A proposed terminology of the dentition of gomphodont cynodonts and dental morphology in Diademodontidae and Trirachodontidae (#25716)

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A proposed terminology of the dentition of gomphodont cynodonts and dental morphology in Diademodontidae and Trirachodontidae

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Gomphodont cynodonts were close relatives of mammals and are one of the two Mesozoic lineages of cynodont therapsids that became extinct at the end of the Triassic. Gomphodonts were omnivorous to herbivorous animals characterized by labiolingually expanded postcanines, which allowed tooth-to-tooth occlusion. The morphology of the upper and lower postcanines presents important means of distinguishing among major lineages within Gomphodontia, i.e., Diademodontidae, Trirachodontidae, and Traversodontidae, but the dentition of most Diademodontidae and Trirachodontidae remain poorly documented. Here we present a comprehensive description of the dentition of each diademodontid and trirachodontid taxon, as well as detailed illustrations of each dental unit, based on firsthand examination of material and 3d reconstructions of postcanine teeth. We also provide a list of autapomorphic dental features for members of both clades. Based on the dentition morphology, *Trirachodon berryi* and '*Trirachodon kannemeyeri*', considered as separate taxa by some authors, likely represent different ontogenetic stage of the same species. Likewise, *Sinognathus* and *Beishanodon*, thought to belong to non-cynognathian cynodonts by some authors, are confidently referred to gomphodonts. A standardized list of terms and abbreviations for each incisor, canine and postcanine anatomical entity is finally proposed, with the goal of facilitating future descriptions of the gomphodont dentition.

A proposed terminology of the dentition of gomphodont cynodonts and dental morphology in Diademodontidae and Trirachodontidae.

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Abstract

Gomphodont cynodonts were close relatives of mammals and are one of the two Mesozoic lineages of cynodont therapsids that became extinct at the end of the Triassic. Gomphodonts were omnivorous to herbivorous animals characterized by labiolingually expanded postcanines, which allowed tooth-to-tooth occlusion. The morphology of the upper and lower postcanines presents important means of distinguishing among major lineages within Gomphodontia, i.e., Diademodontidae, Trirachodontidae, and Traversodontidae, but the dentition of most Diademodontidae and Trirachodontidae remain poorly documented. Here we present a comprehensive description of the dentition of each diademodontid and trirachodontid taxon, as well as detailed illustrations of each dental unit, based on firsthand examination of material and 3d reconstructions of postcanine teeth. We also provide a list of autapomorphic dental features for members of both clades. Based on the ~~dentition~~ morphology, *Trirachodon berryi* and '*Trirachodon kannemeyeri*', considered as separate taxa by some authors, likely represent different ontogenetic stage of the same species. Likewise, *Sinognathus* and *Beishanodon*, thought to belong to non-cynognathian cynodonts by some authors, are confidently referred to

~~gomphodonts~~. A standardized list of terms and abbreviations for each incisor, canine and postcanine anatomical entity is finally proposed, with the goal of facilitating future descriptions of the gomphodont dentition.

Introduction

Gomphodont cynodonts form a radiation of Triassic therapsids known from the Late Olenekian to the Norian on all continents but Oceania (e.g., Battail, 1983; Abdala & Ribeiro, 2003; Hopson, 2005, 2014; Abdala & Gaetano, 2018; Figure 1). Members of this clade were small to medium-sized (from approximately 30 cm to 2 m in body length), quadrupedal animals characterized by labiolingual expansion of the upper postcanines (gomphodont morphology) allowing crown-to-crown occlusion (e.g., Seeley, 1895, 1908; Crompton, 1972; Reisz & Sues, 2000; Abdala, Neveling & Welman, 2006; Hopson, 2014). Such morphology of the postcanines suggests that gomphodonts were omnivorous or possibly exclusively herbivorous animals, feeding on hard plant material (Reisz & Sues, 2000; Abdala, Neveling & Welman, 2006; Liu & Abdala, 2014). Three clades, mainly differentiated by the postcanine morphology, are currently recognized among Gomphodontia, the Diademodontidae, Trirachodontidae and Traversodontidae (Hopson, 2005; Liu & Abdala, 2014; Hendrickx, Abdala & Choiniere, 2016).

Diademodontid~~s~~ is an early diverging lineage of gomphodonts with low taxonomic diversity at the generic and species level (Figure 1). Two valid taxa (i.e., *Diademodon* and *Titanogomphodon*) known from the Olenekian and Anisian of southern and East Africa, Argentina and possibly Antarctica currently compose this group (Keyser, 1973; Hammer, 1995; Martinelli, Fuente & Abdala, 2009). A possible lazarus diademodontid from the Lower Jurassic of South Africa (Bordy et al., 2017; Abdala & Gaetano, 2018) was described by Abdala (2007) but most likely represents a non-gomphodont tetrapod (Abdala pers. obs.). The postcanine dentition of diademodontids is heterogeneous and separated into conical, gomphodont and sectorial teeth, which represents the most primitive condition of dental morphology among Gomphodontia (Hopson, 2005; Hendrickx, Abdala & Choiniere, 2016; Abdala & Gaetano, 2018). The upper and lower gomphodont postcanines of diademodontids display several ridges and accessory cusps whose position varies on the crown and along the tooth row. The distalmost part of the diademodontid tooth row is also characterized by a transitional postcanine and a minimum of three sectorial teeth gradually changing from a gomphodont morphology to a more labiolingually compressed carnassial type of crown (Crompton, 1972; Hopson, 2005).

Trirachodontids are represented by five valid taxa restricted to the Olenekian and Anisian of Southern Africa and Asia (Abdala, Neveling & Welman, 2006; Gao et al., 2010; Figure 1). Trirachodontids were relatively small animals (i.e., <1m), and some had a burrowing/fossorial lifestyle (Groenewald, Welman & Maceachern, 2001; Smith & Swart, 2002). The postcanine tooth row of trirachodontids encompasses a lower number of sectorial teeth than that of diademodontids, which occur immediately distal to the gomphodont postcanines (Hopson, 2005). The gomphodont postcanine of trirachodontids shows a clearly defined centrally positioned transverse crest made of labial, central and lingual cusps and ringed by mesial and distal cingula on the rim of the tooth (Abdala, Neveling & Welman, 2006).

Similar to other cynodonts, the dentition of diademodontids and trirachodontids is the most diagnostic element of the skeleton (Liu & Sues, 2010). Because of their high resistance due to greater density and lower permeability (Martin, 1999), teeth are also the most common material in Gomphodontia, with dental elements known in every gomphodont taxa hitherto described (C.H. pers. observ.). Given the postcanine diversity and complexity among gomphodonts, the dentition of these cynodonts typically receives particular attention and is often relatively well-described. Nonetheless, thorough description of the dental material is often provided for gomphodont postcanines, whereas information as well as detailed figures on the incisor, canine and conical and sectorial postcanines are omitted in most gomphodont taxa (C.H. pers. observ.). In addition, we have noticed inconsistencies in the terminology and abbreviations used in discussions of the dental gomphodont anatomy, with several authors providing different terms for the same dental structure.

This paper aims to: i) propose a standardized list of terms and abbreviations for each incisor, canine and postcanine anatomical entity, with the goal of facilitating future descriptions of the gomphodont dentition; ii) provide a comprehensive description and detailed illustrations of the dentition of all known diademodontid and trirachodontid taxa. Tooth replacement pattern and postcanine occlusion, which were treated in detail by several authors for Diademodontidae and Trirachodontidae (e.g., Crompton, 1955, 1972; Fourie, 1963; Ziegler, 1969; Hopson, 1971; Osborn, 1974; Sidor & Hopson, 2018), is beyond the scope of this paper. Likewise, a comprehensive description of the dentition of Traversodontidae will form the base of another contribution. Finally, the evolution of the gomphodont dentition will be explored in a third contribution based on the cladistic analysis performed on a dentition-based datamatrix encompassing all gomphodont cynodonts.

Institutional abbreviations: AM, Albany Museum, Grahamstown, South Africa; **AMNH**, American Museum of Natural History, New York City, New York, USA; **BP**, Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; **BSP**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CGP**, Council for Geosciences, Pretoria, South Africa; **GSN**, Geological Survey of Namibia, Windhoek, Namibia; **IVPP**, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MB**, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; **MHNSR–Pv**, Museo de Historia Natural de San Rafael, Mendoza, Argentina; **NHCC**, National Heritage Conservation Commission, Lusaka, Zambia; **NHMUK**, Natural History Museum, London, UK; **NMQR**, National Museum, Bloemfontein, South Africa; **NMT**, National Museum of Tanzania, Dar es Salaam, Tanzania; **OUMNH TSK**, Oxford University Museum of Natural History, T.S. Kemp Collection, University of Oxford, Oxford, UK (now deposited at the Natural History Museum of London and waiting for a specimen number to be provided); **PKUP**, Peking University Paleontological Collections, Beijing; **SAM-PK**, Iziko, the South African Museum, Cape Town, South Africa; **UMZC**, University Museum of Zoology, Cambridge, UK.

Material and methods

Dental features were investigated on incisors, canines and gomphodont and sectorial postcanines preserved within the upper and lower jaws as well as isolated teeth of non-traversodontid gomphodonts. The dentition of six taxa deposited in twelve scientific collections from South Africa, Namibia, Argentina, Germany, the United Kingdom and China were examined first-hand (Table 1). Denticles, crown ornamentations and enamel texture were observed with a digital microscope AM411T-Dino-Lite Pro. Only *Beishanodon youngi* could not be examined first hand, and we relied on Gao et al.'s (2010) publication in which the dentition was comprehensively described and illustrated. 3D-models of teeth were generated for lower and upper postcanines in all taxa but *Sinognathus* and *Beishanodon* (Table 1) through photogrammetric techniques using Agisoft Photoscan Standard (Version 1.3.4); Software; 2017; Retrieved from http://www.agisoft.com/downloads/installer/). A total twenty 3d-models are deposited and freely downloadable in the MorphoBrowser database (http://pantodon.science.helsinki.fi/morphobrowser/). The dental morphology of *Trirachodon berryi* was also investigated based on CT-scan data from the specimen AM 461 (holotype of '*Trirachodon kannemeyeri*').

Neotrirachodon expectatus (Tatarinov, 2002) and *Redondagnathus hunti* (Lucas et al., 1999; Spielmann & Lucas, 2012), classified as trirachodontids by their authors, were not included in this study as they probably do not represent gomphodont cynodonts. *Neotrirachodon* likely belongs to a bauriid therocephalian (Battail & Surkov, 2000; Abdala, Neveling & Welman, 2006; Abdala & Smith, 2009; Gao et al., 2010; Sues & Hopson, 2010) whereas *Redondagnathus*' dental material display several features absent in Trirachodontidae, namely: a central cusp strongly mesially/distally deflected from the labial and lingual cusps and much higher than the two latter cusps, no valley-like concavities separating the central cusp from the labial and lingual cusps, a cingulum significantly apically higher than the other one, apically pointed cingular cuspules varying dramatically in size along the cingulum, presence of a basally inclined spalling surface extending below the cingulum as well as an important protuberance on the basal part of the root (Sidor & Hopson, 2018); C.H. pers. observ.). We, therefore, agree with (Sidor & Hopson, 2018) and consider that the teeth of *Redondagnathus* do not share enough dental features with trirachodontids and gomphodonts to be confidently referred to these clades. Likewise, CGP JSM 100, interpreted as a possible juvenile *Trirachodon* by Hopson (2005), was not considered in this study as the specimen likely represents a new taxon of basal traversodontid (C.H. and F.A. pers. observ.). The dentition and phylogenetic position of this specimen will, however, be thoroughly discussed in the two following contributions on the evolution of the dentition in gomphodonts.

Proposed dental terminology

Dental positional and morphometric nomenclature follows Smith & Dodson (2003) and Hendrickx, Mateus & Araújo (2015), with the following abbreviations being used in this study:

Crown Base Length (CBL)—Maximum mesiodistal extent of the crown base at the level of the cervix (i.e., the transition between the crown and the root and forming the basal extension of the enamel layer; Smith, Vann & Dodson, 2005; Hendrickx, Mateus & Araújo, 2015).

Crown Base Width (CBW)—Labiolingual extent of the crown base at mid-length, perpendicular to the CBL, and at the level of the cervix (Smith, Vann & Dodson, 2005).

Crown Height (CH)—Maximum apicobasal extent of the distal margin of the crown (Hendrickx, Mateus & Araújo, 2015).

Crown Base Ratio (CBR)—Ratio expressing the labiolingual elongation of the base crown and corresponding to the quotient of CBW by CBL (CBR = CBW ÷ CBL; Smith, Vann & Dodson, 2005).

Denticle Size Density Index (DSDI)—Ratio expressing the size difference between mesial and distal denticles (Rauhut & Werner, 1995) and corresponding to the quotient of the number of denticles per five millimeters on the mesial carina at mid-crown (MC) by the number of denticles per five millimeters on the distal carina (DC) at mid-crown (DSDI = MC ÷ DC).

Crown microstructure nomenclature uses the terminology proposed by Sander (1997a, 1999). The anatomical nomenclature used to describe and annotate the external tooth morphology (Figure 2) follows the terminology and abbreviations proposed below. For a consistent terminology, the positional terms mesial, distal, labial and lingual, proposed as standard terms by Smith & Dodson (2003), were favored, with length, width and height referring to the dimension of an anatomical entity in the mesiodistal, labiolingual and apicobasal directions, respectively.

Accessory cusp (ac)—Minor pointed or rounded projection of dentine covered with enamel on the mesial/distal ridge (i.e., the labiomesial (lamc), labiodistal (ladc), linguomesial (limc) and linguodistal (lidc) accessory cusps; Figure 2C-G) and/or transverse crest (i.e., the central accessory cusp (cac); Figure 2C) of a gomphodont postcanine as well as on the carina (i.e., the mesial (mac) and distal (dac) accessory cusps; Figure 2I) of a sectorial postcanine.

Basin (ba)—Deep concavity located on the occlusal surface of a gomphodont postcanine, on the mesial and/or distal surfaces of the crown (i.e., the mesial (mb) and distal (mb) basins, respectively; Figure 2C, D, E, G), and receiving the crown of the opposite jaw during occlusion.

Canine (c)—Maxillary and dentary tooth located between the distalmost incisor and the mesialmost postcanine and specialized for cutting and/or piercing (Figure 2A, B). It is usually the largest tooth of the series.

Carina (ca)—A sharp, narrow, and well-delimited ridge or keel-shaped structure running apicobasally on the crown and, in some case, on the root base, and typically making the cutting edge of the tooth (Hendrickx, Mateus & Araújo, 2015; Figure 2A). Incisors and canines of gomphodont cynodonts often have serrated mesial and distal carinae, whereas the carinae of sectorial teeth bear accessory cusps and/or minute denticles.

Central accessory cusp (cac)—Minor pointed or rounded projection labial and/or lingual to the central cusp on the transverse crest of upper gomphodont postcanine (Figure 2C).

Central cusp (cc)—Main centrally positioned projection of dentine covered with enamel on the transverse crest of the gomphodont postcanine (Figure 2C).

Central ridge (cri)—Labiolingually oriented crest centrally positioned on the mesial basin of a gomphodont postcanine (Figure 2E).

Centrolabial ridge (clar)—Labiolingually oriented crest-like structure running on the labial surface of the central cusp, following the edge of the transverse crest, and connected to the labiocentral ridge of the labial cusp (Figure 2C).

Centrolingual ridge (clir)—Labiolingually oriented crest-like structure running on the lingual surface of the central cusp, following the edge of the transverse crest, and connected to the linguocentral ridge of the lingual cusp (Figure 2F).

Cingular cuspule (cic)—Small accessory cusp on a cingulum of a gomphodont or sectorial postcanine (Figure 2D).

Cingulum (ci)—Bulge or shelf made of a succession of cingular cuspules on the rim of the occlusal surface of the gomphodont postcanine and on the basolingual or basolabial side of a sectorial tooth (Figure 2G).

Concave surface (cos)—Apicobasally elongated concavity adjacent to the mesial and/or distal carinae on the labial and/or lingual surfaces of the crown in incisors and canines (Figure 2B). The presence of concave surfaces on the lingual surface of the incisors and canines results in the salinon-shaped cross-section outlines of the crown, i.e., an outline with both mesial and distal carinae facing linguomesially and linguodistally, respectively, subsymmetrical mesial and distal crown sides, a convex labial margin, and a biconcave lingual margin (Hendrickx, Mateus & Araújo (2015), figure 5R).

Conical postcanine (cpc)—Conidont tooth located in the mesialmost part of the postcanine tooth row (Figure 2A, B). While *Diademodon* bears three or more conical postcanines, trirachodontids and some traversodontids (e.g., *Andescynodon*, *Massetognathus*, *Boreogomphodon*) have fewer than three conical teeth, and the most derived traversodontids do not possess conical postcanine at all.

Crown (co)—Portion of the tooth covered with enamel, typically situated above the gum and protruding into the mouth (Hendrickx, Mateus & Araújo, 2015; Figure 2I).

Cusp (cu)—Pointed or rounded projection of dentine covered with enamel on the occlusal surface of a gomphodont postcanine or on the carina of sectorial teeth (Figure 2G).

Denticle (de)—An elaborate type of serration being formed by a projection of dentine covered with enamel along the carina of incisors, canines and sectorial postcanines (modified from Hendrickx, Mateus & Araújo (2015); Figure 2J).

Diastema (dia)—Space separating the last upper incisor from the canine and the upper and/or lower canine from the first postcanine (Figure 2B).

Distal accessory cusp (dac)—Minor pointed or rounded projection of a sectorial postcanine, distal to the main cusp (Figure 2I).

Distal accessory ridge (dar)—Crest-like structure on the distal surface of the transverse crest, perpendicular, diagonally oriented or even parallel from the latter (Figure 2H).

Distal basin (db)—Main concavity distal to the transverse crest on the occlusal surface of a postcanine (Figure 2C, D, G, H). The distal basin, which is typically delimited by the distal ridge/cingulum distally, is also known as the 'posterior basin' (e.g., Hopson, 2005; Liu & Sues, 2010; Sues & Hopson, 2010).

Distal cingular cuspule (dcc)—Minor pointed or rounded projection on the distal cingulum (dci) of a gomphodont postcanine (Figure 2G).

Distal cingulum (dci)—Labiolingually oriented row of distal cingular cuspules (dcc) distal to the transverse crest and typically delimiting the distal rim of the occlusal surface of a gomphodont postcanine (Figure 2C, D, F). The distal cingulum is also known as the 'posterior cingulum' (e.g., Hopson, 2005; Liu & Sues, 2010; Sues & Hopson, 2010).

Distal ridge (dri)—Labiolingually oriented crest-like structure distal to the transverse crest and delimiting the distal rim of the occlusal surface of a gomphodont postcanine (Figure 2H).

Enamel texture (ent)—Pattern of sculpturing on the crown surface at a sub-millimeter scale (Hendrickx, Mateus & Araújo, 2015; Figure 2K). The enamel surface texture of incisors, canines, and postcanines of gomphodont cynodonts shows different patterns (Hendrickx, Mateus & Araújo (2015), figure 6). A smooth enamel texture is here defined as the absence of enamel texture so that the crown surface does not show any irregularity. A non-oriented enamel texture with no pattern is referred as irregular. Finally, the enamel surface texture is called braided if the texture is oriented and made of alternating and interweaving grooves and short, moderately elongated or long sinuous ridges that are typically apicobasally oriented on the crown (Hendrickx, Mateus & Araújo, 2015; Figure 2K).

Gomphodont postcanine (gpc)—Oval, quadrangular, subrectangular or subtriangular tooth comprising most, if not all, the postcanine tooth row and allowing tooth-to-tooth occlusion (Figure 2A, B). Upper gomphodont postcanines are typically labiolingually expanded whereas lower gomphodont postcanines can be labiolingually expanded, quadrangular or mesiodistally expanded.

Incisor (i)—Premaxillary or dentary tooth mesial to the canine and specialized for cutting (Figure 2B).

Labial cingular cuspule (lacc)—Minor pointed or rounded projection on the labial cingulum of a gomphodont and/or sectorial postcanine (Figure 2C).

Labial cingulum (laci)—Mesiodistally oriented row of accessory cuspules on the labiobasal surface of a sectorial postcanine and/or delimiting the labial rim of the occlusal surface of a gomphodont postcanine (Figure 2C). The labial cingulum is also known as the 'external cingulum' (e.g., Flynn et al., 2000; Abdala & Ribeiro, 2003; Abdala & Sa-Teixeira, 2004; Hopson, 2005, 2014; Abdala, Neveling & Welman, 2006).

Labial cusp (lac)—Main labially positioned projection on the transverse crest of a gomphodont postcanine (Figure 2C-H).

Labial ridge (lar)—Labiolingually oriented and labially positioned crest-like structure delimiting the labial rim of the occlusal surface of a lower gomphodont postcanine in Traversodontidae (Figure 2D).

Labiocentral ridge (lacr)—Labiolingually oriented crest-like structure running on the lingual surface of the labial cusp, following the edge of the transverse crest, and connected to the centrolabial ridge of the central cusp (Figure 2F).

Labiodistal accessory cusp (ladc)—Minor pointed or rounded projection distal to the labial cusp and located on the labiodistal margin of the occlusal surface of a gomphodont postcanine (Figure 2C-D, F-H).

Labiodistal ridge (ladr)—Mesiodistally oriented crest-like structure running on the distal surface of the labial cusp and typically connected to the distal ridge/cingulum (Figure 2C, F).

Labiomesial accessory cusp (lamc)—Main pointed or rounded projection mesial to the labial cusp and located on the labiomesial margin of the occlusal surface of a gomphodont postcanine (Figure 2C).

Labiomesial ridge (lamr)—Mesiodistally oriented crest-like structure running on the mesial surface of the labial cusp and typically connected to the mesial ridge/cingulum (Figure 2C).

Lingual cingular cuspule (licc)—Minor pointed or rounded projection on the lingual cingulum of a sectorial postcanine (Figure 2I).

Lingual cingulum (lici)—Mesiodistally oriented row of cuspules on the basolingual surface of a sectorial postcanine and/or delimiting the lingual rim of the occlusal surface of a gomphodont postcanine (Figure 2I).

Lingual cusp (lic)—Main lingually positioned projection on the transverse crest of the postcanine (Figure 2C-H).

Linguocentral ridge (licr)—Labiolingually oriented crest-like structure running on the labial surface of the lingual cusp, following the edge of the transverse crest, and connected to the centrolingual ridge of the central cusp (Figure 2F).

Lingual ridge (lir)—Labiolingually oriented and lingually positioned crest-like structure delimiting the lingual rim of the occlusal surface of a gomphodont postcanine (Figure 2E).

Linguodistal accessory cusp (lidc)—Minor pointed or rounded projection distal to the lingual cusp and located on the linguodistal margin of the occlusal surface of a gomphodont postcanine (Figure 2C, F).

Linguodistal ridge (lidr)—Mesiodistally oriented crest-like structure running on the distal surface of the lingual cusp and typically connected to the distal ridge/cingulum (Figure 2C, F).

Linguomesial accessory cusp (limc)—Main pointed or rounded projection mesial to the lingual cusp and located on the linguomesial margin of the occlusal surface of a gomphodont postcanines (Figure 2C, H).

Linguomesial ridge (limr)—Mesiodistally oriented crest-like structure running on the mesial surface of the lingual cusp and typically connected to the mesial ridge/cingulum (Figure 2C).

Longitudinal ridge (lri)—Apicobasally high and mesiodistally short convexity on the labial and/or lingual surface of incisors and/or canines (modified from Hendrickx, Mateus & Araújo (2015); Figure 2B).

Main cusp (mc)—Major projection of dentine covered with enamel on the sectorial postcanine (Figure 2I). The main cusp can be denticulated on both their mesial and distal carinae.

Mesial accessory cusp (mac)—Minor pointed or rounded projection on the mesial carina of a sectorial postcanine, mesial to the main cusp (Figure 2I). If two or more mesial accessory cusps are present in some sectorial postcanines of *Cynognathus*, diademodontids, trirachodontids and some traversodontids (e.g., *Boreogomphodon*, *Plinthogomphodon*) bear a single mesial accessory cusps in some of their sectorial postcanines.

Mesial accessory ridge (mar)—Crest-like structure on the mesial surface of the transverse crest, perpendicular, diagonally-oriented or parallel to the latter (Figure 2H).

Mesial basin (mb)—Main concavity mesial to the transverse crest on the occlusal surface of a gomphodont postcanine (Figure 2C, E, H).

Mesial cingular cuspule (mcc)—Minor pointed or rounded projection on the mesial cingulum of a gomphodont postcanine (Figure 2C, H).

Mesial cingulum (mci)—Labiolingually oriented row of accessory cuspules mesial to the transverse crest and typically delimiting the mesial rim of the occlusal surface of a gomphodont postcanine (Figure 2C).

Mesial ridge (mri)—Labiolingually oriented crest-like structure mesial to the transverse crest and typically delimiting the mesial rim of the occlusal surface of a gomphodont postcanine (Figure 2C, E).

Paracanine fossa (pcf)—Deep concavity located on the palatal surface of the anterior portion of the snout and receiving the canine of the lower jaw during occlusion (Figure 2A).

Postcanine (pc)—Maxillary or dentary tooth positioned distal to the canine. Postcanines include conical, gomphodont and/or sectorial teeth, which can gradually change from one morphology to the other (Figure 2B).

Root (ro)—Portion of the tooth beneath the gum and embedded in an alveolus (modified from Hendrickx, Mateus & Araújo (2015); Figure 2I).

Sectorial postcanine (spc)—Blade-like tooth located in the distalmost part of the postcanine tooth row, distal to the gomphodont teeth and adapted for cutting in a shearing manner. Sectorial postcanines typically include a main cusp and often one or several accessory cusps mesial and/or distal to the main cusp (Figure 2A, B).

Serration (se)—A projection along a ridge or keel-like structure of a tooth, whether composed of enamel or by both enamel and dentine (modified from Brink & Reisz (2014); Figure 2J). While the carinae of incisors, canines and sectorial teeth often show distinct serrations composed of a core of dentine covered with a layer of enamel (i.e., denticles), the transverse crest as well as the mesial and distal ridges of gomphodont postcanines can bear minute serrations only visible with a microscope. These serrations should not be confused with the elaborate and well-delimited denticles of non-gomphodont postcanines as well as the triangular, hemi-spherical or sub-pyramidal cusps and cuspules present on the transverse crest and/or cingula of gomphodont and sectorial postcanines in some taxa.

Shouldering (sho)—Extension of the labiomesial margin of the upper postcanine forward, producing a 'shoulder-like' process over the preceding postcanine (modified from Romer (1967); Abdala and Ribeiro (2003), figure 10C, D).

Transitional postcanine (tpc)—Labiolingually expanded sectorial postcanine sharing an intermediated morphology between a gomphodont tooth and a labiolingually compressed blade shaped sectorial postcanine (Figure 2A). Transitional postcanines are typically formed by a distally recurved blade shape labial portion and a relatively flat lingual projection.

Transverse crest (tc)—Main labiolingually oriented ridge on the occlusal surface of the gomphodont postcanine and bearing the labial, lingual and often the central cusps (Figure 2C-E, H).

Transverse undulation (tun)—Band like enamel wrinkle extending along most of the incisor or canine length, typically from the mesial to distal carinae (modified from Hendrickx, Mateus & Araújo (2015); Figure 2B).

Results

Diademodontidae (Haughton, 1924)

***Diademodon tetragonus* (Seeley, 1894)**

Holotype: SAM-PK-571, two isolated canines (holotype of *Diademodon brachytiara*), an incomplete upper jaw, a small portion of mandible and two isolated upper postcanines.

Referred dental material: AM 438, 458 (holotype of *Gomphognathus kannemeyeri*), 3753 (holotype of *Octogomphus woodi*); AMNH R5518; BP/1/1195, 2522, 3511, 3639 (holotype of *Diademodon rhodesiensis*), 3754, 3756–3758, 3769, 3771–3773, 3776 (holotype of *Cragievarus kitchingi*), 4529, 4647, 4669, 4677; BSP 1934 VIII 14, 15, 16, 17 (holotype of *Gomphognathus grossarthi*), 18 (holotype of *Gomphognathus broomi*), 19 (holotype of *Gomphognathus haughtoni*), 20, 505; MB R1004; NHMUK R2574, R2575, R2576–7 (holotype of *Gomphognathus polyphagus*), R2578, R3303 (holotype of *Diademodon mastacus*), R3304 (holotype of *Diademodon browni*), R3305 (holotype of *Microgomphodon oligocynus*), R3308, R3581 (holotype of *Microgomphodon eumerus*); R3587, R3588 (referred to *Diademodon browni*), R3724, R3765 (holotype of *Diademodon entomophonus*), R4092, R9216; SAM-PK-3426, 4002, 5877 (*Cyclogomphodon platyrhinus*), 6216, 6218, 6219, ?11265, K175, K177, K180, K183,?K4660, ?K4661, K5223, K5266, K5716, K8971, K9968, K9969; MHNSR–Pv 357; GSN R321, R327, R335, RK3; UMCZ T.430, T.436 (holotype of *Diademodon laticeps*), T.438, T.441, T.445, T.454, T.828, T.971.

Occurrence: Burghersdorp, Aliwal North, Joe Gqabi District, Gariep Municipality, South Africa (type); Lady Frere, Chris Hani District, Emalahleni Municipality, South Africa; Grahamstown, Makana Municipality, Sarah Baartman District, Eastern Cape, South Africa; Etjo Mountain, Otjozondjupa Region, Namibia; Puesto Viejo farm house, 40 km southwest of San Rafael, Mendoza Province, Argentina.

Horizon: Subzones B–C of the *Cynognathus* AZ, Burgersdorp Formation, Karoo Basin; Omingonde Formation; Río Seco de la Quebrada Formation, Upper unit of the Puesto Viejo Group.

Age: Early to Late Anisian, Middle Triassic.

Dental formula: I4/3 : C1/1 : PC12-16/12-13 (CPC2-6 : GPC3-9 : TPC0-2 : SPC1-4).

Dental morphology: The dentition morphology, postcanine microstructure, dental replacement pattern and postcanine occlusion of *Diademodon tetragonus* are fairly well-known (Seeley, 1894, 1895, 1908, Watson, 1911, 1913; Broili & Schröder, 1934; Brink, 1955, 1963, Crompton, 1955, 1972; Fourie, 1963; Ziegler, 1969; Hopson, 1971; Osborn, 1974; Grine, 1977). Few of these studies provide, however, detailed information and illustrations on the dentition morphology and a thorough description of the anatomy of the incisors, canines and postcanines is here provided.

Incisors

The incisors of BSP 1934 VIII 14 appear to be salinon-shaped in cross-section at mid-crown and both mesial and distal carinae are serrated. The distal carina faces distally whereas the mesial carina is mesiolingually displaced and almost reaches the cervix (Figure 3A, C). The denticles are minutes, well-delimited, apicobasally elongated to subquadrangular, and their external margin, made of a thin layer of enamel, is weakly convex (Figure 3B, D). There are eight and six denticles per millimeter on the mesial and distal carinae at mid-crown in BSP 1934 VIII 14, respectively. This suggests that the distal denticles of the incisors are larger than the mesial ones (DSDI > 1.2) in *Diademodon*. Concave surfaces adjacent to the mesial carina are present on the lingual surface and marginal to the distal carina on the labial side of the crown (Figure 3A).

Canines

The two isolated canines of the holotype specimen SAM-571b bear two poorly defined longitudinal ridges on both labial and lingual sides. These ridges extend along the whole crown and delimit narrow labial and lingual depressions mesiodistally that extend also on the root (Figure 3E). Although the canines of several specimens of *Diademodon* do not bear any ridges (e.g., BSP 1934 VIII 14, 15 and 505; BP 4669), three to four longitudinal ridges can also be seen on the canines in AM 3753. The mesial and distal carinae of the canines are also denticulated and the mesial carina extends well-above the cervix in the holotype. The denticles are well-preserved in this specimen and clearly show the peculiar condition of changing sporadically in size along the carinae (Figure 3F). As in the incisors, the denticles of the canines are apicobasally elongated in shape and their external margin is weakly symmetrically convex. Seven and 7.5 denticles per millimeter are present at mid-crown in canine of the holotype (CH ~ 10 mm), whereas three and

3.5 to four denticles per millimeter can be counted at mid-crown in the canines of the larger specimens BSP 1934 VIII 14 (CH ~ 14 mm) and BP 4669 (CH ~ 19 mm), respectively.

Conical postcanines

The upper and lower conical postcanines vary from three to five. As described by Crompton (1955), the upper postcanines are straight, apically pointed, slightly labiolingually compressed and ~~serrated~~ on both mesial and distal carinae (Figure 3G–K). In MB R1004, the upper conical teeth are also mesiodistally constricted at the cervix but this may result from taphonomical deformation (Figure 3G). The third and fourth lower conical postcanines of AM 458 are wide and wider than the upper conical postcanines of *Diademodon*. In this specimen, the mesial carina of conical postcanines faces mesiolingually while the distal carina is positioned distally (Figure 3I, J). The distal denticles are large and apically inclined whereas the mesial serrations are low and show a widely convex external margin. Cingular cuspules are clearly visible on the linguodistal surface, at the base of the third and fourth conical postcanines of AM 458 (Figure 3J). A distal accessory cusp also appears to be present in the lower conical teeth of SAM-5877 (Figure 3K).

Upper gomphodont postcanines

The best-preserved upper gomphodont postcanines are from the holotype specimen SAM-571a, which includes in situ teeth within the maxillae (Figure 3N–O) as well as two well-preserved isolated postcanines from the more distal portion of the jaw (Figure 3L–M). With a CBR ranging from one to 1.7, most of the upper gomphodont postcanines are wider than the lower gomphodont postcanines. Gomphodont postcanines of *Diademodon* are characterized by the presence of several accessory ridges and bumps on the mesial and distal surfaces of the transverse crest. The mesial and distal accessory ridges vary in length, orientation and extension along the tooth row so that each gomphodont postcanine has a unique morphology along the jaw. All upper postcanines, however, bear a large labial cusp longer and slightly higher than the lingual cusp (Figure 3L, N). A smaller and lower yet well-demarked labiodistal accessory cusp always follows the labial cusp. The mesial and distal crests of the labial cusp appear to be weakly serrated, with the largest denticles being at the base of the cusp. The lingual cusp is always adjacent to a mesiolingual accessory cusp, and the latter is as long and tall as the lingual cusp. In the fourth right gomphodont postcanine of BSP 1934 VIII 14, the mesiolingual accessory cusp is in fact much longer than the lingual cusp (Figure 3P) and is followed by a second shorter mesiolingual accessory cusp. Although the presence of accessory ridges and bumps on the transverse crest makes it difficult to delimit and located the central cusp in SAM-571a, this cusp is centrally positioned on the crest. Both mesial and distal margins of the upper gomphodont postcanines are delimited by one or several accessory cusps forming a cingulum (Figure 3L). The size, position and height of these cingular cuspules vary in each upper postcanine along the tooth row (see below). The isolated upper postcanines of the holotype bear a single mesial cingular cuspule (Figure 3M) and perhaps some other minor cingular cuspules, whereas the distal cingulum is made of four to five cuspules increasing in height and width lingually. The distal basin is longer than but as deep as the mesial basin. The root is more than twice as long as the crown and bears a deep, wide and centrally positioned depression on its distal surface.

The upper gomphodont postcanines from the mesial half of the maxilla (Figure 3N, O) follow the same pattern of ridges and cusps seen in the isolated upper postcanines, i.e., they have two main labial and lingual cusps adjacent to two prominent labiodistal and linguomesial cingular cuspules, respectively. The labial and lingual cusps share, however, the same height. The labiodistal accessory cusp is significantly lower and shorter than the labial cusp, whereas the linguomesial accessory cusp is longer and as high or higher than the lingual cusp. The transverse crest of these postcanines bears accessory ridges and bumps on the mesial surface only, the distal surface being smooth (Figure 3N). In one of the two in-situ upper postcanines, the mesial surface shows an accessory ridge running perpendicular to the transverse crest and parallel to a second, poorly marked ridge, as well as a single accessory bump on its linguomesial portion. The central cusp of the transverse crest is long, low and appears to bear some poorly defined serrations on its labial and lingual crests. Some portions of the mesial and distal cingula and labiomesial, labiodistal, linguomesial and linguodistal ridges also show a beaded appearance and are finally serrated in the three best-preserved upper postcanines. The distal basin of the distalmost preserved postcanine is narrow, well defined and bounded by the distal cingulum. The distal basin is, however, shallow and poorly defined in the preceding tooth and absent in the mesialmost preserved postcanine (Figure 3N). The mesial basin of the two first postcanines has also been worn out, a feature shared with *Titanogomphodon* among diademodontids. Similar to the isolated upper postcanines, the mesial margins of the in-situ postcanines have a single and weakly lingually deflected cingular cuspule. Likewise, the distal cingulum is formed by four cingular cuspules that increase in width and height lingually. Two distal cingular cuspules are seen on the linguodistal margin of the preceding tooth (Figure 3N). A higher number of cingular cuspules can, however, been counted on the cingula of other *Diademodon* specimens, with five, possibly six, cingular cuspules in the mesial cingulum of the best-preserved right upper postcanine of NHMUK R3303, and five to six cingular cuspules in the distal cingulum of the largest left and right upper postcanines of NHMUK R3765. If the width and height of the mesial cingular cuspules also increase lingually in NHMUK R3303, the cingular cups of the distal carina decrease in size either towards the center of the cingulum or sporadically along the cingulum in NHMUK R3765.

Lower gomphodont postcanines

Two lower gomphodont postcanines from the distal portion of an incomplete left mandible of the holotype SAM-571a are also among the best-preserved lower postcanines known (Figure 4A–E). Their morphology shows some difference with that of upper postcanines. The best-preserved lower postcanine, which is the most distal one, is longer than wide and the lingual cusp is as wide but slightly shorter and lower than the labial cusp (Figure 4A, C). It is difficult to know whether accessory cusps were present. Based on the size of the cusps, it appears that the linguomesial and labiodistal accessory cusps are present and are not cingular cuspules. These two cusps are lower and shorter than the lingual and labial cusps (Figure 4A, B). It is unknown whether the lingualmost cingular cuspule of the mesial cingulum is homologous to the linguomesial accessory cusp (Figure 4A, B). The mesial and distal accessory ridges are prominent, higher than the low and poorly delimited transverse crest and diagonally oriented from it. Three accessory ridges can be counted on the mesial surface of the transverse crest and one on the distal surface (Figure 4A). A second much shorter distal ridge extending linguodistally is present at the level of the distal basin. Three protuberant and well-delimited mesial cingular cuspules composed the mesial cingulum whereas the distal cingulum encompasses four smaller and poorly delimited cingular cuspules (Figure 4A, C). As observed in some upper postcanines, the mesial and distal edges of the labial cusp are serrated (Figure 4E). The second more mesial lower gomphodont postcanine is more sub-circular in outline and the mesial and distal accessory ridges on the transverse crest are not so prominent. We assume the presence of a labiodistal and linguomesial accessory cusps in this tooth, but the mesialmost and distalmost cingular cuspules are as wide and as well-delimited as these two putative accessory cusps. Both labial and lingual cusps are incomplete and it is unknown whether they had the same width and height.

The lower gomphodont postcanines of the large majority of other more mature specimens of *Diademodon* preserving the lower dentition (e.g., BMNH R3588; BSP 1934 VIII 16, 505; MB R1004; GSN R321) are worn out and only the distalmost mandibular postcanines of AM 458, AM 3753 and SAM-PK-5877 are complete enough to provide some information on their morphology. In all specimens, the labial cusp is the largest, and is significantly longer, wider and higher than the lingual cusp. The transverse crest connecting the two cusps forms a narrow ridge bearing a low and poorly defined central cusp. One or two large pointed mesial cingular cuspules are visible in the three specimens, mesial to the lingual cusp (Figure 4D). Based on their size, these cingular cuspules may correspond to the mesiolingual accessory cusps of more derived gomphodonts. A wide and high centrally positioned mesial cingular cuspules is well-visible in SAM-PK-5877 (Figure 4D) but worn out in AM 458 and AM 3753. The central cingular cuspules is wider than the mesial cuspules directly mesial to the lingual cusp but narrower than the preceding one situated on the mesiolingual margin of the lower postcanine. The distal cingulum, well-preserved in the left and right distalmost lower postcanines of SAM-PK-5877, bears four to six well-delimited cingular cuspules (Figure 4D). These distal cingular cuspules extend on the labiodistal ridge of the labial cusp in the left postcanine where they increase in length mesially. As in the holotype, several accessory ridges of variable length and orientation (i.e., perpendicular, diagonally oriented or parallel to the transverse crest) are present on the mesial and distal surfaces of the transverse crest in SAM-PK-5877, AM 458 and AM 3753. In SAM-PK-5877, one of the mesial accessory ridges reaches the largest mesial cingular cuspules (Figure 4D).

Transitional postcanines

The transitional upper and lower postcanines, which are relatively well preserved in MB R1004, SAM-PK-K177 and AM 3753, have an intermediate morphology between the distalmost gomphodont and the sectorial postcanines. They are subcircular, weakly labiolingually elongated or mesiodistally short, drop-shaped or oval in outline. These teeth show a large distally recurved cusp on the labial portion of the crown homologous to the labial cusp and the main cusp of gomphodont and sectorial postcanines, respectively. A lingual cingulum formed by three to five well-delimited and strongly protruding cingular cuspules are also visible (Figure 4F, G).

Labiodistally oriented ridges connecting the main cusp to one or several of these cingular cuspules can be seen in some specimens (Figure 4F). One or two distal accessory cusps are also present distal to the main cusp, with the mesial one being homologous to the labiodistal accessory cusp of gomphodont postcanines. Two transitional postcanines can be observed in the lower jaw of SAM-PK-K177 (Figure 4F). Although incomplete, the main cusp of those two teeth appears to be mesiolingually oriented and subcircular in outline. The transitional upper postcanines (the 'intermediate gomphodont of Osborn 1974) were lost in some specimens of *Diademodon* such as BSP 1934 VIII 14 in which they were replaced by a gomphodont postcanine, following the replacement model proposed by Hopson (1971) and Osborn (1974).

Sectorial postcanines

The upper and lower sectorial postcanines always bear a distally recurved main cusp followed by one, or, more commonly, two smaller distal accessory cusps (Figure 4H–I). The distalmost accessory cusp of the sectorial teeth is either of the same length or slightly shorter than the mesial one. Some sectorial teeth also bear a minute mesial accessory cusp on the basal third of the mesial margin of the main cusp (Figure 4H). The mesial and distal carinae of the main cusp are usually serrated along the whole crown height. The specimen BP/1/4529 shows the unique feature of having both mesial and distal denticles divided into two parts, i.e., a large sub-denticle apically and a smaller one basally (Figure 4J, K). The two distal accessory cusps are also denticulated in this specimen (Figure 4J). A lingual cingulum composed of six to seven cuspules is clearly present in the mesial lower sectorial teeth of AM 3753, MB R1004 and SAM-PK-K177. This lingual cingulum is, however, absent in the upper sectorial postcanines of BSP 1934 VIII 14 and in the distalmost upper and lower sectorial teeth of MB R1004. The enamel texture of incisors, canines and postcanines is braided and oriented.

Crown microstructure

Histological studies of the postcanine of *Diademodon tetragonus* were done by Grine (1977, 1978), Osborn & Hillman (1979) and Sander (1997b). The enamel microstructure of this taxon was revealed to be prismless and columnar (the synapsid columnar enamel (SCE) of Sander (1997b), and to include incremental lines and enamel tubules.

***Titanogomphodon crassus* (Keyser, 1973)**

Holotype: GSN R323, an incomplete cranium missing the mesial tip of the rostrum.

Referred dental material: None.

Occurrence: Northern slope of Etjo Mountain, Otjozondjupa Region, Namibia.

Horizon: Etjo Beds, Omingonde Formation, Karoo Basin.

Age: Anisian-Early Ladinian?, Middle Triassic.

Dental formula: I?/? : C?/? : PC>7/? (CPC?: GPC>3: TPC1 : SPC3).

Dental morphology: Keyser (1973) described the dentition of *Titanogomphodon* in relative details given the poor preservation of the teeth. The holotype specimen GSN R323 preserves the distal portion of the three distalmost upper gomphodont postcanines as well as a transitional postcanine and the mesialmost and distalmost upper sectorial teeth (Figure 5).

Upper gomphodont postcanines

As noted by Keyser (1973), the transverse crest of the upper gomphodont postcanine, which connects the labial and lingual cusps (both unpreserved in all gomphodont postcanines of GSN R323), is slightly mesially displaced (Figure 5B). As seen in the *Diademodon* upper postcanines, a faint mesial accessory ridge can be observed in the distalmost gomphodont tooth (Figure 5A, C). Unlike Keyser's (1973) description of the upper gomphodont postcanines, no labiodistal accessory cusp or distinct cuspules forming a distal cingulum can be observed in the preserved teeth (Figure 5A). Nonetheless, the damaged right mesialmost gomphodont postcanine appears to show a labiomesial accessory cusp, mesial to the unpreserved labial cusp as well as a mesial cingular cuspule (Figure 5D, F). Many portions of the enamel and dentine surface of this tooth are, however, missing and the presence of these two accessory cusps/cingular cuspules ~~requires~~ to be confirmed in better preserved specimens in the future. Similar to some upper postcanines of *Diademodon* that have been worn out, and unlike trirachodontid postcanines, the mesial and distal basins are absent in all preserved postcanines of *Titanogomphodon*.

Transitional and sectorial postcanines

According to Keyser (1973), *Titanogomphodon* is diagnosed by the diagonal orientation of the sectorial postcanines, of which the long axis is linguomesially oriented. Such orientation of the sectorial teeth indeed contrasts with the mesiodistally oriented upper sectorial postcanines of other gomphodont cynodonts such as *Diademodon*, *Langbergia*, *Trirachodon*, *Andescynodon* and *Boreogomphodon*, in which the long axis is parallel to the labial margin of the upper jaw. As in *Diademodon* and unlike trirachodontids, a transitional postcanines is present between the gomphodont and sectorial tooth rows. Little information can be extracted from the transitional and sectorial postcanines due to wear and the incompleteness of the crowns. No main, accessory or cingular cuspules are preserved in the sectorial postcanines and only a concavity centrally positioned on the lingual surface of the root is present in the two sectorial teeth (Figure 5A, E).

Trirachodontidae (Crompton, 1955)

***Langbergia modisei* (Abdala, Neveling & Welman, 2006)**

Holotype: NMQR 3255, an incomplete cranium.

Referred dental material: NMQR 3251, 3256, 3268, 3280, 3281; BP/1/5362, 5363, 5400, 5401, 5404; CGP/1/33, 120; SAM-PK-11481.

Occurrence: Langberg 556 (type), Rexford Store 433, Eerste Geluk 131, Bethlehem District; Moerbeidal 648, Kaaimansgat 146 and Hugo's Kop 620, Paul Roux District; Goedgedacht 15, Marquard District; Bosrand 12, Senekal District; Palmiet Fontein 94, Tarkastad District; Free State and the Eastern Cape Province; South Africa.

Horizon: Lower horizons of the Burgersdorp Formation, Beaufort Group, Karoo Supergroup.

Age: Late Olenekian, Early Triassic.

Dental formula: I4/3 : C1/1 : PC7-9/8 (CPC1-2: GPC3-7?: SPC2-4).

Dental morphology: The dentition of *Langbergia modisei* has been relatively well-described by Abdala, Neveling & Welman (2006). Here we provide additional information based on firsthand examination of the best-preserved specimens.

Incisors

The mesial carina of the incisors does not seem to be serrated, whereas the distal carina is denticulated and bears around 30 denticles per 5 mm (contra Abdala, Neveling & Welman (2006); Figure 6A-C). The distal denticles of the first right lower incisor of NMQR 3251 have a symmetrically convex external margin and are poorly delimited. They are apicobasally elongated and change sporadically in size along the carina (Figure 6A, B). The largest denticles are at mid-crown whereas the basalmost and apicalmost serrations do not reach the root and the crown apex (Figure 6A, B). The distal denticles of the fourth upper incisor of NMQR 3281 and SAM-PK-K11481 share the same morphology, with the largest denticles at mid-crown and the basalmost and apicalmost serrations extending far above the root (Figure 6C) and below the crown apex, respectively. A concave surface adjacent to the distal carina is also present on the labial surface of the third? right incisor in SAM-PK-K11481. Based on the first and best-preserved lower incisor of NMQR 3280, the mesial carina faces mesially whereas the distal carina is distally and almost linguodistally oriented, giving a lenticular to D-shaped cross-section outline at mid-crown. The distal profile of the upper incisors of this specimen is sigmoid in labial view, with the basal one-third and the apical two-thirds of the crown being convex and concave, respectively. The incisors are apically recurved and some of them are weakly mesiodistally constricted at the cervix.

Canines

Both upper and lower canines of *Langbergia modisei* have serrated carinae (BP/1/5362; NMQR 3251, 3268) with a denticle density ranging from 20 to 32 denticles per 5 mm. In NMQR 3251 and 3268, the mesial and distal denticles of the canines do not extend to the cervix basally, but do reach the crown apex in NMQR 3251. Similar to the incisors, the mesial and distal denticles change sporadically in size along the carinae and have a symmetrically to asymmetrically convex external margin (Figure 6F, G). However, the denticles of the canines tend to be better delimited and mesiodistally longer than those of the incisors so that denticles are apicobasally elongated and sometimes subquadrangular in shape. Despite the fact of changing randomly in size, the basal and apicalmost denticles are smaller than those of the mid-crown on both mesial and distal carinae. Faint longitudinal ridges delimiting mesiodistally short, flat facets can be observed on the labial surface of the canines of BP/1/5362 (Figure 6H) and SAM-PK-K11481. In the latter specimen, the mid-crown cross-section outline of the upper canine is roughly salinon-shaped (sensu Hendrickx, Mateus & Araújo, 2015), with a wide convex labial margin showing a weakly concave labiodistal surface, and a biconcave lingual margin, of which the mesial concavity is longer than the distal one (Figure 6E). A concave surface is also present on the mesial and distal surfaces of the erupting right and left upper canines of NMQR 3268, respectively. The cross-section outline of the canine of NMQR 3251 is, however, parabolic at mid-crown. This indicates that there is variation in cross-section outline in the canines of *Langbergia*. No transverse undulations could be observed on the upper and lower canines of the specimens examined. The enamel surface texture of NMQR 3268 is clearly braided and curves basally close to the carinae (Figure 6I).

Gomphodont postcanines

As noted by Abdala, Neveling & Welman (2006), the first upper and lower postcanines differ in morphology. The first upper postcanine of NMQR 3251 is significantly smaller than the more distal ones, has a sub-circular cross-section outline and only bears a single main cusp, a morphology that ~~recalls~~ the conical postcanines of *Diademodon*. In NMQR 3255, the first upper postcanine has an oval cross-section outline and is only slightly smaller than the other gomphodont postcanines. Given the incomplete preservation of the first upper postcanines on both sides, it is unknown whether they were monocuspid as well. The morphology of the first lower postcanine appears to be more complex. It is formed by a main centrally positioned and slightly labially displaced cusp (Figure 6N), which is homologous to the central cusp of more distal gomphodont postcanines. This main cusp is bordered by a small apically pointed mesial accessory cusp and a low lingual cingulum formed by at least three minute cingular cuspules (Figure 6N). Because the distal portion of this tooth is missing, it is unknown whether an accessory cusp was present distal to the main cusp.

Unlike other trirachodontids, the upper and lower gomphodont postcanines of *Langbergia* roughly share the same morphology, i.e., they are elliptical in cross-section, slightly labiolingually elongated and their long axis is mesiolingually oriented (Abdala, Neveling & Welman, 2006). If the upper and lower gomphodont postcanines of NMQR 3251 and NMQR 3255 share a crown base ratio (CBR) varying between 1.3 and 1.45, the upper gomphodont postcanines of NMQR 3268 are more labiolingually elongated, with a CBR around 2 in the widest teeth. Both upper and lower gomphodont postcanines increase in size up to the penultimate tooth, which is slightly larger than the last gomphodont postcanine. The long axis of the upper gomphodont postcanines is parallel in all teeth, yet it changes in orientation in the lower postcanines, with the long axis of the first two postcanines being strongly mesially oriented and almost parallel to the long axis of the mandibular tooth row. All gomphodont teeth bear a high, wide, centrally positioned central cusp bordered labially and lingually by the labial and lingual cusps, respectively (Figure 6J-M). The central cusp always appears to be higher and wider than both labial and lingual cusps. It is separated from these two cusps by a deep and narrow concavity extending basally at a certain distance above the mesial and distal basins (Figure 6L). The labial, central and lingual cusps that form the transverse crest are not perfectly aligned on the same plane of elongation of the postcanine. The long axis of the central cusp either follows that of the transverse crest or is diagonally oriented from it (Figure 6J, K, M). Likewise, the labial cusp of the upper postcanines is significantly deflected mesially from the diagonally oriented axis of the transverse cusp whereas the lingual cusp of the lower postcanines is weakly deflected distally in some teeth (Figure 6J, K, M). The lingual and central cusps are, however, aligned in the same plane of elongation of the postcanine while the labial cusp remains mesially displaced from that plane. A cingulum formed by three to four large and sometimes strongly protruding cingular cuspules delimits both the mesial and distal margin of the upper and lower gomphodont postcanines in NMQR 3251 and NMQR 3255. It is difficult to assess homologies of the linguomesial, linguodistal, labiomesial and labiodistal cuspules of the upper and lower postcanines of *Langbergia* in relation to those cuspules of some traversodontids such as *Luangwa*, *Traversodon* and *Mandagomphodon*. We assume their homology here based on similarity in the size of these cusps, but acknowledge that our hypothesis is tentative. The labiomesial and linguodistal cusps are the largest accessory cusps of the cingula in the upper gomphodont postcanines whereas the labiomesial, linguomesial and linguodistal are the largest in the lower postcanines. Although incomplete and badly preserved, the upper postcanines of NMQR 3268 do not seem to bear these large accessory cusps on the cingula. The mesial and distal cingula instead comprise a large number of small cingular cuspules, as seen in *Cricodon* and *Trirachodon*. The incompleteness of the upper postcanines of NMQR 3268 does not permit to know whether the cingular cuspules extend along the whole width of the crown or are restricted to a certain part of the cingulum. The cingular cuspules, however, increase in width towards the center of the crown at least on the distal cingulum in this specimen. The mesial and distal basins, delimited by the transverse crest and the cingulum, are deep and mesiodistally short in *Langbergia* (Figure 6J, K, M). As observed for the canines, the enamel texture of the gomphodont postcanines is braided and oriented.

Sectorial postcanines

The sectorial postcanines always include a main distally recurved cusp followed by one or two distal accessory cusps distally and one or no mesial accessory cusp mesially (Figure 6O, P). The mesial margin of the main cusp is serrated on the apical third of the crown in BP/1/5362 (Figure 6P). The denticles are poorly defined, low, apicobasally elongated projections on the carina. As in the denticles of the incisors and canines, they sporadically change in size and their external margin is symmetrically to asymmetrically convex. The first distal accessory cusp is the longest whereas the first and second distal accessory cusps are smaller and sometimes appear as minute projections. The mesial accessory cusp is often large, projects apically and strongly protrudes from the basal third of the crown (Figure 6O). The largest distal accessory cusp also projects distally in some specimens. As observed by Abdala, Neveling & Welman (2006), a lingual cingulum composed of five cingular cuspules is present in the second upper sectorial postcanine of NMQR 3255 (Figure 6Q). The mesialmost cingular cuspule is long and followed distally by two short cusps, a much longer one, and then a medium sized one. A sigmoid and basally inclined cingulum formed by minute cingular cuspules is also visible on the basolingual surface of the third lower sectorial postcanine of NMQR 3251. In the latter, the last upper sectorial crown is shorter than the mesial ones. It is also a tricuspid postcanine, in which the distalmost accessory cusp is widely parabolic instead of being pointed and subtriangular, as seen in the main and accessory cusps of the sectorial tooth row (Figure 6O).

***Cricodon metabolus* (Crompton, 1955)**

Holotype: UMZC T905, incomplete upper and lower jaws with several loose teeth.

Referred dental material: BP/1/5540, 5835, 6102, 6159; NHCC LB28; NMT RB227; NHMUK R3722, R36800; SAM-PK-6212, K5881.

Occurrence: Stockley's bone locality B11, Njalila, Tanzania (type); Avilion and Norwood farms, Bamboeshoek Valley, Sterkstroom District, Eastern Cape Province, South Africa; Aliwal North, Joe Gqabi District, Gariep Municipality, South Africa; 5 km west of Sitwe, Eastern Province, Zambia.

Horizon: Manda Formation (type); Subzone B and C of the *Cynognathus* Assemblage Zone (AZ), Burgersdorp Formation, Karoo Basin; Ntawere Formation.

Age: Early and Late Anisian, Middle Triassic.

Dental formula: I4/3 : C1/1 : PC9-10/11 (CPC0 : GPC7-9 : SPC0-2).

Dental morphology: The dentition of the holotype specimen of *Cricodon metabolus* was described by Crompton (1955) and additional information was given by Abdala, Hancox & Neveling (2005) based on referred specimens. A detailed examination of the holotype and referred material enable us to provide additional information on the morphology of incisors, canines and both gomphodont and sectorial postcanines. Based on the large size, the low denticle density of the incisors and canines, the drop-shaped outline of the distalmost upper postcanines, the step-like disposition of distalmost upper gomphodont postcanines, and the long axis of lower postcanines perpendicular to the mandibular tooth row, BP/1/5540, 5835, 6102, 6159 as well as NHMUK R3722, R36800 as well as SAM-PK-6212 and K5881, all from Aliwal North (Subzone B of the *Cynognathus* AZ), are here referred to *Cricodon metabolus*. On the other hand, BP/1/5538 from the Burgersdorp Formation of the Avilion farm (Sterkstroom District) is excluded from this taxon. This specimen, represented by the posterior portion of the snout and orbits with the three last gomphodont and the first sectorial postcanines preserved, differ from *Cricodon* by the following dental features: i) longer and more ovoid upper distal gomphodont postcanines (CBR of 1.5); ii) no step-like disposition of the antepenultimate and penultimate upper gomphodont postcanines; iii) upper postcanines with a large labiomesial accessory cusp and no distal cingulum; iv) sectorial upper postcanines with a large strongly pointed and strongly apically recurved main cusp and two distal accessory cusps. This specimen instead appears to belong a new gomphodont taxon that will be described in a forthcoming paper.

Incisors

The mesial and distal carinae of the partially erupted first left lower incisor of the holotype UMZC T905 are clearly serrated and include apicobasally elongated to subquadrangular and weakly apically inclined denticles with a symmetrically convex external margin (Figure 7A, B). Both mesial and distal denticles decrease in size apically and reach the crown apex, although the tip of the apex remains unserrated. There are around 1.75 denticles per mm (denticle density of ~9/5mm) in the basalmost erupted part of the mesial and distal carinae, and 3.5 denticles per mm at the apex. The incisors of the referred specimen BP/1/6102 and BP/1/5540 share the same denticle density, with 7 to 10 denticles per 5 mm in the distal carina (Figure 7C, D). This contrasts with the much higher denticles density (>20/5mm at mid-crown) on the incisors of other trirachodontids. The mesial carina and denticles of BP/1/6102 are not visible and are ~~most likely~~ covered by sediment. Only the apical denticles of the first left upper incisor can be seen on the mesial carina of BP/1/5540. These mesial denticles are apicobasally elongated, have a flat external margin and extend one millimeter below the crow apex. The denticles of the distal carina of BP/1/6102 and BP/1/5540 also extend from the cervix to the base of the crown apex (Figure 7C). In BP/1/6102, the distal denticles decrease in size apically and basally, and are apicobasally elongated at mid-crown and in the apical part of the crown and almost subquadrangular in the basal third of the carina (Figure 7D). On the other hand, the distal denticles of BP/1/5540 are apically inclined and subquadrangular on most of the carina. The external margin of the denticles in BP/1/5540 is symmetrically to asymmetrically convex and weakly parabolic. The interdenticular space is apicobasally wide in the basal denticles and narrow in the mid-crown and apical denticles in BP/1/6102 whereas it is wide in most of the denticles in BP/1/5540. The distal denticles of the incisors change sporadically in size along the carina in *Cricodon*. The mesial carina faces mesially in this taxon whereas the distal carina is oriented linguodistally and distally in the first two and last two upper incisors, respectively. The incisors are distally recurved and the mesial and distal profiles of the incisors are strongly convex and straight to slightly concave, respectively. The crowns do not seem to be constricted at the cervix, and no information can be provided on the cross-section outline of the incisors.

Canines

The morphology of the canines of *Cricodon* is based on the upper canines of the referred specimens BP/1/6102, BP/1/5540, NHMUK R3722 and the lower canines of SAM-PK-K5881, as none of the upper and lower canine is preserved in the holotype (Crompton, 1955). As noted by Abdala, Hancox & Neveling (2005), both carinae of the upper canine are serrated (Figure 7E). The denticles of the canines are slightly bigger than those of the incisors, with 6 to 7 denticles per 5 mm on the distal carinae at mid-crown in BP/1/6102 and BP/1/5540 (Figure 7G-I). The denticle density of the smaller specimens NHMUK R3722 and SAM-PK-K5881 vary between 12.5 and 14 denticles per 5 mm. The distal denticles appear to be larger than the mesial ones in BP/1/6102 and BP/1/5540, with a denticle density of 8.5 and 6.8 in the mesial and distal carinae, respectively, in BP/1/6102 (Figure 7G, H), and 8 and 6.6 denticles/5mm in BP/1/5540. There is, however, no difference between the mesial and distal denticle density in the upper and lower canines of NHMUK R3722 and SAM-PK-K5881. The denticles are apicobasally elongated in the mesial and distal carinae of NHMUK R3722 and SAM-PK-K5881, and apicobasally elongated to subquadrangular in the distal carina of BP/1/6102 and BP/1/5540. Similar to the incisors, there is a sporadic variation in denticle size along the carina, with a minute denticle followed by a much larger one in some portion of the carina. The interdenticular space is particularly wide in the mid-crown denticles of the distal carina in BP/1/5540 (Figure 7I). The cross-section outline is lenticular at mid-crown in the upper canines of BP/1/6102 and weakly salinon-shaped in the lower canine of SAM-PK-K5881 (Figure 7F) due to the presence of a concave surface adjacent to both carinae (Figure 7E. In the latter specimen, several transverse undulations are present on the lingual surface of the lower canine at mid-crown (Figure 7E). Unlike the postcanines, the surface texture of the incisors and canines of the referred specimens is irregular and non-oriented.

Upper gomphodont postcanines

The morphology of the first to the fifth upper postcanines relies on the referred specimen of SAM-PK-K5881. The first upper postcanine, incomplete and worn in this specimen, is labiolingually expanded and comprises a transverse crest made of a labial, lingual and most likely central cusps, as well as both mesial and distal cingula. No mesial and distal basins can be seen but they might have been worn out. The more distal upper postcanines, which are relatively worn, share the same morphology and only their size and labiolingual elongation increase distally. The mesial margin of the second and third upper postcanines are slightly concave and follows the convexity of the distal margin of the preceding crown. This morphology is reminiscent of the incipient development of a shouldering present in some traversodontids such as *Menadon*, though the postcanines do not seem to be in direct contact in *Cricodon* and the convexity occurs distally and not labiomesially, as it is the case in traversodontids.

All isolated and in-situ upper gomphodont postcanines of the holotype, which belong to the distal half of the maxilla, are labiolingually expanded, ovate in outline, with an CBR of 2.5, 2.3, 2 and 1.85 for the sixth, seventh, eighth and ninth left postcanines, respectively. Their long axis is roughly perpendicular to the long axis of the tooth row, and only the last gomphodont tooth is labiomesially oriented. A striking feature of the upper tooth row of *Cricodon* is the step-like disposition of the antepenultimate and penultimate gomphodont postcanines, so that each erupted tooth is at the level of the base-crown or root of the preceding postcanine. The upper gomphodont teeth are slightly mesiodistally constricted at the labial one-third of the crown giving an asymmetrical outline of the postcanine in apical view, with the labial one-third of the tooth being shorter than the lingual one (Figure 7J). This constriction has similar development on the mesial and distal margins of the ninth upper gomphodont postcanine, but the constriction is slightly more pronounced on the distal surface of the eighth postcanine and particularly well-developed on the distal margin of the sixth and seventh teeth. A wide concavity can be seen on the distal labial third of the surface of the crown in these postcanines. Upper gomphodont postcanines include a low and centrally positioned transverse crest, which is straight (Figure 7J), sigmoid or weakly parabolic in outline, with the concavity directed distally, in apical view. The transverse crest is made of a wide and lingually displaced central cusp bordered by two prominent labial and lingual cusps. No preserved upper postcanines bear fully complete labial, central and lingual cusps but the labial cusp appears to be as high as the central cusp, and as high as or slightly higher than the lingual cusp. As described by Crompton (1955), the labial and lingual ridge of the central cusp are denticulated, with the widest denticles being close to the apex (Figure 7N). The denticles of the central cusp are wide, with a weakly convex external margin. Denticles are also clearly visible on the mesial, distal and central ridges of the labial and lingual cusps, being particularly numerous and well-developed on the labiomesial and labiodistal ridges of the labial cusp (Figure 7O). Unlike the central cusp, the denticles of the mesial, distal and central ridges of the labial and lingual cusps diminish in size apically. Similar to the serrations of incisors and canines, they are apicobasally elongated and change sporadically in size. Their external margin is, however, flattened or weakly convex (Figure 7O). The serrations on the labiomesial and labiodistal ridges either extend along the whole cusp up to its apex, or are restricted to the basal half of the cusp.

The mesial and distal cingula of the upper postcanines bear a large number (>7) of small and well-delimited cingular cuspules along most, if not all, the width of the mesial and distal rims of the crown (Figure 7J, N). Unlike more mesial teeth, the distal cingulum of the ninth left upper postcanine does not extend to the labial cusp. The same can be said of the mesial cingulum of a loose postcanine from the left upper jaw. The cingular cuspules sporadically vary in size along the crown, yet the widest cuspules are found in the central and/or lingual parts of the cingulum. We counted ten and seven cingular cuspules on the mesial and distal cingula in the ninth left upper gomphodont postcanine, respectively, and seven cusps in the preserved labial half of the distal cingulum of the eight left upper postcanine. The preserved portion of the mesial and distal cingula of the upper gomphodont postcanine sampled by Hendrickx, Abdala & Choiniere (2016) includes nine and eleven cingular cuspules, respectively. The widest cingular cuspules are found in the labiocentral and lingual parts of the mesial cingulum and in the labial portion of the distal cingulum (Figure 7N). The mesial cingulum is parabolic or weakly sigmoid and slopes labiobasally in mesial view. The distal cingulum, on the other hand, is symmetrically parabolic or biconcave. In two loose upper gomphodont postcanines, the denticulated labiodistal ridge of the labial cusp does not connect to the distal cingulum as the lingual extremity of the latter extends on the labiodistal surface of the labial cusp, so that the lingualmost distal cingular cuspules are situated apical to the labiodistal ridge.

The upper postcanines of the holotype and two specimens with the same specimen number (SAM-PK-K5881) largely follow the same morphology, yet a few differences can be noted. If the CBR of the largest upper postcanine (i.e., third right gomphodont postcanine; CBR of 2.3) of SAM-PK-K5881*a* (represented by a badly crushed snout and the anterior portion of the mandible) falls within the range of values obtained in the holotype, the upper postcanines of SAM-PK-K5881*b*preserving the left maxillary tooth row are more ovoid, with a CBR beyond 1.7. In addition, the long axis of the last upper postcanine is not diagonally oriented in SAM-PK-K5881*b*. A deep and narrow concavity is also present in the central portion of the distal cingulum of the two distalmost upper postcanines in this specimen, so that the cingulum of these last two crowns is strongly biconvex (Figure 7M).

Lower gomphodont postcanines

As described by Crompton (1955), the upper and lower gomphodont postcanines roughly share the same morphology, but their crown base ratio is significantly lower in the latter teeth, varying from 1.2 to 1.6 (Figure 7K). Similar to the upper postcanines, the first lower postcanine, preserved in SAM-PK-K5881, is weakly labiolingually elongated and includes a labial, central and lingual cusps ringed by the mesial and distal cingula. The central cusp of the lower postcanine is, however, long and wide at its base and surrounded by the mesial and distal basins, merged to form a subcircular groove. Three and four cingular cuspules are preserved on the lingual part of the mesial cingulum and on the labial portion of the distal cingulum, respectively, and it is assumed that both mesial and distal cingula bore between six to eight cuspules. A mesiodistal constriction is present at the cervix in the first postcanine, which is also constricted at the same level on its labial surface. The morphology of the second to fifth lower postcanines of SAM-PK-K5881 follow that of the more well-preserved distal teeth of the holotype. The size and CBR of these teeth increase up to the fifth lower postcanines (CBR of 1.6), then decrease more distally.

A comparative analysis of the upper and lower postcanines of the holotype allows providing major anatomical differences between them. If the lower postcanines include a transverse crest composed of a labial, central and lingual cusps ringed by the mesial and distal cingula, large cingular cuspules appear to be present labio- and linguodistally and linguomesially (Figure 7K). These cusps are most likely homologous to the putative labiodistal, linguomesial and linguodistal accessory cusps of *Langbergia*. The central cusp forms a centrally positioned dome on the transverse crest and, as the upper postcanines, its labial and lingual ridges are serrated. It is, however, unknown whether the central, mesial and distal ridges of the labial and lingual cusps also bore denticles. The labial, central and lingual cusps all share the same height in the eighth lower postcanine, the only one having these cusps complete. Unlike the upper postcanines, the labiodistal surface is angular in apical view in the eighth and ninth lower postcanines, the best preserved of the mandible, with the labiodistal margin connecting to the labial surface of the crown at a slightly obtuse angle (Figure 7K). There are ten mesial and seven distal cingular cuspules on the cingula in the ninth lower postcanine, the only lower crown preserving the majority of these elements. Both cingula extend along the whole width of the postcanine, and the shorter cingular cuspules are found in the central portions of the cingulum. Both upper and lower postcanines show a braided and oriented enamel surface texture best visible on the mesial and distal surface of the central cusp (Figure 7N).

The preserved lower gomphodont postcanines of the referred specimen NHMUK PV R36800, represented by a distal portion of a mandible, differ at some points from those of the holotype. As the latter, there is a decrease in size and elongation in the distalmost postcanines of the mandible, yet the last two lower gomphodont postcanines are particularly small and subcircular in outline in NHMUK PV R36800. As seen in the last lower gomphodont tooth of the holotype, the long axis of the antepenultimate lower gomphodont postcanine is slightly diagonally oriented from the labial margin of the mandible. The long axis of the two last gomphodont lower postcanines is, however, perpendicular to the long axis of the mandibular tooth row. The transverse crest of all preserved lower postcanines is composed of three high subtriangular cusps, of which the central cusps is the widest, even in the subcircular postcanines. The labial, lingual and central cusps appear to share the same height. Unlike the holotype, the labiodistal margin of the lower gomphodont postcanines of NHMUK PV R36800 is not angular but smoothly convex, whereas the linguodistal surface is concave in the third and second gomphodont teeth. Six distal cingular cuspules decreasing in size toward the central part of the cingulum can be counted in the antepenultimate gomphodont postcanine. Likewise, there are at least seven mesial cingular cuspules in the last gomphodont postcanine and their size diminishes towards the mid-width of the crown. As in the holotype, the enamel surface texture, well-visible on the surface of the central cusp, is braided in NHMUK PV R36800.

Sectorial postcanines

An isolated sectorial postcanine (Figure 7P-Q) belonging to the holotype was illustrated and briefly described by Hendrickx, Abdala & Choiniere (2016). This tooth most likely represents the shearing-type crown underlying the ninth right upper postcanine described by Crompton (1955). The postcanine consists of a mesiodistally long main cusp adjacent to a poorly developed mesial accessory cusp, and a well-developed subtriangular and apically pointed distal accessory cusp. Given this morphology, we assume that this is the distalmost tooth of the sectorial tooth row, probably the tenth right upper postcanine, as suggested by Crompton (1955). The mesial and distal carinae are serrated along the apical portion of the main cusp and the serrations extend across the apex of the cusp (Figure 7P-Q). The denticles are low, apicobasally elongated and show a symmetrically convex external margin. There is no trace of a cingulum on the labial or lingual margins of the crown. Two sectorial postcanines are present in NHMUK PV R36800 but little information can be extracted from their morphology due to their poor preservation. The first sectorial postcanine is being replaced by a mesiodistally elongated gomphodont? postcanine with a narrow and apically pointed lingual cusp and a much longer and higher central cusp. Both lower sectorial postcanine include a large distally recurved main cusp bounded mesially and distally by a mesial and distal accessory cusps. No lingual cingulum or serrated carinae appear to be visible in these badly preserved lower sectorial postcanines and their presence cannot be excluded.

Crown microstructure

Hendrickx, Abdala & Choiniere (2016) recently explored the enamel and dentin microstructure in two isolated gomphodont and sectorial postcanines of the holotype specimen of *Cricodon metabolus*. This study reveals that the enamel microstructure of this taxon is prismless and composed of discontinuous columnar divergence units (SCE). Abundant tubules and around 19 irregularly spaced striae of Retzius were also observed in the enamel layer, which is 11.5 thicker in gomphodont postcanines (176.5 µm in average in horizontal section) compared to sectorial teeth (15.4 µm in average in horizontal section). The dentin layer of *Cricodon* postcanine includes a large amount of tubules and approximately 100 incremental growth lines of von Ebner were counted in the gomphodont tooth.

***Trirachodon berryi* (Seeley, 1894)**

Holotype: NHMUK R3579, the mesial portion of the cranium with poorly preserved teeth.

Referred dental material: AM 434, 461 (holotype of *Trirachodon kannemeyeri*); BP/1/3511, 3775, 4258, 4658, 4661, 5050; BSP 1934 VIII 21, 22, 23; CGP INN 2000-7-2A, CGP unnumbered; GSN R327; NHMUK R2807, R3306, R3307, R3350, R3721 (holotype of *Trirachodon browni*); NMQR 122, 1399, 3279; SAM-PK-987, 5873 (holotype of *Trirachodon minor*), 5880, 5881, K142, K170, K171, K4801, K4803, K5821 (=12168?), K7888, K10157, K10161, K10176, K10207, K10411.

Occurrence: Lady Frere (type), Chris Hani District, Emalahleni Municipality, South Africa; Burghersdorp, Aliwal North, Joe Gqabi District, Gariep Municipality, South Africa; western buttress of Etjo Mountain, Otjozondjupa Region, Namibia.

Horizon: Subzone B of the *Cynognathus* AZ, Burgersdorp Formation, Karoo Basin; Omingonde Formation.

Age: Late Olenekian–Early Anisian, Middle Triassic.

Dental formula: I4/3 : C1/1 : PC6-12/8-9 (CPC1 : GPC4-10 : SPC0-2).

Dental morphology: The dentition of *Trirachodon* has received particularly little attention compared to other gomphodonts, and information on the dental anatomy of this taxon mostly rely on the rather limited descriptions and illustrations of Seeley (1894) and Broili & Schröder (1934). Firsthand examination of *Trirachodon* specimens with the best-preserved dental material ~~allows to provide~~ a comprehensive description of the dentition of this taxon. Dental differences in the specimens referred to *T. berryi* and *T. kannemeyeri*, considered to be separated species by several authors, are also discussed in the Discussion section.

Incisors

The incisors, well-preserved in the specimens CGP INN 2000-7-2A, SAM-PK-K171, SAM-PK-K5821 and BP/1/4658, have serrated mesial and distal carinae at least in the first upper and lower incisors of SAM-PK-K5821 (Figure 8A-C) and SAM-PK-K171, respectively. Mesial denticles are also visible in the third upper incisor of BP/1/4658. No denticles could be seen in the lower incisors of BP/1/4658 and 4661. It is unknown whether the absence of denticles in some upper and lower incisors is a genuine condition of *Trirachodon*. The presence of unserrated canines in some specimens would, however, suggests so. The mesial denticles of SAM-PK-K5821 are well-separated, apicobasally elongated and almost subquadrangular at the base of the carina (Figure 8B). As other diademodontids and trirachodontids, they sporadically change in size and their external margin is weakly symmetrically to asymmetrically convex. Unlike *Cricodon*, which counts much larger denticles, there are 6 and 10 mesial denticles per mm in the *Trirachodon* specimens SAM-PK-K5821 and BP/1/4658, respectively. The largest denticles are situated apically, and given the fact that the apex and basal portions of the crown is missing, it is unknown whether the denticles reached the apex and cervix. The distal denticles of the first and second incisors of SAM-PK-K5821 are incipiently developed and form poorly delimited convexities changing sporadically in size along the carina (Figure 8C). These serrations appear to extend well-above the cervix and get flared at mid-crown. Some upper and lower incisors are weakly mesiodistally constricted at the cervix, conferring a folidont (i.e., leaf-shaped) morphology to the crown. The cross-section outline of the upper and lower mesial incisors is D- to salinon-shaped, with the mesial carina positioned mesially and the distal carina facing linguodistally (Figure 8D, E). The incisors from the distal half of the jaw appear to have a more semi-circular cross-section outline, with the distal carina facing distally. Similar to *Langbergia*, a concave surface adjacent to the distal margin of the crown is visible on the labial surface of the second? upper incisor of SAM-PK-K5821.

Canines

The canines of the specimens of *Trirachodon* SAM-PK-K171, K5821, K10157 and BP/1/4658, 4661 and 3511 have both mesial and distal carinae serrated. Unserrated canines are, however, present in the specimens BSP 1934 VIII 21 and 22 as well as SAM-PK-K7888. The denticles are minute, sometimes barely discernable, and always apicobasally elongated (Figure 8H). They sporadically change in size along the carina and have symmetrically to asymmetrically convex external margins. In some specimens, the denticles are incipiently developed or restricted to a small portion of the crown (e.g., BP/1/3511, SAM-PK-K5821). The denticles of the canines are larger than those of the incisors, with mesial and distal denticle density ranging from four to nine denticles per mm in the canines. In BP/1/4658, the mesial carina is lingually deflected whereas the distal carina is centrally positioned on the distal margin of the crown. A long concave surface adjacent to the distal carina is clearly present on the labial and sometimes lingual sides of the canine in BSP 1934 VIII 22, SAM-PK-K171, K5821, K10157 and BP/1/4658, 4661. A similar concave surface adjacent to both carinae on the lingual side can be seen in the lower canine of SAM-PK-K171. Transverse undulations and/or faint or conspicuous longitudinal ridges can be observed on the labial surface of the canine of BP/1/4661 (Figure 8F, G) and SAM-PK-K12168. The cross-section outline of the incisor is elliptical, lenticular or salinon-shaped at mid-crown, indicating some important variation in cross-section outline in *Trirachodon*. The enamel texture of BP/1/4661 is clearly braided and oriented, curving basally adjacent to the carinae (Figure 8G). The texture of the enamel appears to be smooth in the canines of the other specimens though.

Upper gomphodont postcanines

The morphology of the upper postcanines is based on the specimens BSP 1934 VIII 21, SAM-PK-K171, SAM-PK-K4801, NHMUK R3307 and BP/1/4658. As *Cricodon* and *Sinognathus*, the upper postcanines are labiolingually expanded and ovate in outline. They increase in size and elongation distally up to the antepenultimate or penultimate gomphodont tooth. The first upper postcanine is the smallest and, with a CBR ranging from 1.1 to 1.6, the least labiolingually elongated of the upper gomphodont tooth row. This tooth is missing, badly preserved or in occlusion and obscured by the lower postcanines in all specimens examined first hand but CT-scan data of AM 461 allows to provide some information on its morphology. The tooth is subconical, i.e., the crown is simple, slightly labiolingually elongated, labiolingually constricted at the cervix and bears a centrally positioned central cusp but no labial and lingual cusps nor a mesial and distal cingula.

The CBR of the more distal upper postcanines varies from 1.4 to 2.4 and the outline of the crown in apical view only slightly changes along the tooth row. In BSP 1934 VIII 21 and BP/1/4658, the postcanines from the mesial half of the upper postcanine are reniform (sensu Hendrickx, Mateus & Araújo, 2015), with a weakly to strongly concave mesial margin. This outline results from the presence of a distal 'shouldering' between each tooth, which are in close contact in these two specimens. In SAM-PK-K171 and SAM-PK-K4801, the reniform outline is restricted to the third and fourth upper postcanines, yet the mesial margin is only weakly concave in the fourth tooth. If the distal margin of the upper postcanines from the mesial half of the *Trirachodon* crown is typically convex, this distal margin is sigmoid in BSP 1934 VIII 21 due to the presence of a narrow concavity on the lingual third of the distal surface of the crown. Such dental feature is, however, restricted to this specimen. The more distal upper postcanines of *Trirachodon* are roughly ovate in outline, but a weak mesiodistal constriction occurs at the labial third of the crown in SAM-PK-K171, SAM-PK-K4801, and NHMUK R3307 (Figure 8I, K-M). This constriction, created by the presence of a concavity on the labial third/half of the distal margin of the postcanine, leads to an asymmetrical crown-shape, in which the labial third is shorter than the lingual two-thirds of the postcanine (Figure 8I, K-M). Such concavity is particularly pronounced in the last upper gomphodont postcanines. It is, however, absent in the postcanines of BSP 1934 VIII 21 and BP/1/4658 so that the upper postcanines are subsymmetrical in shape in these two specimens (Figure 8J).

As other trirachodontids, the upper postcanines of *Trirachodon* consist of a mesial and distal cingula extending on the mesial and distal rims of the crown as well as a labiolingually elongated transverse crest. The latter is made of a labial, central and lingual cusps and bounded mesially and distally by the wide mesial and distal basins, respectively (Figure 8I-K). The transverse crest is centrally positioned on the crown in the postcanines from the mesial half of the upper tooth row in BP/1/4658, SAM-PK-K171 and NHMUK R3307, and distally deflected in BSP 1934 VIII 21. Unlike *Cricodon*, the transverse crest runs diagonally on the crown in the distalmost gomphodont postcanines. The diagonal orientation of the transverse crest, particularly noticeable in NHMUK R3307, SAM-PK-K171 and SAM-PK-K4801, results from the distal deflection of the labial cusp, which points apicodistally in these specimens (Figure 8I, K-M). The central cusp is closer to the lingual cusp in most specimens, and centrally positioned on the transverse crest in SAM-PK-K4801. The central cusp is typically apicolingually inclined in distal view, so that the concavity bordering the central cusp on the transverse crest is deeper between the central and labial cusps. The latter consists of a three-faced pyramidal structure, in which the edges form the labiomesial, labiodistal and labiocentral ridges. The lingual cusp shares the same shape, with a labiodistally shorter linguocentral ridge. Similar to *Cricodon*, the labiomesial and labiodistal ridges of the labial cusp are serrated in at least one postcanine of SAM-PK-K171 and SAM-PK-K4801. The linguomesial, linguodistal, centrolabial and centrolingual ridges do not, however, appear to have serrations. The mesial and distal cingula typically bear a low number (i.e., < 6) of cingular cuspules restricted to a certain portion of the cingulum or along the whole width of the cingulum (Figure 8M-N). We counted three, four and five cingular cuspules on the mesial cingulum of the best-preserved postcanines of NHMUK R3307, SAM-PK-K171 and BSP 1934 VIII 21, respectively, and three to four, four, five, and six to seven distal cingular cuspules in SAM-PK-K171, BSP 1934 VIII 21, SAM-PK-K4801 and NHMUK R3307, respectively. The size of the cingular cuspules varies sporadically along the cingulum and does not follow any pattern along the tooth row. We, however, note that the widest cingular cuspules are often located in the middle or lingual part of the crown. When restricted to a certain portion of the postcanine, the cingular cuspules variously occupy the central, lingual or labial part of the crown. Large cingular cuspules have been observed in the labiomesial, labiodistal, linguomesial and linguodistal sides of the fully complete postcanines. Given the fact that none of these large cingular cuspules are present in all postcanines of the tooth-row, they may not be homologous to the accessory cusps of some gomphodonts. The presence of labiomesial, labiodistal, linguomesial and linguodistal accessory cusps in the upper gomphodont postcanines *Trirachodon* cannot, however, be ruled out.

The morphology of the distalmost upper gomphodont postcanine of the holotype and referred specimens NHMUK R3579 and BSP 1934 VIII 21, respectively, which represent the specimens of *Trirachodon* with the highest number of gomphodont postcanines (i.e., 11 and 12, respectively), departs from that more mesial upper postcanines. In NHMUK R3579, the last postcanine is half the size of the preceding teeth, elliptical, long and short (CBR of 1.3) and displays a centrally positioned transverse crest ringed by the mesial and distal basins and cingula. The transverse crest includes a long and wide labial cusp, a lingually displaced central cusp and a narrow lingual cusp. The labial cusp, of which the base is preserved, was the largest and likely the highest of all three, while the central and lingual cusps appears to have the same height. The mesial cingulum seems to encompass four cingular cuspules, in which the widest, which may correspond to the labiomesial accessory cusp, is directly mesial to the labial cusp. Two particularly wide distal cingular cusps adjacent to the labial and lingual cusps may also represent the labio- and linguodistal accessory cusps of other gomphodont upper postcanines. Unlike NHMUK R3579, the last upper postcanines of BSP 1934 VIII 21 appears to be strongly labiolingually elongated and includes a long, high and lingually deflected central cusp and a much shorter, apically pointed labial cusp (Figure 8O). Unlike NHMUK R3579 and more mesial gomphodont postcanines, this tooth does not have a lingual cusp nor a distal basin and cingulum. Given that the mesial portion of the tooth is still embedded in matrix, it is unknown whether the mesial basin and cingulum were present or not. The root is twice as long as the crown at mid-width of the tooth, tapers apically and has a linguobasally inclined lingual margin and sub-vertical labial border (Figure 8O). The basolingual portions of the crown and root of BSP 1934 VIII 21 also show an extensive parallelogram-shaped wear facet on its distal surface.

Lower gomphodont postcanines

Well-preserved lower gomphodont postcanines are present in SAM-PK-K171, SAM-PK-K4801 and BP/1/4658. The first postcanine, only seen in BP/1/4658 (Figure 9D), is significantly smaller than the more distal postcanines, as witnessed by the particularly small size of the alveoli in SAM-PK-K171. Its morphology does not differ from that of more distal gomphodont postcanines (Figure 9D). Similar to *Langbergia* and unlike *Cricodon*, the long axis of the lower gomphodont postcanines is linguomesially oriented and never perpendicular to the mandibular tooth row (Figure 9A-C). The mesiolingual inclination of the first and last gomphodont teeth is more pronounced than the others in BP/1/4658 and SAM-PK-K171. The lower postcanines decrease in size from the middle of the mandibular tooth row in BP/1/4658, so that the last gomphodont tooth is as small as the first postcanine. As in *Langbergia* and unlike *Cricodon*, such decrease in size occurs from the penultimate lower postcanine in SAM-PK-K171 and SAM-PK-K4801. The lower gomphodont postcanines share the same morphology than that of upper postcanines, yet they are symmetrical in the transverse and sagittal axes and narrower, with a CBR varying from 1.3 to 1.6 (Figure 9A-C). The central cusp is centrally positioned on the crown and occupies most of the transverse crest width. As in other trirachodontids, this cusp is bordered by the labial and lingual cusps, and the three cusps all share the same height. The mesial and distal basins are deep and both surround the dome-like central cusp mesially and distally, respectively (Figure 9A-C). The mesial and distal cingula are symmetrically concave and parabolic in shape in mesial and distal views. They include a variable number of cingular cuspules extending between the labial and lingual cusps. There are two to three and four cingular cuspules on the mesial cingulum in the best-preserved lower postcanines of SAM-PK-K171 (Figure 9A, E) and SAM-PK-K4801 (Figure 9B-C), respectively, and four distal cingular cuspules in both specimens. Six to seven cingular cuspules appear to be present on the distal cingulum of the fifth right and left postcanines of BP/1/4658, respectively, while more than seven distal cuspules were present on the sixth left lower tooth. Unlike *Cricodon*, the widest cuspules typically occur in the center or labial portions of the crown. The last lower gomphodont postcanine of SAM-PK-K4801 (Figure 9C) has the peculiarity of having a particularly high transverse crest, higher than this of more mesial postcanines. The central cusp strongly protrudes apically and is higher than both the labial and lingual cusps. The distal cingulum comprises six well-separated cingular cuspules whereas the mesial cingulum includes three cuspules in its labial half (Figure 9C). The last lower postcanine of SAM-PK-K171 and BP/1/4658 share the same morphology with the other lower postcanines. The enamel texture of *Trirachodon*'s upper and lower postcanines, clearly visible on the mesial and distal surfaces of the central cusp, is braided and oriented.

Sectorial postcanines

One or two upper and lower sectorial teeth are ~~bore~~ by the specimens SAM-PK-K4801, SAM-PK-K171, SAM-PK-K12168, BP/1/4658, BP/1/4661, BP/1/3511, and CGP INN 2000-7-2A. The first right upper sectorial tooth of SAM-PK-K4801 is simpler and shorter than the second one (Figure 9F). It includes a main distally positioned and recurved cusp followed mesially by a smaller accessory cusp. This mesial accessory cusp is symmetrically convex and projects from the mesial surface at one third of the crown. The single or distalmost upper sectorial postcanine shares the same morphology, i.e., it comprises a main cusp, a mesial accessory cusp at one half of the crown and two distal accessory cusps occupying the distal third of the crown (Figure 9F). The main cusp typically occupies the two and three fifth of the crown length. It consists of a subtriangular, apicodistally pointed or strongly distally recurved (Figure 9F) projection, and its external margin is strongly parabolic and asymmetrically convex. The mesial accessory cusp can be minute and forms a tiny bump on the mesial surface of the main cusp, or a large, apically pointed projection similar in size or slightly longer than the distalmost accessory cusp. The two distal accessory cusps are straight, decrease in size distally, and either point apically or apicodistally. The first distal accessory cusp either forms a low, weakly pointed and mesiodistally long convexity or a high and short projection. No cingular cuspule were observed on the labial and lingual margin of the upper sectorial postcanines of *Trirachodon*. Variation in the morphology of the last sectorial appears to occur between the left and right sides of the cranium, as seen in SAM-PK-K4801. In this specimen, the mesial accessory cusp of the last upper sectorial postcanine consists of a poorly-developed bump on the right side (Figure 9F) and a large and strongly protruding projection on the left side. Likewise, the first distal accessory cusp of this sectorial postcanine is mesiodistally short and high on the right side (Figure 9F) and long and low on the left side.

The morphology of the single or first lower sectorial postcanine is significantly different from that of the upper sectorial teeth. The crown is particularly wide, especially in BP/1/4658 (CBR of 0.6 to 0.65). The crown consists of a large and high apically pointed main cusp bordered by two small apically projected mesial and distal accessory cusps (Figure 9I). The distal accessory cusp is larger than the mesial one in SAM-PK-K171 and BP/1/4658. The three cusps are bounded lingually by a mesiodistally concave cingulum made of minute cingular cuspules (Figure 9G). This lingual cingulum either extends along the whole length of the crown or is restricted to the mesial half of the postcanine, as seen in SAM-PK-K171. A labial cingulum is also present on the lower sectorial postcanine and occupies the whole length, as seen in the right lower postcanine of BP/1/4658 (Figure 9I), or a small portion of the distal surface of the crown only, as in SAM-PK-K4801 (Figure 9H).

The second lower postcanine, only well-preserved on the left jaw of BP/1/4658 (Figure 9I-J), is narrower, with an CBL of 0.54. The tooth includes a main cusp occupying slightly more than the mesial half of the crown, and two distal accessory cusp, of which the mesial one is the longest. No mesial accessory cusps appear to be present in the second left and right lower sectorial postcanines. The distal accessory cusp points apically and is not distally recurved (Figure 9I-J). The main cusp, of which only the base is visible, was likely significantly higher than the distal accessory cusp on the left side of the jaw. The distal accessory cusp of the second right sectorial postcanine is, however, much larger and probably only slightly lower than the main cusp. The distal accessory cusp consists of a symmetrically parabolic convexity while the second accessory cusp is a minute and pointed projection (Figure 9I-J). A lingual cingulum bearing several minute cuspules extends along the whole length of the crown (Figure 9J). The second right lower sectorial postcanine of BP/1/4658 is significantly shorter than the preceding one (65% smaller) and is being replaced by another sectorial postcanine (Figure 9I-J). This tooth erupts distally from the second sectorial postcanine, and its morphology is reminiscent to that of the upper sectorial postcanines in that it has an apically recurved main cusp. No mesial or distal accessory cusps appear to be present on this erupting postcanine but they might be hidden by the matrix. The main cusp has an unserrated mesial carina twisting lingually and no cingulum is present at the base of the lingual surface of the crown (Figure 9J).

Dent~~ition~~ morphotypes in Trirachodon berryi

As noticed by previous authors such as Sidor and Hopson (2018), two dental morphotypes of *Trirachodon* can be observed. AM 461, SAM-PK-K171, SAM-PK-K5821, NHMUK R3307 (included in the taxon '*Cricodon kannemeyeri*' by Sidor and Hopson (2018), see Discussion below), as well as CGP INN 2000-7-2A, SAM-PK-K4801, BP/1/4661 and BP/1/3511, share a combination of dental features not seen in other specimens of *Trirachodon*, i.e., serrated canines, less than ten upper postcanines comprising one or two upper and lower sectorial teeth, transversely asymmetrical distal upper gomphodont postcanines, in which the lingual half of the crown is longer than the labial one, a diagonally oriented transverse crest on the crown, and a slightly apicodistally pointed labial cusp. These specimens indeed differ from NHMUK R3579, BSP 1934 VIII 21 to 23 and SAM-PK-K7888 (classified among *Trirachodon berryi* by Sidor and Hopson (2018), see below), characterized by the following dental features: unserrated canines, more than nine upper postcanines, no sectorial teeth, transversely symmetrical distal upper postcanines (i.e., labial and lingual halves of the crown of the same length, apically pointed labial cusp, and non-diagonally oriented transverse crest on the crown) and last upper gomphodont postcanine being significantly smaller than the preceding tooth.

It should, however, be noted that the specimen NHMUK R3307 does not have a sectorial postcanine on the right portion of the maxilla while a particularly low number of upper postcanines (i.e., seven) is present in this specimen. The absence of a diagonally oriented transverse crest in the upper postcanines of BSP 1934 VIII 21 could also be explained by the fact that the labial cusp of some gomphodont postcanines is worn out. All specimens classified in the morphotype of *Trirachodon berryi* do not preserve incisors and only two of them (i.e., BSP 1934 VIII 21, SAM-PK-K7888) bear canines. The latter are, however, incomplete and/or badly preserved and the absence of denticles could be explained by the fact that they have been worn out from the carinae due to the advanced age of the individuals (see Discussion). We also note that BP/1/4658 appears to represent a transitional form between the dental morphotypes of *T. berryi* and '*T. kannemeyeri*', as this specimen includes finally serrated canines, subsymmetrical and non-mesiodistally constricted upper gomphodont postcanines with a non-diagonally oriented transverse crest and a complete distal cingulum (present at least in the fifth right upper postcanine), penultimate and last upper gomphodont postcanines with a CBR > 2, seven upper postcanines, as well as one upper sectorial postcanines and two lower tricuspid sectorial postcanines bearing a lingual cingulum. We propose that the dental differences between these two morphotypes are ontogenetic and not interspecific, as some authors suggest, an hypothesis developed in the Discussion section.

***Sinognathus gracilis* (Young, 1959)**

Holotype: IVPP V2339, an almost complete skull.

Occurrence: Peipanching Shihpi, Wuhsiang-Yüshe area, Shanxi Province, China.

Horizon: Upper Ermaying Formation.

Age: Early Anisian, Middle Triassic.

Dental formula: I4/2 : C1/1 : PC6/7 (CPC? : GPC5 : SPC?).

Dental morphology: The dentition of *Sinognathus gracilis*, briefly described by Young (1959) due to the lack of preparation of the skull, has received a relatively good description from Sun (1988) following a re-preparation of the postcanines teeth. Firsthand examination of the holotype allows providing a few additional details on the dental material of this taxon.

Incisors and canines

The incisors, poorly preserved in the holotype and only specimen of *Sinognathus*, do not show a constriction at the level of the cervix (Figure 10A). Minute denticles can be seen at the base and apex of the distal carina of the fourth left upper incisor (Figure 10B, C). We counted eight denticles per mm on this tooth. No other incisor appears to bear serrations. The cross-section through the root base of the first left upper incisor is more or less subcircular (Figure 10D). The root base of the left and right upper canines, the crown base of the right lower canine as well as the root, crown base and a small portion of the mesial part of the left lower canine are preserved (Figure 10E, F). None of these portions of the canines show serrations (Figure 10F) and it is unknown whether denticles are unpreserved or absent. The cross-section outline through the root base of the left upper canine is roughly lenticular (Figure 10G). The left lower canine is mostly projected apically, whereas the right canine appears to be weakly procumbent. The root base of the left lower canine is slightly longer than the crown base. The root is two-thirds the height of the crown and tapers basally (Figure 10E).

Gomphodont postcanines

All postcanines are in occlusion. Information on their morphology can, however, be extracted from the right upper postcanines, of which the lingual portion has been prepared and is visible in medioventral view (Figure 10J-L), and from a mid-crown sagittal section through the upper and lower postcanines of the left jaw side of the skull (Figure 10H, I, N). Some parts of the labial portion of the right lower postcanines can also be seen in labial view (Figure 10M). As described by Sun (1988), the upper postcanines are labiolingually elongated and consist of a labiolingually oriented and slightly distally positioned transverse crest. The latter is apically high and comprises labial, central and lingual cusps of the same height. A small concavity separates the central and lingual cusps in the best-prepared upper postcanine (Figure 10J-L). The central cusp is wide, the widest of the three cusps, and centrally located on the transverse crest. The mesial and distal ridges, visible in the sagittal cross-section through the fourth left upper postcanines, bound the mesial and distal margins of the gomphodont postcanines (Sun, 1988).

These ridges are not visible in the lingual portion of the exposed upper postcanines, yet poorly preserved cingular cuspules appear to be present on what would then be the distal cingulum of the third upper postcanine (Figure 10K). A linguomesial accessory cusp may have been present in the upper gomphodont postcanine (Figure 10K). No other accessory cusps are visible in the upper postcanines. The mesial basin is longer than the distal one, and both basins are horizontal and shallow.

Few details on the lower gomphodont postcanines of the holotype can be observed. They are labiolingually elongated and bear an apically high transverse crest bounded by the mesial and distal basins. Both basins are mesiodistally concave, yet the distal basin is horizontally positioned and shallow whereas the mesial basin is basally inclined and shorter. The transverse crest is slightly mesially deflected and includes labial, central and lingual cusps roughly sharing the same height. A faint mesial ridge is present at the rim of the lower postcanine. Remnant of mesial cuspules appear to be present on this ridge (Figure 10M), but this need to be confirm with CT-data in better preserved postcanines. Based on the sagittal cross-section through the left lower postcanines, no distal ridge or cingulum appears to be present.

The sixth right upper postcanine was interpreted as a sectorial by Sun (1988). The crown is, however, incomplete, with the labial and central portion missing, and only an horizontal cross-section through the root can be seen in ventromedial view (Figure 10O). A closer look at the cross-section outline reveals that the sixth upper tooth was a gomphodont and not a sectorial postcanine. This is corroborated by the fact that the preserved portion of this crown shows a labiolingually oriented transverse ridge in the middle of the crown (Figure 10O-P), whereas no sectorial postcanines bear such ridge in gomphodont cynodonts ~~(pers. obs.)~~. In addition, sectorial teeth/alveoli are typically labially positioned from the long axis of the tooth row in all gomphodont cynodonts (with the possible exception of *Beishanodon*; see discussion below), at the level of the labial half of the gomphodont postcanines. The preserved portion of the sixth upper postcanine is, however, at the same level as the lingual half of the preceding tooth (Figure 10P). Based on firsthand examination of the specimen IVPP V2339, nothing support the presence of sectorial postcanines in *Sinognathus*.

***Beishanodon youngi* (Gao et al., 2010)**

Holotype: PKUP V3007, an incomplete cranium.

Occurrence: Beishan locality, Quarry-3, in Beishan Hills, northern Gansu Province, China.

Horizon: Lower Triassic dark shales, Hongyanjing Formation.

Age: Late Olenekian, Middle Triassic.

Dental formula: I4/? : C1/? : PC8/? (CPC2 : GPC7 : SPC?).

Dental morphology: The dentition of this taxon, which is only known from six upper gomphodont postcanines belonging to the mesial and central portions of the cranium, has been comprehensively described by Gao et al. (2010). The dental morphology of *Beishanodon*, which departs from that of other trirachodontids in many aspects, is addressed in the next section.

Discussion

The dentition of diademodontid and trirachodontid gomphodonts, one of the most complex among non-mammaliaform cynodonts, show a large variety of dental features previously unknown or undescribed. The following homologous dental characters were shown to be present and relatively common in the dentition of non-traversodontid gomphodonts: i) concave surfaces adjacent to the carinae in the incisors and canines; ii) transverse undulations, longitudinal ridges and a sporadic variation in denticles size along the carinae in the canines; iii) denticulated carinae in the incisors, canines and sectorial postcanines; iv) serrated transverse crest and labial cusps, mesial and distal cingular cuspules, and a braided enamel surface texture in the gomphodont postcanines; and v) lingual and labial cingula in the sectorial postcanines. In diademodontids, we revealed the presence of denticles changing sporadically in size along the carinae in the canines, lingual cingular cuspules in the conical postcanines, serrated labial cusp in the gomphodont postcanines and biserrated denticles in the sectorial postcanines in *Diademodon*, and a labiomesial accessory cusp as well as mesial cingular cuspules, in the upper gomphodont postcanines of *Titanogomphodon*. The presence of these dental characters in *Titanogomphodon*, however, requires confirmation with better-preserved specimens. In trirachodontids, we described for the first time serrated carinae in the incisors and sectorial postcanines as well as longitudinal ridges in the canines of *Langbergia*, concave surfaces adjacent to the carinae in the canines and a biconvex distal cingulum in the upper postcanines of *Cricodon*, transverse undulations and longitudinal ridges in the canines as well as labial and lingual cingular cuspules in the lower sectorial postcanines of *Trirachodon*, and serrated incisors and no sectorial postcanine in *Sinognathus*.

A thorough examination of the dentition of Diademodontidae and Trirachodontidae enable us to provide a list of apomorphic dental features for both clades and their respective taxa. Unambiguous apomorphic characters are underlined:

- Diademodontidae: presence of a transitional postcanine in the upper and lower tooth row; presence of one or several accessory rides on the mesial surfaces of the transverse crest; absence of mesial and distal basins in some upper gomphodont postcanines.
- *Diademodon tetragonus*: presence of accessory ridges on the distal surface of the transverse crest in the upper and lower gomphodont postcanines (possibly present in *Titanogomphodon* given the particularly worn upper postcanines of the holotype specimen); absence of a labiomesial accessory cusp on the upper gomphodont postcanines.
- *Titanogomphodon crassus*: transverse crest located on the mesial half of the upper gomphodont postcanines; elongation axis of the upper sectorial postcanines strongly diagonally and mesiolingually oriented from the labial margin of the cranium and the main axis of the upper tooth row.
- Trirachodontidae: presence of labial and lingual cusps of the same height in the lower postcanines, absence of shearing planes between the outer surface of the main cusp of the lower and the inner surfaces of the main cusps of the upper postcanines.
- *Langbergia modisei*: denticles restricted to the distal carina of the incisors; long axis of the upper postcanines diagonally and labiodistally oriented from the long axis of the cranial tooth row; ovoid-/ellipsoid-shaped upper gomphodont postcanines; a transverse crest of the upper gomphodont postcanine forming a high crest; presence of deep concavities extending to or close to the level of the mesial and distal basins between the labial/lingual cusps and the central cusp in the upper and lower gomphodont postcanines.
- *Cricodon metabolus*: large denticles, i.e., less than 20 denticles along the crown height, in the incisors; presence of distally inclined distalmost upper gomphodont teeth in relation to the axis of the skull; step-like disposition of distalmost upper gomphodont postcanines; asymmetrical upper gomphodont postcanines, in which the lingual half of the crown is significantly longer than the labial half; transverse crest of the upper gomphodont postcanines forming a high crest; central cusp of the upper postcanines close to the lingual cusp; more than ten lower postcanines.

- *Trirachodon berryi*: shallow and poorly delimited paracanine fossa; strongly labiolingually elongated upper and lower postcanines (i.e., CBR of more than 1.8 and 1.5 for upper and lower postcanines, respectively); last upper postcanine extending ~~at~~ the same level ~~than~~ the anteriormost margin of the subtemporal fossa; presence of labial cingular cuspules in the sectorial postcanines.
- *Sinognathus gracilis*: no more than two lower incisors; non-cusp~~idated~~ distal ridge in the upper gomphodont postcanines.
- *Beishanodon youngi*: small size of the upper postcanines compared to the skull dimension (shared with *Diademodon*, see below; Figure 11); labial position of the upper postcanines from the paracanine fossa; presence of a small central cusp adjacent to a larger labial cusp in the upper conical postcanines; asymmetrical upper gomphodont postcanines, in which the labial half of the crown is significantly longer than the lingual half; transverse crest located on the distal half of the crown.

The peculiar dentition and affinities of *Beishanodon*

According to Gao et al. (2010), the placement of *Beishanodon* within Trirachodontidae is supported by an ovoid-elliptical outline of the upper postcanines and a long axis of the postcanine tooth row directed toward the center of the subtemporal fenestra. The upper postcanines of *Beishanodon* also share with trirachodontids a low transverse crest made of a labial, central and lingual cusps combined with a distal cingulum comprising a large number of cingular cuspules. One, possibly two, sectorial postcanines, also appear to be present based on the alveol~~i~~ outline of the right maxilla, at the end of the tooth row (Gao et al., 2010, figure 5 and 6a) but this cannot be confirmed with the absence of the actual postcanines. The dentition of this taxon is nonetheless unusual in many aspects for a trirachodontid: the upper postcanine are particularly small in relation to the skull size and only *Diademodon* shares a low upper postcanine/skull length ratio (Figure 10). The first upper conical postcanine comprises a small central cusp adjacent to a larger labial cusp (Gao et al., 2010), a feature absent in other gomphodont taxa. In addition, the transverse crest of the postcanines three and four is distally positioned and directly located near the distal border of the tooth, giving the impression that the postcanine of *Beishanodon* has a traversodontid-like occlusal basin. According to ~~the~~ figure 6A from Gao et al. (2010), the central cusp of at least the second right postcanine is also strongly labiodistally oriented, a feature absent in all other trirachodontids. Finally, the sectorial postcanine(s), if present, would be weakly lingually deflected from the long axis of the tooth row (Gao et al. (2010), figure 5 and 6a) whereas all gomphodont cynodonts have their sectorial postcanine labial to this axis ~~(C.H. pers. observ.).~~

Beishanodon and *Sinognathus* were recently suggested to be basal probainognathians close to *Aleodon brachyrhamphus* by Hopson (2014) and Sidor & Hopson (2018). Nonetheless, the dentition of *Aleodon*, the only non-tritylodontid probainognathian with labiolingually elongated and ovoid postcanines, strongly differs from that of *Beishanodon* and *Sinognathus* in the following features: upper postcanine tooth row curved, with a long axis of the posterior portion directed towards the lateral part of the subtemporal fossa, postcanines strongly protruding from the alveoli, second and third upper postcanines subcircular and smaller than the more distal postcanines, no transverse crest, central cusps or mesial and distal cingula in the postcanines, labial cusp significantly larger (i.e., longer, wider and higher) than the lingual 'cusp' (when present) in the upper postcanines, and the absence of a wide lingual platform directly laterodorsal to the postcanines. For those reasons, we consider both *Beishanodon* and *Sinognathus* to be confidently classified among gomphodont cynognathians. Likewise, given the presence of a single conical postcanine, six upper gomphodont postcanines comprising a distal cingulum and a low transverse crest made of a labial, central and lingual cusps, a straight postcanine tooth row directed towards the centromedial portion of the temporal fenestra, and possibly one or two sectorial postcanines, *Beishanodon* is here tentatively referred as a trirachodontid. This suggests that the two gomphodonts *Diademodon* and *Beishanodon* convergently evolved large skulls compared to the upper postcanines, the latter remaining particularly small in mature individuals of these two taxa.

Dental differences between *Trirachodon berryi* and '*Trirachodon kannemeyeri*'

Two species of *Trirachodon*, *T. berryi* and '*T. kannemeyeri*', were distinguished by Seeley (1894) based on the snout expansion and the number and labiolingual elongation of the maxillary teeth. Although these two taxa were synonymized by Hopson & Kitching (1972) (n.b., along with *Trirachodon minor*, *Trirachodontoides berryi* and *Inusitatodon smithi*) and Abdala, Neveling & Welman (2006), they were considered as separate species by Broom (1932), Kitching (1977) and more recently by Hopson and Sidor (2015) and Sidor and Hopson (2018).

According to the two latter authors, *T. berryi* includes the specimens NHMUK R3579, BSP 1934 VIII 21 to 23 and SAM-PK-K7888, whereas the specimens AM 461, SAM-PK-K171, SAM-PK-K5821 (=SAM-PK-K12168), and NHMUK R3307 belong to '*T. kannemeyeri*'. SAM-PK-K11481 is also included in the latter taxon by Sidor and Hopson (2018), yet, as stated by Abdala, Neveling & Welman (2006), SAM-PK-K11481 is here referred to *Langbergia* based on the absence of the maxillary lateral platform and the curvature of the ventral margin of the dentary. CT-scanning data and reconstruction of the dentition, in occlusion in this specimen, will, however, confirm referral to this taxon in the future.

Sidor and Hopson (2018) list the following apomorphic characters in the dentition of *Trirachodon berryi*: i) the upper gomphodont postcanines are slightly less than twice as wide as long (i.e., CBR < 2) and are transversely symmetrical in apical view; ii) the mesial and distal cingula are usually complete and typically bear small cingular cuspules; iii) the sectorial upper postcanines are absent; and iv) the last upper gomphodont postcanine is transversely expanded, and about two-thirds the transverse diameter of the preceding tooth, with reduced labial and lingual cusps. Sidor and Hopson (2018) also suggest that the dentition of '*T. kannemeyeri*' and *Cricodon* are closer than that of *Trirachodon berryi*, so ~~that~~ these authors place *T. kannemeyeri* among the genus *Cricodon*. According to Sidor and Hopson (2018), *Cricodon metabolus* and '*Cricodon kannemeyeri*' share the following dental synapomorphies: i) transversely expanded upper and lower gomphodont postcanines with one or two sectorial teeth at the rear of the tooth row; ii) distal upper gomphodont postcanines more than twice as wide as long (i.e., CBR > 2) and transversely asymmetrical in apical view, with the lingual half of the crown usually being mesiodistally longer than the labial half of the crown; iii) cingular cuspules varying in size, with some being particularly large; iv) mesial and, less frequently, distal cingula often incomplete, and sometimes even absent; v) distalmost one or two postcanines sectorial and formed by three main cusps oriented mesiodistally and often with a narrow lingual cingulum.

Although Sidor and Hopson (2018) note that the mesial and distal cingula are usually complete and bear small cingular cuspules in *T. berryi*, the distal cingulum is complete and includes a large number of cingular cuspules in NHMUK R3307 and SAM-PK-K4801. Likewise, important variations in size in the mesial and distal cingular cuspules, which are as large as other *Trirachodon* specimens, can be noticed in BSP 1934 VIII 21. Seeley (1894) and Sidor and Hopson (2018) also note difference in the elongation of the upper gomphodont postcanines between the two *Trirachodon* species, yet the CBR of the penultimate upper gomphodont postcanine of BSP 1934 VIII 21 is 2.3 whereas the crown of SAM-PK-K171 from the same position has a CBR of 2.

As stated before, we, nonetheless, agree with Sidor and Hopson (2018) that two morphotypes can be observed among the specimens referred to *Trirachodon berryi* and '*T. kannemeyeri*' but propose that the dental differences between these morphotypes can be explained by ontogeny. *Trirachodon berryi* sensu Sidor and Hopson (2018) can be considered as an older ontogenetic stage of '*T. kannemeyeri*', in which: i) the last sectorial postcanines were replaced by transversely symmetrical gomphodont postcanines; and ii) two to three upper gomphodont postcanines, with the last one bearing a large central cusp, and reduced labial cusp and lingual cusps (Figure 8O), were added in the distal portion of the tooth row. Such dental replacement and increase in the number of gomphodont teeth throughout ontogeny are common in gomphodont cynodonts and were observed in the closely related trirachodontid *Cricodon metabolus* (Crompton, 1955) as well as the basal traversodontids *Scalenodon angustifrons* (Crompton, 1955) and *Andescynodon mendozensis* (Goñi & Goin, 1988).

Given that both morphotypes of *T. berryi* and '*T. kannemeyeri*' are represented by large-sized specimens with a skull of more than ten centimeters (see Abdala, Neveling & Welman (2006), Table 4; pers. observ.), this suggests that the largest specimens referred to '*T. kannemeyeri*' were subadult/non-fully grown individuals in which: i) the maximum size was reached; and ii) the sectorial postcanines remained to be replaced by subsymmetrical upper gomphodont postcanines latter in their life. Specimens classified as *T. berryi* would consequently represent fully grown, most likely old, individuals in which all sectorial postcanines were replaced by gomphodont postcanines. This hypothesis is supported by size and wear in the upper and lower gomphodont postcanines. All specimens belonging to *T. berryi* have skulls of more than nine centimeters (see Abdala, Neveling & Welman (2006), Table 4) and show extensive wear in the upper and lower gomphodont postcanines (e.g., NHM R3579, BSP 1934 VIII21-23; SAM-PK-K7888; Sidor & Hopson (2018), figure 9C). On the other hand, wear is barely present or less extensive on the upper and lower gomphodont postcanines of specimens belonging to '*T. kannemeyeri*' (e.g., SAM-PK-K171, SAM-PK-K171, NHMUK R3307), which includes individuals whose skull length varies from 5.2 to ten centimeters (see Abdala, Neveling & Welman (2006), Table 4; pers. obs.). An exception to this rule is BP/1/4658 which bears seven particularly worn out upper and lower postcanines, and one upper and two lower sectorial teeth. As stated before, BP/1/4658 however appears to represent a transitional form between the dental morphotypes of *T. berryi* and '*T. kannemeyeri*' and likely belongs to a subadult individual. Consequently, all specimens previously referred to the species '*T. kannemeyeri*' are here interpreted as younger individuals of *T. berryi*.

Conclusions

The teeth of diademodontids and trirachodontids are particularly complex. Even the most comprehensive descriptions of the dentition of these gomphodont cynodonts have inadvertently omitted some dental features. The main differences between the dentition of diademodontids and trirachodontids include: i) the presence of a transitional postcanine in the upper and lower tooth row; ii) one or several accessory rides on the mesial and/or distal surfaces of the transverse crest; and iii) the absence of mesial and distal basins in some upper gomphodont postcanines in diademodontids; and i) the presence of labial and lingual cusps of the same height in the lower postcanines; as well as ii) the absence of shearing planes between the outer surface of the main cusp of the lower and the inner surfaces of the main cusps of the upper postcanines in trirachodontids. The most important autapomorphic dental characters for each diademodontid and trirachodontid taxa are: the absence of a labiomesial accessory cusp on the upper gomphodont postcanines in *Diademodon*, the diagonally oriented elongation axis of the sectorial and gomphodont postcanines in *Titanogomphodon* and *Langbergia*, respectively, the step-like disposition of the distalmost upper gomphodont postcanines in *Cricodon*, a labial cingulum in the lower sectorial postcanines in *Trirachodon*, no more than two lower incisors in *Sinognathus*, and a distally positioned transverse crest in the upper gomphodont postcanines in *Beishanodon*. Based on the morphology of the dentition, *Trirachodon berryi* and *T. kannemeyeri* more likely correspond to two morphotypes of the same species, with *T. kannemeyeri* representing younger individuals of *T. berryi*. This study reveals the importance of describing the dentition of gomphodonts comprehensively and providing information on the denticle, cusps and cingular cuspules morphology and density as well as crown ornamentations and surface texture, with the goal of facilitating the identification of isolated gomphodont teeth and clarifying the phylogenetic position of gomphodont taxa, an objective that we wish to tackle in subsequent contributions.

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Figure captions

Figure 1. Phylogeny and stratigraphic distribution of cynodont clades based on the results of the cladistic analyses of Liu & Abdala (2014) for cynognathians and Martinez, Fernandez & Alcober (2013) and Martinelli, Soares & Schwanke (2016) for probainognathians. *Titanogomphodon*,

considered to be a close relative of *Diademodon* by Keyser (1973) and Martinelli, Fuente & Abdala (2009), is placed among Diademodontidae. Node 1, Eucynodontia; Node 2, Probainognathia; Node 3, Cynognathia; Node 4, Gomphodontia; Node 5, Diademodontidae; Node 6, Trirachodontidae. Arrows indicate that the clades extend beyond the Lower Jurassic. Silhouettes from José Eduardo Camargo Martínez.

Figure 2. Dental terminology used in this study. **A**-**B**, *Diademodon* rostrum in **A**, palatal and **B**, labial views; **C**, **F**, idealized right upper gomphodont postcanine in **C**, apical and **F**, distal views (based on the upper gomphodont postcanine of *Scalenodon angustifrons* by Hopson (2005); modified); **D**, **G**, idealized left lower gomphodont postcanine in **D**, apical and **G**, distal views (based on the lower gomphodont postcanine of *Scalenodon angustifrons* by Hopson (2005); modified); **E**, upper right gomphodont postcanine of *Menadon besairiei* (UA 10601) in apical view; **H**, upper right gomphodont postcanine of *Diademodon tetragonus* (SAM-571) in apical view; **I**, idealized sectorial postcanine of *Diademodon tetragonus* in lingual view (based on the second right upper sectorial postcanine of *Diademodon tetragonus* BP/1/4529); **J**, apex of main cusp of an upper sectorial postcanine of *Diademodon tetragonus* with close up on the denticles, in labial view; **K**, close up on the enamel surface texture of the second right upper sectorial postcanine of *Diademodon tetragonus* (BP/1/4529). **Abbreviations**: **c**, canine; **ca**, carina; **cap**, crown apex; **cc**, central cusp (in green); **ci**, cingulum; **cic**, cingular cuspules; **clar**, centrolabial ridge; **clir**, centrolingual ridge; **co**, crown; **cpc**, conical postcanine; **cri**, central ridge; **cu**, cusp; **db**, distal basin; **dac**, distal accessory cusp; **dad**, distal accessory cusp; **dar**, distal accessory ridge; **dca**, distal carina; **dcc**, distal cingular cuspule; **dci**, distal cingulum (in violet); **de**, denticle; **dia**, diastema; **dri**, distal ridge; **ec**, ectopterygoid; **ent**, enamel texture; **gpc**, gomphodont postcanine; **i**, incisor; **j**, jugal; **lac**, labial cusp (in red); **lacc**, labial cingular cusp; **laci**, labial cingulum (in orange); **lacr**, labiocentral ridge; **ladc**, labiodistal accessory cusp; **ladr**, labiodistal ridge; **lamr**, labiomesial ridge; **lar**, labial ridge; **lic**, lingual cusp (in blue); **licc**, lingual cingular cuspule; **lici**, lingual cingulum (in turquoise); **licr**, linguocentral ridge; **lidc**, linguodistal accessory cusp; **lidr**, linguodistal ridge; **limc**, linguomesial accessory cusp; **limr**, linguomesial ridge; **lir**, lingual ridge; **lri**, longitudinal ridge; **mac**, mesial accessory cusp; **mar**, mesial accessory ridge; **mb**, mesial basin; **mc**, main cusp; **mca**, mesial carina; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum (in beige); **mri**, mesial ridge; **mx**, maxilla; **pal**, palatine;

pc, postcanine; **pcf**, postcanine fossa; **pmx**, premaxilla; **ro**, root; **se**, serration; **spc**, sectorial postcanine; **tc**, transverse crest (in yellow); **tpc**, transitional postcanine; **tun**, transverse undulation.

Figure 3. Dentition of *Diademodon tetragonus* I. **A**, Isolated upper incisor (first left incisor?) of BSP 1934 VIII 14, with **B**, close up on the distal denticles, in labial view; **C**, Isolated upper incisor (first or second right incisor?) of BSP 1934 VIII 14, with **D**, close up on the mesial denticles, in lingual view; **E**, Isolated canine of SAM-PK-571b, with **F**, close up on the distal denticles, in lingual? view; **G**, First to third right upper conical postcanines of MR R1004 in labial view; **H**, Fifth right upper conical postcanine of BSP 1934 VIII 14 in apicolabial view; **I**, **J**, Third and fourth left lower conical postcanines of AM 458 in **I**, labial and **J**, lingual views; **K**, Second to fourth left lower conical postcanines of SAM-PK-5877 in labial view; **L**, **M**, Isolated upper gomphodont postcanine of SAM-PK-571 in **L**, apical and **M**, mesial views; **N**, **O**, Second and third right upper gomphodont postcanines of SAM-PK-571 in **N**, apical and **O**, distal view; **P**, Fourth right upper gomphodont postcanine of BSP 1934 VIII 14 in apical view. **Abbreviations**: **cc**, central cusp; **cic**, cingular cuspules; **dac**, distal accessory cusp; **dar**, distal accessory ridge; **dca**, distal carina; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **dde**, distal denticle; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lic**, lingual cusp; **limc**, linguomesial accessory cusp; **lri**, longitudinal ridge; **mar**, mesial accessory ridge; **mca**, mesial carina; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **tc**, transverse crest.

Figure 4. Dentition of *Diademodon tetragonus* II. **A-C**, **E**, Lower gomphodont postcanine from the posterior portion of the mandible of SAM-PK-571, with **E**, close up on the labial cusp of the distal postcanine, in **A**, apical, **B**, **E**, labial and, **C**, distal views; **D**, Distalmost right lower gomphodont postcanine of SAM-PK-5877 in apical view; **F**, Sixth? gomphodont, first and second transitional, and first sectorial postcanines from the left mandible of SAM-PK-K177 in apical view; **G**, First transitional and first sectorial postcanines of the right mandible of MB R1004 in apical view; **H**, First and second left upper sectorial postcanines of MB R1004 in labial view; **I-K**, Second right upper sectorial postcanine of BP/1/4529, with close up on the **J**, first distal accessory cusp, and **K**, mesial denticles, in labial view. **Abbreviations**: **cc**, central cusp; **dac**, distal accessory cusp; **dar**, distal accessory ridge; **dcc**, distal cingular cuspule; **dci**, distal

cingulum; **dde**, distal denticle; **de**, denticle; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lic**, lingual cusp; **licc**, lingual cingular cuspule; **lri**, longitudinal ridge; **mar**, mesial accessory ridge; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **tc**, transverse crest.

Figure 5. Dentition of *Titanogomphodon crassus*. **A-C**, **E**. Right upper gomphodont, transitional and sectorial postcanines of GSN R322, with close up on **B**, the penultimate gomphodont, **C**, mesial accessory ridge of the distalmost gomphodont, and **E**, distalmost sectorial postcanine in apical view; **D-F**, left mesialmost preserved upper gomphodont postcanine of GSN R322 in **D**, apical and **F**, mesial views. **Abbreviations**: **lac**, labial cusp; **lamc**, labiomesial accessory cusp; **lic**, lingual cusp; **mar**, medial accessory ridge; **mcc**, mesial cingular cusp; **spc**, sectorial postcanine; **tc**, transverse cusp; **tpc**, transitional postcanine.

Figure 6. Dentition of *Langbergia modisei*. **A-B**, First left lower incisor of NMQR 3251, with **B**, close up on the distal carina in labial view; **C**, close up on the distal carina of the fourth left upper incisor of NMQR 3281 in labial view; **D**, **F-G**, right lower canine of NMQR 3251, with close up on the **F**, distal and **G**, mesial carina, in labial view; **E**, cross-section outline of the right upper canine of SAM-PK-K11481 in apical view (labial and mesial sides to the top and the right, respectively); **H**, right upper canine of BP/1/5362 in labial view; **I**, mesiocentral portion of the erupting left upper canine of NMQR 3268 in labial view; **J**, fourth and fifth left upper gomphodont postcanines of NMQR 3251 in apical view. **L**, Close up on the fourth left upper postcanine of NMQR 3251 in mesial view (crown upside down); **K**, third left upper postcanine of NMQR 3255 in apical view; **M**, third and fourth right lower gomphodont postcanine of NMQR 3251 in apical view; **N**, first left lower gomphodont postcanine of NMQR 3251 in apicodistal view; **O**, first and second right upper sectorial postcanine of NMQR 3251 in labial view; **P**, first right upper sectorial postcanine of BP/1/5362 in labial view; **Q**, second left upper sectorial postcanine of NMQR 3255 in linguomesial view. **Abbreviations**: **cc**, central cusp; **dac**, distal accessory cusp; **db**, distal basin; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **dde**, distal denticle; **de**, denticle; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lamc**, labiomesial accessory cusp; **lic**, lingual cusp; **licc**, lingual cingular cuspule; **lidc**, linguodistal accessory cusp; **limc**, linguomesial accessory cusp; **lri**, longitudinal ridge; **mac**, mesial accessory cusp; **mb**,

mesial basin; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **tc**, transverse crest. Elongation axes of the crown and the central cusp in green and red, respectively.

Figure 7. Dentition of *Cricodon formosus*. **A-B**, First left lower incisor of UMCZ T905 in **A**, labial and **B**, labiodistal views; C-D, fourth left upper incisor of BP/1/6102, with **D**, close up on the distal denticles, in labial view; **E-F**, left lower canine of SAM-PK-K5881, with **F**, cross-section outline at mid-crow, in **E**, lingual and **F**, apical views; **G**, mesial and **H**, basodistal denticles of the right and left upper canines, respectively, of BP/1/6102 in labial view; **I**, centrodistal denticles of the right upper canine of BP/1/5540 in labial view; **J**, eight? and nine? right upper gomphodont postcanines of UMCZ T905 in apical view; **K**, eight and nine right lower gomphodont postcanines of UMCZ T905 in apical view; **L**, first left lower gomphodont postcanine of SAM-PK-K5881 in apical view; **M**, last right upper gomphodont postcanine of SAM-PK-K5881 in distal view; **N**, last left upper gomphodont postcanine of UMCZ T905 in labiodistal view; **O**, close up on the denticles on the labiodistal ridge of an isolated left upper postcanine of UMCZ T905 in labiodistal view; **P-Q**, ninth right upper sectorial postcanine of UMCZ T905 in **P**, labial and **Q**, apical views. **Abbreviations**: **cac**, central accessory cusp; **cc**, central cusp; **cos**, concave surface; **dac**, distal accessory cusp; **db**, distal basin; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **dde**, distal denticle; **de**, denticle; **ent**, enamel surface texture; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lic**, lingual cusp; **lidc**, linguodistal accessory cusp; **limc**, linguomesial accessory cusp; **lri**, longitudinal ridge; **mac**, mesial accessory cusp; **mb**, mesial basin; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **tc**, transverse crest; **tun**, transverse undulation. The red lines highlight the angular labiodistal margin of the lower postcanines.

Figure 8. Dentition of *Trirachodon berryi* I. **A-C**, First? left upper incisor, with close up on **B**, mesial and **C**, distal denticles of SAM-PK-K5821 in labial view; **D**, first left and right upper and **E**, first right lower incisors of BP/1/4658 in apical views; **F-G**, right upper canine of BP/1/4661 with **G**, close up on the distocentral part of the crown, in labial view; **H**, distal denticles of the right lower canine of BP/1/4658 in labial view; **I**, fifth and sixth right upper gomphodont postcanines of SAM-PK-K171 (‘*T. kannemeyeri*’ morphotype) in apical view; **J**, tenth and

eleventh left (reversed) upper gomphodont postcanines of BSP 1934 VIII 21 (*T. berryi* morphotype) in apical view; **K**, penultimate right upper gomphodont postcanine of SAM-PK-K4801 ('*T. kannemeyeri*' morphotype) in apical view; **M**, penultimate left upper gomphodont postcanine of NHMUK PV R3307 ('*T. kannemeyeri*' morphotype) in apical view; **N**, tenth left upper gomphodont postcanine of BSP 1934 VIII 21 (*T. berryi* morphotype) in apical view; **O**, partially erupted twelfth (and last) upper gomphodont postcanine of BSP 1934 VIII 21 in distal view. **Abbreviations**: **cc**, central cusp; **dac**, distal accessory cusp; **db**, distal basin; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **ent**, enamel surface texture; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lamc**, labiomesial accessory cusp; **lic**, lingual cusp; **lidc**, linguodistal accessory cusp; **limc**, linguomesial accessory cusp; **lri**, longitudinal ridge; **mb**, mesial basin; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **tc**, transverse crest; **tun**, transverse undulation.

Figure 9. Dentition of *Trirachodon berryi* II. **A**, fifth and sixth right lower gomphodont postcanines of SAM-PK-K171 in apical view; **B**, penultimate and **C**, ultimate (and linguobasally rotated) right lower gomphodont postcanines of SAM-PK-K4801 in apical view; **D**, first left lower gomphodont postcanine of BP/1/4658 in apical view; **E**, fifth (bottom) and sixth (top) right lower gomphodont postcanines of SAM-PK-K171 in mesioapical view; **F**, first (left) and second (right) right upper sectorial postcanines of SAM-PK-K4801 in labial view; **G**-**H**, first right lower sectorial postcanine of SAM-PK-K4801 in **G**, labial and **H**, lingual views; **I-J**, first and second (erupted and replacing tooth) right lower sectorial postcanines of BP/1/4658 in **I**, labial and **J**, apical views. **Abbreviations**: **cc**, central cusp; **dac**, distal accessory cusp; **db**, distal basin; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **dde**, distal denticle; **de**, denticle; **ent**, enamel surface texture; **lac**, labial cusp; **lacc**, labial cingular cuspule; **laci**, labial cingulum; **lic**, lingual cusp; **licc**, lingual cingular cuspules; **lici**, lingual cingulum; **mac**, mesial accessory cusp; **mb**, mesial basin; **mc**, main cusp; **mca**, mesial carina; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum.

Figure 10. Dentition of *Sinognathus gracilis* (IVPP V2339). **A**, second left upper incisor in labial view; **B**, fourth left upper incisor, with **C**, close up on basodistal denticles, in labial views; **D**,

basal root cross-section outline of the first left upper incisor in apical view; **E**, left and F, right lower canines in labial view; **H**, first to sixth upper and lower left gomphodont postcanines (sagittal cross-section through mid-crown), with close up on the fourth upper gomphodont postcanine, in labial view; **J**, right second to sixth upper (bottom) and second to seventh lower (top) gomphodont postcanines in linguodistal view (and apicodistal and basodistal views for the upper and lower gomphodont postcanines, respectively); **K-L**, third right upper gomphodont postcanine in **K**, apicodistal and **L**, apicolingual views; **M**, third right lower gomphodont postcanine in labial view; **N**, fourth left lower gomphodont postcanine in labial view; **O-P**, sixth (and last) upper gomphodont postcanine in **O**, linguodistal and **P**, apicolingual views. **Abbreviations**: **cc**, central cusp; **dci**, distal cingulum; **de**, denticle; **lac**, labial cusp; **lic**, lingual cusp; **limc**, linguomesial accessory cusp; **mci**, mesial cingulum; **mde**, mesial denticle; **ro**, root; **tc**, transverse crest; **I-VI**, first to sixth gomphodont postcanines.

Figure 11. Comparison of skull size and widest upper gomphodont postcanine width in gomphodont cynodonts, with linear regression trendlines for gomphodont taxa (in black) and *Diademodon* (in yellow). *Diademodon* I, II and III refer to specimens BSP 1934 VIII 14, MB R1004 and BSP 1934 VIII 19, respectively. **Abbreviations**: **CBW**, crown base width.

Figure 1

Figure 1. Phylogeny and stratigraphic distribution of cynodont clades based on the results of the cladistic analyses of Liu & Abdala (2014) for cynognathians and Martinez, Fernandez & Alcober (2013) and Martinelli, Soares & Schwanke (2016) for probainogna

Titanogomphodon, considered to be a close relative of *Diademodon* by Keyser (1973) and Martinelli, Fuente & Abdala (2009) , is placed among Diademodontidae. Node 1, Eucynodontia; Node 2, Probainognathia; Node 3, Cynognathia; Node 4, Gomphodontia; Node 5, Diademodontidae; Node 6, Trirachodontidae. Arrows indicate that the clades extend beyond the Lower Jurassic. Silhouettes from José Eduardo Camargo Martínez.

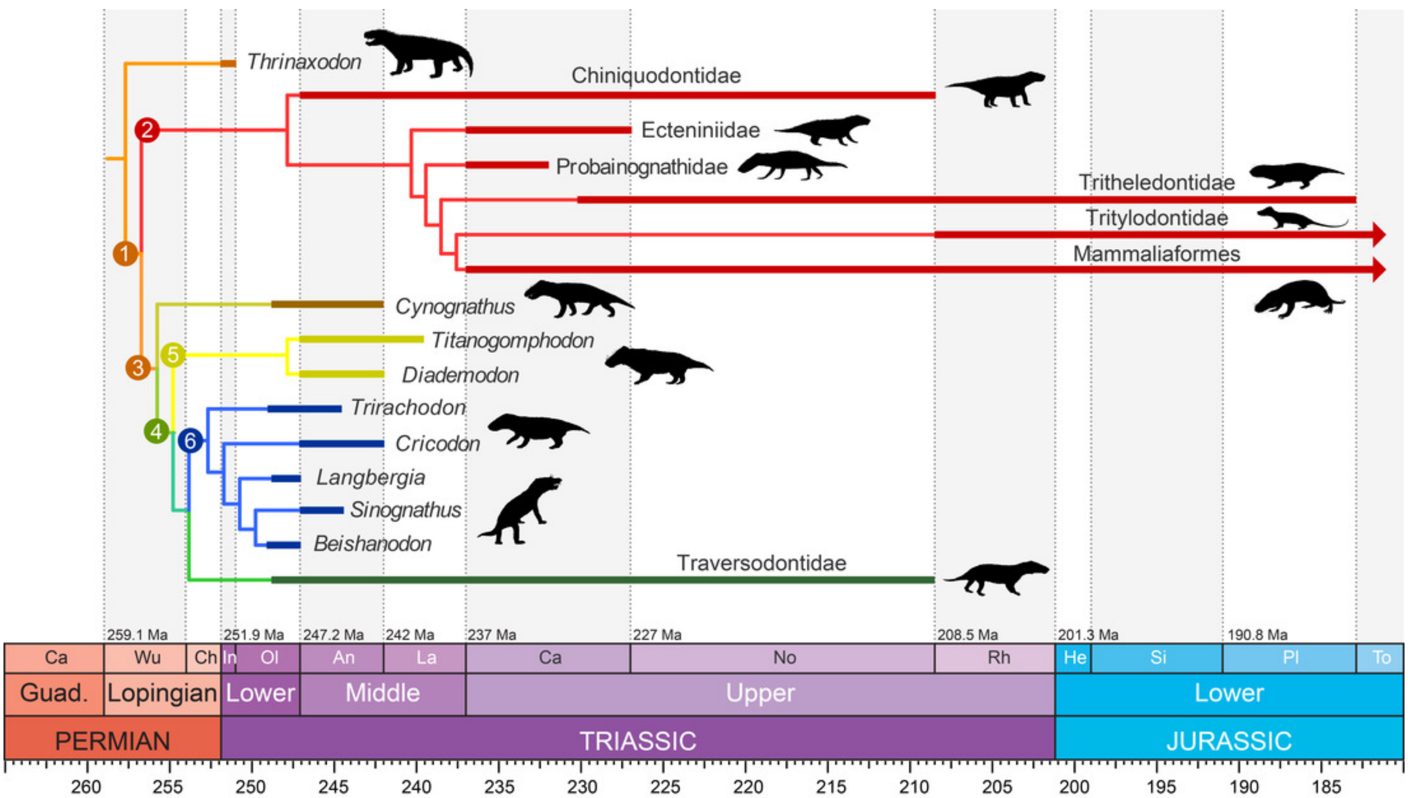

Figure 2

Figure 2. Dental terminology used in this study.

A-**B**, *Diademodon* rostrum in **A**, palatal and **B**, labial views; **C**, **F**, idealized right upper gomphodont postcanine in **C**, apical and **F**, distal views (based on the upper gomphodont postcanine of *Scalenodon angustifrons* by Hopson (2005) ; modified); **D**, **G**, idealized left lower gomphodont postcanine in **D**, apical and **G**, distal views (based on the lower gomphodont postcanine of *Scalenodon angustifrons* by Hopson (2005) ; modified); **E**, upper right gomphodont postcanine of *Menadon besairiei* (UA 10601) in apical view; **H**, upper right gomphodont postcanine of *Diademodon tetragonus* (SAM-571) in apical view; **I**, idealized sectorial postcanine of *Diademodon tetragonus* in lingual view (based on the second right upper sectorial postcanine of *Diademodon tetragonus* BP/1/4529); **J**, apex of main cusp of an upper sectorial postcanine of *Diademodon tetragonus* with close up on the denticles, in labial view; **K**, close up on the enamel surface texture of the second right upper sectorial postcanine of *Diademodon tetragonus* (BP/1/4529). **Abbreviations**: **c**, canine; **ca**, carina; **cap**, crown apex; **cc**, central cusp (in green); **ci**, cingulum; **cic**, cingular cuspules; **clar**, centrolabial ridge; **clir**, centrolingual ridge; **co**, crown; **cpc**, conical postcanine; **cri**, central ridge; **cu**, cusp; **db**, distal basin; **dac**, distal accessory cusp; **dad**, distal accessory cusp; **dar**, distal accessory ridge; **dca**, distal carina; **dcc**, distal cingular cuspule; **dci**, distal cingulum (in violet); **de**, denticle; **dia**, diastema; **dri**, distal ridge; **ec**, ectopterygoid; **ent**, enamel texture; **gpc**, gomphodont postcanine; **i**, incisor; **j**, jugal; **lac**, labial cusp (in red); **lacc**, labial cingular cusp; **laci**, labial cingulum (in orange); **lacr**, labiocentral ridge; **ladc**, labiodistal accessory cusp; **ladr**, labiodistal ridge; **lamr**, labiomesial ridge; **lar**, labial ridge; **lic**, lingual cusp (in blue); **licc**, lingual cingular cuspule; **lici**, lingual cingulum (in turquoise); **licr**, linguocentral ridge; **lidc**, linguodistal accessory cusp; **lidr**, linguodistal ridge; **limc**, linguomesial accessory cusp; **limr**, linguomesial ridge; **lir**, lingual ridge; **lri**, longitudinal ridge; **mac**, mesial accessory cusp; **mar**, mesial accessory ridge; **mb**, mesial basin; **mc**, main cusp; **mca**, mesial carina; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum (in beige); **mri**, mesial ridge; **mx**, maxilla; **pal**, palatine; **pc**, postcanine; **pcf**, postcanine fossa; **pmx**, premaxilla; **ro**, root; **se**, serration; **spc**, sectorial postcanine; **tc**, transverse crest (in yellow); **tpc**, transitional postcanine; **tun**, transverse undulation.

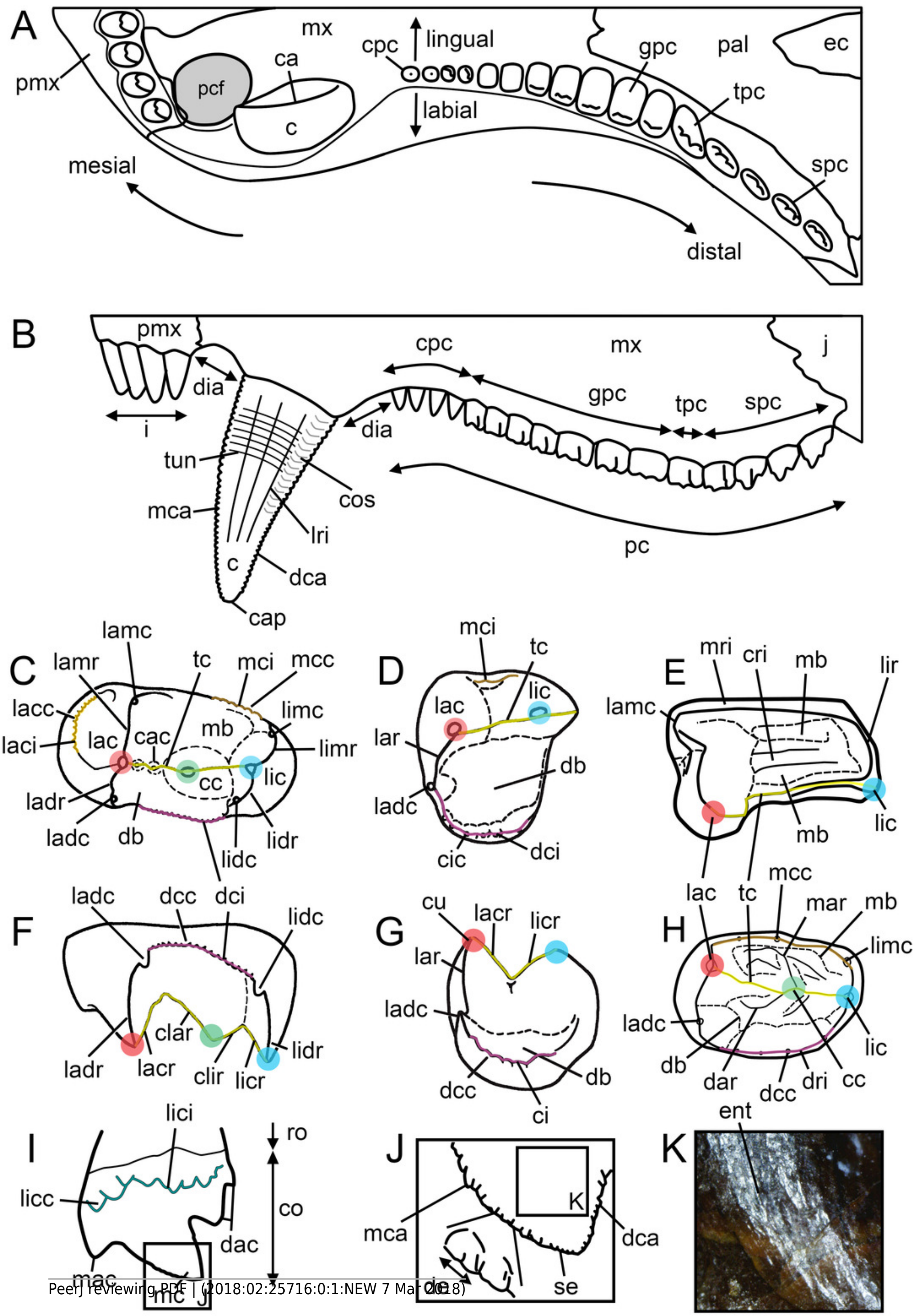
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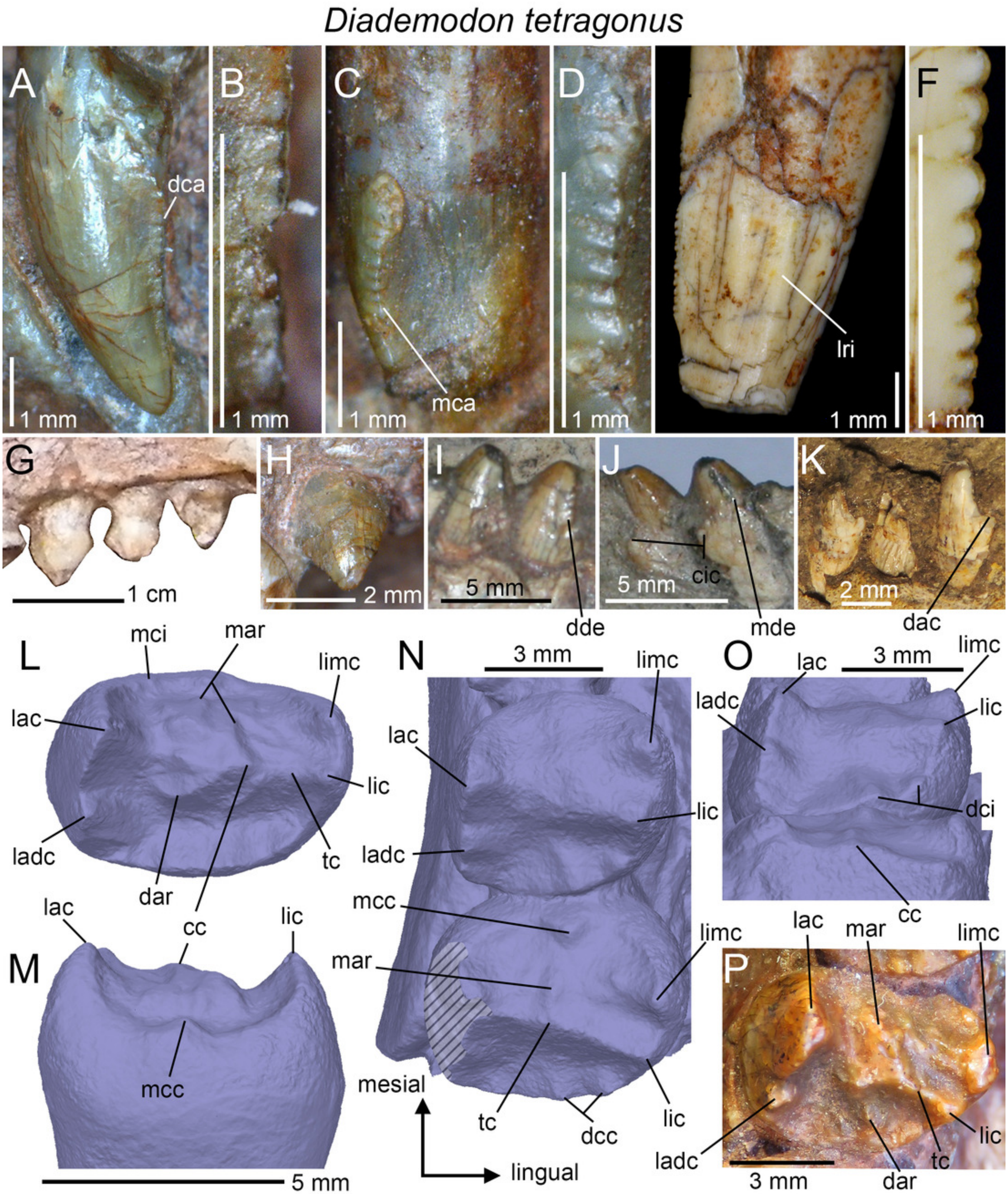
Figure 3

Figure 3. Dentition of *Diademodon tetragonus* I.

A, Isolated upper incisor (first left incisor?) of BSP 1934 VIII 14, with **B**, close up on the distal denticles, in labial view; **C**, Isolated upper incisor (first or second right incisor?) of BSP 1934 VIII 14, with **D**, close up on the mesial denticles, in lingual view; **E**, Isolated canine of SAM-PK-571b, with **F**, close up on the distal denticles, in lingual? view; **G**, First to third right upper conical postcanines of MR R1004 in labial view; **H**, Fifth right upper conical postcanine of BSP 1934 VIII 14 in apicolabial view; **I**, **J**, Third and fourth left lower conical postcanines of AM 458 in **I**, labial and **J**, lingual views; **K**, Second to fourth left lower conical postcanines of SAM-PK-5877 in labial view; **L**, **M**, Isolated upper gomphodont postcanine of SAM-PK-571 in **L**, apical and **M**, mesial views; **N**, **O**, Second and third right upper gomphodont postcanines of SAM-PK-571 in **N**, apical and **O**, distal view; **P**, Fourth right upper gomphodont postcanine of BSP 1934 VIII 14 in apical view. **Abbreviations**: **cc**, central cusp; **cic**, cingular cuspules; **dac**, distal accessory cusp; **dar**, distal accessory ridge; **dca**, distal carina; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **dde**, distal denticle; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lic**, lingual cusp; **limc**, linguomesial accessory cusp; **lri**, longitudinal ridge; **mar**, mesial accessory ridge; **mca**, mesial carina; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **tc**, transverse crest.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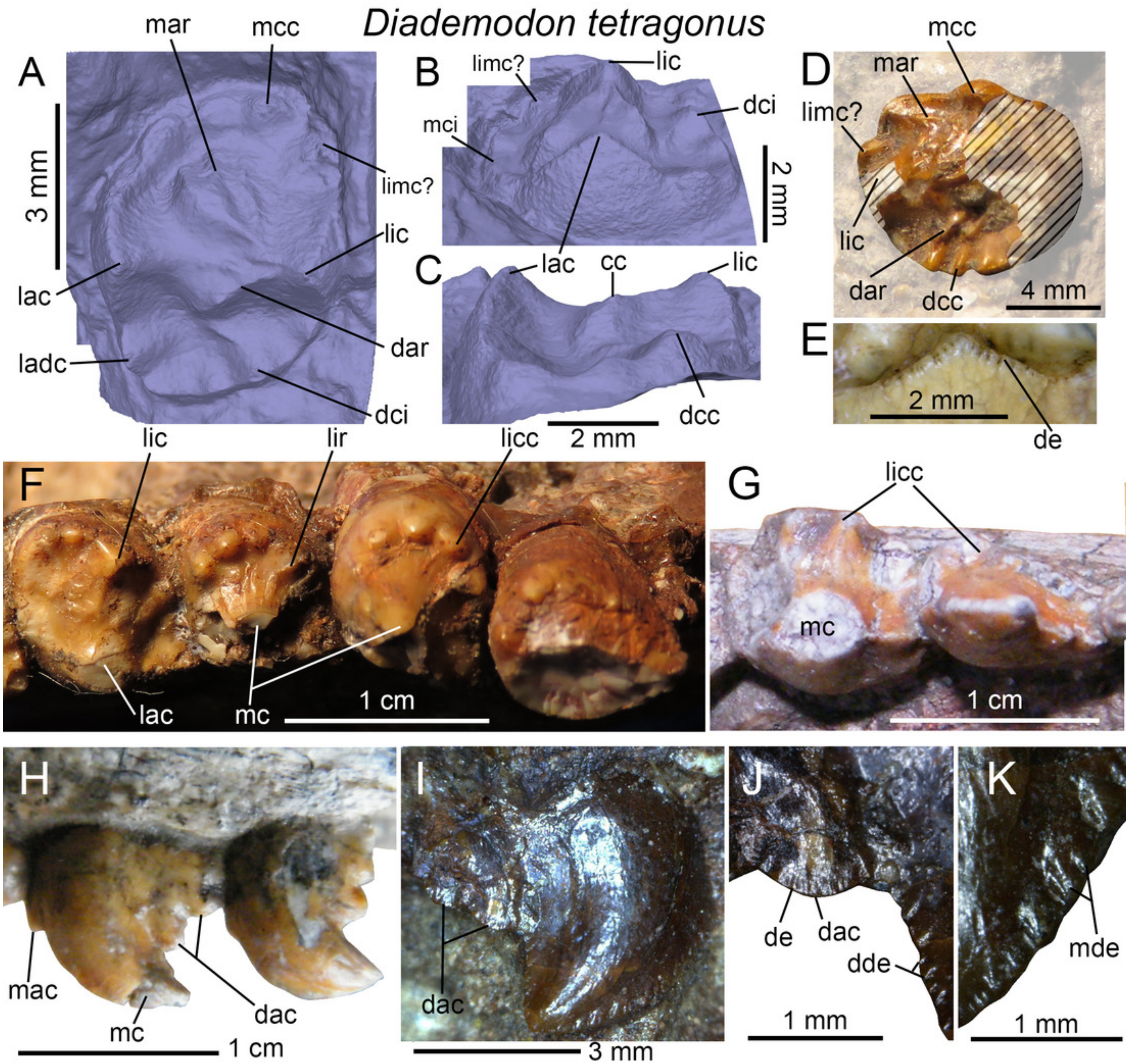
lingual

Figure 4

Figure 4. Dentition of *Diademodon tetragonus* II

A-C, **E**, Lower gomphodont postcanine from the posterior portion of the mandible of SAM-PK-571, with **E**, close up on the labial cusp of the distal postcanine, in **A**, apical, **B**, **E**, labial and, **C**, distal views; **D**, Distalmost right lower gomphodont postcanine of SAM-PK-5877 in apical view; **F**, Sixth? gomphodont, first and second transitional, and first sectorial postcanines from the left mandible of SAM-PK-K177 in apical view; **G**, First transitional and first sectorial postcanines of the right mandible of MB R1004 in apical view; **H**, First and second left upper sectorial postcanines of MB R1004 in labial view; **I-K**, Second right upper sectorial postcanine of BP/1/4529, with close up on the **J**, first distal accessory cusp, and **K**, mesial denticles, in labial view. **Abbreviations**: **cc**, central cusp; **dac**, distal accessory cusp; **dar**, distal accessory ridge; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **dde**, distal denticle; **de**, denticle; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lic**, lingual cusp; **licc**, lingual cingular cuspule; **lri**, longitudinal ridge; **mar**, mesial accessory ridge; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **tc**, transverse crest.



Diademodon tetragonus
A
mar
mcc
3 mm
limc?
lic
lac
dar
ladc
dci
B
limc?
lic
dci
mci
2 mm
lac
C
cc
lic
dcc
2 mm
D
mcc
mar
limc?
lic
dar
dcc
4 mm
E
2 mm
de
F
lic
lir
licc
lac
mc
1 cm
G
licc
mc
1 cm
H
mac
mc
dac
1 cm
I
dac
3 mm
J
de
dac
dde
1 mm
K
mde
1 mm

Figure 5

Figure 5. Dentition of *Titanogomphodon crassus*.

A-C, **E**. Right upper gomphodont, transitional and sectorial postcanines of GSN R322, with close up on **B**, the penultimate gomphodont, **C**, mesial accessory ridge of the distalmost gomphodont, and **E**, distalmost sectorial postcanine in apical view; **D-F**, left mesialmost preserved upper gomphodont postcanine of GSN R322 in **D**, apical and **F**, mesial views. **Abbreviations**: **lac**, labial cusp; **lamc**, labiomesial accessory cusp; **lic**, lingual cusp; **mar**, medial accessory ridge; **mcc**, mesial cingular cusp; **spc**, sectorial postcanine; **tc**, transverse cusp; **tpc**, transitional postcanine.

Titanogomphodon crassus

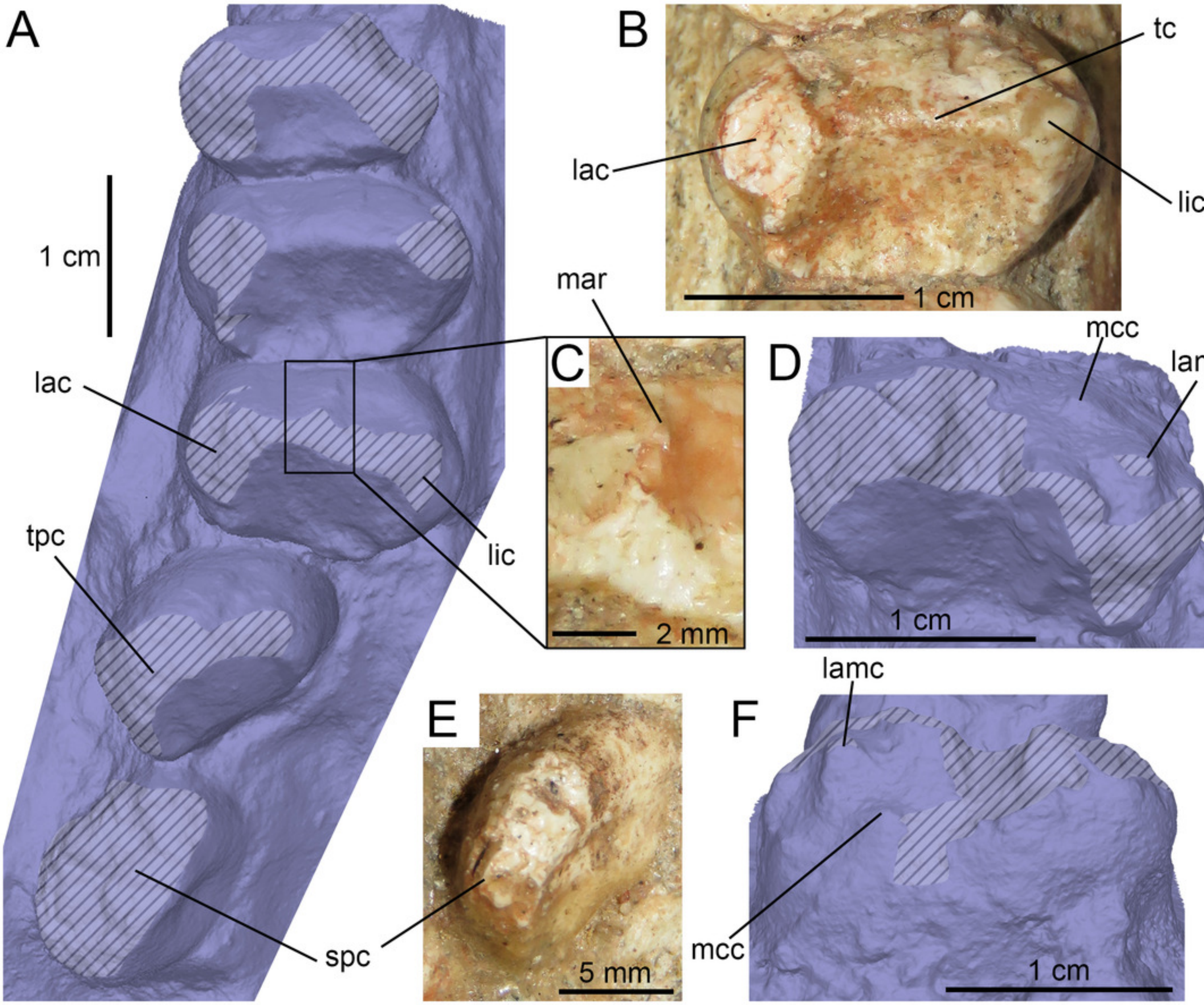
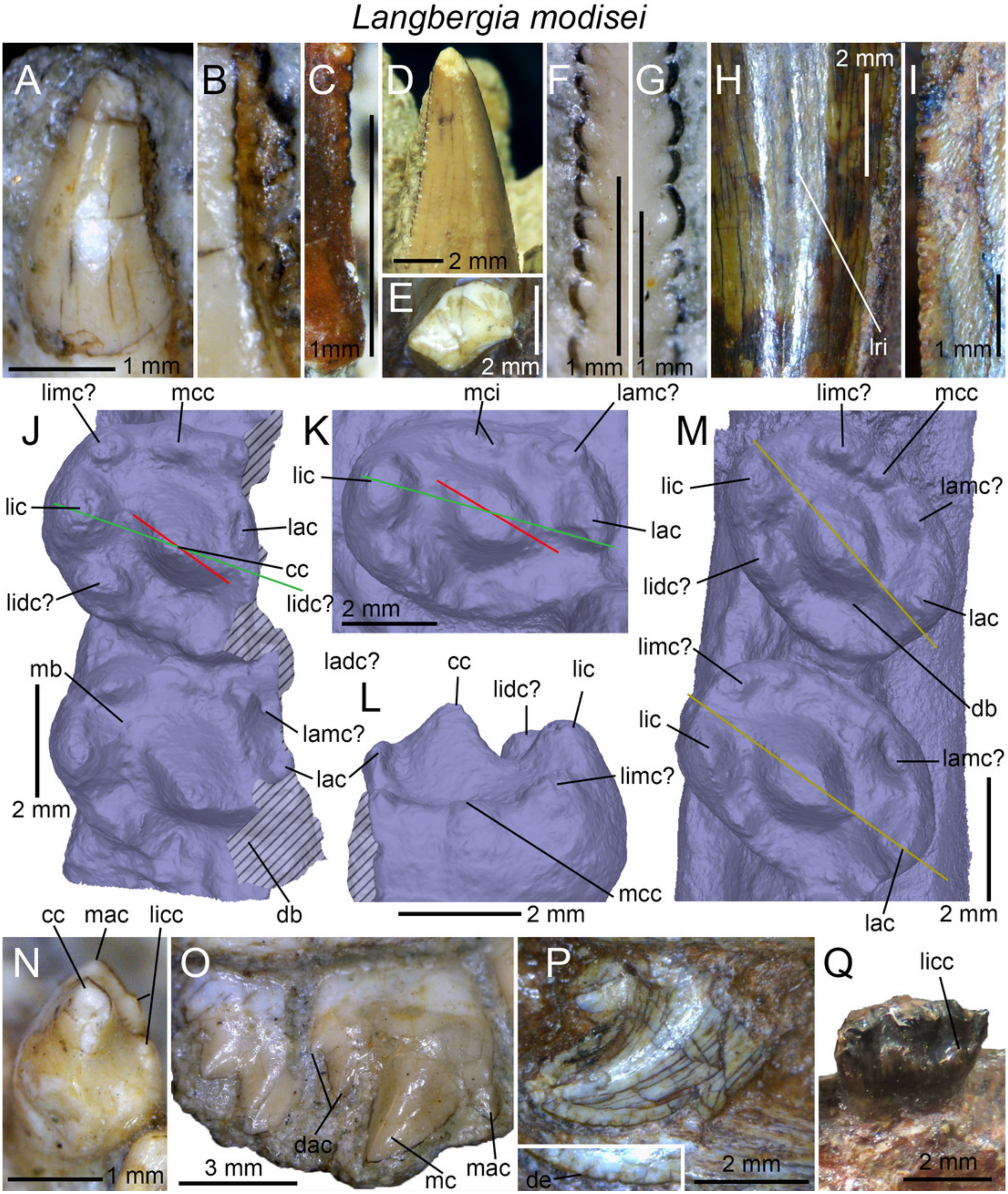


Figure 6

Figure 6. Dentition of *Langbergia modisei*

A-B, First left lower incisor of NMQR 3251, with **B**, close up on the distal carina in labial view; **C**, close up on the distal carina of the fourth left upper incisor of NMQR 3281 in labial view; **D**, **F-G**, right lower canine of NMQR 3251, with close up on the **F**, distal and **G**, mesial carina, in labial view; **E**, cross-section outline of the right upper canine of SAM-PK-K11481 in apical view (labial and mesial sides to the top and the right, respectively); **H**, right upper canine of BP/1/5362 in labial view; **I**, mesiocentral portion of the erupting left upper canine of NMQR 3268 in labial view; **J**, fourth and fifth left upper gomphodont postcanines of NMQR 3251 in apical view. **L**, Close up on the fourth left upper postcanine of NMQR 3251 in mesial view (crown upside down); **K**, third left upper postcanine of NMQR 3255 in apical view; **M**, third and fourth right lower gomphodont postcanine of NMQR 3251 in apical view; **N**, first left lower gomphodont postcanine of NMQR 3251 in apicodistal view; **O**, first and second right upper sectorial postcanine of NMQR 3251 in labial view; **P**, first right upper sectorial postcanine of BP/1/5362 in labial view; **Q**, second left upper sectorial postcanine of NMQR 3255 in linguomesial view. **Abbreviations**: **cc**, central cusp; **dac**, distal accessory cusp; **db**, distal basin; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **dde**, distal denticle; **de**, denticle; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lamc**, labiomesial accessory cusp; **lic**, lingual cusp; **licc**, lingual cingular cuspule; **lidc**, linguodistal accessory cusp; **limc**, linguomesial accessory cusp; **lri**, longitudinal ridge; **mac**, mesial accessory cusp; **mb**, mesial basin; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **tc**, transverse crest. Elongation axes of the crown and the central cusp in green and red, respectively.



Langbergia modisei
A
1 mm
B
C
1mm
D
2 mm
E
2 mm
F
1 mm
G
1 mm
H
2 mm
lri
I
1 mm
J
limc?
mcc
lic
lac
cc
lidc?
lidc?
mb
lamc?
lac
2 mm
db
K
mci
lamc?
lic
lac
2 mm
L
ladc?
cc
lidc?
lic
lac
limc?
mcc
2 mm
M
limc?
mcc
lic
lamc?
lidc?
lac
limc?
db
lic
lamc?
lac
2 mm
N
cc
mac
licc
1 mm
O
3 mm
dac
mc
mac
P
2 mm
de
Q
licc
2 mm

Figure 7

Figure 7. Dentition of *Cricodon formosus*

A-B, First left lower incisor of UMCZ T905 in **A**, labial and **B**, labiodistal views; C-D, fourth left upper incisor of BP/1/6102, with **D**, close up on the distal denticles, in labial view; **E-F**, left lower canine of SAM-PK-K5881, with **F**, cross-section outline at mid-crow, in **E**, lingual and **F**, apical views; **G**, mesial and **H**, basodistal denticles of the right and left upper canines, respectively, of BP/1/6102 in labial view; **I**, centrodistal denticles of the right upper canine of BP/1/5540 in labial view; **J**, eight? and nine? right upper gomphodont postcanines of UMCZ T905 in apical view; **K**, eight and nine right lower gomphodont postcanines of UMCZ T905 in apical view; **L**, first left lower gomphodont postcanine of SAM-PK-K5881 in apical view; **M**, last right upper gomphodont postcanine of SAM-PK-K5881 in distal view; **N**, last left upper gomphodont postcanine of UMCZ T905 in labiodistal view; **O**, close up on the denticles on the labiodistal ridge of an isolated left upper postcanine of UMCZ T905 in labiodistal view; **P-Q**, ninth right upper sectorial postcanine of UMCZ T905 in **P**, labial and **Q**, apical views. **Abbreviations**: **cac**, central accessory cusp; **cc**, central cusp; **cos**, concave surface; **dac**, distal accessory cusp; **db**, distal basin; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **dde**, distal denticle; **de**, denticle; **ent**, enamel surface texture; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lic**, lingual cusp; **lidc**, linguodistal accessory cusp; **limc**, linguomesial accessory cusp; **lri**, longitudinal ridge; **mac**, mesial accessory cusp; **mb**, mesial basin; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **tc**, transverse crest; **tun**, transverse undulation. The red lines highlight the angular labiodistal margin of the lower postcanines.

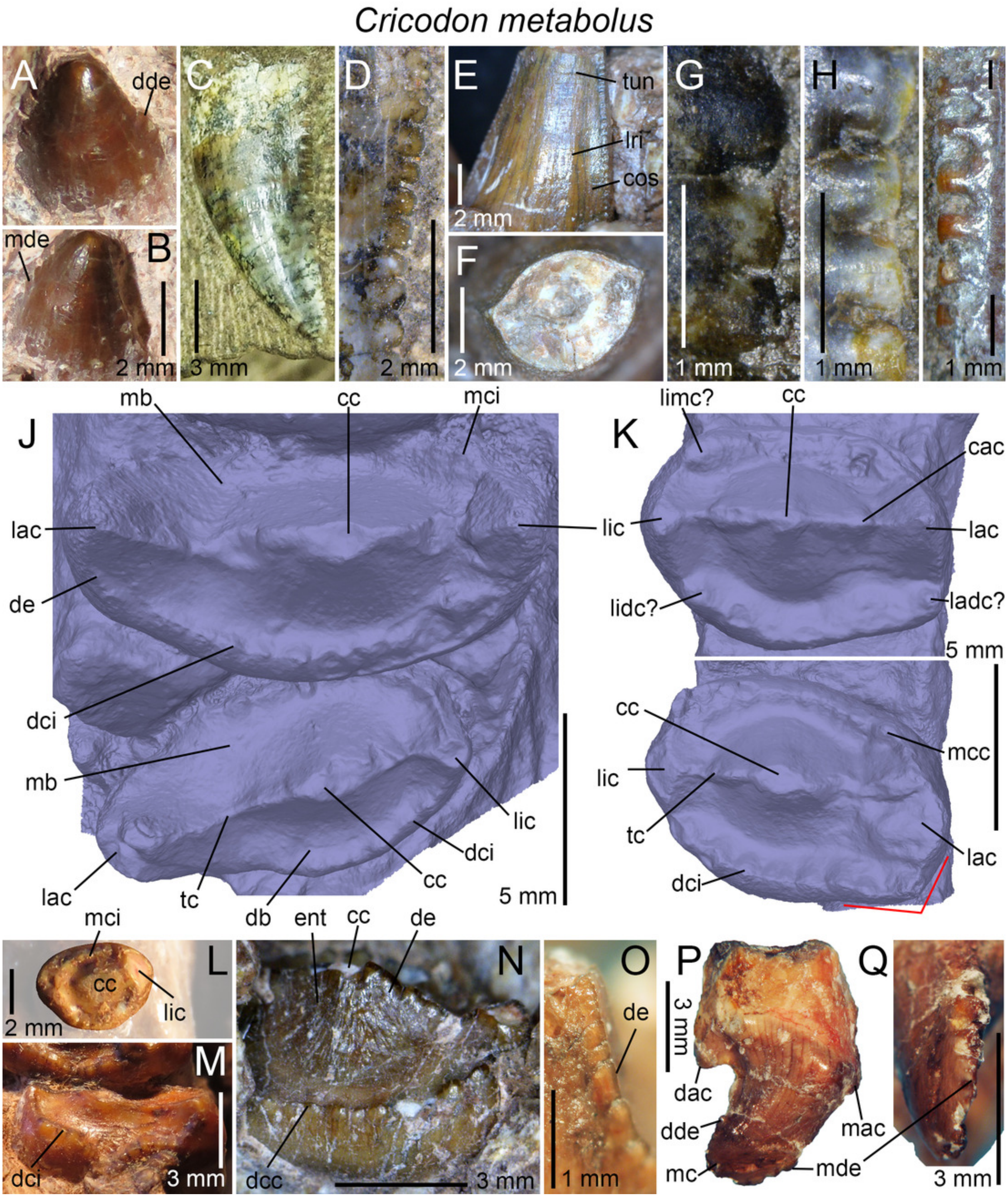
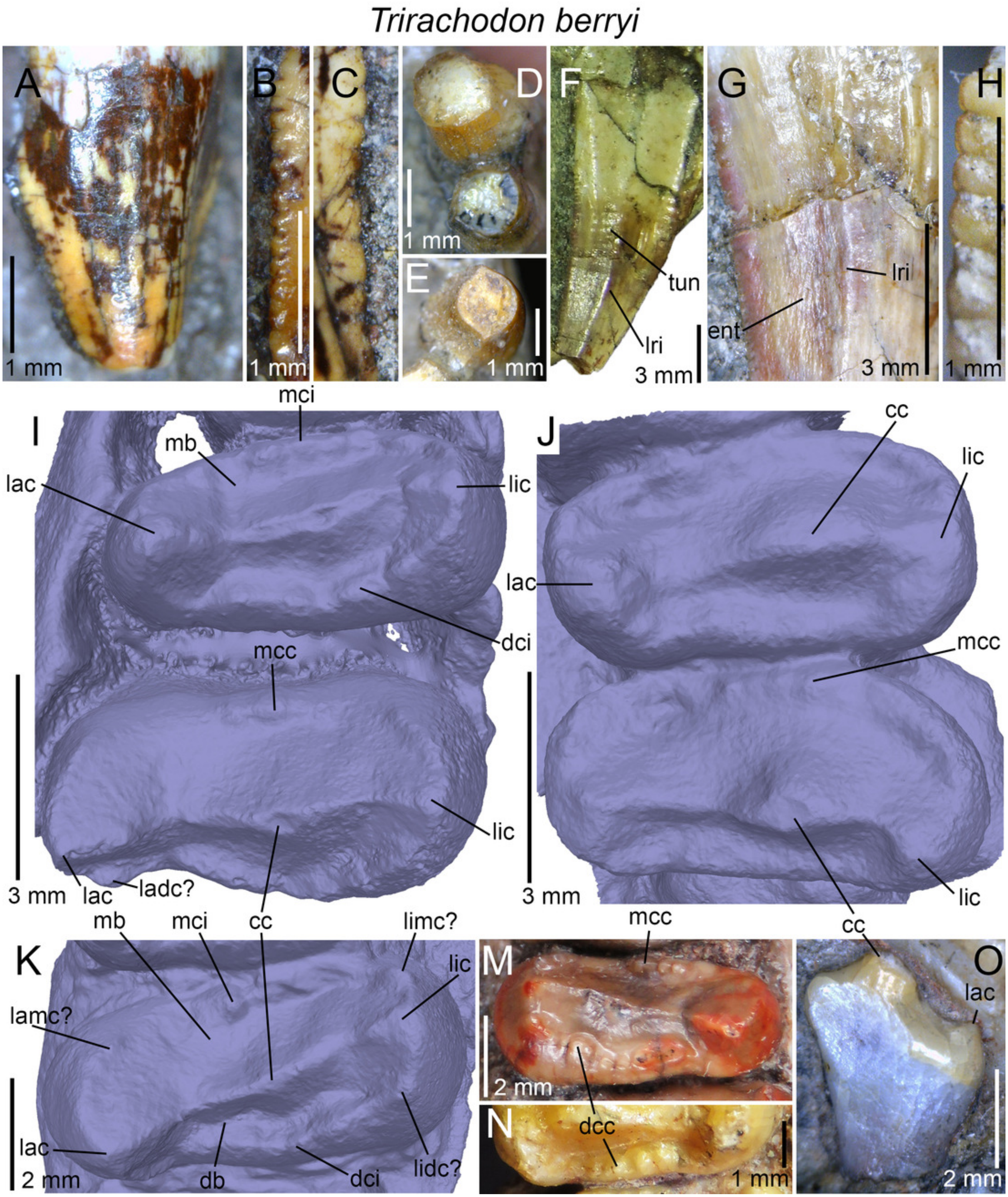

Cricodon metabolus
A
dde
B
mde
2 mm
C
3 mm
D
2 mm
E
tun
lri
cos
2 mm
F
2 mm
G
1 mm
H
1 mm
I
1 mm
J
mb
cc
mci
lac
de
dci
mb
lic
dci
cc
lac
tc
db
5 mm
K
limc?
cc
cac
lic
lac
lidc?
ladc?
5 mm
cc
mcc
lic
tc
lac
dci
L
mci
cc
lic
2 mm
M
dci
3 mm
N
ent
cc
de
dcc
3 mm
O
de
1 mm
P
3 mm
dac
dde
mac
mc
mde
Q
3 mm

Figure 8

Figure 8. Dentition of *Trirachodon berryi*

A-C, First? left upper incisor, with close up on **B**, mesial and **C**, distal denticles of SAM-PK-K5821 in labial view; **D**, first left and right upper and **E**, first right lower incisors of BP/1/4658 in apical views; **F-G**, right upper canine of BP/1/4661 with **G**, close up on the distocentral part of the crown, in labial view; **H**, distal denticles of the right lower canine of BP/1/4658 in labial view; **I**, fifth and sixth right upper gomphodont postcanines of SAM-PK-K171 ('*T. kannemeyeri*' morphotype) in apical view; **J**, tenth and eleventh left (reversed) upper gomphodont postcanines of BSP 1934 VIII 21 (*T. berryi* morphotype) in apical view; **K**, penultimate right upper gomphodont postcanine of SAM-PK-K4801 ('*T. kannemeyeri*' morphotype) in apical view; **M**, penultimate left upper gomphodont postcanine of NHMUK PV R3307 ('*T. kannemeyeri*' morphotype) in apical view; **N**, tenth left upper gomphodont postcanine of BSP 1934 VIII 21 (*T. berryi* morphotype) in apical view; **O**, partially erupted twelfth (and last) upper gomphodont postcanine of BSP 1934 VIII 21 in distal view. **Abbreviations**: **cc**, central cusp; **dac**, distal accessory cusp; **db**, distal basin; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **ent**, enamel surface texture; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lamc**, labiomesial accessory cusp; **lic**, lingual cusp; **lidc**, linguodistal accessory cusp; **limc**, linguomesial accessory cusp; **lri**, longitudinal ridge; **mb**, mesial basin; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **tc**, transverse crest; **tun**, transverse undulation.



Trirachodon berryi
A
1 mm
B
1 mm
C
D
1 mm
E
1 mm
F
tun
lri
3 mm
G
lri
ent
3 mm
H
1 mm
I
mci
mb
lac
lic
dci
mcc
lic
3 mm
lac
ladc?
J
cc
lic
lac
mcc
3 mm
lic
cc
K
mb
mci
cc
limc?
lic
lamc?
lac
2 mm
db
dci
lidc?
M
mcc
2 mm
dcc
N
1 mm
O
lac
2 mm

Figure 9

Figure 9. Dentition of *Trirachodon berryi* II

A, fifth and sixth right lower gomphodont postcanines of SAM-PK-K171 in apical view; **B**, penultimate and **C**, ultimate (and linguobasally rotated) right lower gomphodont postcanines of SAM-PK-K4801 in apical view; **D**, first left lower gomphodont postcanine of BP/1/4658 in apical view; **E**, fifth (bottom) and sixth (top) right lower gomphodont postcanines of SAM-PK-K171 in mesioapical view; **F**, first (left) and second (right) right upper sectorial postcanines of SAM-PK-K4801 in labial view; **G**-**H**, first right lower sectorial postcanine of SAM-PK-K4801 in **G**, labial and **H**, lingual views; **I-J**, first and second (erupted and replacing tooth) right lower sectorial postcanines of BP/1/4658 in **I**, labial and **J**, apical views. **Abbreviations**: **cc**, central cusp; **dac**, distal accessory cusp; **db**, distal basin; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **dde**, distal denticle; **de**, denticle; **ent**, enamel surface texture; **lac**, labial cusp; **lacc**, labial cingular cuspule; **laci**, labial cingulum; **lic**, lingual cusp; **licc**, lingual cingular cuspules; **lici**, lingual cingulum; **mac**, mesial accessory cusp; **mb**, mesial basin; **mc**, main cusp; **mca**, mesial carina; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum.

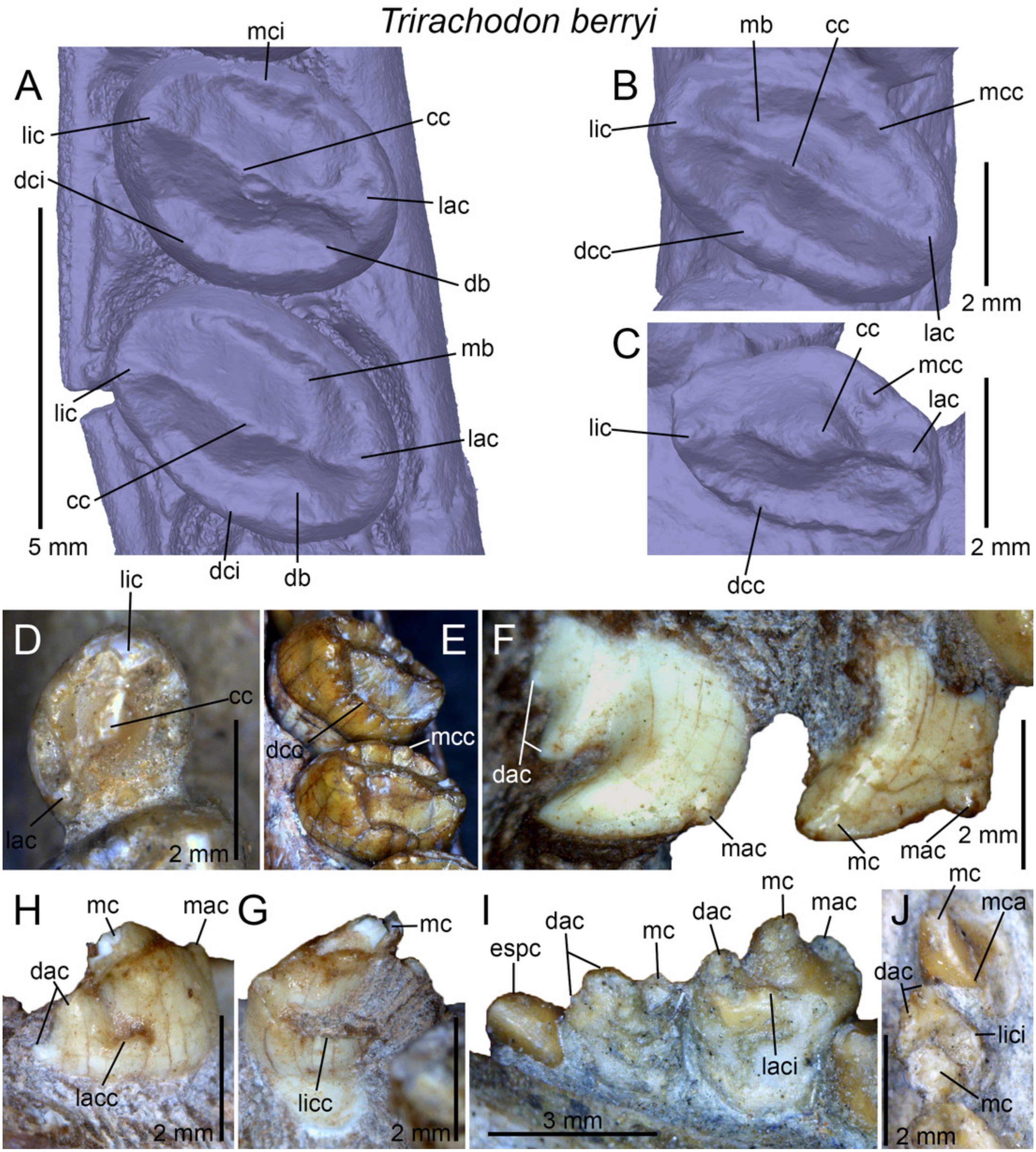

Trirachodon berryi
A
mci
lic
dci
cc
lac
db
mb
lic
lac
cc
5 mm
dci
db
B
mb
cc
mcc
lic
dcc
lac
2 mm
C
cc
mcc
lac
lic
dcc
2 mm
D
lic
cc
lac
2 mm
E
dcc
mcc
F
dac
mac
mc
mac
2 mm
H
mc
mac
dac
lacc
2 mm
G
mc
licc
2 mm
I
espc
dac
mc
dac
mc
mac
laci
3 mm
J
mc
mca
dac
lici
mc
2 mm

Figure 10

Figure 10. Dentition of *Sinognathus gracilis* (IVPP V2339)

A, second left upper incisor in labial view; **B**, fourth left upper incisor, with **C**, close up on basodistal denticles, in labial views; **D**, basal root cross-section outline of the first left upper incisor in apical view; **E**, left and F, right lower canines in labial view; **H**, first to sixth upper and lower left gomphodont postcanines (sagittal cross-section through mid-crown), with close up on the fourth upper gomphodont postcanine, in labial view; **J**, right second to sixth upper (bottom) and second to seventh lower (top) gomphodont postcanines in linguodistal view (and apicodistal and basodistal views for the upper and lower gomphodont postcanines, respectively); **K-L**, third right upper gomphodont postcanine in **K**, apicodistal and **L**, apicolingual views; **M**, third right lower gomphodont postcanine in labial view; **N**, fourth left lower gomphodont postcanine in labial view; **O-P**, sixth (and last) upper gomphodont postcanine in **O**, linguodistal and **P**, apicolingual views. **Abbreviations**: **cc**, central cusp; **dci**, distal cingulum; **de**, denticle; **lac**, labial cusp; **lic**, lingual cusp; **limc**, linguomesial accessory cusp; **mci**, mesial cingulum; **mde**, mesial denticle; **ro**, root; **tc**, transverse crest; **I-VI**, first to sixth gomphodont postcanines.

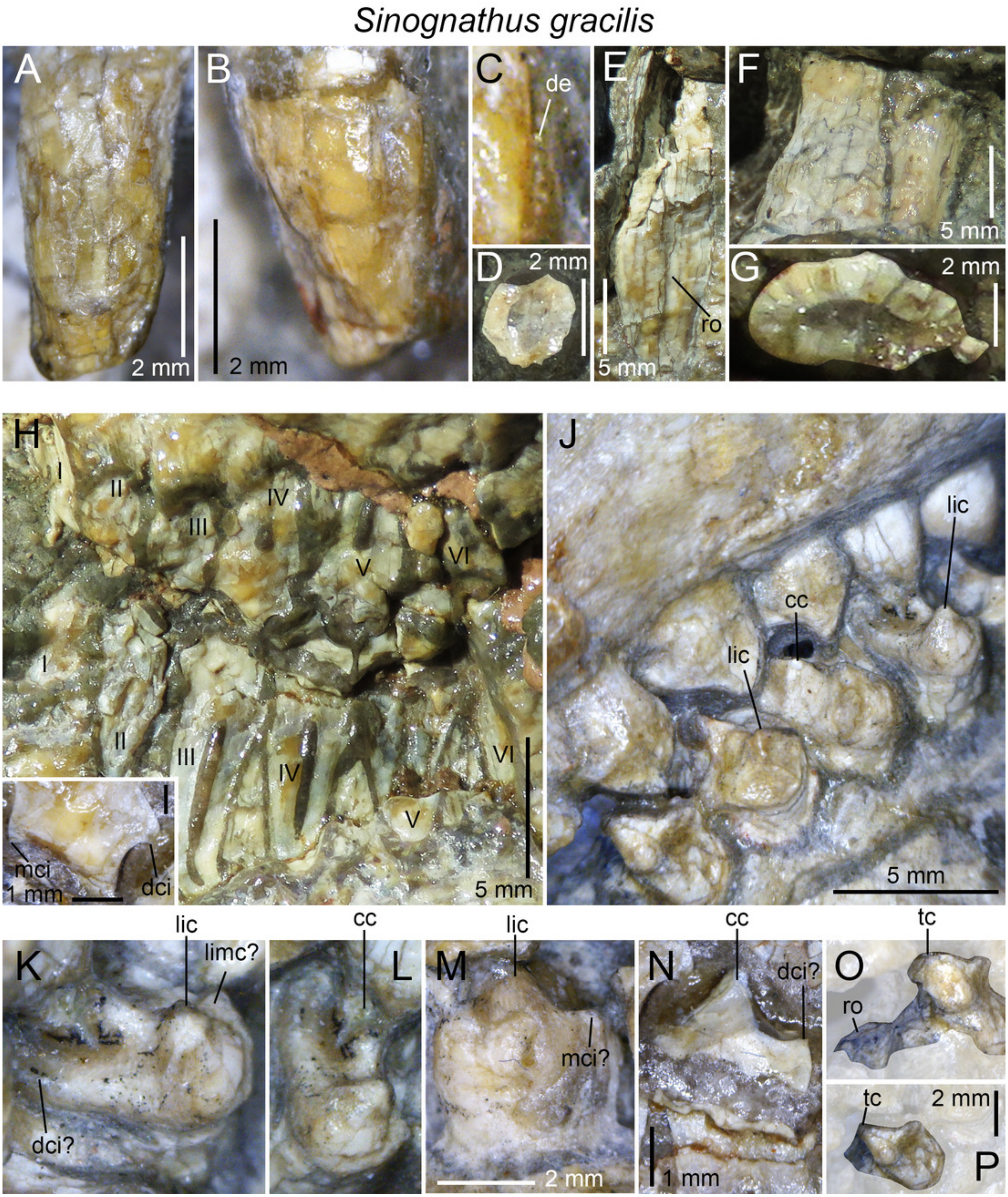

Sinognathus gracilis
A
2 mm
B
2 mm
C
de
D
2 mm
E
ro
5 mm
F
5 mm
G
2 mm
H
I
II
III
IV
V
VI
I
II
III
IV
V
VI
5 mm
I
mci
dci
1 mm
J
lic
cc
lic
5 mm
K
lic
limc?
dci?
L
cc
M
lic
mci?
2 mm
N
cc
dci?
1 mm
O
tc
ro
P
tc
2 mm

Figure 11

Figure 11. Comparison of skull size and widest upper gomphodont postcanine width in gomphodont cynodonts, with linear regression trendlines for gomphodont taxa (in black) and *Diademodon* (in yellow)

Diademodon I, II and III refer to specimens BSP 1934 VIII 14, MB R1004 and BSP 1934 VIII 19, respectively. **Abbreviations**: **CBW**, crown base width.

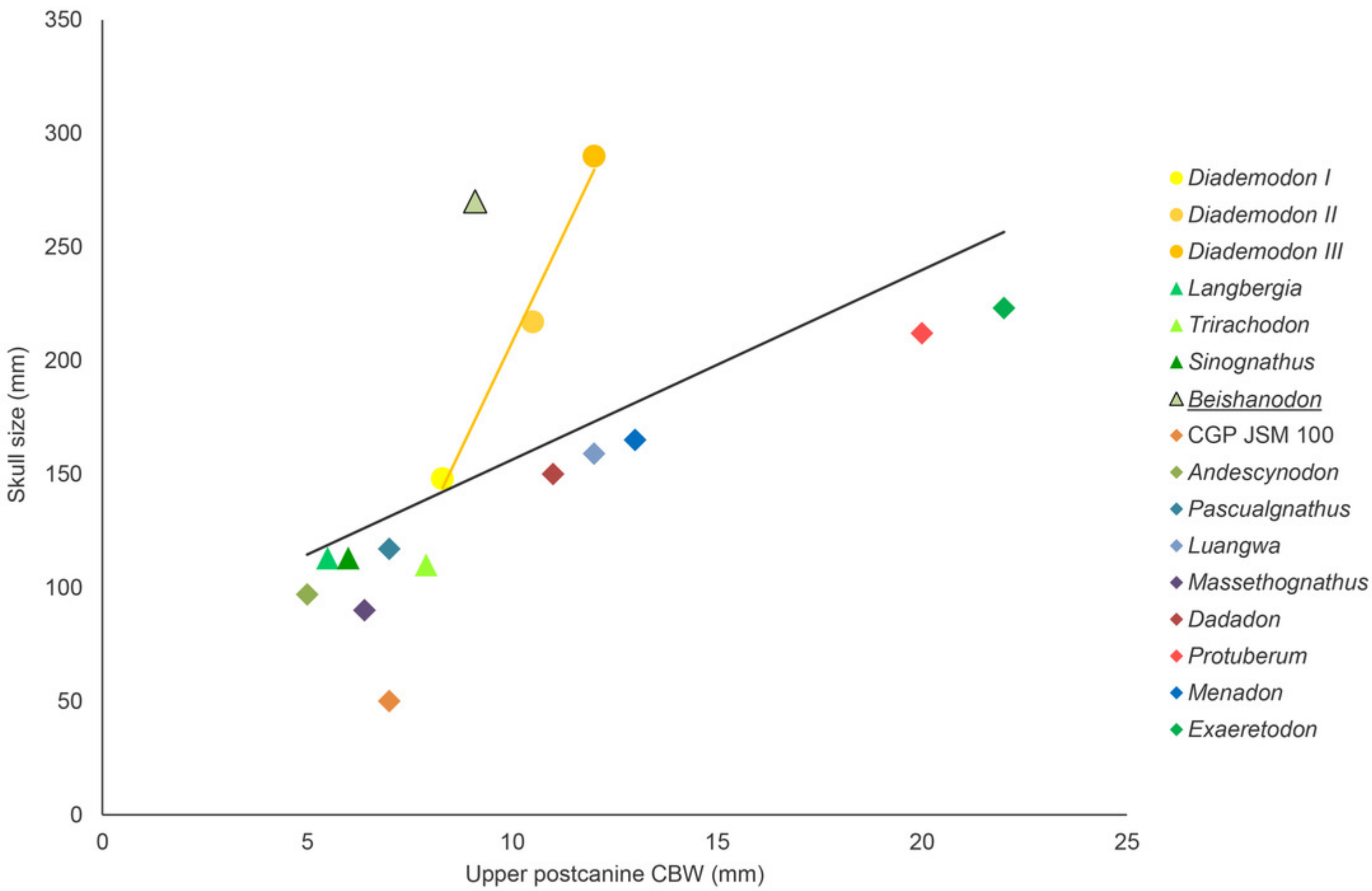


Table 1(on next page)

Table 1: List of specimens of non-traversodontid gomphodonts examined in this study.

Specimens with the best-preserved dentition are underlined.

Table

Table 1: List of specimens of non-traversodontid gomphodonts examined in this study. Specimens with the best-preserved dentition are underlined.

Taxa	Specimens
Diademodon tetragonus	AM 458, 3753; BP/1/2522, 3639, 3756, 4529, 4669, 4677; BSP 1934 VIII 14, 15, 16, 19, 20, 505; MB R1004; NHMUK R3303, R3588, R3765; SAM-PK-571, 4002, 5877, 6216, 6218, 6219, 11265, K175, K177, K180, K183, ?K4660, ?K4661, K5223, K5266, K8971, K9968, K9969; GSN R321, RK3
Titanogomphodon crassus	GSN R323
Langbergia modisei	NMQR 3251, 3255, 3256, 3268, 3280, 3281; BP/1/5362, 5363; SAM-PK-11481
Cricodon metabolus	BP/1/5540, 5835, 6102, 6159; NHMUK R3722, K36800; SAM-PK-6212, K5881; UMZC T905
Trirachodon berryi	AM 434, 461; BP/1/4258, 4658, 4661; BSP 1934 VIII 21, 22, 23; CGP INN 2000-7-2A, CGP unnumbered; NHMUK R2807, R3306, R3307, R3350, R3579, R3721; NMQR 1399; SAM-PK-987, 5880, K142, K170, K171, K4801, K4803, K5821 (=12168?), K7888, K10157, K10161, K10176, K10207, K10411

Sinognathus gracilis	IVPP V2339