smaller distal cusp.

Jasinoski and Abdala (2017a) noted the presence of a small accessory cusp mesial to the main recurved cusp in the maxillary postcanines of two small specimens: BP/1/4597 (BSL ~70 mm) and NMQR 3716 (BSL 75 mm). Specimens previously attributed to *Glochinodontoides* have been described as having an mesial cusp that

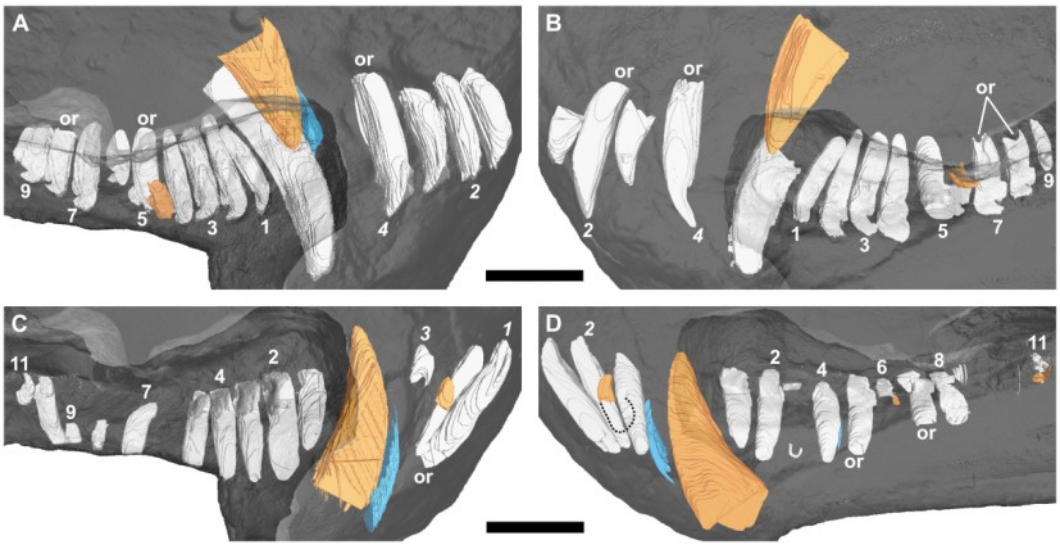

Figure 25. Three-dimensional rendering of the tooth rows of a subadult *Galesaurus planiceps* (RC 845) in medial view.
A, upper left; B, upper right; C, lower left; D, lower right. Note the more procumbent orientation of i1 and i2, in comparison to the straighter orientation of i3 (C and D). Replacement teeth/crypts in orange, old remnant roots in blue. Resorption of the right functional i2 and i3 indicated with a dashed line (D). Abbreviation: or, open root. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bar equals 10 mm.

is longer, and not as distally curved as that of *Galesaurus* (Brink, 1954). In some specimens (e.g., BP/1/4602), the entire postcanine series has elongated mesial cusps, whereas in RC 845 only the anterior postcanines (PC1–PC3) have elongated mesial cusps and the posterior teeth have shorter, more recurved mesial cusps. The distal cusp of the first maxillary postcanine is reduced in size in several smaller specimens (e.g., RC 845 and BP/1/4602) such that it is almost indistinguishable. In some larger specimens (e.g., SAM-PK-K9956), however, the first erupted postcanine has the typical bicuspid crown morphology. The number

of postcanines recorded in the study sample varies from seven to 12 in the maxilla, and nine to 14 in the dentary. There does not appear to be any noticeable differences between the crown morphologies of the upper and lower postcanines within an individual.

Both the maxillary and mandibular postcanine series are arranged in a slight imbricate pattern such that the mesial portion of the tooth crown is directed lingually, whereas the distal margin of the crown is directed labially.

6.4.2 Tooth replacement

Evidence of tooth replacement was recorded in all μCT-scanned specimens of *Galesaurus planiceps*. Several specimens facilitated an evaluation of replacement activity for the full dental complement of the same individual. Replacement teeth for the incisors and postcanines are situated lingual to the functional tooth. Replacement canines are usually not erupted. The following section describes the state of replacement of the teeth (i.e., presence of replacement teeth, developmental condition of roots, etc.) for the eight μCT-scanned specimens of *Galesaurus*. These descriptions are presented in order from smallest to largest basal skull length (BSL).

6.4.3 RC 845 (BSL 69 mm)

6.4.3.1 Incisors

There is no evidence of replacement teeth amongst the maxillary incisors. On both sides, I4 is the largest tooth and I2 the second largest. On the left (Figure 25A), I1

and I3 are similar in size, but on the right (Figure 25B), I1 is smaller than the I3, both of which have open roots.

Replacement teeth of the mandibular i2 are visible on both sides (Figure 25C, D), with noticeable resorption of the tooth roots of the functional i2 and i3 visible in the right (Figure 25D). There is no evidence of replacement for the i1 and i3 loci in the mandibular rami. The left i3 is open-rooted and was still in the process of developing. In contrast, the root of the right i3 was fully developed.

6.4.3.2 Canines

A large replacement canine is present anteromedial to the functional canine in both maxillae (Figure 25A, B). A remnant canine root is retained in the left, labial and mesial to the functional canine, and it is evident that the replacement canines have slightly eroded the roots of the functional teeth. The lower canines were still in the process of erupting, with the left being slightly more developed (Figure 25C, D).

The newly erupted replacement mandibular canines do not appear to have associated replacement teeth developing in the dentaries. Mesial to the newly erupting functional canine there appear to be partially resorbed roots of remnant teeth present in both rami (Figure 25C, D).

6.4.3.3 Postcanines

Ten postcanine teeth are present in the left maxillary series (Figure 25A). In both maxillae, the root of PC1 is closed and does not make contact with the functional canine. An open root is observed for PC5 and PC8. A partially erupted tooth is preserved between the crowns of PC4 and PC5, and is interpreted as the replacement PC4, based on its lingual position to the functional tooth row. In the right maxillary series (Figure 25B) nine postcanine teeth are preserved. The root of PC6 has been resorbed, and a replacement crown was in the process of forming dorsolingually to the functional tooth. Open roots are present in PC7 and PC8. An old remnant root between PC6 and PC7 is preserved labially (not visible in lingual view).

In the left mandibular series (Figure 25C), 11 alveoli and 10 postcanines are preserved (pc6 absent), and there is no evidence of postcanine replacement. The ventral part of the hemimandible, distal to pc4 is lost, such that the root apices are not preserved. It is assumed that this damage had no impact on the preservation of any replacement postcanines in the left dentary, as the replacement teeth in the right hemimandible (Figure 25D) are situated more dorsal in the dentary corpus than the region missing from the left. In the right mandibular series (Figure 25D) 11 postcanine teeth are present. The crowns of pc3 and pc6 are present, despite the almost complete resorption of the roots, whereas the roots of pc5 and pc7 are still open. An old root is preserved distal to pc4. There is no evidence for mineralised replacement teeth, however, crypts are associated with pc6 and pc11.

6.4.4 BP/1/4714 (BSL 81 mm)

6.4.4.1 Incisors

In the left premaxilla, only the I1 and I4 are preserved, with no evidence of replacement teeth (Figure 26A). Only I3 and I4 of the right series are present (Figure 26B). Replacement teeth are present lingually for the second to fourth incisors. The replacement element of I4 is remarkably smaller than those of the mesial incisors. Only i1 and i3 are present in the left dentary, with evidence for a developing germ in i2 (Figure 26C). In the right dentary all three incisors are preserved (Figure 26D). Only i1 and i3 show evidence of replacement, in the form of associated replacement germs, of which that of i1 is larger.

6.4.4.2 Canines

An unusual structure is associated with the root apex of the left maxillary canine (Figure 26A). This structure is located too far dorsally to represent a replacement tooth and is instead interpreted as the last unresorbed remnants of the previous canine based on its resemblance to a closed root apex. A developing replacement canine is present lateral to the functional canine in the right maxilla (Figure 26B). No replacement of the lower canines is evident (Figure 26C, D). The root apices of the four functional canines are fully developed.

6.4.4.3 Postcanines

Nine of a total of 11 postcanines are preserved in the left maxilla, with empty alveoli present at PC5 and PC6 (Figure 26A). A single replacement tooth is preserved in association with the locus of PC10. Only five postcanines of the right

maxilla (PC1, PC4, PC5, and PC10) are preserved *in situ* (Figure 26B). An additional postcanine tooth is preserved distal to pc10. This element is interpreted as being *ex situ*, due to the horizontal orientation of the tooth, but may represent the exfoliated pc11/12. There are no preserved roots from shed teeth, and there is evidence for three replacement teeth. The replacement associated with the locus of PC7 is the largest, whereas those of PC4 and PC5 are very small.

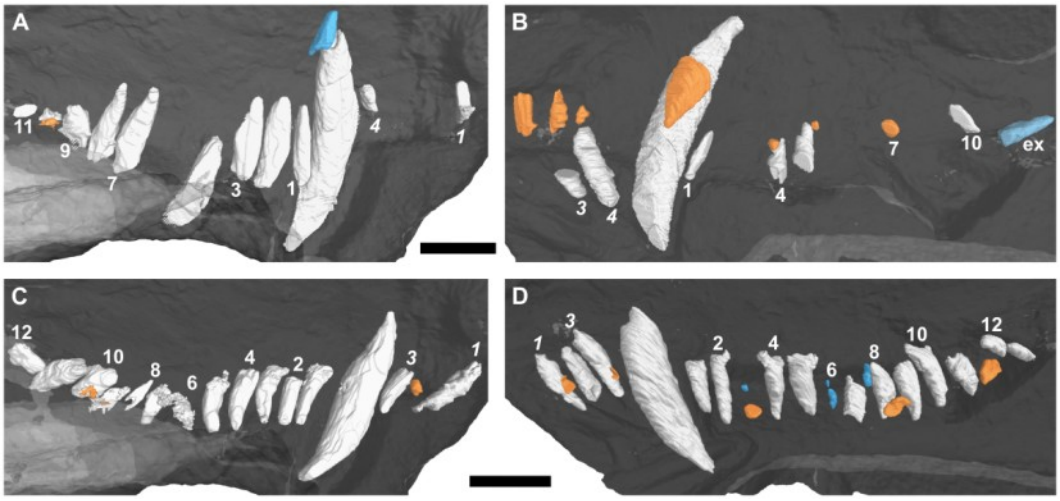

Figure 26. Three-dimensional rendering of the tooth rows of a subadult *Galesaurus planiceps* (BP/1/4714) in medial view.
A, upper left; B, upper right; C, lower left; D, lower right. Replacement teeth in orange, old remnant roots in blue. Abbreviation: ex, *ex situ* postcanine. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bars equal 20 mm.

Twelve erupted postcanines are preserved in the left dentary (Figure 26C). Two replacement teeth are present in the left dentary at the pc9 and pc10 positions, the latter being larger. Eleven functional postcanines and two empty alveoli are preserved on the right dentary, with empty alveoli at the positions of pc3 and pc6

(Figure 26D). Both pc3 and pc12 have replacement teeth below the gingival margin, whereas old roots from previously shed teeth are present at pc3 and pc6. Another root of a shed tooth is preserved labially to pc8. The alveolus of pc8 also preserves the developing crown of a replacement tooth.

6.4.5 BP/1/4602 (BSL 88 mm)

6.4.5.1 Incisors

Four incisors are preserved in the left premaxilla (Figure 27A). Open roots are visible in I2 and I4. The only replacement tooth is associated with I3. The root of the functional I3 shows signs of resorption associated with the replacing tooth. In the right premaxilla I1, I3, and I4 are preserved. The roots of the I1 and I4 are open, whereas the root of I3 is closed (Figure 27B). An *ex situ* crown, possibly shed from I2 is preserved lingual to I3. There is no evidence of replacement activity in the right premaxilla.

Three incisors are present in each dentary, and in both instances, only i2 shows replacement activity. On the left, the root of i2 has been completely resorbed (Figure 27C). The crown of the functional tooth is situated higher than those of the neighbouring incisors, which indicates that the tooth was about to be shed.

Unlike the left i2, the right i2 has not undergone as much resorption such that the crown and root are still connected (Figure 27D). The roots of i2 and i3 appear longer, and more slender than that of i1, possibly due to the incomplete development of i1, as the root is still open.

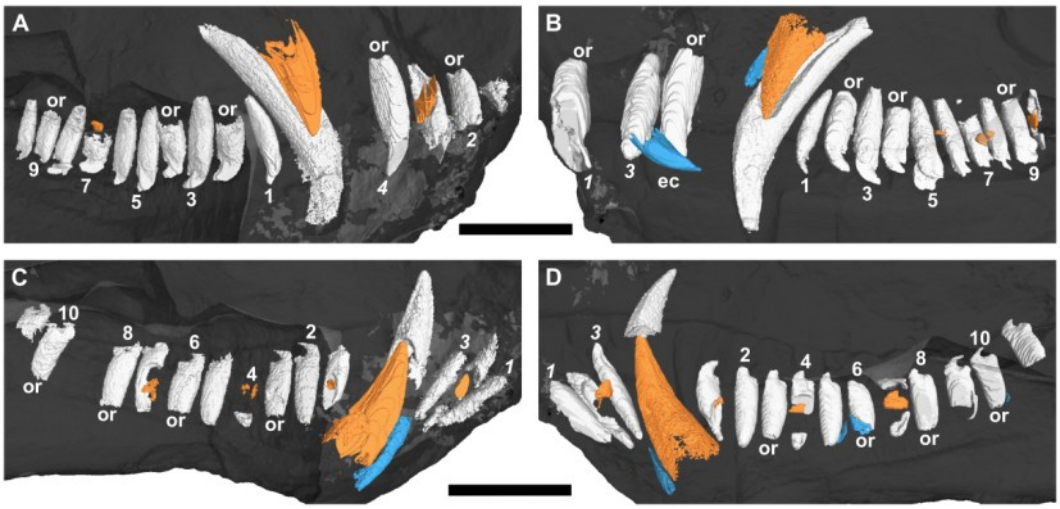

Figure 27. Three-dimensional rendering of the tooth rows of a subadult *Galesaurus planiceps* (BP/1/4602) in medial view.
A, upper left; B, upper right; C, lower left; D, lower right. Replacement teeth in orange, old remnant roots in blue. Abbreviations: ec, exfoliated crown; or, open root. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bars equal 20 mm.

6.4.5.2 Canines

Both maxillae present a large unerupted replacement canine, in similar developmental stages, anteromedial to the functional tooth (Figure 27A, B). A remnant canine root is retained in the right maxilla, mesial to the functional canine. The roots of the functional maxillary canines are closed. Two tooth generations of the left mandibular canine are present (Figure 27C); a functional crown nearing exfoliation with corresponding root remnants, and a moderately developed crown of a replacing canine. The replacement canine has pierced the root of the crown to be shed. In the right dentary the replacement crown is slightly more developed than the left, and much of the old crown has been resorbed

(Figure 27D). The crown to be shed has been displaced such that it no longer lies in the same plane as the remnant root mesial to the erupting tooth. The apex of the replacing crown does not pierce the old crown and is instead directed labially.

6.4.5.3 Postcanines

In the left maxillary series (Figure 27A), 10 postcanine teeth are preserved. The root of PC1 is very close to, but does not contact, the root of the functional canine. The roots are open in PC2, PC4, and PC9. A replacement tooth is present lingual to PC7. The root morphology of PC7 is similar to that of PC2 and PC4, but is likely caused by resorption of the root by the associated replacement tooth, rather than the incomplete development of the root. The roots of PC3, PC5, PC6, PC8, and PC10 are not yet fully closed, but are more developed than those mentioned above. In the right maxillary series (Figure 27B), 10 functional postcanine teeth are preserved. The root of PC1 does not contact the functional canine. A small, partially developed replacement crown is preserved between PC5 and PC6. Larger, more developed crowns of replacement teeth are present lingual to PC7 and PC10. Open roots are preserved for PC2, PC4, and PC9. The root of PC10 has been eroded away to the extent that the root and crown are no longer in contact.

There are 11 alveoli in the left mandibular series (Figure 27C), and nine functional teeth are preserved. An alveolus containing a retained root is situated in the locus of pc4, whereas the alveolus of pc9 is empty. Replacement germs are associated with pc1, pc4, and pc7, the latter being more developed. In the right mandibular series (Figure 27D), 11 teeth are preserved. The root of pc1 is closed

and shows signs of resorption where the root is in close proximity to the replacing canine. There are replacement teeth associated with pc1, pc4, and pc7, the same condition observed on the left. The root of pc9 shows signs of resorption, but no replacement germ is identifiable. There are old root structures preserved distally to pc5 and pc10, and mesially to pc6. Open roots are present in the pc3, pc6, pc8 and pc10 positions in both dentaries.

6.4.6 NMQR 135 (BSL 94 mm)

There is no mandible preserved for this specimen.

6.4.6.1 Incisors

The crowns of the functional incisors in both premaxillae have been lost either prior to, or during fossilisation. The second alveolus of the left premaxilla is the smallest. In contrast, in the right premaxilla the first has the smallest diameter (Figure 28A). A remnant root is preserved in the first alveolus of the left premaxilla (Figure 28B). There is a small structure lingually between the I3 and I4 of the right premaxilla, which is not paired, and appears to have a mesial ridge. It is interpreted as the crypt of a developing replacement tooth (Figure 28B).

6.4.6.2 Canines

The crowns of the functional canines have been broken. There is no replacement activity associated with either maxillary canine (Figure 29A, B). The roots of both canines are open.

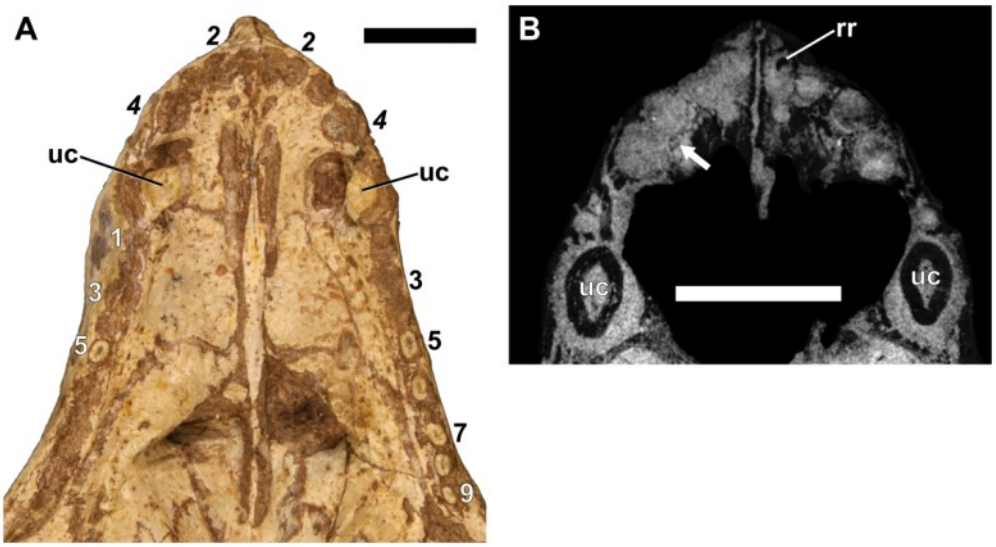

Figure 28. Dentition of an adult *Galesaurus planiceps* (NMQR 135).
A, ventral view; B, virtual transverse section through premaxilla. Abbreviations: rr, remnant root, uc, maxillary canine. Arrow indicates the crypt of a replacement incisor. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bars equal 10 mm.

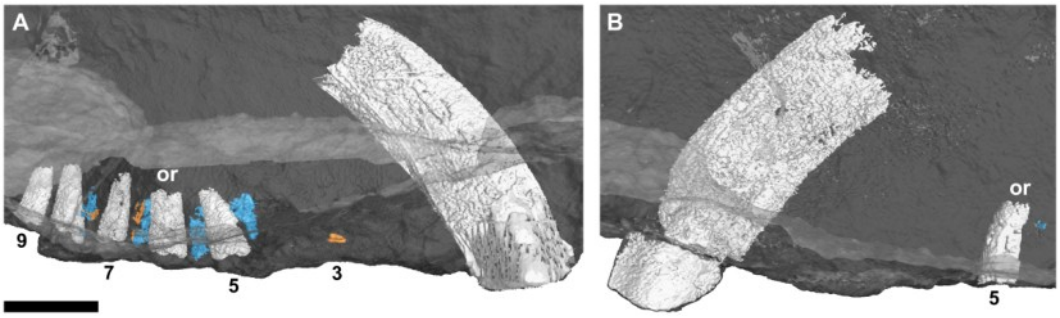

Figure 29. Three-dimensional rendering of the tooth rows of an adult *Galesaurus planiceps* (NMQR 135) in medial view.
A, upper left; B, upper right. Replacement teeth in orange, old remnant roots in blue. Abbreviation: or, open root. Arabic numerals indicate postcanine positions. Scale bar equals 5 mm.

6.4.6.3 Postcanines

Neither maxilla contains a complete postcanine series as several of the teeth have fallen from their alveoli (Figure 28 and Figure 29). In the left maxilla, PC1–PC4 are represented by empty alveoli (Figure 29A). Roots are preserved in the positions of PC5–PC9. A small replacement germ is preserved lingual to the alveolus of PC3. Old root structures are preserved in an alternating pattern with the functional teeth from position PC4 to PC8. These remnant roots show signs of partial resorption and are smaller in root diameter than the associated functional postcanines. No remnant root is preserved between PC8 and PC9, suggesting that the tooth in the PC9 locus was the most recent tooth in the series to erupt, and no replacement had yet taken place at the PC9 (and possibly PC8) locus. Only the root of PC5 is preserved in the right maxillary postcanine series (Figure 29B). There does not appear to be any remnant roots preserved between the alveoli of functional postcanines to the same extent as the left maxilla.

6.4.7 NMQR 3542 (BSL ~102 mm)

6.4.7.1 Incisors

Four incisors are preserved in each premaxilla. Replacement teeth are situated lingual to the left I3 and I4, with the latter being larger (Figure 30A). No replacement activity is recorded in the right premaxilla. Three incisors are preserved in each hemimandible. No replacement teeth are evident (Figure 30B). Remnants of the root of a replaced tooth are associated with the left i2.

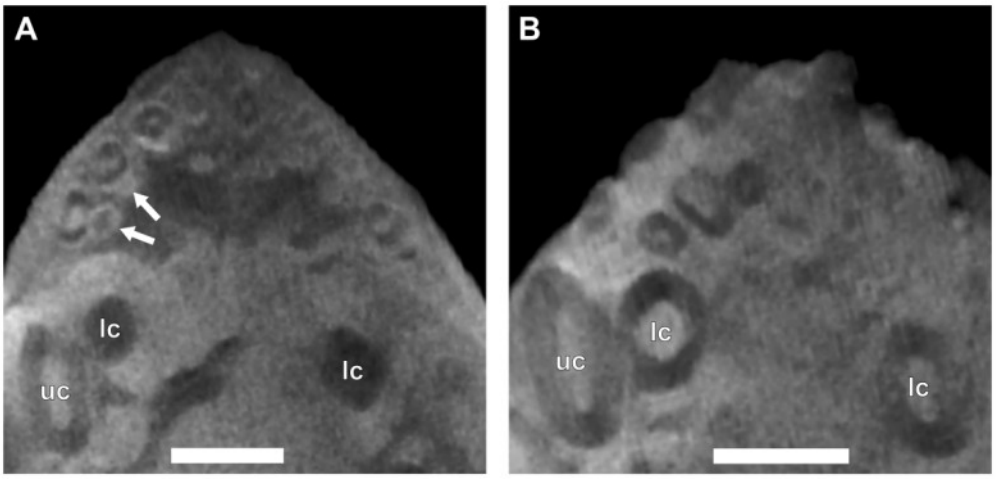

Figure 30. Virtual transverse cross-sections through the anterior dentition of an adult *Galesaurus planiceps* (NMQR 3542).
A, section through premaxillary incisors; B, section through mandibular incisors. Abbreviations: lc, mandibular canine; uc, maxillary canine. Arrows indicate crypts of replacement incisors. Scale bars equal 5 mm.

6.4.7.2 Canines

No replacement canines are present in the upper or lower jaws. The maxillary and mandibular canines are open-rooted.

6.4.7.3 Postcanines

Eleven functional postcanines are preserved in the left maxilla. Replacements are associated with PC3, PC7, and PC8. The right postcanine series also comprises 11 erupted teeth. Of these, PC3, PC4, and PC10 have associated replacement teeth developing. Fourteen functional postcanines are present in the left dentary, with an empty alveolus at pc8. Twelve functional teeth are present in the right lower postcanine series. The only replacement tooth is associated with pc4.

6.4.8 BP/1/5064 (BSL 103 mm)

6.4.8.1 Incisors

The broken roots of three incisors are preserved in each premaxilla (Figure 31A, B), with the I1 of both sides being absent. Although the crowns are damaged, the largest tooth in each series appears to be I4, based on observable root length and diameter. There is evidence of replacement for the first three incisors (I1–I3) of each premaxilla (Figure 32A). In the left premaxilla, the replacement of I2 is the most developed, and that of I1 the least developed. In the right premaxilla, the replacement I3 is the most developed, whereas the replacements of I1 and I2 are almost equal in size. Crypts associated with the development of replacing teeth are present lingual to the mandibular i1 on both sides, and the left i3 has preserved remnants of an old root (Figure 32B).

6.4.8.2 Canines

The left maxillary canine socket is empty (Figure 31A). The right maxilla (Figure 31B) and left mandible (Figure 31C) preserve almost complete canines, whereas only the root and partial crown of the right mandibular canine is preserved (Figure 31D). The apices of the preserved canine roots are not pointed, suggesting that they were not yet fully developed, and are thus interpreted as being open. There is no replacement activity for either the upper or the lower canines, and there are no old root remnants preserved.

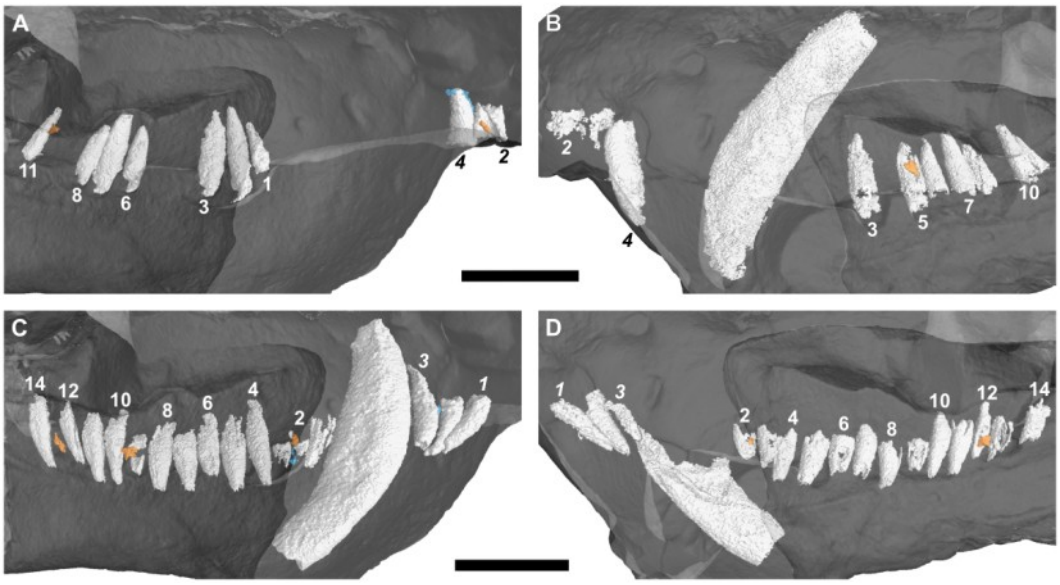

Figure 31. Three-dimensional rendering of the tooth rows of an adult *Galesaurus planiceps* (BP/1/5064) in medial view.

A, upper left; B, upper right; C, lower left; D, lower right. Replacement teeth in orange, old remnant roots in blue. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bar equals 20 mm.

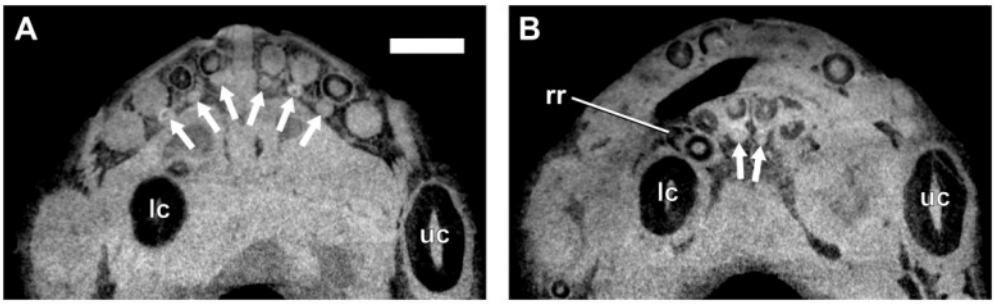

Figure 32. Virtual transverse cross-sections through the anterior dentition of an adult *Galesaurus planiceps* (BP/1/5064).

A, section through premaxillary incisors; B, section through mandibular incisors. Abbreviations: lc, mandibular canine; rr, remnant root; uc, maxillary canine. Arrows indicate crypts of replacement incisors. Scale bar equals 10 mm.

6.4.8.3 Postcanines

In the left maxillary series (Figure 33A) the positions of 11 postcanines can be identified from the preserved teeth and empty alveoli. Developing crypts are evident lingual to the functional PC2, PC3, PC6, PC8, and PC9. A small replacement germ is present at the locus for PC11 (Figure 31A). The crypt associated with PC8 is the largest, whereas the crypts for PC3 and PC6 are of comparable developmental stages. The replacement for PC2 is minute in comparison to the others. In the right maxillary series (Figure 33B), 11 postcanine teeth are preserved. Replacement crypts are present lingually to PC1, PC3, PC6, and PC8. A mineralised replacement crown is present lingual to PC5 (Figure 31B). PC1 is poorly preserved and appears to be in contact with the functional canine. The replacement crypt associated with PC3 is the largest, followed by those of PC6 and PC8.

In the left mandibular series (Figure 31C and Figure 33C), 13 teeth are preserved with an empty alveolus at pc13. The roots of pc9 are partially resorbed, and replacement teeth are situated lingual to pc2, pc9 and in the alveolus of pc13. Replacement crypts are recorded for pc2, pc3, pc6, pc7, pc9, pc10, and pc12. In the right mandibular series (Figure 33D), 13 alveoli, and 12 teeth are preserved. Replacement crypts are associated with pc2, pc6, pc7, pc9, pc11, pc12, and pc14. A small crypt is present mesial to the first erupted postcanine. The replacement crypt of pc6 is the largest, followed by those of pc2, pc7, and pc9. The germ lingual to pc6 is of a similar size to the mineralised crown of the replacement pc12.

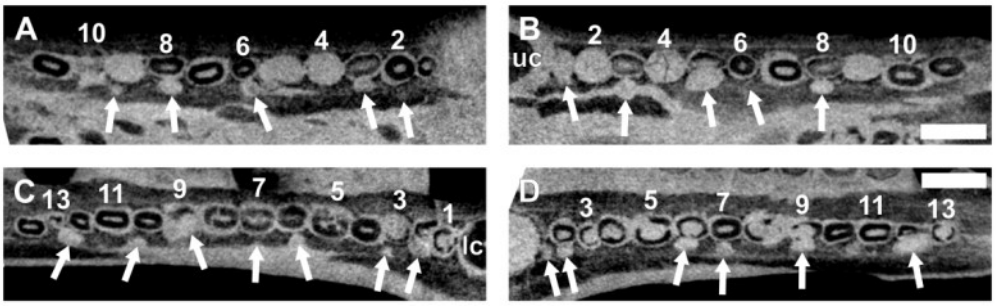

Figure 33. Virtual transverse cross-sections through the maxillae and dentaries of an adult *Galesaurus planiceps* (BP/1/5064).
A, left maxillary postcanine series; B, right maxillary postcanine series; C, left mandibular postcanine series; D, right mandibular postcanine series.
Abbreviations: lc, left mandibular canine; uc, right maxillary canine. Arrows indicate crypts of replacement postcanines. Arabic numerals indicate postcanine positions. Scale bars equal 2 mm.

6.4.9 SAM-PK-K10468 (BSL 105 mm)

6.4.9.1 Incisors

Four functional incisors are preserved in the left premaxilla (Figure 34A), with a replacement tooth preserved lingual to I3. A similar condition is present in the right premaxilla, with an additional replacement tooth present lingual to the I1. Three incisors are preserved in each dentary (Figure 34B). In the left, a replacement tooth is associated with each functional tooth. The replacement lingual to i1 is the smallest, and that lingual to i2 is the largest. Replacement germs are present lingual to the i1 and i3 in the right dentary. The lower incisors of the right are at a more advanced stage of development than those of the left.

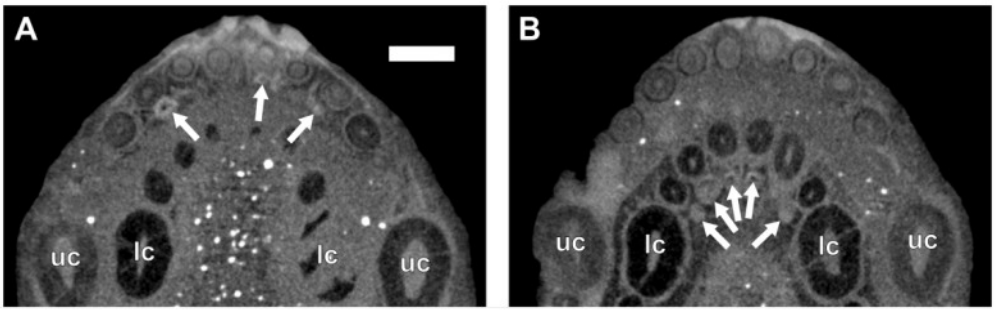

Figure 34. Virtual transverse cross-sections through the anterior dentition of an adult *Galesaurus planiceps* (SAM-PK-K10468).
A, section through premaxillary incisors; B, section through upper and lower incisors. Abbreviations: lc, mandibular canine; uc, maxillary canine. Arrows indicate crypts of replacement incisors. Scale bar equals 10 mm.

6.4.9.2 Canines

Canines are present in all four quadrants of the buccal cavity (Figure 34), and their roots are open. Remnant canine roots are preserved distal to the functional canines. These teeth are much smaller than the functional canines (comparable in size to the postcanines) and have a closed root morphology.

6.4.9.3 Postcanines

Nine functional postcanines are present in each maxilla (Figure 35A, B). The right maxilla preserves a crypt on the distal margin of the postcanine series, indicating that a tooth was beginning to develop in the PC10 position. There is good synchrony of the replacement patterns of the two maxillae, with replacement activity present at positions PC2, PC4, and PC5 in both maxillae, with an additional replacement at PC8 in the right maxilla. In both series, the root of the first tooth appears to have been partially resorbed by the developing canine.

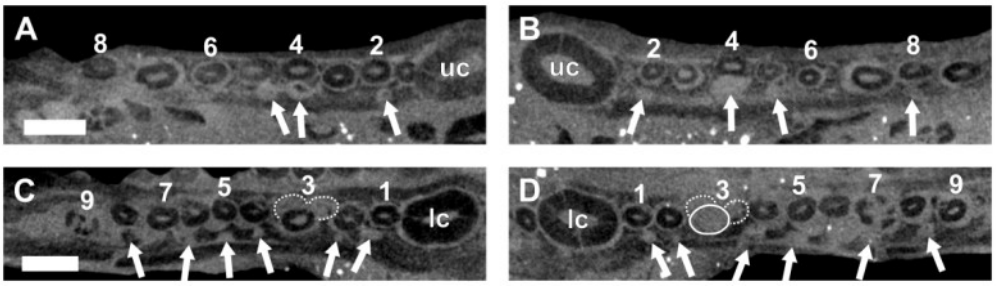

Figure 35. Virtual transverse cross-sections through the maxillae and dentaries of and adult *Galesaurus planiceps* (SAM-PK-K10468).
A, left maxillary postcanine series; B, right maxillary postcanine series; C, left mandibular postcanine series; D, right mandibular postcanine series. Note the replacement tooth at the third locus (C and D) appears to be occupying the loci of two exfoliated teeth. Abbreviations: lc, mandibular canine; uc, maxillary canine. Arrows indicate crypts of replacement postcanines. Solid line indicates the outline of replacement postcanine (pc3); dashed lines indicate empty alveoli associated with the pc3 locus. Arabic numerals indicate postcanine positions. Scale bars equal 4 mm.

The left lower postcanine series comprises nine erupted teeth and two empty alveoli, whereas the right series includes 10 erupted teeth (Figure 35C, D). Both hemimandibles have crypts associated with the pc1 and pc2 positions. Of particular interest is the region associated with the erupting pc3 in the left dentary. This tooth is larger than the surrounding teeth and appears to be filling the position of two previous loci (Figure 35C). A similar condition is observed in the right dentary, but the alveolus is empty (Figure 35D). Additional replacement teeth are recorded in the pc4, pc5, pc6 and pc8 positions of the left dentary, and the pc4, pc5, pc7 and pc8 positions of the right. A good degree of synchrony is

observed between the anterior postcanine loci of the two hemimandibles, but developmental stages in positions distal to pc5 become asynchronous.

6.4.10 NMQR 860 (BSL 114 mm)

6.4.10.1 Incisors

Each premaxilla preserves four incisors (Figure 36A). On the left, I2 is represented by a large empty alveolus. The crown of the right I4 is damaged, and the position of the root in the alveolus suggests that the tooth was in the process of being lost. Whether this exfoliation was due to a natural or taphonomic process is unclear. A resorption pit associated with the left I4 contains a mineralised germ of the replacement tooth. There are three lower incisors preserved in each mandible, and no replacement teeth are visible. The roots of the i3 in each series lie lingual, almost posterior, to those of the neighbouring i2. In contrast, the crowns of all three elements lie in the same plane in the dental arcade.

6.4.10.2 Canines

Functional canines are preserved in all four quadrants of the buccal cavity. No replacement canines are preserved, and the root morphology of all four canines is open.

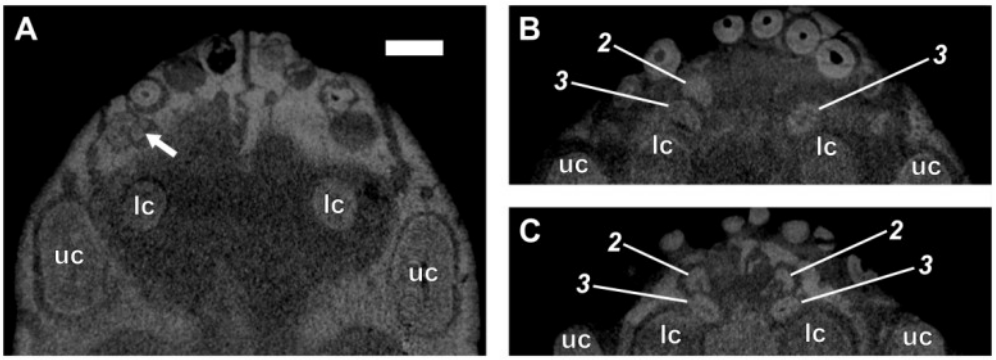

Figure 36. Virtual transverse cross-sections through the anterior dentition of an adult *Galesaurus planiceps* (NMQR 860).
A, section through premaxillary incisors; B, section through mandibular incisor crowns; C, section through mandibular incisor roots. Abbreviations: lc, mandibular canine; uc, maxillary canine. Arrow indicates crypt of replacement incisor. Arabic numerals indicate lower incisor (italicised) positions. Scale bar equals 4 mm.

6.4.10.3 Postcanines

Twelve postcanines are preserved in the left maxilla, with small replacement teeth located lingual to PC3 and PC8. The right maxilla contains a postcanine series comprising 10 teeth. Replacements are associated with PC2 and PC5. Small crypts are located lingual to PC6 and PC8, but neither contains mineralised tooth tissue. There are 13 mandibular postcanines in the left dentary. Several alveoli are empty; pc3, pc6, pc9. Replacement germs are present lingual to the alveoli of pc6 and pc9, and what appear to be the remains of the tooth root is preserved in pc3. At least 12 postcanine loci are evident in the right dentary. The first 10 positions show erupted teeth, whereas those of pc11 and pc12 are empty alveoli. A retained root is situated between the first and second erupted teeth, suggesting that the full series may have been 13 teeth, as is the condition in the left dentary.

6.4.11 Anatomical specimen

Several specimens of *Galesaurus planiceps* were studied for gross morphological patterns. Because most of these specimens have not been fully prepared, or are not very well preserved, little information regarding the tooth replacement patterns could be added from direct observation of the specimens. One noticeable exception is SAM-PK-K1119, a specimen that was subjected to acid preparation prior to this study (Jenkins, 1971; Butler, 2009).

6.4.12 SAM-PK-K1119 (BSL 72 mm)

6.4.12.1 Incisors

Four teeth are preserved in each premaxilla. A pit is present lingual to the right I3, which may be indicative of an associated replacement tooth (Figure 37A). Three incisors are preserved in each dentary, with resorption pits lingual to the left i3 and between the right i2 an i3 (Figure 37B).

6.4.12.2 Canines

An erupting replacement canine is present posterolingually to the functional canine in both dentaries (Figure 37B). On the right, the tips of both the functional and replacing crowns are broken. In contrast, the crowns are well preserved in the left dentary. The tip of the replacing canine is not in contact with the functional tooth. No replacement activity can be seen for the upper canines.

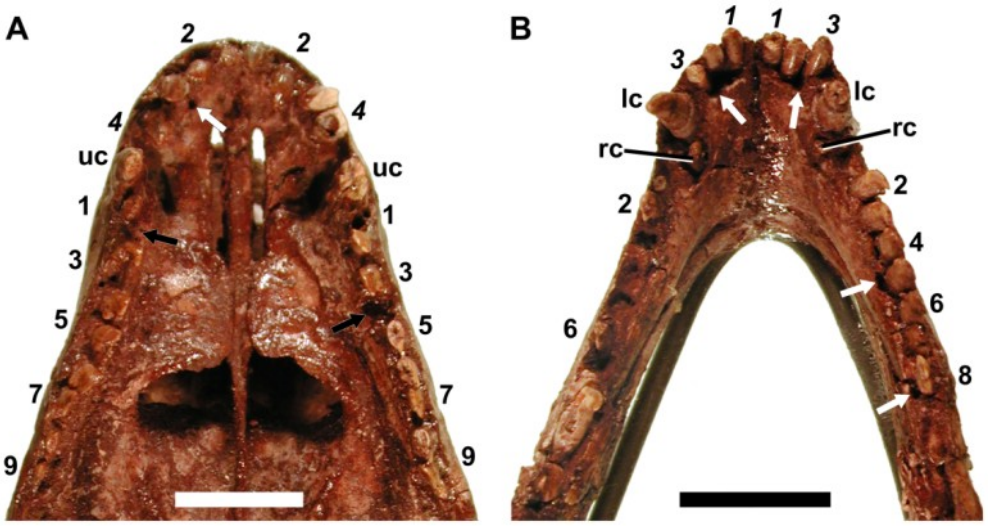

Figure 37. Dentition of a subadult *Galesaurus planiceps* (SAM-PK-K1119). A, upper dentition; B, lower dentition. Abbreviations: lc, mandibular canine; rc, replacement mandibular canine; uc, maxillary canine. White arrows indicate resorption pits; black arrows indicate spaces between erupted teeth. Arabic numerals indicate incisor (italicised) and postcanine positions. Scale bars equal 10 mm.

6.4.12.3 Postcanines

Seven postcanine teeth are present in the left maxilla (Figure 37A). There is a space between the second and third tooth, which appears to be an empty alveolus corresponding to PC4. The erupted postcanine count on the right maxilla is seven, however, there is a gap between the first and second tooth, which is of sufficient size to have once held a tooth (Figure 37A).

The postcanine series is poorly preserved in the left dentary (Figure 37B). The crown of pc1 is broken at the level of the bone, and the alveoli of pc3–pc5 and pc7 are empty. Evidence for at least two, possibly three, additional teeth distal to

the alveolus of pc7 is visible. These crowns are damaged, with the potential of pc9 being displaced. Eight postcanine positions are preserved in the right dentary. The crown of pc1 is broken, and pc7 is represented by an alveolus with an unerupted replacement tooth. The alveoli surrounding pc5 and pc8 are wider than those of the other teeth. In addition, the pc2, pc5, and pc8 stand out of their respective alveoli such that the tooth neck is visible. It is suggested that these teeth were in the process of being exfoliated. In both dentaries, pc1 has a noticeably smaller root diameter than the other teeth of the series.

6.5 Discussion

6.5.1 Tooth morphology and number

6.5.1.1 Anterior dentition

The dental formula of four upper and three lower incisors, as is present in most basal Permian cynodonts, also applies to *Galesaurus planiceps* (Broom, 1932a; Hopson and Kitching, 2001). This dental formula is retained in the majority of the Early to Middle Triassic cynodonts (Hopson and Barghusen, 1986; Abdala, 2007). The crowns of the upper and lower incisors are conical with the upper incisors being slightly more recurved than the lowers.

The upper incisors of all specimens are evenly spaced, and the roots are round in cross-section. In contrast, the crowns of the lower incisors are evenly spaced, but the roots are tightly packed. The lower incisors of the larger specimens (BP/1/5064 and NMQR 860) show more pronounced crowding of the roots of the i2 and i3 than in the smaller specimens. In both specimens, the root of the left i3 is

positioned lingual to that of i2, whereas the erupted crowns are situated laterally to one another (Figure 32B). In NMQR 860, the roots of i2 and i3 are in such close association that it appears that partial resorption of the root of i2 has taken place (Figure 36B, C). The crown of the erupted left i3 in BP/1/5064 is positioned more lingual than that of the neighbouring i2 (Figure 32B). This is interpreted as the result of i3 having not migrated completely into its natural position. Presence of a retained root labial to the erupting i3 is further evidence that the process of replacement at the locus was not yet complete (Figure 32B). This crowding of the incisors lead van Hoepen (1916) to originally interpret the number of lower incisors in TM 24 (BSL ~71 mm) as two.

A single functional canine tooth is present in each quadrant of the buccal cavity. The lateral ridges of the canines resemble the 'cutting edges' present in the 'incisiform dentition' of the Nile crocodile (*Crocodylus niloticus*) (Poole, 1961; Kieser *et al.*, 1993). The maxillary canines of *Galesaurus* do not bear the dorsoventrally directed facets on the distal surface of the canine, which are present in *Thrinaxodon* (Abdala *et al.*, 2013). These structures in *Thrinaxodon* are not interpreted as occlusal wear surfaces, as the mandibular canine passes mesial to the maxillary canine, suggesting that they may rather represent an adaptation relating to feeding. Furrowed canine teeth, on the other hand, are present in *Cynosaurus* and *Progalesaurus* (Sidor and Smith, 2004) and may be an adaptation to strengthen the tooth crown.

The canine roots of specimens RC 845, BP/1/4714, and BP/1/4602 are closed, whereas those of the large specimens NMQR 135, NMQR 3542, BP/1/5064, SAM-PK-K10468 and NMQR 860 are open. Interestingly, the remnant roots of the shed maxillary canines of SAM-PK-K10468 have a closed morphology. This indicates that skulls with a BSL ≤ 88 mm have closed roots, whereas the larger skulls (BSL ≥ 94 mm) have open canine roots, a condition previously reported in various dicynodont taxa (Hopson, 1964; Camp, 1956; Cox, 1968; Froebisch, 2005; Jinnah and Rubidge, 2007; Fröbisch and Reisz, 2008; Rozefelds *et al.*, 2011; Hancox *et al.*, 2013; Whitney *et al.*, 2019). This change in canine root morphology is accompanied by the cessation of replacement of the canines and coincides with the transition from subadult to adult skull size (Jasinoski and Abdala, 2017a).

6.5.1.2 Postcanines

The number of postcanines recorded in the study sample varies from nine to 12 maxillary, and 11 to 14 mandibular teeth, with the larger specimens having the largest number of teeth. The number of postcanine teeth agrees with those reported in previous descriptions (Owen, 1860; van Hoepen, 1916; Watson, 1920; Broom, 1932a, 1932b; Parrington, 1934) and confirms the idea that the length of the postcanine series varies with basal skull length. Specimen FMNH PR 1774 (WM 1563 in Rigney [1938]), which has seven teeth in each maxilla, has the least number of upper postcanines. The largest number of upper postcanines is in TM 83 with 12 teeth, although BP/1/5064 shows evidence for the development of a twelfth postcanine in both maxillae.

RC 845, the smallest specimen included in the study, has the fewest mandibular postcanines, with only 11 in each dentary. The larger BP/1/5064 exhibits the most postcanines, with evidence for 14 functional postcanines in the left, and 13 in the right dentary. The functional teeth of the right dentary are, however, interpreted as representing loci pc2–pc14, as a crypt is evident mesial to the position of pc2 (Figure 33D).

In the smaller specimens that were µCT-scanned, the first tooth of the postcanine series has a simplified crown morphology; with a straighter mesial cusp and an incipient distal cusp. This morphology of PC1 was first described and illustrated by Broom (1932a, 1932b). The tooth is also mesially inclined and is smaller than the following teeth in the series. This gives an overall more conical, caniniform appearance compared to PC2. A comparable condition has been described for the fourth upper incisor of *Thrinaxodon* (Abdala *et al.*, 2013). Abdala *et al.* (2013) suggested that the simplification of the fourth incisor to a canine-like morphology in *Thrinaxodon* was related to the manner in which the animal captured prey. Similarly, the simplification of the first maxillary postcanine in *Galesaurus* to a canine-like morphology could be related to the role the tooth played in prey capture.

It appears that the distal cusp of the postcanine teeth became more prominent with each successive replacement generation, as is evidenced by the fact that PC2 already has a more distinguishable distal cusp in all specimens. All teeth distal to PC2 exhibit the bicuspid crown morphology of *Galesaurus*. This condition differs

from that reported for *Diademodon* (Osborn, 1974) and *Thrinaxodon* (Abdala *et al.*, 2013), where the postcanine crown morphologies become more simplified with each successive replacement. This observation, coupled with those of Hopson and Kitching (1972) and van Heerden (1976) support the idea that the morphological variation of the postcanine crowns seen in the sample may be the result of ontogenetic variation, rather than taxonomic variation. Additionally, small mesial accessory cusps have been described in two small specimens of *Galesaurus* (Jasinoski and Abdala, 2017a), and the presence of these is also attributed to ontogenetic variation.

In *Thrinaxodon* there is a reduction in the number of postcanine teeth in the series with each successive replacement (Brink, 1955a; Estes, 1961; Hopson, 1964). *Galesaurus*, on the other hand, increases the length of the postcanine series with size (Figure 38). This condition has a superficial resemblance to that of *Diademodon*, but the manner in which it is achieved in *Galesaurus* is not the same. In *Diademodon*, the mesial-most tooth of the postcanine series had no replacement (Fourie, 1963, 1964; Hopson, 1971; Osborn, 1974). Once the first postcanine was exfoliated, the alveolus became filled with bone, which was subsequently remodelled to the extent that the filled alveoli mesial to the postcanine series are indistinguishable from the surrounding bone (Osborn, 1974). Each successive exfoliation of the first postcanine results in the distal shift of the postcanine series by one locus, and an increase in size of the diastema between the canine and postcanine series. This is not observed in *Galesaurus*, as replacement crypts are present lingual to the first postcanine in the maxilla of BP/1/5064

(Figure 33B), and the dentaries of BP/1/5064 (Figure 33D) and SAM-PK-K10468 (Figure 35C, D).

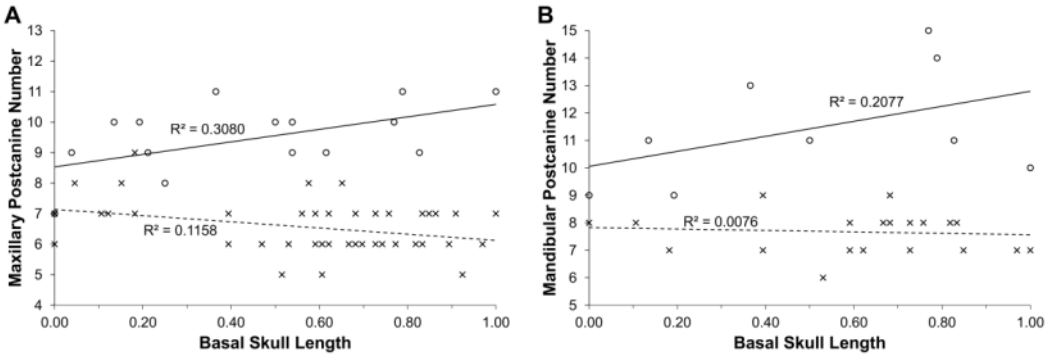

Figure 38. Number of postcanines in *Galesaurus planiceps* (○) and *Thrinaxodon liorhinus* (×).
A, maxillary dentition; B, mandibular dentition. X-axis represents the normalised basal skull length (BSL), and Y-axis the number of postcanines present. Solid trend line, *Galesaurus planiceps*; dashed trend line, *Thrinaxodon liorhinus*.

Estes (1961) wrote that the tooth morphology in *Thrinaxodon* was similar in specimens of various sizes, but juvenile specimens of *Thrinaxodon* had more postcanine teeth (seven) when compared to adults (six postcanines). Abdala *et al.* (2013) considered the typical number of postcanines in adult *Thrinaxodon* to be six maxillary and seven–eight mandibular teeth. It was demonstrated that crown morphologies of the upper postcanines were simpler than those of the lower teeth, with the most complex maxillary postcanines being tricuspid, lacking a cingular collar. Abdala *et al.* (2013) also demonstrated a reduction in mandibular postcanine crown complexity with increased size. Specimens with a BSL ≤ 80

mm have multicusped crowns, whereas larger specimens only have tricuspid crowns.

The postcanine crown morphology of the contemporaneous *Progalesaurus* (SAM-PK-K9954) is more complex than that of *Galesaurus*, bearing well developed mesial accessory cusps, and several distal accessory cusps (Sidor and Smith, 2004). Additional mesial accessory cusps have recently been observed in two subadult specimens of *Galesaurus* (Jasinoski and Abdala, 2017a): BP/1/4597 (BSL ~70 mm) and NMQR 3716 (BSL 75 mm). No such accessory cusps were observed in adult specimens, suggesting a simplification of crown cusp morphology with each successive replacement, as has been reported for *Thrinaxodon* (Abdala *et al.*, 2013) and *Diademodon* (Hopson, 1971; Osborn, 1974). The specimen of *Progalesaurus* is much larger (BSL 93.5 mm) than either of the *Galesaurus* specimens reported with mesial accessory cusps on the postcanines. At present *Progalesaurus* is represented by one specimen, and consistently falls as the sister taxon to *Galesaurus* in phylogenetic analyses (Sidor and Smith, 2004; Abdala, 2007; Botha *et al.*, 2007; Ruta *et al.*, 2013).

Van Heerden and Rubidge (1990: 43) describe the recurved mesial cusp of the postcanine dentition as forming "a long cutting edge." The proposed cutting edges of the postcanine dentition of *Galesaurus* may have acted in a 'shearing' action, and may have been specialised to deal with soft-bodied prey. This is markedly different from the 'piercing' morphology of the dentition of the other basal cynodonts, such as *Procynosuchus* (Kemp, 2005).

In *Galesaurus*, the teeth of the postcanine series are arranged in a slight imbricate pattern. Similar overlapping patterns are seen in the maxillary postcanine series of the Late Triassic eucynodont, *Ecteninion lunensis* from Argentina (Martinez *et al.*, 1996), and the mandibular postcanine series of the Early Triassic epicynodont, *Progalesaurus lootsbergensis* from South Africa (Sidor and Smith, 2004). In contrast, an increased degree of overlapping is seen in the distal maxillary postcanines in the tritheledontid, *Riograndia guaibensis* from the Brazilian Norian (Bonaparte *et al.*, 2001; Soares *et al.*, 2011).

6.5.2 Tooth replacement

The pattern of tooth replacement observed in *Thrinaxodon* (Crompton, 1963; Abdala *et al.*, 2013) corresponds with Edmund's (1960, 1962) Zahnreihe theory, whereby teeth are replaced in successive waves that move through the jaw in a back to front direction. In *Galesaurus,* replacement of the anterior teeth (incisors and canines) matches that of *Thrinaxodon*, whereas the pattern of the postcanine replacement differs.

Replacement teeth are always positioned lingual to the functional tooth they are to replace. As the new tooth develops, it moves labially, etching at, and causing the resorption of the root of the functional tooth. Once the root has been sufficiently eroded through this process, the crown is shed (Wu *et al.*, 2013). A similar sequence of resorption of the functional tooth root coinciding with the development of the replacing crown in the postcanine series of *Galesaurus* is described in the Diadectomorpha (LeBlanc and Reisz, 2013).

6.5.2.1 Incisors

A typical pattern of alternating replacement is recorded for both the upper and lower incisor compliments in the sample. A good example of this for the upper series is seen in the right premaxilla of RC 845 (Figure 25B), where the even-numbered incisors (I2 and I4) are at a later developmental stage than the odd-numbered incisors (I1 and I3). The odd-numbered incisors show only the crown up to the approximate level of the tooth neck, whereas the even-numbered incisors have more prominently developed roots. The condition is less obvious in the left premaxilla of RC 845, but again the even-numbered teeth are more developed. A noticeable exception is observed in BP/1/5064, which has replacement crypts associated with the first three incisors (I1–I3) in each premaxilla. In both sides, the third crypt is larger than the others, which are all of similar size.

An alternating replacement pattern is evident in the lower dentition of several specimens. In RC 845 and BP/1/4602, replacement incisors are only associated with the even-numbered teeth (i2), with a fair amount of synchrony of the developmental stages in each hemimandible. Asynchronous replacement is, however, evident in BP/1/4714 (Figure 26C, D), where replacement germs are associated with i2 in the left dentary, and i1 and i3 in the right.

6.5.2.2 Canines

Specimen RC 845, which has the smallest BSL in the study, is considered a subadult (Butler, 2009; Jasinoski and Abdala, 2017a). The advanced stage of development of the maxillary replacement canines (Figure 25A, B), and the

presence of remnant roots associated with three of the four canines (Figure 25A, C, D), indicates that the teeth present in RC 845 do not represent the earliest canine dentition of the individual. Specimen BP/1/4602 is the only skull of *Galesaurus* that exhibits replacement of all four canines simultaneously. This degree of canine replacement was present in the whole sample of µCT-scanned *Thrinaxodon* specimens (Abdala *et al.*, 2013), with the exception of the largest specimen, BP/1/5905 (BSL 87 mm), where replacement maxillary canines are evident, but there are no replacement canines in the mandible. This is similar to the condition reported for the subadult *Galesaurus* RC 845 (Figure 25).

No replacement of the canines was documented for specimens of *Galesaurus* with a BSL of 90 mm or more. Replacement of the canines thus appears to be restricted to juvenile and subadult *Galesaurus* (BSL < 90 mm), whereas open rooted canine morphology with no signs of replacement activity is observed only in adult specimens larger than 94 mm (e.g., NMQR 135). This suggests that there are a finite number of replacement generations for the canines in *Galesaurus* and that the final 'permanent' generation has a different root morphology to that of 'deciduous' generations. This differs from the condition seen in *Thrinaxodon* where continual replacement of the canine teeth has been recorded well into adulthood (Abdala *et al.*, 2013).

The condition of continuously growing, open-rooted canines is a feature previously considered to have been a unique specialisation of dicynodonts amongst the therapsids (Jinnah and Rubidge, 2007). It is important to note that the

caniniform teeth (tusks) of dicynodonts are not homologous to the canine teeth of the Theriodontia (Froebisch, 2005; Fröbisch and Reisz, 2008; Cisneros *et al.*, 2011, 2015). Among non-mammaliaform cynodonts open canine roots have previously been hypothesised to be present in the Middle Triassic traversodontid, *Andescynodon* due to hypertrophy of the canines (Liu and Powell, 2009).

Several examples of open-rooted dentitions, or 'tusks,' exist in extant mammalian lineages. Proboscideans (Tiedemann, 1997), rodents, and lagomorphs have open-rooted incisors, whereas walruses (Fay, 1985), beaked whales (Heyning, 1984; Mead, 1989), narwhal (Silverman and Dunbar, 1980), dugong (Anderson, 2002) and hippopotamus (Laws, 1968) have open-rooted canines (Ungar, 2010). In many of these examples, these teeth are adapted to serve a secondary purpose not necessarily related to feeding: such as intraspecific competition (e.g., elephant and hippopotamus [Kingdon, 1989]) or even as a sensory organ (e.g., narwhal [Nweeia *et al.*, 2014]). Often the teeth are also influenced by sexual dimorphism (Ungar, 2010) (e.g., primates and narwhal [Nweeia *et al.*, 2012, 2014]). Sexual dimorphism has recently been suggested to have occurred in *Galesaurus* (Jasinoski and Abdala, 2017a), however, open-rooted canines are present in both 'female' (e.g., NMQR 135 and NMQR 3542) and 'male' morphotypes (e.g., BP/1/5064, SAM-PK-K10468, and NMQR 860).

It is hypothesised that by the time an individual had attained a basal skull length of ~90 mm, the rate of mineralisation of the canine teeth had slowed to such an extent that the root apex would not have fully developed prior to the animal's

death. Possible reasons for such sudden slowing of canine tooth formation, and cessation of the formation of replacement teeth may be related to the attainment of skeletal maturity. This implies that individuals may also have attained sexual maturity. Sexual maturity has been inferred to have been attained at a larger size in *Galesaurus* compared to *Thrinaxodon* (Jasinoski and Abdala, 2017a). Parental care has also been demonstrated to have occurred in *Galesaurus* (Jasinoski and Abdala, 2017b). Changes in behaviour, such as spending less time hunting/foraging and more time caring for young may have resulted in physiological changes such as a slower rate of mineralisation of the canine teeth in larger specimens.

There is no evidence of multiple canine tooth families in *Galesaurus*, such that at any one time only a single functional canine is present in each quadrant of the mouth. In contrast, several specimens of *Thrinaxodon* present evidence for multiple tooth families (e.g., BP/1/5372, TM 80A, BP/1/7199, and TM 180) (Abdala *et al.*, 2013). In the maxilla of these specimens, both the replacing canine and retained roots from the previous canine are positioned mesial to the functional canine. Abdala *et al.* (2013) interpreted this arrangement as being caused by the migration of the functional canine. This condition is not seen in *Galesaurus*, as in all the μCT-scanned specimens the roots of the previous maxillary canines have been almost completely resorbed. Similarly, in the mandible of several specimens of *Thrinaxodon* (e.g., BP/1/5372, TM 80A, and BP/1/7199) the replacement, and remnant roots are both situated distal to the functional canine. Osborn and Crompton (1973) proposed a similar hypothesis for the migration of the

mandibular canines. Several small *Thrinaxodon* specimens; BP/1/1376 (BSL ~30 mm), TM 1486 (BSL ~33 mm), and SAM-PK-K10016 (BSL 42 mm), have replacement maxillary canines distal to the functional canine, a condition described as being rare in this taxon (Abdala *et al.*, 2013). In addition to the distal eruption of the replacing canine, TM 1486 is unusual in that it also has a smaller replacement bud lingual to the root of the functional canine (Abdala *et al.*, 2013), suggesting the presence of multiple replacement generations. Eruption of replacement canines lingual to the functional tooth has been described in the basal cynodont *Procynosuchus* (Broom, 1937a, 1938), as well as the Gorgonopsia and Therocephalia (Kermack, 1956) (Chapter 3).

The data from the smallest *Galesaurus* specimen scanned (RC 845, BSL 69 mm) indicates that the development and eruption of the mandibular canines took place earlier than that of the maxillary canines (Figure 25). This interpretation holds true also for the condition seen in SAM-PK-K1119 (BSL 72 mm), where the replacement mandibular canines have already erupted, and the maxillary canines are not yet visible (Figure 37).

The largest *Thrinaxodon* specimen scanned by Abdala *et al.* (2013) that shows replacement of the maxillary canines, (BP/1/5905) has a BSL of 87 mm and represents an adult approximately 91% of the size of the largest specimen in their study (SAM-PK-K1461, BSL 96 mm). In contrast, the largest specimen of *Galesaurus* to show replacement of the canines (BP/1/4602) is only 77% of the size of the largest *Galesaurus* specimen (NMQR 860) and is considered to be a

subadult (Jasinoski and Abdala, 2017a). Abdala *et al.* (2013) proposed a higher rate of replacement of the canines in juvenile specimens of *Thrinaxodon*, noting two instances of multiple replacement generations occurring at the same time.

6.5.2.3 Postcanines

It has been demonstrated in both *Thrinaxodon* (Abdala *et al.*, 2013) and *Diademodon* (Osborn, 1974) that replacement of the anterior teeth in the postcanine series ceases, and new teeth are added to the distal margin of the postcanine series, causing a distal shift in the series. This distal shift in the postcanine series is also observed in *Galesaurus*, however, the presence of replacement crypts mesial to the first functional postcanine in the right dentary of the adult specimen BP/1/5064 (Figure 33D) suggests that the mesial-most elements of the postcanine series may have undergone at least one replacement.

A brief account of the tooth replacement in a juvenile *Galesaurus* specimen (FMNH PR 1774) was given by Rigney (1938). A replacement germ is present for the eighth postcanine in the left dentary. Owing to the greater length of the third and fifth postcanines, Rigney (1938) deduced that an alternating pattern of replacement was present in the postcanines series.

As an individual increased in size, additional postcanine teeth were added to the dental series distally. In contrast, *Thrinaxodon* tends to show a reduction in the number of postcanines in both the maxillary and mandibular series at the transition from juvenile (BSL ≤ 42 mm) to subadult (BSL ~56–68 mm) (Jasinoski

et al., 2015). The number of postcanines in *Thrinaxodon* specimens larger than 56 mm still shows some variability (Figure 38), but stabilises at 6–7 elements in the maxillary, and 7–8 elements in the mandibular series (Abdala *et al.*, 2013).

The apparent addition of postcanine teeth mesial to the series in the largest specimen of *Galesaurus* (BP/1/5064) (Figure 33B) lends support to the Zone of Inhibition (ZOI) theory (Osborn, 1971, 1973) used to describe sequences of tooth replacement. Such 'prevention' of the development of the mesial postcanine teeth, may also explain the noticeable decrease in anteroposterior crown length as BSL increases. This further suggests that the PC1 in RC 845 is not homologous to PC1 in BP/1/5064.

The waves of replacement in the maxillae of *Galesaurus* are not as clear as those in the mandibles. This is similar to the findings for *Thrinaxodon* (Abdala *et al.*, 2013), where an alternating replacement pattern was well documented in the mandibular postcanine series, whereas the replacement pattern of the maxillary series was not simple to identify. However, it appears that there are two replacement waves that pass down the hemimandible simultaneously: one affecting even numbered teeth, and the second affecting odd-numbered teeth. In addition, it appears that these two waves originate in each hemimandible alternately, such that odd teeth on one side may be more advanced than the odd teeth of the other side, whereas the converse is true for the even teeth. Instead of a replacement tooth being associated with every second tooth in the series, replacements are associated with every third tooth in the anterior region of the

series, i.e., pc1, pc4, and pc7. The replacement wave runs from back to front as the replacement pc7 is more developed than that of pc4, with pc1 being the least developed. Specimen BP/1/4602 (Figure 27C, D) shows the best example of this.

In at least one specimen (SAM-PK-K10468), there is indication of a single replacement tooth filling the loci of two erupted teeth (locus 3 in Figure 35C, D). This may explain the reduction in the number of postcanines in the series seen in some specimens with regard to the BSL. This anomaly may be due to the alternating waves of replacement, and could explain the complexity seen in the patterns of the replacement waves. There appears to be a slowing in the rate of replacement of the postcanines as BSL increases, such that the waves replacing odd and even numbered may begin to move along the postcanine series at differing rates. This may account for the condition of two teeth adjacent to one another both being in the process of replacement (e.g., BP/1/5064 and SAM-PK-K10468).

It was not possible to determine the number of replacement waves present in either postcanine series of *Galesaurus*. However, in the maxilla, it is inferred that a minimum of five replacement waves took place, as there is an increase in the number of postcanines from the smallest (FMNH PR 1774, seven maxillary postcanines) to the largest (TM 83, 12 maxillary postcanines) count of five elements. Assuming that each successive wave would add one element to the distal margin of the postcanine series, five replacement waves are estimated.

However, it is likely that the first postcanine tooth was shed to accommodate the expanding alveolus of the canine (Abdala *et al.*, 2013), especially in juveniles. Thus, the increase in the number of postcanine teeth with an increase in skull length suggests that teeth are added to the distal margin of the postcanine series faster than they are exfoliated from the mesial margin of the same series. Given the perceived alternating pattern of three, it is plausible to consider that the first locus of the series ceases to be active after two or three tooth generations. Thus, every three replacement waves would comprise a complete replacement cycle resulting in a net gain of two postcanine teeth (+ 1 distal locus per each wave and − 1 mesial locus per cycle). Specimens with a BSL smaller than 81 mm appear to adhere to this proposed replacement triplet of + 3: − 1 (i.e., two teeth are gained after one complete replacement cycle), whereas in adult specimens the pattern is not as clear, and may more closely resemble + 2: − 1 due to the slowing of the replacement waves.

In the sample, there is a decline in the number of maxillary postcanine teeth (from 11 to 9) in specimens with a BSL between 80 and 90 mm (Figure 39A), which represents the transition between subadults and adults. This corresponds to the skull size at which replacement of the canines is no longer recorded. Similar observations were not possible for the mandibular postcanine series, as there were no specimens in the BSL range of 90 to 100 mm that have accessible mandibular teeth (Figure 39B). Interestingly, there is a decline in the number of mandibular postcanine teeth with increased BSL in specimens larger than 102 mm.

For the maxillary series, it is interpreted that at a BSL of approximately 80 to 90 mm the replacement rates of the postcanine series slows such that two replacement waves are present in the tooth row at the same time. This may account for the perceived increase in replacement activity based solely on observations of the number of crypts being present in larger specimens (e.g., BP/1/5064; Figure 33). Whereas the + 3: − 1 replacement triplet may still apply, it is likely masked by the presence of the first wave of the next triplet occurring concurrently with the last wave of the preceding triplet, leading to observations that do not follow the original model proposed. Such instances are observed in the maxilla at the transition from 90 to 94 mm, and 103 to 105 mm. These account for the first tooth of the leading wave having been shed, but as the leading wave was still developing, it has yet to reach the point of adding an additional tooth to the series.

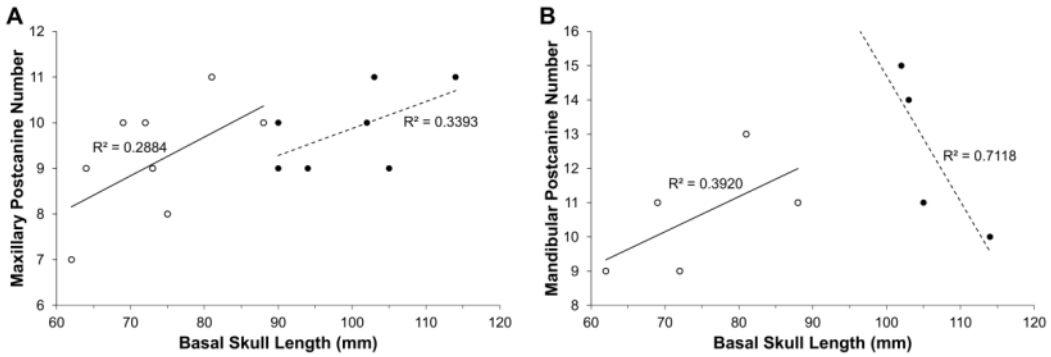

Figure 39. Number of postcanines in subadult (○) and adult (●) *Galesaurus planiceps*.

A, maxillary dentition; B, mandibular dentition. X-axis represents the basal skull length (BSL), and Y-axis the number of postcanines present. Solid trend line, subadults; dashed trend line, adults.

It has been demonstrated in the Gorgonopsia and Therocephalia (Kermack, 1956; Hopson, 1964) that replacement of the postcanines ceased first, followed by the canines, and lastly the incisors. However, in *Galesaurus* replacement of the canines ceases at the attainment of adult size (BSL ~90 mm), and replacement of the incisors and postcanines continues even in the largest specimens.

6.5.3 Maxillary postcanine replacement model

The model presented in Figure 40 is not perfect for the following reasons: (1) it assumes a constant rate of development of replacing teeth through ontogeny, and (2) it assumes that each replacing tooth erupts directly into the locus of the associated functional tooth. The latter has been observed to be not always the case, with some specimens showing a replacement tooth erupting between two functional teeth (e.g., RC 845).

Developmental stages 1–7 are not observed in the sample, as specimens of such early ontogenetic stages of *Galesaurus* have yet to be discovered. However, the smallest known specimen (FMNH PR 1774) approximates the condition of developmental stage 8. In addition, three larger specimens can also be matched to subsequent developmental stages, providing some support for the model.

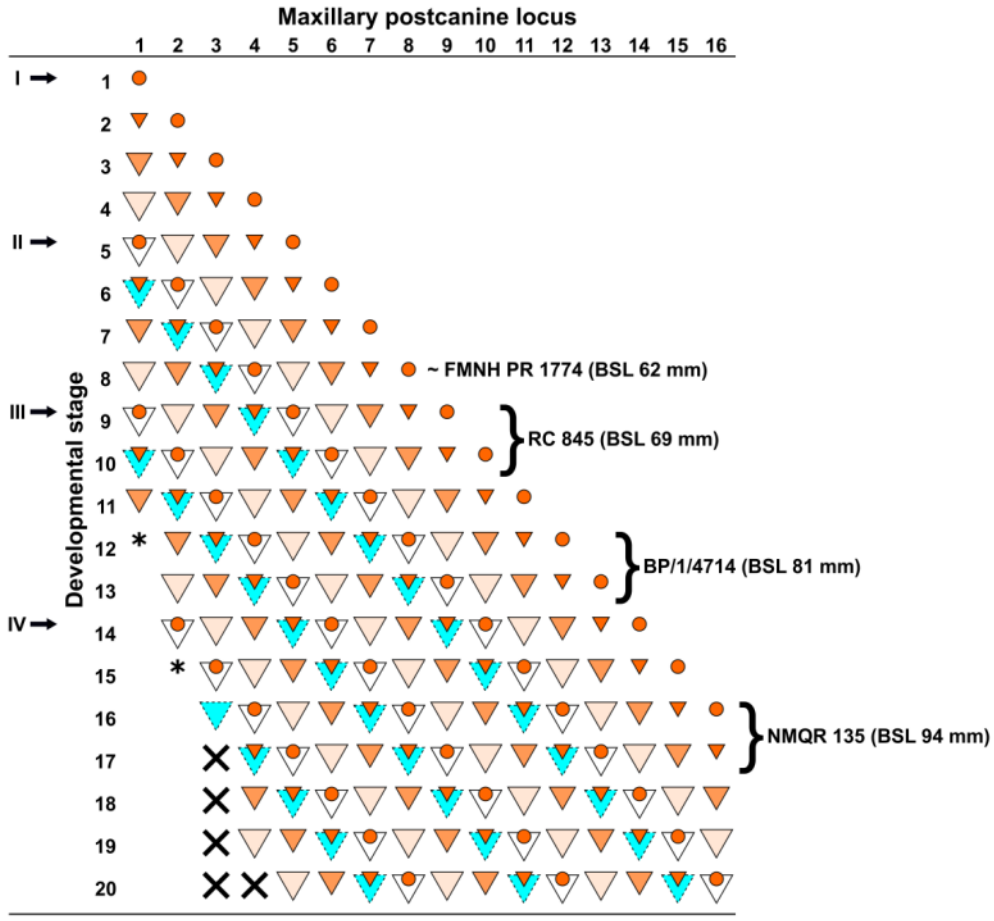

Figure 40. Hypothetical model of maxillary postcanine replacement in *Galesaurus planiceps* through ontogeny.

Replacement crypts and teeth are indicated by orange circles and small orange triangles respectively. Functional teeth are indicated by large triangles, with shading representing tooth age. Darker tones of orange indicate younger teeth still in the process of developing/erupting, white indicates fully erupted functional teeth, and blue indicates a crown about to be shed due to resorption of the roots. Roman numerals indicate the initiation of a wave of replacement, asterisks (*) indicate the stages at which it is hypothesised that the first active postcanine locus is invaded by the alveolus of the replacement canine, X indicates that a locus has ceased replacement and the alveolus may be filled by bone. Not to scale.

6.5.4 Palaeobiology of *Galesaurus*

Although *Galesaurus* lived contemporaneously with *Thrinaxodon* (Groenewald and Kitching, 1995; Ruta *et al.*, 2013), the vastly different stratigraphic ranges (Botha and Smith, 2006: fig. 6) recorded for these two closely related taxa has led to the belief that they occupied different niches (Butler, 2009). The laterally compressed postcanine teeth of *Galesaurus* have been interpreted as forming a shearing surface (LeBlanc *et al.*, 2018), and the enlarged, distally directed main cusp of the postcanines might be an adaptation for capturing and grasping small, wriggling prey. These assumptions agree with the previous proposals of the diet of *Galesaurus* to likely have consisted of invertebrates and small lizards (McLoughlin, 1980; Kemp, 2005).

The widespread loss of vegetation (Smith and Ward, 2001), and the change-over to a *Dicroidium* dominated flora (Retallack, 1995), inferred to have been experienced after the end-Permian mass extinction event (Wignall *et al.*, 2009; Jia *et al.*, 2010; Joachimski *et al.*, 2012), as well as changes in fluvial style (to ephemeral, braided streams) and lowered water tables, are indicative of severe drought conditions during the Early Triassic (Smith, 1995; Kemp, 2005; Smith and Botha-Brink, 2014). This change in environment may have resulted in a decline in the abundance of suitable prey items for *Galesaurus* to subsist on. In contrast, the generalist dentition of *Thrinaxodon* may have allowed it to survive the gruelling climatic changes by becoming an obligate omnivore; the tricuspid and mulitcuspid dentition of *Thrinaxodon* potentially being better suited for processing plant material than the specialised bicuspid dentition of *Galesaurus*.

Not only are the crown morphologies and replacement patterns of *Galesaurus* different to those of *Thrinaxodon*, but so too is the manner in which the teeth are attached to the jaw. In *Galesaurus* the teeth do not become fused to the bone, instead exhibiting the mammalian condition of permanent gomphosis (LeBlanc *et al.*, 2018). In contrast, the teeth of *Thrinaxodon* were shown to ankylose to the bone, in a possible reversal to the basal state (LeBlanc *et al.*, 2018). It has been demonstrated that both *Galesaurus* (Butler, 2009; Butler *et al.*, 2019) and *Thrinaxodon* (Botha and Chinsamy, 2005) grew rapidly for a period of about a year before reaching skeletal maturity. *Thrinaxodon* did so at a smaller body size than has been estimated for *Galesaurus*, suggesting that *Thrinaxodon* may have retained juvenile characters (such as continued replacement of maxillary canines) into adulthood. Alternatively, the hypothesised reversal to the ancestral condition of attachment of the teeth to the jaw via ankylosis, may be coupled with the reversal to the state of continued replacement of the maxillary canine dentition too.

6.6 Conclusion

This study is the first to apply scanning techniques to determine the changes in dental replacement patterns across an ontogenetic series of *Galesaurus*, and has demonstrated that tooth replacement patterns observed in the canines and postcanines of *Galesaurus planiceps* differ from those of *Thrinaxodon liorhinus*. Cessation of the canine replacement occurs in adult *Galesaurus* specimens, i.e., specimens with a BSL larger than ~90 mm, whereas postcanine replacement was recorded in several larger specimens (BSL 94–114 mm). Additionally, the

functional canines of adult specimens have an open-rooted morphology, whereas subadults (BSL < 90 mm) have functional canines with closed roots. This change from closed to open-rooted morphology of the canines in *Galesaurus* may be linked to the cessation of replacement of the canines, and the hypothesised subsequent slowing in the rate of mineralisation of the tooth.

Galesaurus shows an increase in the number of postcanine teeth in the maxilla and mandible with an increase in skull length, which differs from the condition reported for *Thrinaxodon*. As in *Thrinaxodon*, the postcanine teeth of *Galesaurus* are replaced in an alternating pattern. However, for *Thrinaxodon* the replacement waves follow each second tooth in the series, whereas in *Galesaurus* the replacement wave affects every third tooth in the series. In both taxa, this pattern has been best observed in the postcanine series of the mandibles.

Although *Thrinaxodon* is widely considered to be a more derived member of the Epicynodontia, the evidence for the cessation of replacement of the canines in *Galesaurus* hints that the tooth replacement patterns of *Galesaurus* could be more derived than that of *Thrinaxodon*. Reduction of the number of generations of replacement teeth has previously been described for the postcanine dentition of the gomphodont cynodont *Diademodon*, and the probainognathian *Brasilodon* (Martinelli and Bonaparte, 2011). The earliest record of the mammalian condition of true diphyodonty occurs in *Morganucodon* (Luo *et al.*, 2004). The evolutionary pressure behind this adaptation may be as a result of a specialised diet/foraging behaviour. Evidence shows that both *Galesaurus* and *Thrinaxodon* utilised

burrows (Brink, 1959; Damiani *et al.*, 2003; Butler, 2009; Fernandez *et al.*, 2013; Jasinoski and Abdala, 2017b; Butler *et al.*, 2019). Since *Thrinaxodon* is more prevalent in the fossil record, and has a much longer stratigraphic range after the PTB than *Galesaurus*, it may be that specialised dependence on a particular food source lead to the earlier extinction of *Galesaurus*, whereas *Thrinaxodon* was able to survive on alternative food sources because of the more generalised morphology of its postcanine crowns.

7 DISCUSSION

7.1 Outline

Independent discussions of the tooth replacement patterns of the basal therocephalian family Lycosuchidae (Chapter 3), the derived therocephalian *Bauria cynops* (Chapter 4), and the basal epicynodonts *Cynosaurus suppostus* (Chapter 5) and *Galesaurus planiceps* (Chapter 6) are presented at the end of each chapter.

This chapter compares the results relating to patterns of tooth replacement amongst the Therocephalia, followed by a comparison of the Cynodontia. Lastly, similarities/differences in tooth replacement patterns in Eutheriodontia are discussed. These trends are noted according to the three tooth types, i.e., incisors, canines, and postcanines, as there is considerable variation amongst and between these different tooth types.

Given that both *Thrinaxodon* (Crompton and Jenkins, 1968; Hopson and Crompton, 1969; Hopson and Barghusen, 1986) and *Bauria* (Broom, 1911) have been suggested as the model for the precursor of mammals by different authors at different times, a model describing the transition to the mammalian condition of (hemi)diphyodonty from the patterns of alternating replacement in these theriodont ancestors is proposed and discussed.

To conclude, some shortfalls of this study are addressed, with suggestions of how to possibly enhance future studies of the tooth replacement patterns of taxa included in this thesis, as well as suggestions of which taxa to prioritise for future studies, in order to fill the gaps in our knowledge in theriodont tooth replacement.

7.2 Comparison of tooth replacement in Therocephalia

7.2.1 Incisors

Both µCT-scanned specimens of Lycosuchidae showed replacement of the incisors in the premaxilla (Figure 6A, B and Figure 8A, B), whereas replacement amongst the mandibular incisors is evident only in US D173 (Figure 6C, D). In contrast, of the four specimens of *Bauria cynops* subjected to µCT-scanning, only BP/1/1180 showed possible evidence for replacement associated only in the upper incisors (Figure 11).

The incisor replacement pattern of Lycosuchidae is alternating, and is the same as that described by Kermack (1956) in his study of tooth replacement in basal theriodonts. Due to only the single occurrence of incisor replacement in the four µCT-scanned specimens of *Bauria*, it is difficult to describe a replacement pattern with certainty. It is possible that *Bauria* retained the ancestral amniote condition of alternating replacement of the incisors.

7.2.2 Canines

The results showed that Lycosuchidae retains the basal synapsid condition of two maxillary canine families (Romer and Price, 1940; Sigogneau-Russell, 1989), and

a single mandibular canine. Kermack (1956) described double maxillary canines in several specimens of Therocephalia. The presence of two large maxillary canines was previously considered diagnostic for the Lycosuchidae (Haughton and Brink, 1954). Van den Heever (1980) proposed that the presence of two maxillary canines was a result of one tooth replacing the other. The results presented in Chapter 3 show that Lycosuchidae does indeed have two active tooth families of maxillary canines.

The presence of a single functional canine in each maxilla of *Bauria* suggests that only one canine family remained active. However, because of the lack of evidence of canine replacement in the sample studied, it is not possible to determine a pattern of canine replacement. This suggests that somewhere in the therocephalian phylogenetic lineage, between the basal Lycosuchidae and derived *Bauria* (Figure 1), the number of maxillary canine families was reduced from two to one.

7.2.3 Postcanines

Determining patterns of maxillary postcanine replacement in the Lycosuchidae is problematic due to the reduction in the number of teeth in the series. Additionally, the µCT-scanned specimens of Lycosuchidae are quite large (Table 16). Specimen US D173 has a BSL of 77.85% and SL of 76.51% that of the largest specimen of *Lycosuchus* (BP/1/7162, BSL = 298, SL = 149), and CGS C60 has an SL of 79.87% compared to BP/1/7162. Due to these proportionately large sizes (i.e., ontogenetically advanced individuals), the rate of replacement of the postcanines may have already begun to decrease in the lycosuchid specimens sampled.

Table 16. Ranges of basal skull length in the sampled taxa.

Taxon	Known BSL* range (mm)	µCT range (mm)	% BSL sampled
Lycosuchidae (SL)	21–226[a]	114–119	2.91
Lycosuchidae (BSL)	218–370[a]	232[b]	0.65
Bauria	80–132[c]	114–132	35.85
Cynosaurus	49–122[d]	49–115	90.54
Galesaurus	62–114[e]	69–114	86.79
Thrinaxodon	~30–96[e]	37–87	76.12

Abbreviations: BSL, basal skull length; SL, snout length.

* Snout length included for Lycosuchidae

[a] Measurements from Abdala *et al.* (2014a) with NHMUK PV R 49422 omitted

[b] no BSL for CGS CC60

[c] Measurements from Abdala *et al.* (2014b)

[d] Measurements from Van den Brandt and Abdala (2018)

[e] Measurements from Jasinoski and Abdala (2017a)

[f] Measurements from Abdala *et al.* (2013)

In the mandibles of US D173 replacement was taking place at pc2 (Figure 6D) and pc3 (Figure 6C, D), and in CGS C60 replacement was taking place in pc5 (Figure 8C, D). If the replacement waves moved from front to back, this suggests that the waves have already passed through the mesial elements of the series, and that the distal elements are of an older generation.

Bauria presents a different scenario: the number of teeth in the postcanine series has increased to include 8–10 maxillary, and 10–12 mandibular postcanines. Additionally, the sample included at least two specimens (BP/1/2837 and BP/1/4678) that may represent juveniles/subadults (Table 6 and Table 16). Thus, it could be expected that these specimens would have exhibited more replacement activity. In contrast, replacement of the postcanines was observed in only a single

μCT-scanned specimen (BP/1/1180, BSL 114 mm), with historical accounts of possible replacement in two more specimens: SAM-PK-1333 (BSL ~122 mm) (Crompton, 1962) and AMNH FARB 5622 (BSL 130 mm) (Broom, 1937b; Boonstra, 1938). Of particular interest in *Bauria* is evidence for sequential addition of postcanine teeth to the distal margin of the postcanine series in BP/1/1180 (Figure 12), as has been described for several gomphodont cynodonts (Abdala *et al.*, 2002, 2013).

7.3 Comparison of tooth replacement in Cynodontia

7.3.1 Incisors

The alternating patterns of replacement described in the incisors of *Cynosaurus* and *Galesaurus* showed very little variation between the two genera. In addition, the replacement pattern described in the incisors of *Cynosaurus* and *Galesaurus*, matches that of the closely related *Thrinaxodon* (Abdala *et al.*, 2013). This indicates little variation in incisor replacement patterns, perhaps reflecting their close phylogenetic relationships (Figure 2).

7.3.2 Canines

The results presented in Chapters 5 and 6 provide the first evidence for ontogenetic cessation of replacement of the maxillary canines in basal Cynodontia. Specimens of *Cynosaurus* and *Galesaurus* that had attained a basal skull length of more than 90 mm, and are therefore considered adult (Butler, 2009; Jasinoski and Abdala, 2017a; Van den Brandt and Abdala, 2018; Butler *et al.*, 2019), showed no evidence for the replacement of either maxillary or

mandibular canines. This suggests that the cessation of replacement of the canine teeth is linked to the attainment of skeletal (and possibly sexual) maturity. Interestingly, in the closely related *Thrinaxodon*, replacement of the maxillary canines appears to have continued well into adulthood (Abdala *et al.*, 2013) (Table 17).

Table 17. Smallest and largest specimens of Epicynodontia included in studies of tooth replacement using micro-computed tomography.

Taxon	Smallest BSL (mm)	Largest BSL recording canine replacement (mm)	Largest BSL (mm)
Cynosaurus	49 (40.16%)	~88[a] (72.13%)	122
Galesaurus	62 (54.39%)	88 (77.19%)	114
Thrinaxodon	~30 (31.25%)	87 (90.63%)	96

Percentages in parenthesis are relative to largest known specimen. Abbreviation: BSL, basal skull length.

[a] This value is an estimate calculated from the methods described in Chapter 5.3.2

Of further interest is the presence of canine replacement distal to the functional maxillary canine reported in small specimens of *Thrinaxodon* (Fourie, 1963, 1974; Gow, 1985b; Abdala *et al.*, 2013). Fourie (1963) noted the eruption of the replacement maxillary canine alternating between the mesial and distal position of the functional tooth. Fourie (1963) added that similar observations have been made for cynognathids, but did not offer specimen numbers, or any further taxonomic identification. Gow (1985b) further proposed that juvenile specimens of *Thrinaxodon* had two maxillary canine families, whereas adults had a single maxillary canine family. Eruption of the replacement maxillary canine distal to

the functional canine was not seen in the studies of *Cynosaurus* and *Galesaurus*. This is possibly due to the samples not including similarly small specimens (Table 16 and Table 17).

Fourie (1963: 211) described a *Diademodon* specimen for which, "the root of a replaced lower canine is preserved mesial to the functional tooth," further noting that, "[t]his condition is opposite to that found in all the mandibles investigated." From Fourie's (1963) wording it is interpreted that the "replaced" tooth is a retained root from a previous replacement generation, and the "functional" tooth represents a more recently erupted tooth. Such an arrangement, with the replacement mandibular canine erupting distal to the functional tooth, was observed for all μCT-scanned specimens of *Cynosaurus* (Chapter 5), *Galesaurus* (Chapter 6), and *Thrinaxodon* (Abdala *et al.*, 2013), in which replacement mandibular canines were recorded. It is therefore of interest, that according to Fourie (1963) (Table 18), seven specimens of *Diademodon* show the opposite condition of the replacement mandibular canine erupting mesial to the functional tooth. Kermack (1956) noted that he was not aware of any theriodont specimens showing evidence for two tooth families of mandibular canine.

Table 18. Summary of the *Diademodon* specimens included in a study of tooth replacement by Fourie (1963).

Element	No. fragments with canine replacement	Estimated no. of canine replacement generations
Maxilla	3	7 +
Mandible	8	3–4

7.3.3 Postcanines

The replacement pattern of the postcanines of *Cynosaurus* and *Galesaurus* showed the most variation from one another. Although an alternating pattern is present in both taxa, in *Cynosaurus*, there is clear evidence for the cessation of replacement at the first postcanine locus in the maxilla (PC1) (e.g., Figure 17 and Figure 18). From the model of maxillary postcanine replacement (Figure 24), it was estimated that at least three tooth generations erupted at PC1 before the locus became dormant, and the alveolus was invaded by the maxillary canine. There were insufficient mandibles in the sample to determine if such a cessation of replacement of the first locus (pc1) also occurred in the mandible. However, the presence of a replacement tooth in pc1 of each hemimandible of SAM-PK-K10694 (Figure 19C, D), and the broken crown of the left pc1 in AM 4947 (Figure 20C), suggest that the pc1 may also have undergone a finite number of replacement generations before the locus became dormant. This condition of the PC1 becoming dormant is the same as that described by Abdala *et al.* (2013) for *Thrinaxodon*.

In contrast, *Galesaurus* showed evidence for the continued replacement of PC1, in the largest specimen (Figure 33B). *Galesaurus* also exhibited an increase in the number of teeth in the maxillary and mandibular postcanine series through ontogeny (Figure 38and Table 14). However, it must be noted that there is a decrease in the number of postcanines in the maxilla at the transition from subadult to adult (Figure 39A), and a decrease in the number of mandibular postcanines in the largest (BSL > 110 mm) adults (Figure 39B). Similarly,

Cynosaurus also showed a tendency to increase the length of the postcanine series (Figure 23 and Table 9), whereas *Thrinaxodon* maintained a similar number of postcanines in the maxilla and mandible through ontogeny (Figure 38). As such, it is interpreted that each of the three epicynodont taxa show a replacement pattern that is derived from the same common ancestor, but with slightly different modifications.

7.4 Trends in replacement patterns in Synapsida

This section follows replacement pattern trends observed in the four taxa studied (two therocephalians and two cynodonts). Due to differences in the degree of variation in the different tooth types, replacement patterns in the incisors, canines, and postcanines are addressed separately.

7.4.1 Incisors

The incisors of the sampled taxa showed little variation in the patterns of replacement, with alternating replacement reported in all four taxa. The greatest variation from the ancestral theriodont condition to the more derived cynodonts is a reduction in number of incisor teeth, as opposed to the manner in which they are replaced. It is thus apparent that an alternating pattern of replacement of both upper and lower incisors is retained through both ontogeny and phylogeny.

This is possibly because the incisors show the least specialisation: they are not enlarged like the canines, and the crown morphology is not highly ornate as is the situation in the postcanines. However, therapsid taxa that do show specialisation

of the incisors for food processing (e.g., tapinocephalid dinocephalians) also maintain an alternating pattern of replacement (Norton *et al.*, 2009). One difference between the dinocephalians and eutheriodonts included in this study is that the former show multiple replacement teeth associated with each locus, whereas the eutheriodonts have only a single replacement associated with each locus, at any given developmental stage.

7.4.2 Canines

The ancestral condition of two maxillary caniniforms is present in sphenacodonts, as well as the basal therapsid *Raranimus dashankouensis* (Liu *et al.*, 2009). Additionally, *Tetraceratops insignis* is of interest, as its relationship to the pelycosaurs and therapsids is quite contentious. First described as a pelycosaur by Matthew (1908), the specimen has been considered to fall within the crown-clade Therapsida by Laurin and Reisz (1990, 1996) and Amson and Laurin (2011), whereas Conrad and Sidor (2001) and Liu *et al.* (2009) consider it to be more "pelycosaurian" in nature.

Matthew (1908) described a single maxillary canine in *Tetraceratops*, although his figure (p. 183) depicts the crown of a second caniniform with a dashed line. In their reconstructions, Laurin and Reisz (1990: fig. 1a, b) removed the second caniniform in lateral view, and depicted a depression/diastema distal to the erupted functional canine in ventral view. Later, Laurin and Reisz (1996: fig. 3) showed a reconstructed caniniform erupting mesial to the preserved tooth in the lateral and ventral aspects.

The sample of Lycosuchidae (Chapter 3) showed that double maxillary canines (i.e., two functional tooth families) are prevalent in the taxon. As in "pelycosaurs" and gorgonopsians, there appears to have been "functional distichial replacement" between the two canine loci. Similar observations of the alternation of the functional canine being situated in the mesial and distal locus through ontogeny have been made for *Theriognathus* (e.g., BP/1/512 and BP/1/870, Norton, personal observation).

The replacement maxillary and mandibular canines in the two scanned specimens of Lycosuchidae are positioned at almost the same level as the functional tooth (this is especially evident in the mandibular canines of CGS C60 [Figure 8C, D]). Replacement maxillary canines in *Cynosaurus* (e.g., Figure 18A, B) and *Galesaurus* (e.g., Figure 25A, B) are positioned mesial to the functional canine, whereas the replacement mandibular canines in *Cynosaurus* (e.g., Figure 19C, D) and *Galesaurus* (e.g., Figure 25C, D) are positioned more distal in relation to the functional canine.

This change in relative positions of the replacement canine to the functional canine may be attributable to growth. As the mandible of the epicynodonts lengthened in an anteroposterior direction, so each subsequent replacement canine erupted 'further back' along the length of the jaw. This 'migration' of the canine locus was hypothesised by Osborn and Crompton (1973) for the mandibular canine in *Thrinaxodon*, and was also more recently proposed by Abdala *et al.* (2013) to have occurred in the maxillary canines of *Thrinaxodon*.

There is a wide gap in the phylogeny of the therocephalians sampled in this study (Figure 1), transitioning from the Lycosuchidae of the middle Permian (Chapter 3), to the derived, Middle Triassic therocephalian *Bauria cynops* (Chapter 4). There is no evidence of canine replacement in the specimens of *Bauria* included in the study. It is therefore suggested that the number of maxillary canine tooth families in *Bauria* has been reduced to one. This could be interpreted as convergence towards the derived cynodontian condition of a single maxillary canine tooth family. However, further study is needed in order to determine where in the therocephalian lineage this reduction may have occurred.

The two cynodont taxa included in this study are both representatives of basal cynodonts (Figure 2). Both *Cynosaurus* (Chapter 5) and *Galesaurus* (Chapter 6) show evidence for only a single maxillary canine family, as the replacement maxillary canine was always recorded erupting mesial to the functional tooth. This is the same as the pattern in modern mammals, the most important difference is that replacement takes place only once in mammals, whereas in the epicynodonts *Cynosaurus* and *Galesaurus* there is evidence for several replacement generations. However, for the first time, this study has revealed a cessation of replacement of the maxillary canines during ontogenetic growth, suggesting that a finite number of tooth generations (i.e., oligophyodonty) in these taxa had been established.

Hopson (1964: fig. 9) illustrated two maxillary canine loci in the specimen of *Thrinaxodon* (Olson's [1944] "Cynodont B") included in his study. The

arrangement of both a retained root of an old tooth and developing replacement mesial to the functional canine is the same as that observed by Abdala *et al.* (2013) in four of the five µCT-scanned specimens of *Thrinaxodon* included in their study. Such an arrangement was also observed for the subadults of *Cynosaurus* (BP/1/4469, left maxilla) and *Galesaurus* (RC 845, left maxilla; BP/1/4602, both maxillae). The largest µCT-scanned *Thrinaxodon* specimen of Abdala *et al.* (2013) (BP/1/5905), showed a replacement maxillary canine developing mesial to the functional canine, but with no signs of retained roots from a shed canine. In the largest specimen of *Cynosaurus* (AM 4947) the retained root is situated distal to the functional canine with no signs of a developing replacement.

Additionally, Abdala *et al.* (2013) recorded the distal eruption of the replacement maxillary canine in three small (BSL < 42 mm) specimens of *Thrinaxodon* (BP/1/1376, TM 1486, SAM-PK-K10016), as well as the continued replacement of the maxillary canine well into adulthood. No eruption of the replacement maxillary canine distal to the functional tooth was seen in any of the µCT-scanned specimens of *Cynosaurus* or *Galesaurus* (n = 14). Abdala *et al.* (2013) attributed this arrangement of old retained roots, and the developing replacement being situated mesial to the functional canine, to be due to distal migration of the replacement during the process of eruption. A similar hypothesis of migration of the mandibular canines in *Thrinaxodon* was proposed by Osborn and Crompton (1973).

Interestingly, LeBlanc *et al.* (2018) demonstrated differences in tooth attachment between *Thrinaxodon* and *Galesaurus*. *Thrinaxodon* shows a possible reversion to the ancestral condition of mineralisation of the periodontal ligament and delayed ankylosis, whereas *Galesaurus* has the mammalian condition of permanent gomphosis. It has also been demonstrated that *Thrinaxodon* attained sexual maturity at a smaller body size, relative to that of *Galesaurus* (Botha-Brink *et al.*, 2016). Thus, *Thrinaxodon* may have attained adulthood while still exhibiting juvenile characters relating to the mode of tooth replacement (e.g., continued replacement of maxillary canines through ontogeny). In contrast, the retention of tooth ankylosis in *Thrinaxodon* may represent a reversal to the ancestral condition. Such a reversal may also have manifested as the retention of two maxillary canine tooth families in small specimens of *Thrinaxodon* (BSL ~30 mm), with the distal locus ceasing to produce replacement teeth at a BSL ≥ 42 mm. This hypothesis of the transition from two maxillary canines in juveniles to a single maxillary canine in subadults and adults remains to be tested. This could be accomplished by using μCT to re-examine the very small (BSL < 40 mm) specimens of *Thrinaxodon* previously studied by Gow (1985b).

Finally, the most derived condition appears to be that found in *Bauria*. A single canine tooth family is present, and shows no signs of replacement through the ontogenetic sequence studied. This may also be linked to the transition from a carnivorous to omnivorous diet, meaning that the canines were not relied upon for a carnivorous lifestyle including prey capture. Furthermore, some therocephalian forms, such as *Ericiolacerta* seem to have reduced the reliance on canines even

further, resulting in the teeth being reduced in size, such that they are morphologically indistinguishable from the neighbouring incisor and postcanine dentition (Watson, 1931; Crompton, 1962).

The condition of distal replacement of the maxillary canine could also have been present in juveniles of other epicynodonts, but at present comparatively small specimens are not known (Table 17). The smallest known specimens of *Thrinaxodon* (BSL ~30 mm) are those that show the distal eruption of the maxillary canine. These specimens are approximately 31.25% the size of the largest known *Thrinaxodon* (BSL 96 mm), and 34.48% of the largest μCT-scanned specimen.

In comparison, the smallest *Cynosaurus* (BSL 49 mm) specimen is 40.16% of the size of the largest known specimen, and 55.68% of the largest specimen with canine replacement. Similarly, for *Galesaurus* the smallest specimen (BSL 62 mm) is 54.39% relative to the size of the largest specimen, and 70.45% of the largest specimen to show signs of replacement of the maxillary canine. These percentages suggest that *Thrinaxodon* continued to replace its canines to a much larger proportional size than either *Cynosaurus* or *Galesaurus*. Additionally, the smallest known specimens of *Thrinaxodon* are considerably smaller than the smallest known specimens of *Cynosaurus* and *Galesaurus*, and as such may represent an ontogenetic stage not currently represented in the *Cynosaurus* and *Galesaurus* samples. Building upon this idea of the hypothetical two maxillary canine tooth families in juvenile epicynodonts, there are two mechanisms to arrive

at the pattern of replacement in the sampled specimens (Figure 41). A simple reduction in the number of replacements to one is all that would be required to move from this hypothetical condition to the true state of diphyodonty present in most modern mammals.

Amongst Eutheriodontia, the maxillary canines show more variation with regard to replacement patterns than the mandibular canines, likely as a result of the loss of one of the maxillary canine tooth families. Interestingly there are no known accounts of two mandibular caniniforms being present in the synapsid lineage (Kermack, 1956).

This study highlights a possible phylogenetic trend from two maxillary canine tooth families in sphenacodont pelycosaurs, towards true mammalian diphyodonty of the maxillary canine (i.e., one tooth locus, with a single replacement generation) (Figure 41). Two intermediate stages in this trend are represented by the basal Theriodontia (Figure 41B), and the smallest individuals (BSL < 30 mm) of *Thrinaxodon* (Figure 41C). The transition from two maxillary canine families in juvenile *Thrinaxodon*, to a single tooth family in adults has been previously proposed by Gow (1985b).

It is possible that in other epicynodonts the second canine tooth family (present in Lycosuchidae) could be represented in specimens smaller than those preserved, or that it was only present in embryos. Similar conditions occur within certain mammal lineages, such as Rodentia, Pinnipedia and Monodontidae, where only a

single tooth generation is present. In the northern harbour seal and common seal, the deciduous dentition is exfoliated into the surrounding amniotic fluid *in utero* (Kubota and Togawa, 1970; Kubota *et al.*, 2000; Meyer and Matzke, 2004).

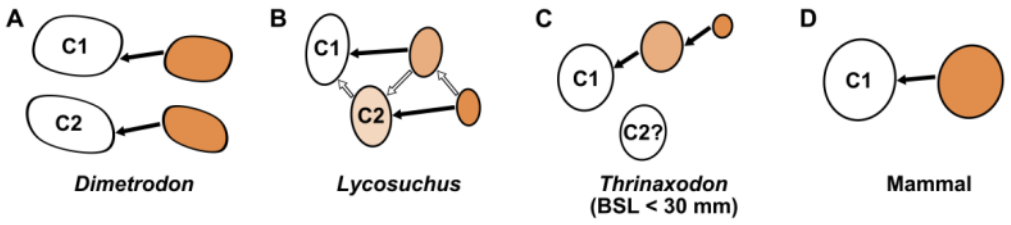

Figure 41. Hypothetical model for the derivation of mammalian diphyodonty in the maxillary canines from the polyphyodont condition of basal synapsids. A, *Dimetrodon*: two tooth families that are replaced simultaneously by multiple replacement generations; B, basal theriodonts: two tooth families, replaced independently by multiple generations, such that the functional canine alternates between the mesial and distal canine locus; C, juvenile *Thrinaxodon*: two tooth families, with the distal canine locus lost through ontogeny and the mesial canine replaced multiple times; D, crown Mammalia: a single tooth family replaced once. Abbreviations: BSL, basal skull length; C1, mesial maxillary canine; C2, distal maxillary canine. Replacement teeth are shown in orange, with darker tones representing younger generations (B and C). Black arrows indicate tooth replacement by members of the same canine family; white arrows indicate the "functional distichial replacement" of the maxillary canines in Lycosuchidae, such that the functional tooth alternated between the mesial (C1) and distal (C2) locus. Not to scale.

There are two possible mechanisms to achieve the condition of diphyodonty in the maxillary canines of crown Mammalia, from the condition of oligophyodonty in the canines in the epicynodonts. These entail either: (1) the maintenance of two

canine tooth families with no replacement, or (2) the loss of a maxillary canine tooth family, with the number of replacements reduced to a single generation. Scenario 1 would mean that the replacement tooth is not of the same tooth family as the functional tooth, whereas in the second scenario, both teeth are of the same family.

7.4.3 Postcanines

It appears that in the majority of basal eutheriodonts, postcanine replacement occurred throughout the animal's life. Evidence for this is the presence of postcanine replacement in the largest, and therefore presumably adult, specimens of Lycosuchidae, *Cynosaurus*, and *Galesaurus*. Concerning replacement patterns, the postcanine series showed the most variation between the taxa studied. It makes sense that the group of teeth that show the most specialisations with regard to crown morphology, also exhibit the most variation in replacement patterns. However, it is possible to derive the mammalian condition of diphyodonty from the polyphyodont replacement of the basal eutheriodonts, via sequential replacement seen in the gomphodont cynodonts and possibly the derived Triassic therocephalian *Bauria* (Chapter 4). It could even be argued that the pattern of diphyodonty is merely the reduction of sequential replacement from several replacement waves to only two.

There is a phylogenetic trend towards a reduction in the number of replacement waves present in the postcanine series. This trend is for modification of the functional distichial replacement pattern of the postcanines in basal vertebrates

(Figure 42A), to an alternating replacement of replacement (i.e., each tooth replaced by a member of its own tooth family) (Figure 42B), and finally towards the sequential addition of teeth to the distal region of postcanine series. Sequential replacement of the postcanines is present in derived non-mammalian cynodonts (Figure 42C) and crown Mammalia (Figure 42D). This final state can be achieved with the number of replacement waves reduced to two, with the eruption of the second wave delayed until adulthood/maturity of the individual. In this manner, the distal-most teeth of the first wave would erupt at a later ontogenetic stage, and due to either the advanced age of the animal, and/or the hypothesised slowed development of replacement teeth of the second wave, the teeth of the distal-most teeth of the postcanine series are never replaced (i.e., are analogous to true molars).

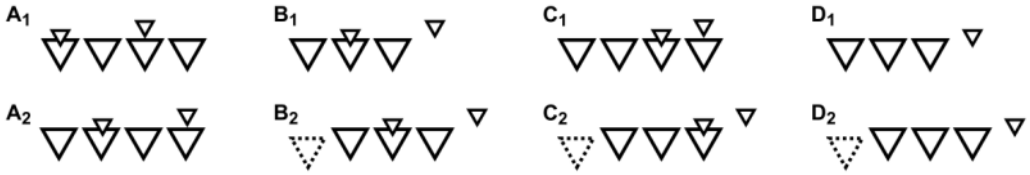

Figure 42. Comparison of replacement patterns of the postcanines in Amniota. A, basal amniote replacement pattern; B, alternating replacement present in the Epicynodontia (e.g., *Cynosaurus* and *Thrinaxodon*); C, sequential replacement 1; D, sequential replacement 2: where the distal-most teeth of the series have no precursors (e.g., Tritylodontidae and crown Mammalia). Small triangles represent replacement teeth, large triangles represent functional teeth, and dashed triangles represent exfoliated teeth. Adapted from Abdala *et al.* (2013: fig. 16). Not to scale.

7.5 Development of the mammalian condition of tooth replacement

7.5.1 Incisors

As demonstrated in the sample of two therocephalian and two cynodont taxa studied, and from the discussion above, there is little variation in replacement pattern of the incisors in the synapsid lineage. The biggest change from the therocephalian condition to that of true Mammalia is not related to replacement pattern, but rather the reduction in the number of incisor teeth.

7.5.2 Canines

It is apparent that the ancestral condition for the basal Theriodontia is to have two maxillary canines. In the Therocephalia the phylogenetic change from having two maxillary canine families, to a single family happens somewhere between Lycosuchidae (Chapter 3) and *Bauria* (Chapter 4) (Figure 1). Given that the replacement pattern in the epicynodonts could approximate this intermediate therocephalian condition, a model showing the transition from two canines to a single canine is proposed (Figure 41).

What remains to be established in the mammalian condition is whether the replacement canine is a member of the same tooth family as the functional tooth (i.e., one canine locus is lost), or if the functional and replacement canines are of different families (i.e., the functional canine represents the distal locus [C2], and the replacement the mesial locus [C1]).

7.5.3 Postcanines

Replacement of the postcanines likely took place throughout the animal's life in the majority of basal theriodonts. The findings of Abdala *et al.* (2013) for postcanine replacement in *Thrinaxodon*, are similar to those observed for *Cynosaurus*. That is, the mesial-most elements of the series ceased replacement as the canine alveolus expanded and moved distally to occupy the space that previously held the PC1. For *Cynosaurus* (Chapter 5), it is estimated that the first postcanine was replaced at least twice before the locus was invaded by the canine. With the loss of the mesial-most position, an additional locus was added to the distal margin of the postcanine series, so that the number of teeth in the postcanine series remained relatively consistent through ontogeny.

Despite the reduction in replacement activity in *Bauria*, replacement was evident in the middle, and distal-most loci of the mandibular series (Chapter 4). This pattern closely matches that of sequential addition described for many gomphodont cynodonts. In this type of pattern, the mesial teeth are replaced once, whereas the distal-most teeth are not replaced at all. This resembles the hemidiphyodont pattern of tooth replacement in most modern mammals, where the premolars (= mesial-most postcanines) are replaced once, and the true molars (= distal postcanines) are added sequentially, and are not replaced at all. This apparent convergence in the tooth replacement patterns of *Bauria* towards that observed in gomphodont cynodonts (and to an extent mammals) are possibly an adaptation towards a predominantly herbivorous lifestyle.

7.6 Conclusion

This study has shown that there is a greater variability amongst the Eutheriodontia with regard to tooth replacement patterns (particularly of canine and postcanine dentition) than previously recognised. This is especially evident in the three closely related epicynodont taxa which have received scrutiny. *Thrinaxodon* (Abdala *et al.*, 2013), *Cynosaurus* (Chapter 5), and *Galesaurus* (Chapter 6) each show a different pattern of alternating replacement of the postcanine dentition. The pattern observed in *Thrinaxodon* and *Cynosaurus* is more similar to each other than to *Galesaurus*. In contrast, *Cynosaurus* and *Galesaurus* manifested cessation of canine replacement with attainment of skeletal maturity, which was not evident in *Thrinaxodon* (Abdala *et al.*, 2013). Of particular interest is the apparent reduction of replacement activity for all tooth types in *Bauria*. This is likely due to a change from a carnivorous to herbivorous diet, requiring a precise tooth-on-tooth occlusion of the postcanine dentition during mastication. This is apparently convergent with the condition of sequential replacement of the traversodontid cynodonts.

7.7 Problems encountered in the computed tomography analyses

7.7.1 Low contrast due to Metallic Inclusions

High metal content in the surrounding rock matrix of fossils recovered from the Karoo Supergroup causes a resultant loss of contrast between the structures of the fossil and surrounding matrix. This was particularly evident in scans of *Lycosuchus vanderrieti* (US D173), which manifested many metallic inclusions in the anterior dentition (Figure 7 and Figure 43).

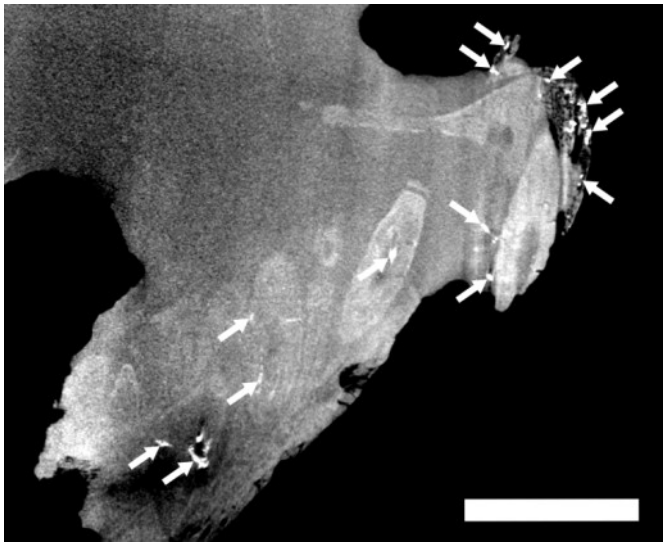

Figure 43. Virtual sagittal section through the snout of *Lycosuchus vanderrieti* (US D173).
Arrows indicate possible metallic inclusions represented by bright spots in the upper and lower dentition. Scale bar equals 20 mm.

Neutron computed tomography (NCT) scanning has been proposed as an alternative to high-resolution X-ray scanning when scanning specimens that contain a large amount of metallic material (de Beer *et al.*, 2008; Sutton, 2008; de Beer, 2017). The use of neutrons as opposed to electrons also has shortcomings. The two most relevant to heritage studies are:

(1) Irradiation of the specimen due to high-intensity neutron bombardment. After scanning, specimens need to be stored in a special vault for the radiation to decay to an acceptable background level. Depending on the size of the specimen and exposure time, the decay time could range from mere hours to weeks, or even years after NCT study (Sutton, 2008; de Beer, 2017).

(2) Change of the atomic weight of the isotopes. This would result in isotopic dating of the specimen giving incorrect results.

It has been demonstrated in a previous study by du Plessis (2010) that NCT often does not provide suitable scan results for the study of internal structures. Of the 35 cynodont specimens scanned using NCT, only three (8.57%) had results that could be considered successful. Similarly, of the 11 specimens subjected to high-energy X-ray computed tomography (HEXCT), only one result (9.09%) was successful (du Plessis, 2010: appendix table 2). Four specimens of *Galesaurus* μCT-scanned for the present study (RC 845, NMQR 135, SAM-PK-10468, and NMQR 860) were included in the study of du Plessis (2010), and scanned using NCT. Of these, usable images were only obtained for RC 845 (see du Plessis, 2010: appendix table 2). In comparison, the μCT scans for all four specimens were usable.

7.8 Future Directions

7.8.1 Increasing Sample Sizes

In addition to the points raised above, the sampled taxa already studied could be expanded to increase specimens at the extremes of the size range of that already subjected to μCT-scanning (see Table 16 and Table 17).

Thrinaxodon would be the best candidate as there are four specimens with a BSL less than that of the smallest scanned specimen (BP/1/5372, BSL 37 mm), as well as five specimens larger than the largest scanned specimen (BP/1/5905, BSL 87

mm) included in the study of Abdala *et al.* (2013). Additionally, the scanning of smaller specimens would allow for the determination of the presence of a second maxillary canine tooth family in the smallest preserved developmental stages of *Thrinaxodon*. Larger specimens should also be scanned to determine whether *Thrinaxodon* ceased to replace the maxillary canines upon reaching adulthood, as reported in *Cynosaurus* (Chapter 5) and *Galesaurus* (Chapter 6).

It is also necessary to increase the number of sampled specimens, especially for the Lycosuchidae for which < 5% of the total BSL range was included in the study (Table 16). This would require further preparation of specimens of the same species but different sizes to cover an ontogenetic sequence. This is especially important given the amount of variation evident in the patterns of replacement of the postcanine dentition observed in the Epicynodontia.

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