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

Christophe Hendrickx [Corresp., 1] , **Fernando Abdala** [1, 2] , **Jonah N Choiniere** [1]

[1] Evolutionary Studies Institute and School of Geosciences, University of the Witwatersrand, Johannesburg, Gauteng, South Africa

[2] CONICET-Fundación Miguel Lillo, Unidad Ejecutora Lillo, San Miguel de Tucumán, Argentina

Corresponding Author: Christophe Hendrickx
Email address: christophendrickx@gmail.com

Gomphodont cynodonts were close relatives of mammals and one of the 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 species, as well as detailed illustrations of each dental unit, after firsthand examination of material and 3d reconstructions of postcanine teeth. Based on dental morphology, *Trirachodon berryi* and '*Trirachodon kannemeyeri*', considered as separate taxa by some authors are here interpreted as representing different ontogenetic stages of the same species. Likewise, *Sinognathus* and *Beishanodon*, thought to belong to non-cynognathian cynodonts and traversodontids by some authors, are referred to Trirachodontidae and Gomphodontia based on dental characters, respectively. Finally, we propose a standardized list of terms and abbreviations for incisors, canines and postcanines anatomical entities, with the goal of facilitating future descriptions and communication between researchers studying the gomphodont dentition.

1 # A proposed terminology for the dentition of gomphodont

2 # cynodonts and dental morphology in Diademodontidae and

3 # Trirachodontidae.

5 CHRISTOPHE HENDRICKX[1*], FERNANDO ABDALA [1,2] & JONAH CHOINIERE[1]

7 [1]Evolutionary Studies Institute and School of Geosciences, University of the Witwatersrand,

8 Johannesburg, South Africa.

9 [2]Unidad Ejecutora Lillo, CONICET-Fundación Miguel Lillo, Miguel Lillo 251, San Miguel de

10 Tucumán 4000, Tucumán, Argentina.

12 Emails: christophendrickx@gmail.com, 1viutiabdala2@gmail.com, jonah.choiniere@wits.ac.za.

13 *Corresponding author.

15 Abstract

16   Gomphodont cynodonts were close relatives of mammals and one of the Mesozoic

17 lineages of cynodont therapsids that became extinct at the end of the Triassic. Gomphodonts

18 were omnivorous to herbivorous animals characterized by labiolingually expanded postcanines,

19 which allowed tooth-to-tooth occlusion. The morphology of the upper and lower postcanines

20 presents important means of distinguishing among major lineages within Gomphodontia, i.e.,

21 Diademodontidae, Trirachodontidae, and Traversodontidae, but the dentition of most

22 Diademodontidae and Trirachodontidae remain poorly documented. Here we present a

23 comprehensive description of the dentition of each diademodontid and trirachodontid species, as

24 well as detailed illustrations of each dental unit, after firsthand examination of material and 3d

25 reconstructions of postcanine teeth. Based on dental morphology, *Trirachodon berryi* and

26 '*Trirachodon kannemeyeri*', considered as separate taxa by some authors are here interpreted as

27 representing different ontogenetic stages of the same species. Likewise, *Sinognathus* and

28 *Beishanodon*, thought to belong to non-cynognathian cynodonts and traversodontids by some

29 authors, are referred to Trirachodontidae and Gomphodontia based on dental characters,

30   respectively. Finally, we propose a standardized list of terms and abbreviations for incisors,

31   canines and postcanines anatomical entities, with the goal of facilitating future descriptions and

32   communication between researchers studying the gomphodont dentition.

34   Introduction

35   Gomphodont cynodonts form a radiation of Triassic therapsids known from the late

36   Olenekian to the Norian on all continents but Australia (e.g., Battail, 1983; Abdala & Ribeiro,

37   2003; Hopson, 2005, 2014; Abdala & Gaetano, 2018; Figure 1A). Members of this clade were

38   small to medium-sized (from approximately 30 cm to 2 m in body length), quadrupedal animals

39   characterized by labiolingual expansion of the upper and sometimes lower postcanines

40   (gomphodont morphology) allowing crown-to-crown occlusion (e.g., Seeley, 1895, 1908;

41   Crompton, 1972; Reisz & Sues, 2000; Abdala, Neveling & Welman, 2006; Hopson, 2014). Such

42   morphology of the postcanines suggests that gomphodonts were omnivorous or possibly

43   exclusively herbivorous animals, feeding on hard plant material (Reisz & Sues, 2000; Abdala,

44   Neveling & Welman, 2006; Liu & Abdala, 2014). Three clades, mainly differentiated by their

45   postcanine morphology, are currently recognized among Gomphodontia, the Diademodontidae,

46   Trirachodontidae and Traversodontidae (Hopson, 2005; Liu & Abdala, 2014; Hendrickx, Abdala

47   & Choiniere, 2016).

48   Diademodontidae is an early diverging lineage of gomphodonts with low taxonomic

49   diversity at the generic and species level (Figure 1A). Two valid taxa (i.e., *Diademodon* and

50   *Titanogomphodon*) known from the Olenekian and Anisian of southern and East Africa,

51   Argentina and possibly Antarctica currently compose this group (Keyser, 1973; Hammer, 1995;

52   Martinelli, de la Fuente & Abdala, 2009; Figure 1B). A possible lazarus diademodontid from the

53   Lower Jurassic of South Africa (Bordy et al., 2017; Abdala & Gaetano, 2018) was described by

54   Abdala et al. (2007) but most likely represents a non-gomphodont tetrapod (F.A. pers. obs.). The

55   postcanine dentition of diademodontids is heterogeneous and separated into conical, gomphodont

56   and sectorial teeth, which is considered as the most primitive condition of dental morphology

57   among Gomphodontia (e.g., Crompton, 1972; Gow, 1978; Hopson, 2005). The upper and lower

58   gomphodont postcanines of diademodontids display several ridges and accessory cusps whose

59   position varies on the crown and along the tooth row. The distalmost part of the diademodontid

60   tooth row is also characterized by a minimum of three sectorial teeth, and one or several

61   transitional postcanines gradually changing from a gomphodont morphology to a more

62   labiolingually compressed sectorial type of crown (Crompton, 1972; Hopson, 2005).

63   Trirachodontidae are represented by five valid species restricted to the Olenekian and

64   Anisian of Southern Africa and Asia (Abdala, Neveling & Welman, 2006; Gao et al., 2010;

65   Sidor & Hopson, 2018; Figure 1A, B). Trirachodontids were relatively small animals (i.e., <1m),

66   and some had a burrowing/fossorial lifestyle (Groenewald, Welman & Maceachern, 2001; Smith

67   & Swart, 2002). The postcanine tooth row of trirachodontids encompasses a lower number of

68   sectorial teeth than that of diademodontids, which occur immediately distal to the gomphodont

69   postcanines (Hopson, 2005). The gomphodont postcanine of trirachodontids shows a clearly

70   defined centrally positioned transverse crest made of labial, central and lingual cusps and ringed

71   by mesial and distal cingula on the rim of the tooth (Abdala, Neveling & Welman, 2006).

72   The most derived and most taxonomically diverse gomphodont radiation are the

73   Traversodontidae, which form a major element of tetrapod communities in Gondwana during the

74   Middle and Late Triassic (Liu & Sues, 2010). This clade currently encompasses more than

75   twenty taxa known from the Anisian to the Norian and possibly Rhaetian of Africa, South

76   America, North America and Europe (e.g., Hopson, 2014; Liu & Abdala, 2014; Figure 1A).

77   Traversodontids increased in body size throughout the Triassic, with younger members reaching

78   up to two meters in length (Reisz & Sues, 2000; Liu & Abdala, 2014). The upper and lower

79   postcanines of traversodontids typically encompass gomphodont teeth, and only a few taxa

80   retained one or several sectorial postcanines at the distal rear of the tooth row in small, possibly

81   young individuals (Liu & Sues, 2010).

82   Similar to other cynodonts, the dentition of gomphodonts is the most diagnostic element

83   of the skeleton (Liu & Sues, 2010). Because of their high resistance compared to other parts of

84   the skeleton due to greater density and lower permeability (Martin, 1999), teeth are also the most

85   commonly preserved material in Gomphodontia, with dental elements known in every

86   gomphodont taxa hitherto described. Given the postcanine diversity and complexity among

87   gomphodonts, the dentition of these cynodonts typically receives particular attention and is often

88   relatively well-described. Nonetheless, thorough description of the dental material is often

89   provided for gomphodont postcanines, whereas information as well as detailed figures on the

90   incisors, canines and conical and sectorial postcanines are omitted in the descriptions of many

91 gomphodont taxa. In addition, we have noticed inconsistencies in the terminology and

92 abbreviations used in discussions of the dental gomphodont anatomy, with several authors

93 providing different terms for the same dental structure. The labiomesial accessory cusp seen in

94 the gomphodont postcanines of some traversodontids has, for instance, received no less than

95 eleven different terms, and more than eight terms describe the labial and labiodistal accessory

96 cusps. Such a large number of terms and abbreviations for the same dental structure leads to

97 confusion, and a clear and detailed terminology, which will greatly facilitate the description and

98 communication of the dentition of gomphodont cynodonts, remain to be provided.

99   This paper: i) proposes a standardized list of terms and abbreviations for incisors, canines

100 and postcanines anatomical entities, with the goal of facilitating future descriptions and

101 illustrations of the gomphodont dentition; and ii) provides a comprehensive description and

102 detailed illustrations of the dentition of all known diademodontid and trirachodontid taxa. Tooth

103 replacement pattern and postcanine occlusion, which were treated in detail by several authors for

104 Diademodontidae and Trirachodontidae (e.g., Crompton, 1955, 1972; Fourie, 1963; Ziegler,

105 1969; Hopson, 1971; Osborn, 1974; Sidor & Hopson, 2018), is beyond the scope of this paper.

106 Likewise, a comprehensive description of the dentition of Traversodontidae, which will form the

107 base of another contribution (Hendrickx, Choiniere & Abdala, in preparation), falls outside the

108 scope of this study. Finally, the evolution of the gomphodont dentition will be thoroughly

109 explored in a third contribution based on a cladistic analysis performed on a dentition-based data

110 matrix encompassing all gomphodont taxa (Hendrickx, Abdala & Choiniere, in preparation).

112 **Institutional abbreviations: AM**, Albany Museum, Grahamstown, South Africa; **AMNH**,

113 American Museum of Natural History, New York, New York, USA; **BP**, Evolutionary Studies

114 Institute (formerly Bernard Price Institute for Palaeontological Research), University of the

115 Witwatersrand, Johannesburg, South Africa; **BSP**, Bayerische Staatssammlung für Paläontologie

116 und Geologie, Munich, Germany; **CGP**, Council for Geosciences, Pretoria, South Africa; **GSN**,

117 Geological Survey of Namibia, Windhoek, Namibia; **IVPP**, Institute for Vertebrate Paleontology

118 and Paleoanthropology, Beijing, China; **MB**, Museum für Naturkunde der Humboldt Universität,

119 Berlin, Germany; **MHNSR–Pv**, Museo de Historia Natural de San Rafael, Mendoza, Argentina;

120 **NHCC**, National Heritage Conservation Commission, Lusaka, Zambia; **NHMUK PV**, Natural

121 History Museum, London, UK; **NMQR**, National Museum, Bloemfontein, South Africa; **NMT**,

122   National Museum of Tanzania, Dar es Salaam, Tanzania; **PKUP**, Peking University

123   Paleontological Collections, Beijing; **SAM-PK**, Iziko, the South African Museum, Cape Town,

124   South Africa; **UMZC**, University Museum of Zoology, Cambridge, UK.

125

126   Material and methods

127   Dental features were investigated on incisors, canines and gomphodont and sectorial

128   postcanines preserved within the upper and lower jaws as well as isolated teeth of non-

129   traversodontid gomphodonts. The dentition of 89 specimens belonging to six diademodontid and

130   trirachodontid genus-level taxa deposited in eleven scientific collections from South Africa,

131   Namibia, Germany, the United Kingdom and China were examined first-hand (Table 1). The

132   specimens were referred to a diademodontid/trirachodontid species based on a dental diagnosis

133   that will be provided for each gomphodont taxon in a forthcoming contribution (Hendrickx,

134   Abdala & Choiniere, in preparation). Denticles, crown ornamentations and enamel texture were

135   observed with a digital microscope AM411T-Dino-Lite Pro. Only *Beishanodon youngi* could not

136   be examined first hand, and we relied on Gao et al.'s (2010) publication in which the dentition

137   was comprehensively described and illustrated.

138   3D-models of teeth were generated for lower and upper postcanines in all taxa but

139   *Sinognathus* and *Beishanodon* (Table 1) through photogrammetric techniques using Agisoft

140   Photoscan Standard (Version 1.3.4; Software; 2017; Retrieved from

141   http://www.agisoft.com/downloads/installer/) and the photos taken with the digital microscope

142   AM411T-Dino-Lite Pro. The batch process followed in Agisoft Photoscan to reconstruct the

143   postcanines in 3d consists of four steps: i) more than 150 photos taken in all views were aligned

144   with the highest accuracy using standard options (i.e., with generic pre-selection and 40,000 and

145   4,000 key point limit and tie point limit, respectively); ii) a dense cloud was then built in ultra-

146   high quality with an aggressive depth filtering and no reuse depth map; iii) the mesh was then

147   built with a high face count and default options (i.e., a custom face count of 200,000 faces,

148   arbitrary surface type, interpolation enabled and vertex color calculated); iv) the texture was

149   finally built using the default options (i.e., generic mapping mode, texture from all cameras,

150   mosaic blending mode, texture size and count of 4,096 and 1, respectively, no color correction

151   and using the hole filling option). A total of twenty 3d-models are deposited and freely

152 downloadable in the MorphoBrowser database

153 (http://pantodon.science.helsinki.fi/morphobrowser/).

154   The dental morphology of *Trirachodon berryi* was also investigated based on CT-scan

155 data from the specimen AM 461, a fully preserved skull and the holotype of *Trirachodon*

156 *kannemeyeri*. AM 461 was CT-scanned at the Evolutionary Studies Institute (ESI) of the

157 University of the Witwatersrand (Johannesburg) using a Nikon Metrology computed tomography

158 XTH 225/320 LC, with a voxel size of 0.0668 mm, and generating 1778 of images of 1109*779

159 pixels resolution. The postcanines were visualized and reconstructed using the software

160 VGStudio Max 3.0 available at the ESI.

161   *Neotrirachodon expectatus* (Tatarinov, 2002) and *Redondagnathus hunti* (Lucas et al.,

162 1999; Spielmann & Lucas, 2012), classified as trirachodontids by their authors, were not

163 included in this study as they probably do not represent gomphodont cynodonts (Sidor &

164 Hopson, 2018). *Neotrirachodon*, synonymized with *Antecosuchus* by Ivakhnenko (2011), likely

165 belongs to a bauriid therocephalian (Battail & Surkov, 2000; Abdala, Neveling & Welman, 2006;

166 Abdala & Smith, 2009; Gao et al., 2010; Sues & Hopson, 2010; Ivakhnenko, 2011) whereas

167 *Redondagnathus'* dental material displays several features absent in Trirachodontidae, namely: a

168 central cusp strongly mesially/distally deflected from the labial and lingual cusps and much

169 higher than the two latter cusps, no valley-like concavities separating the central cusp from the

170 labial and lingual cusps, a cingulum significantly apically higher than the other one, apically

171 pointed cingular cuspules varying dramatically in size along the cingulum, presence of a basally

172 inclined spalling surface extending below the cingulum as well as an important protuberance on

173 the basal part of the root (Sidor & Hopson, 2018; C.H. pers. obs.). We, therefore, agree with

174 Sidor & Hopson (2018) and consider that the teeth of *Redondagnathus* do not share enough

175 dental features with trirachodontids and gomphodonts to be confidently referred to these clades.

176 Likewise, CGP JSM 100, interpreted as a possible juvenile *Trirachodon* by Hopson (2005), was

177 not considered in this study as the specimen likely represents a new taxon of basal traversodontid

178 (C.H.; F.A. pers. obs.), a possibility also discussed by Hopson (2005). The dentition of this

179 specimen, indeed, shows several dental features absent in trirachodontids and seen in basal

180 traversodontids. They include unserrated incisors, a central cusp of transverse crest close to

181 lingual cusp in the upper postcanines, quadrangular or subrectangular lower postcanines in

182 occlusal view, a long axis of lower gomphodont postcanine parallel to the long axis of the

183   mandibular tooth row, and a labial cusp lower than lingual cusp in lower postcanines. The

184   dentition and phylogenetic position of CGP JSM 100 will be thoroughly discussed elsewhere.

185

186   Terminology

187   **Quantitative parameters**

188   The dental positional and morphometric nomenclature follows Smith & Dodson (2003)

189   and Hendrickx, Mateus & Araújo (2015), with the following abbreviations being used in this

190   study:

191

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).

192

193   **Proposed dental terminology**

194   Crown microstructure nomenclature uses the terminology proposed by Sander (1997a,

195   1999). The anatomical nomenclature used to describe and annotate the external tooth

196   morphology (Figure 2) follows the terminology and abbreviations proposed below. The notation

197   presented by Crompton and Jenkins (1968) to describe the series of cusps (i.e., *a, b, c, d, e, f* for

198   the lower postcanines, and *A, B, C, D, E* and *F*, for the upper postcanines) in *Thrinaxodon* and

199   Triassic mammals, and used by some authors to describe the sectorial teeth of gomphodonts

200   (e.g., Sues & Hopson, 2010; Sidor & Hopson, 2018) and non-mammaliaform probainognathians

201   (e.g., Oliveira et al., 2011; Soares, Martinelli & Oliveira, 2014; Martinelli, Soares & Schwanke,

202   2016; Martinelli et al., 2017; Pacheco et al., 2018), was incorporated into our proposed

203   terminology. All abbreviations proposed by Crompton and Jenkins (1968) must, however, be

204   italicized to not be confused with similar abbreviations referred to other dental sub-units (e.g., 'c'

205   is for the canine whereas '*c*' is for the distal accessory cusp). Our terminology and the

206   abbreviations we used to annotate the figures do not also take into consideration the position of

207   the tooth within the upper or lower jaw and left or right side of the skull, as done by Crompton

208   and Jenkins (1968) and other authors (e.g., Hopson, 2005; Sidor & Hopson, 2018).

209   Abbreviations in capital and lower case letters can nonetheless be used by authors to annotate

210   dental features from the upper and lower jaw, respectively. In the same way, the letters 'l' and 'r'

211   followed by the corresponding abbreviation can be used to annotate dental features from the left

212   and right jaw, respectively. For instance, 'lGPC' refers to the left upper gomphodont postcanine

213   whereas 'rmmc' refers to the mesial main cusp of the right lower postcanine.

214   For a consistent terminology, the positional terms mesial, distal, labial and lingual,

215   proposed as standard terms by Smith & Dodson (2003), were favored, with length, width and

216   height referring to the dimension of an anatomical entity in the mesiodistal, labiolingual and

217   apicobasal directions, respectively. We also favor the following hierarchy for the combination of

218   positional terms: 1) apico- and baso- (i.e., apicocentral, apicodistal, apicomesial, apicolingual,

219   basocentral, basodistal, basomesial, basolingual, basolabial); 2) centro- (centrolabial,

220   centrolingual, centromesial, centrodistal); 3) labio- and linguo- (labiomesial, labiodistal,

221   linguomesial, linguodistal); and 4) -mesial and –distal. An exception to this relates to the

222   transverse crest, in which the centrolabial, centrolingual, labiocentral and linguocentral ridges

223   describe different entities of the crest. As for the dental formula, we propose the following

224   notation: i4/3 : c1/1 : pc7-16/7-13 (cpc1-6 : gpc2-7 : tpc0-2 : spc1-4), with i for incisors, c for

225   canines, pc for postcanines, cpc for conical postcanines, gpc for gomphodont postcanines, tpc for

226   transitional postcanines, and spc for sectorial postcanines. Each dental sub-unit is separated by a

227   colon, and the numbers, or ranges (noted x-x), before and after the slash correspond to the

228   number of teeth from the upper and lower jaws, respectively, for each dental sub-unit.

229

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 (db) basins, respectively; Figure 2C, D, E, G), and receiving the crown's cusps and crests of postcanines of the opposite jaw during occlusion. The basin seen on gomphodont postcanines is also referred as 'valley' (e.g., Crompton, 1972; Godefroit & Battail, 1997; Hopson, 2005).
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; Figure 3F). 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 (McGraw-Hill, 2003; Brink & Reisz, 2014; Figure 2A). Incisors and canines of gomphodont cynodonts often have denticulated mesial and distal carinae, whereas the carinae of sectorial teeth bear accessory cusps and/or minute denticles. The carinae are also referred as 'cutting edges' (e.g., Crompton, 1955; Sues & Hopson, 2010), 'cutting ridges', 'enamel ridges' (e.g., Kemp, 1980), 'serrated margins', 'marginal ridges' (e.g., Hopson, 1984), 'keeled edges' and 'sectorial edges' (e.g., Kammerer et al., 2012).
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 accessory cusps correspond to the 'buccal accessory cusp' of Sues et al. (1992) and the 'accessory cusps on transverse ridge' of Hopson (2005).
Central cusp (cc)	Main centrally positioned projection of dentine covered with enamel on the

	transverse crest of the gomphodont postcanine (Figure 2C; Figure 3). The central cusp is also known as the 'middle cusp' (Kemp, 1980), 'main central cusp' (e.g., Crompton, 1955; Hopson, 2014; Sidor & Hopson, 2018) and 'upper central cusp'/'lower central cusp' of Hopson (2005).
Central ridge (cri)	Labiolingually oriented crest centrally positioned on the mesial basin of a gomphodont postcanine (Figure 2E).
Central valley (cev)	Depression delimited by the lingual margin of the labial cusp and the labial margin of the lingual cusps on the transverse crest of the lower postcanine (Figure 2G). The central valley corresponds to the 'saddle' of Crompton (1972).
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 2F).
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). Cingular cuspules are also referred as 'cingular cusps' (e.g., Crompton, 1955; Abdala & Ribeiro, 2003; Abdala, Neveling & Welman, 2006).
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 (Modified from Illiger, 1811; Owen, 1840; Sander, 1997c; Langer & Ferigolo, 2013; Figure 2G). Cingula are also referred as 'crenulations' by Seeley (1894).
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-sectional 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; Figure 3B). While *Diademodon* bears three or more conical postcanines (Figure 3B), trirachodontids (Figure 3) and some traversodontids (e.g., *Boreogomphodon*, possibly *Andescynodon* and *Massetognathus*,) have one or two conical teeth, and the most derived traversodontids do not possess conical postcanine at all. Conical postcanine have also been known as 'premolars' by 19th and 20th century authors (e.g., Broom, 1905, 1913; Brink, 1955; Grine, 1977; Gow, 1978).
Crown (co)	Portion of the tooth covered with enamel, typically situated above the gum and protruding into the mouth ('couronne' of Fauchard, 1728; Cuvier, 1805; Schwenk, 2000; McGraw-Hill, 2003; 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, as well as the crests of gomphodont postcanines ('dentelure' of Cuvier, 1805; Owen, 1840; McGraw-Hill, 2003; Brink & Reisz, 2014; Figure 2J). The denticles are also referred as 'denticulations' (e.g., Kammerer et al., 2012), and the large denticles in low number (<15) on the carinae are known as 'mega-serrations'/'megaserrations' (Hopson, 1984), 'cuspules' (e.g., Abdala & Ribeiro, 2003; Sidor & Hopson, 2018), 'marginal cuspules' (Hopson, 1984; Sues, Hopson & Shubin, 1992; Abdala & Ribeiro, 2003; Abdala, Neveling & Welman, 2006; Liu & Abdala, 2014), 'cusps' (Kammerer et al., 2012), 'accessory cusp' and 'posterior accessory cusp' (Ranivoharimanana et al., 2011; Kammerer et al., 2012).
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	Minor pointed or rounded projection of a sectorial postcanine, distal to the

cusp (dac, *D* or *d*)	distal main cusp (Figure 2I; Figure 3Q-R). The distal accessory cusp is also referred as the 'posterior cingular cusp' (e.g., Crompton, 1963; Abdala, Jasinoski & Fernandez, 2013), 'posterior accessory cusp' (e.g., Abdala & Ribeiro, 2003; Abdala, Neveling & Welman, 2006; Sues & Hopson, 2010; Sidor & Hopson, 2018), 'heel cusp' (Sues & Hopson, 2010) and 'cuspule' (Liu & Sues, 2010). The distal accessory cusp of gomphodont is homologous to the 'posterior cingular cusp' (*sensu* Crompton, 1963) *D* and *d* of the upper and lower postcanines, respectively, in Crompton and Jenkins' (1968) notation.
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; Figure 3A, N).
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., Crompton, 1972; Hopson, 1984, 2005, 2014; Godefroit & Battail, 1997; Sues, Olsen & Carter, 1999; Hopson & Sues, 2006; Liu & Sues, 2010; Sues & Hopson, 2010; Sidor & Hopson, 2018) and the 'posterior valley' (e.g., Crompton, 1972; Godefroit & Battail, 1997; Hopson, 2005).
Distal cingular cuspule (dcc)	Minor pointed or rounded projection on the distal cingulum (dci) of a gomphodont postcanine (Figure 2G; Figure 3G). Distal cingular cusps are also known as 'posterior cingular cusps' (e.g., Hopson, 2005; Abdala, Hancox & Neveling, 2005; Abdala, Jasinoski & Fernandez, 2013) and 'heel cusp' (Crompton, 1955).
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., Crompton, 1972; Kemp, 1980; Hopson, 2005; Abdala, Hancox & Neveling, 2005; Liu & Sues, 2010; Sues & Hopson, 2010; Martinelli, 2010; Hendrickx, Abdala & Choiniere,

	2016), 'posterior marginal cingulum' (Hopson, 2005; Sidor & Hopson, 2018), 'posterior cingular crest' (Abdala & Ribeiro, 2003; Kammerer et al., 2012), and 'crenulated posterior ridge' (Crompton, 1955).
Distal main cusp (dmc, *C* or *c*)	Largest pointed or rounded projection of a sectorial postcanine distal to the main cusp (Figure 2I; Figure 3P, S). The distal main cusp is also known as the 'posterior cusp' (e.g., Hopson, 2005; Liu & Sues, 2010; Sidor & Hopson, 2018), and the 'posterior accessory cusp' (e.g., Crompton, 1963; Abdala & Ribeiro, 2003; Abdala, Neveling & Welman, 2006; Sues & Hopson, 2010; Sidor & Hopson, 2018). The distal main cusp is homologous to the 'posterior accessory cusp' (*sensu* Crompton, 1963) *C* and *c* of the upper and lower postcanines, respectively, in the notation proposed by Crompton and Jenkins (1968).
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). Also known as the 'posterior wall' (Godefroit & Battail, 1997; Hopson & Sues, 2006; Hopson, 2014) and 'posterior ridge' (Crompton, 1955; Godefroit & Battail, 1997).
Distal valley (dv)	Depression delimited by the distal margin of the main cusp and the mesial margin of the distal main cusp on a sectorial postcanine (Figure 2I).
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). The term 'crenulation' was used by Sidor and Hopson (2018) to describe the braided enamel

	texture seen on the canines of *Cricodon*.
Gomphodont postcanine (gpc)	Oval, quadrangular, subrectangular or subtriangular tooth in apical view allowing tooth-to-tooth occlusion (Figure 2A, B; Figure 3B). 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; Figure 3F).
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 basolabial 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., Crompton, 1972; Flynn et al., 2000; Abdala & Ribeiro, 2003; Abdala & Sa-Teixeira, 2004; Hopson, 2005, 2014; Abdala, Neveling & Welman, 2006; Melo, Martinelli & Soares, 2017), 'buccal cingulum' (e.g., Sues, Olsen & Carter, 1999; Sues & Hopson, 2010; Melo, Martinelli & Soares, 2017), 'crenulated ridge' (e.g., Crompton, 1955) and 'cingular labial crest' (Martinelli, 2010).
Labial cusp (lac)	Main labially positioned projection on the transverse crest of a gomphodont postcanine (Figure 2C-H; Figure 3). The labial cusp is also know as the 'external cusp' (e.g., Seeley, 1894; Crompton, 1972; Kemp, 1980; Flynn et al., 2000; Hopson, 2005, 2014; Hendrickx, Abdala & Choiniere, 2016; Sidor & Hopson, 2018), 'upper external cusp'/'lower external cusp' (Hopson, 2005), 'main external cusp' (e.g., Hopson, 2005, 2014; Sidor & Hopson, 2018), 'main upper external cusp'/'main lower external cusp' (Hopson, 2014), 'buccal cusp' (e.g., Grine, 1977; Sues, Hopson & Shubin, 1992; Sues, Olsen & Carter, 1999; Hopson & Sues, 2006), 'buccal main cusp' (Melo, Abdala & Soares, 2015; Melo, Martinelli & Soares, 2017), 'posterior buccal main cusp' (Melo, Abdala & Soares, 2015), 'labial main cusp' (e.g., Godefroit & Battail, 1997; Abdala, Barberena & Dornelles,

	2002) and 'main labial cusp' (e.g., Chatterjee, 1982; Hopson, 1984, 2005, 2014; Godefroit & Battail, 1997; Abdala, Barberena & Dornelles, 2002; Abdala & Ribeiro, 2003; Abdala, Hancox & Neveling, 2005; Abdala & Smith, 2009; Martinelli, 2010; Ranivoharimanana et al., 2011; Kammerer et al., 2012; Liu & Abdala, 2014).
Labial ridge (lar)	Mesiodistally oriented and labially positioned crest-like structure delimiting the labial rim of the occlusal surface of a lower gomphodont postcanine in Traversodontidae (Figure 2D). The labial ridge is also referred as the 'external ridge' (e.g., Seeley, 1895; Kemp, 1980; Hopson, 1984), 'shearing ridge' (e.g., Hopson, 1984), 'buccal ridge' (e.g., Sues, Olsen & Carter, 1999; Hopson & Sues, 2006; Liu & Sues, 2010), 'posterior ridge' (Crompton, 1972) and 'buccal longitudinal crest' (Hopson & Sues, 2006).
Labial valley (lav)	Depression delimited by the lingual margin of the labial cusp and the labial margin of the central cusp on the transverse crest (Figure 2F). The labial valley corresponds to the 'embayment' of Crompton (1972) and the 'V-shaped notch' of many authors (e.g., Crompton, 1955; Sues, Olsen & Carter, 1999; Sues & Hopson, 2010; Martinelli, 2010; Hopson, 2014).
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, G).
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). The labiodistal accessory cusp is also known as the 'posterior labial cusp' (e.g., Crompton, 1955; Liu, 2007a; Martinelli, 2010; Liu & Abdala, 2014; Melo, Abdala & Soares, 2015), 'posterolabial cusp' (e.g., Abdala & Ribeiro, 2003; Hopson, 2014), 'posterior labial accessory cusp' (e.g., Kammerer et al., 2012), 'posterior external accessory cusp' (Hopson, 2014), 'posterior accessory labial cusp' (e.g., Abdala, Barberena & Dornelles, 2002; Abdala & Ribeiro, 2003; Abdala & Sa-Teixeira, 2004; Battail, 2005; Abdala, Hancox & Neveling, 2005; Kammerer et al., 2012), 'posterior buccal cusp' (e.g., Liu & Sues, 2010; Melo, Abdala & Soares,

	2015), 'posterobuccal cusp' (e.g., Sues, Olsen & Carter, 1999; Hopson & Sues, 2006; Liu & Sues, 2010; Sues & Hopson, 2010), 'posterior buccal accessory cusp' (Melo, Abdala & Soares, 2015), 'posterolateral accessory cusp' (Hopson, 1985) and 'posterior accessory cusp' (e.g., Crompton, 1972; Hopson, 1985).
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). The labiodistal ridge corresponds to the 'posteroexternal ridge' of Hopson (2005) and Hendrickx, Abdala & Choiniere (2016).
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). The labiomesial accessory cusp is also known as the 'anterior accessory cusp of upper postcanine'/'anterior accessory cusp of lower postcanine' (Crompton, 1972), 'anterior labial cusp' (e.g., Crompton, 1955; Liu, 2007a; Martinelli, 2010), 'anterolabial cusp' (e.g., Flynn et al., 2000; Liu, 2007a; Hopson, 2014; Liu & Abdala, 2014), 'anterolabial accessory cusp' (e.g., Hopson, 2014; Liu & Abdala, 2014; Melo, Martinelli & Soares, 2017), 'anteroexternal accessory cusp' (Hopson, 2014), 'anterior buccal cusp' (e.g., Melo, Abdala & Soares, 2015), 'anterobuccal cusp' (e.g., Sues, Olsen & Carter, 1999; Hopson & Sues, 2006; Liu & Sues, 2010; Sues & Hopson, 2010), 'anterior buccal accessory cusp' (Melo, 2014; Melo, Abdala & Soares, 2015), 'mesiobuccal accessory cusp' (Melo, Martinelli & Soares, 2017), and 'anterior accessory labial cusp' (e.g., Abdala, Barberena & Dornelles, 2002; Abdala & Ribeiro, 2003; Abdala & Sa-Teixeira, 2004; Battail, 2005; Abdala, Hancox & Neveling, 2005; Abdala & Smith, 2009; Ranivoharimanana et al., 2011; Kammerer et al., 2012).
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). The labiomesial ridge corresponds to the 'anterior ridge' (e.g., Crompton, 1972; Hopson, 1985) and 'anteroexternal ridge' (e.g., Hopson, 2005; Hendrickx, Abdala & Choiniere, 2016).

Lingual cingular cuspule (licc)	Minor pointed or rounded projection on the lingual cingulum of a conical or sectorial postcanine (Figure 2I; Figure 3O). The lingual cingular cuspules are also known as the 'lingual cingular cusps' (e.g., Sidor & Hopson, 2018).
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; Figure 3O).
Lingual cusp (lic)	Main lingually positioned projection on the transverse crest of the postcanine (Figure 2C-H; Figure 3). The lingual cusp is also known as the 'internal cusp' (e.g., Romer, 1967; Kemp, 1980; Hopson, 1985), 'main internal cusp' (e.g., Hopson, 2005, 2014; Sidor & Hopson, 2018), 'upper internal cusp'/'lower internal cusp' (Hopson, 2005), 'lingual main cusp' (Melo, Martinelli & Soares, 2017) and 'main lingual cusp' (e.g., Crompton, 1955; Godefroit & Battail, 1997; Godefroit, 1999; Sues & Hopson, 2010; Melo, Martinelli & Soares, 2017).
Lingual ridge (lir)	Mesiodistally oriented and lingually positioned crest-like structure delimiting the lingual rim of the occlusal surface of a gomphodont postcanine (Figure 2E).
Lingual valley (liv)	Depression delimited by the labial margin of the lingual cusp and the lingual margin of the central cusp on the transverse crest (Figure 2F). The labial valley corresponds to the 'embayment' of Godefroit and Battail (1997) and the 'V-shaped notch' of Hopson and Sues (2006).
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).
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). The linguodistal accessory cusp is also known as the 'posterior lingual cusp' (e.g., Crompton, 1955; Abdala, Barberena & Dornelles, 2002; Kammerer et al., 2012; Melo, Abdala & Soares, 2015), 'posterolingual cusp' (e.g., Hopson & Sues, 2006; Liu, 2007a), 'posteromesial accessory cusp' (Hopson, 1985) and 'posterior accessory

	lingual cusp' (e.g., Abdala & Ribeiro, 2003; Kammerer et al., 2012).
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). The linguodistal ridge is equivalent to the 'posterointernal ridge' of Hopson (2005).
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 postcanine (Figure 2C, H). The linguomesial accessory cusp is also known as the 'anterior accessory cusp of upper postcanine'/'anterior accessory cusp of lower postcanine' (Crompton, 1972), 'anterior lingual cusp' (e.g., Crompton, 1955; Abdala & Smith, 2009; Martinelli, 2010; Melo, Abdala & Soares, 2015), 'anterior lingual accessory cusp' (Melo, 2014), 'anterolingual cusp' (e.g., Hopson, 1984; Sues, Hopson & Shubin, 1992; Abdala & Ribeiro, 2003; Abdala, Neveling & Welman, 2006; Gao et al., 2010; Sues & Hopson, 2010; Ranivoharimanana et al., 2011; Liu & Abdala, 2014), 'anterolingual accessory cusp' (e.g., Sues & Hopson, 2010; Hopson, 2014; Liu & Abdala, 2014; Melo, Abdala & Soares, 2015; Sidor & Hopson, 2018) and 'anterointernal accessory cusp' (Hopson, 2014),.
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). The linguomesial ridge is equivalent to the 'anterointernal ridge' of Hopson (2005).
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). Longitudinal ridges are also known as 'flutes'/'fluting' (Seeley, 1894; Crompton, 1955), 'longitudinal striations' (e.g., Hopson, 1984), 'vertical striations' (e.g., Liu & Sues, 2010), and 'vertical ridges' (Sues & Hopson, 2010).
Main cusp (mc, *A* or *a*)	Major projection of dentine covered with enamel on the sectorial postcanine (Figure 2I; Figure 3Q, S). The main cusp can be denticulated on both its mesial and distal carinae. The main cusp is also known as the 'central cusp'

	(e.g., Liu & Sues, 2010; Sues & Hopson, 2010; Sidor & Hopson, 2018), and the 'central main cusp' (Sidor & Hopson, 2018). The main cusp is homologous to the cusps *A* and *a* of the upper and lower postcanines, respectively, in Crompton and Jenkins' (1968) notation..
Mesial accessory cusp (mac, *E* or *e*)	Minor pointed or rounded projection on the mesial carina of a sectorial postcanine, mesial or linguomesial to the mesial main cusp. The mesial accessory cusp is homologous to the 'anterior cingular cusp' (*sensu* Crompton, 1963) *E* and *e* of the upper and lower postcanines, respectively, in Crompton and Jenkins' (1968) notation. Visible in some sectorial postcanines of *Thrinaxodon* and possibly *Cynognathus*, one or several mesial accessory cusps are assumed to be present in the multicuspid/crenulated lower sectorial teeth of juveniles *Andescynodon* (PVL 4390) and *Massetognathus* (MCZ 4267).
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; Figure 3A, C, N).
Mesial basin (mb)	Main concavity mesial to the transverse crest on the occlusal surface of a gomphodont postcanine (Figure 2C, E, H). The mesial basin is also known as the 'anterior excavation in the crown' (Crompton, 1955), 'anterior valley' (Crompton, 1972), 'occlusal basin' (Melo, Martinelli & Soares, 2017) and 'anterior basin' (e.g., Sues, Hopson & Shubin, 1992; Godefroit & Battail, 1997; Sues, Olsen & Carter, 1999; Hopson & Sues, 2006; Liu & Sues, 2010; Hopson, 2014).
Mesial cingular cuspule (mcc)	Minor pointed or rounded projection on the mesial cingulum of a gomphodont postcanine (Figure 2C, H; Figure 3E).
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). The mesial cingulum is also known as the 'anterior cingulum' (e.g., Sues, Hopson & Shubin, 1992; Abdala & Sa-Teixeira, 2004; Battail, 2005; Hopson, 2005; Hopson & Sues, 2006; Abdala, Neveling & Welman, 2006; Kammerer et al., 2008; Gao et al.,

	2010; Sues & Hopson, 2010; Liu & Abdala, 2014; Hendrickx, Abdala & Choiniere, 2016), 'crenulated ridge' (e.g., Kemp, 1980; Abdala, Neveling & Welman, 2006), 'anterior crenulated ridge' (Crompton, 1955), 'anterior marginal cingulum' (Hopson, 2005; Sidor & Hopson, 2018), 'anterior external cingulum' (Hopson, 2005) and 'anterior cingular crest' (e.g., Abdala & Ribeiro, 2003; Kammerer et al., 2012).
Mesial main cusp (mmc, *B* or *b*)	Largest pointed or rounded projection on the mesial carina of a sectorial postcanine directly mesial to the main cusp (Figure 2I; Figure 3Q, S). The mesial main cusp, as used by Sidor and Hopson (2018), is also known as the 'anterior cusp' (e.g., Liu & Sues, 2010; Sues & Hopson, 2010; Sidor & Hopson, 2018), the 'anterior main cusp' (e.g., Abdala, Jasinoski & Fernandez, 2013), the 'anterior accessory cusp' (e.g., Crompton, 1963; Abdala, Neveling & Welman, 2006; Sues & Hopson, 2010; Sidor & Hopson, 2018) and the 'mesial accessory cusp' (e.g., Martinelli, Soares & Schwanke, 2016). The mesial main cusp is homologous to the 'anterior accessory cusp' (*sensu* Crompton, 1963) *B* and *b* of the upper and lower postcanines, respectively, in Crompton and Jenkins' (1968) notation.
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). Also known as 'transverse ridge' (Seeley, 1894), 'anterior wall' (e.g., Hopson, 1985; Sues, Olsen & Carter, 1999; Flynn et al., 2000; Battail, 2005; Martinelli, 2010; Melo, Abdala & Soares, 2015; Melo, Martinelli & Soares, 2017) and 'anterior crest' (Melo, Abdala & Soares, 2015).
Mesial valley (mv)	Depression delimited by the mesial margin of the main cusp and the distal margin of the mesial main cusp on a sectorial postcanine (Figure 2I).
Postcanine (pc)	Maxillary or dentary tooth positioned distal to the canine. Postcanines include conical, gomphodont and sectorial teeth, which can change (e.g., *Diademodon*) from one morphology to the other (Figure 2B).
Root (ro)	Portion of the tooth beneath the gum and embedded in an alveolus ('racine' of Fauchard, 1728; Cuvier, 1805; 'radix dentis' of Illiger, 1811; Owen,

	1840; Hillson, 2005; Figure 2I).
Sectorial postcanine (spc)	Labiolingually compressed tooth typically located in the distalmost part of the postcanine tooth row, distal to the gomphodont teeth, and more rarely in the anteriormost part of the postcanine tooth row, 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; Figure 3F, H).
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). Unlike the carinae of incisors, canines and sectorial teeth which bear large and elaborate serrations (i.e., denticles), the serrated transverse crest and mesial and distal ridges of gomphodont postcanines only have simple and minute serrations visible with a microscope. Besides the well-delimited denticles of non-gomphodont postcanines, these serrations should not be confused with the triangular, hemi-spherical or sub-pyramidal cusps and cuspules present on the transverse crest and/or cingula of gomphodont and sectorial postcanines of 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 intermediate morphology between a gomphodont tooth and a sectorial postcanine (Figure 2A; Figure 3B, D, O). Transitional postcanines are typically formed by a recurved blade shape labial portion and a relatively flat lingual projection (Goñi & Goin, 1988). They are also referred as 'intermediate gomphodont' (Fourie, 1963; Osborn, 1974; Grine, 1977; Goñi & Goin, 1988), 'intermediate sectorial' (Osborn, 1974; Goñi & Goin, 1988), 'semi-gomphodont'(Hopson, 1971; Crompton, 1972; Brink, 1977), 'sub-gomphodont' (Hopson, 1964) and 'sub-sectorial' (Martinelli, 2010) postcanines.

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). The transverse crest is also known as the 'transverse ridge' (e.g., Crompton, 1972; Hopson, 1984, 2005, 2014; Godefroit, 1999; Abdala, Neveling & Welman, 2006; Sues & Hopson, 2010; Sidor & Hopson, 2018), 'anterior ridge' (Martinelli, 2010), 'transverse anterior ridge' (Hopson & Sues, 2006), 'anterior crest' (Liu & Abdala, 2014), 'central crest' (e.g., Hendrickx, Abdala & Choiniere, 2016; Sidor & Hopson, 2018) and 'posterior transverse crest' (e.g., Abdala, Barberena & Dornelles, 2002; Abdala & Ribeiro, 2003; Melo, Abdala & Soares, 2015).
Transverse undulation (tun)	Band like enamel wrinkle extending along most of the incisor or canine length, typically from the mesial to distal carinae, perpendicular from the long axis of the crown (modified from Hendrickx, Mateus & Araújo, 2015; Figure 2B).

230

231   Results

232   **Diademodontidae Haughton, 1924**

233   *Diademodon tetragonus* **Seeley, 1894**

234   **Holotype:** SAM-PK-571a (Wonderboom, subzone B, *Cynognathus* AZ, South Africa), two

235   isolated upper postcanines (holotype of *Diademodon brachytiara*; Seeley, 1894); SAM-PK-571b

236   (Burghersdorp, subzone B, *Cynognathus* AZ, South Africa), two isolated canines, an incomplete

237   upper jaw and a small portion of mandible (holotype of *Diademodon tetragonus*; Seeley, 1894).

238   **Referred dental material:** from Burghersdorp, subzone B, *Cynognathus* AZ, South Africa: AM

239   438, 458 (holotype of *Gomphognathus kannemeyeri*), BP/1/2522 (Luiperdskop locality), 3769,

240   3771–3773, 3776 (holotype of *Cragievarus kitchingi*; Cragievar locality for the four last

241   specimens), NHMUK PV R2574, R2575, R3581 (holotype of *Microgomphodon eumerus*),

242   SAM-PK-3426, K175, K177, K180, K183, K9968, UMCZ T.433 (Luiper Kop locality); from

243   Steynsburg, subzone B, *Cynognathus* AZ, South Africa, AM 3753 (holotype of *Octagomphus*

244 *woodi*); from Winnaars Baken, subzone B, *Cynognathus* AZ, South Africa: AMNH FR 5518 and

245 5519 (holotype of *Cyclogomphodon platyrhinus*), BP/1/3511, NHMUK PV R3587, R3588

246 (referred to *Diademodon browni*), R3765 (holotype of *Diademodon entomophonus*), R4092,

247 R9216, SAM-PK-8015, 11265; from Aliwal North, subzone B, *Cynognathus* AZ, South Africa:

248 NHMUK PV R3303 (holotype of *Diademodon mastacus*), R3304 (holotype of *Diademodon*

249 *browni*), R3305 (holotype of *Microgomphodon oligocynus*), R3308, R3724, SAM-PK-4002,

250 5877 (referred to *Cyclogomphodon platyrhinus*), 6216, 6218, 6219; from Queenstown, subzone

251 B or C, *Cynognathus* AZ, South Africa: SAM-PK-?K4660, ?K4661; from Hofmeyr, subzone B

252 or C, *Cynognathus* AZ, South Africa: SAM-PK-K5266; from Lady Frere, subzone B,

253 *Cynognathus* AZ, South Africa: BP/1/1195, 3754, 3756–3758, BSP 1934 VIII 14, 15, 16, 17

254 (holotype of *Gomphognathus grossarthi*), 18 (holotype of *Gomphognathus broomi*), 19

255 (holotype of *Gomphognathus haughtoni*), 20, 505, BSP 1936 II 8 (holotype of *Sysphinctostoma*

256 *smithi*), MB R1004, NHMUK PV R2576–7 (holotype of *Gomphognathus polyphagus*), R2578,

257 UMCZ T.434, T.436 (holotype of *Diademodon laticeps*), T.438, T.441, T.445, T.454, T.826,

258 T.971; from Rouxville, subzone A, *Cynognathus* AZ, South Africa: BP/1/4529, 4647

259 (Bethel/Slootkraal localities for the two last), 4669 (Gladde Grond 530 locality), 4677

260 (Betjieskraal 36 locality); from Norwood farm, subzone C, *Cynognathus* AZ, South Africa:

261 BP/1/5541; from Avilion farm, subzone C, *Cynognathus* AZ, South Africa: BP/1/5542; from

262 unknown localities in South Africa: NHMUK PV R3767; SAM-PK-K5223 (Cape Province),

263 K5716, K8971, K9969; from the Luangwa Basin, Ntawere Formation, Zambia: BP/1/3639

264 (holotype of *Diademodon rhodesiensis*); from Etjo Mountain, Omingonde Formation, Namibia:

265 GSN R321, R327, R335, RK3; from San Rafael, Río Seco de la Quebrada Formation, Argentina:

266 MHNSR–Pv 357; from Beardmore Glacier region, Fremouw Formation, Antarctica: possibly

267 AMNH FR 24421.

268 **Occurrence:** Wonderboom, Burghersdorp, Aliwal North, Steynsburg, Winnaars Baken,

269 Queenstown and Hofmeyr, Joe Gqabi District, Walter Sisulu Municipality, Eastern Cape

270 Province, South Africa; Avilion and Norwood farms, Chris Hani District, Enoch Mgijima

271 Municipality, Eastern Cape Province, South Africa; Lady Frere, Chris Hani District; Rouxville,

272 Xhariep District, Mohokare Municipality; Free State, South Africa; Drysdall and Kitching's

273 locality 16, north of Sitwe, northern Luangwa Basin, Zambia (Peecook et al., 2018); Etjo

274 Mountain, Otjozondjupa Region, Namibia; Puesto Viejo farm house, 40 km southwest of San

275   Rafael, Mendoza Province, Argentina; possibly Gordon Valley, Beardmore Glacier region,

276   Transantarctic Mountains, Antarctica.

277   **Horizon:** subzones B–C of the *Cynognathus* AZ, Burgersdorp Formation, Karoo Basin; lower

278   Ntawere Formation; lower fauna of the upper Omingonde Formation; Río Seco de la Quebrada

279   Formation, upper unit of the Puesto Viejo Group; possibly upper Fremouw Formation.

280   **Age:** early to late Anisian, Middle Triassic; n.b, Valencio et al. (1975) provided a ^{40}K/^{40}Ar

281   dating of 232±10Ma for the middle section of the Río Seco de la Quebrada Formation of

282   Argentina, placing this unit into the Upper Triassic (Carnian; Figure 1B). Likewise, Ottone et al.

283   (2014) obtained a ^{38}U/^{206}Pb age of 235.8±2.0 Ma for the underlying Quebrada de los Fósiles

284   Formation (Figure 1B), providing additional support to the fact that the Río Seco de la Quebrada

285   Formation is early Carnian. This unit, which has yielded remains of the basal cynognathians

286   *Cynognathus* (Abdala, 1996, 1999) and *Diademodon* (Martinelli, de la Fuente & Abdala, 2009),

287   would thus be at least 10 million years younger than the putative age usually attributed to the

288   African *Cynognathus* AZ (Martinelli et al., 2017; Peecook et al., 2018; Gaetano, Mocke &

289   Abdala, 2018 and references therein). Ottone and colleagues (2014) suggested two scenarios to

290   explain their results: i) the *Cynognathus* AZ and other fossiliferous units from African basins

291   (i.e., Omingonde Formation of Namibia, Manda Beds of Tanzania, Ntawere Formation of

292   Zambia) are wrongly attributed to the Anisian and should be instead assigned to the Carnian

293   (Figure 1B, in green); ii) an Anisian age of the *Cynognathus* AZ and other contemporaneous

294   biostratigraphic units from Southern Africa is correct and the stratigraphic duration of

295   *Cynognathus* and *Diademodon* is much longer than expected, ranging from the Anisian (Africa)

296   to the Carnian (South America).

297   **Dental formula:** i4/3 : c1/1 : pc7-16/7-13 (cpc1-6 : gpc2-7 : tpc0-2 : spc1-4).

298   **Dental morphology:** The dental morphology, postcanine microstructure, dental replacement

299   pattern and postcanine occlusion of *Diademodon tetragonus* are fairly well-known (Seeley,

300   1894, 1895, 1908; Watson, 1911, 1913; Broili & Schröder, 1934; Brink, 1955, 1963, 1977;

301   Crompton, 1955, 1963, 1972; Fourie, 1963; Ziegler, 1969; Hopson, 1971; Osborn, 1974; Grine,

302   1977). Few of these studies provide, however, detailed information and illustrations on the dental

303   morphology and a thorough description of the anatomy of the incisors, canines and postcanines

304   is here provided.

305   *Incisors*

306   Little information on the upper and lower incisors is available in the *Diademodon*

307   specimens examined first hand. Incisors are preserved in the skulls of BP/1/3756 and BP/1/4669,

308   the crania of AM 3753, BP/1/2522 and BSP 1934 VIII 14, and the mandible of MB R1004. The

309   incisors of the latter specimen are, however, the only ones in natural position and visible in

310   lingual view. Only the labial side of the teeth is visible in the other specimens, except for BSP

311   1934 VIII 14, in which three loose upper incisors are preserved and show their labial or lingual

312   sides. The upper incisors of BSP 1934 VIII 14 appear to be salinon-shaped in cross-section at

313   mid-crown and both mesial and distal carinae are denticulated. The distal carina faces distally

314   whereas the mesial carina is linguomesially displaced and almost reaches the cervix (Figure 4A,

315   C). The denticles are minute, well-delimited, apicobasally elongated to subquadrangular, and

316   their external margin, made of a thin layer of enamel, is weakly convex (Figure 4B, D). There

317   are eight and six denticles per millimeter on the mesial and distal carinae at mid-crown in BSP

318   1934 VIII 14, respectively. This suggests that the distal denticles of the incisors are larger than

319   the mesial ones (DSDI > 1.2) in *Diademodon*. Concave surfaces adjacent to the mesial carina are

320   present on the lingual surface and marginal to the distal carina on the labial side of the crown

321   (Figure 4A). The lower incisors of MB R1004 are too badly preserved. They are mildly

322   procumbent and no constriction appears to be present between root and crown. Their

323   morphology does not seem to depart from that of the upper incisors.

324   *Canines*

325   Only the two partially complete isolated canines of the holotypic specimen SAM-PK-

326   571b can be examined in all views. The upper canines of AM 3753, BP/1/3756, BP/1/4669 and

327   BSP 1934 VIII 14 and 15 are relatively well-preserved but BSP 1934 VIII 15 is the only

328   specimen with in-situ upper canines that can be seen in both labial and lingual views. Likewise,

329   only the lower canines of BSP 1934 VIII 505 can be observed in both labial and lingual views,

330   yet they are poorly preserved and incomplete. The isolated canine of the holotype bear two

331   poorly defined longitudinal ridges on both labial and lingual sides (Figure 4E). These ridges

332   extend along the whole crown and delimit narrow labial and lingual depressions mesiodistally

333   that extend also on the root. Although the canines of several specimens of *Diademodon* (e.g.,

334   BSP 1934 VIII 14, 15 and 505; BP/1/4669) do not bear any ridges, three to four faint

335   longitudinal ridges can be seen on the canines of AM 3753 and BP/1/3756. Interestingly, SAM-

336   PK-571b, AM 3753 and BP/1/3756 with ridged canines belong to small individuals whereas

337 large size specimens of *Diademodon* have canines devoid of longitudinal ridges. This strongly

338 suggests that the presence of ridges varies throughout ontogeny, as observed in the canines of

339 some traversodontids (Agustín Martinelli, pers. comm. April 2018). The mesial and distal

340 carinae of the upper canines are centrally positioned on the crown and the cross-sectional outline

341 at mid-crown is lenticular in AM 3753. Both carinae are also denticulated and the mesial carina

342 extends well-apical to the cervix in SAM-PK-571b. The denticles are well-preserved in this

343 specimen and clearly show the peculiar condition of changing sporadically in size along the

344 carinae (Figure 4F). As in the incisors, the denticles of the canines are apicobasally elongated in

345 shape and their external margin is weakly symmetrically convex. Seven and 7.5 denticles per

346 millimeter are present at mid-crown in the canine of the holotype (CH ~ 10 mm), whereas three

347 and 3.5 to four denticles per millimeter can be counted at mid-crown in the canines of the larger

348 specimens BSP 1934 VIII 14 (CH ~ 14 mm) and BP/1/4669 (CH ~ 19 mm), respectively. Due to

349 preservation, it is unknown whether the lower canines of BSP 1934 VIII 505 were denticulated.

350 *Conical postcanines*

351   The upper and lower conical postcanines vary from one in the newly born/juvenile

352 specimen BSP 1936 II 8 (Broili & Schröder, 1936; Hopson, 1971; Brink, 1977) to six in the

353 large-sized and most probably adult specimen NHMUK PV R3308 (Hopson, 1971). As

354 described by Crompton (1955), the upper conical postcanines are straight, apically pointed, and

355 slightly labiolingually compressed or subcircular. The mesial and distal carinae of these teeth are

356 also denticulated in NHMUK PV R3308 (Crompton, 1955) and denticles appear to be present at

357 the base of the distal carina in BSP 1934 VIII 14 (Figure 4H). The upper conical teeth are,

358 however, unserrated in BP/1/3639 and possibly in MB R1004 (Figure 4G). In the latter

359 specimen, the upper conical postcanines are also mesiodistally constricted at the cervix but this

360 may result from taphonomical deformation (Figure 4G). The upper conical postcanines of

361 NHMUK PV R3308 clearly increase in width distally, and the mesial four (possibly also the

362 unpreserved fifth) crowns are monocuspid (i.e., tooth strictly conical in shape, with a single

363 centrally positioned cusp; Crompton, 1955). The sixth postcanine, considered to be a conical

364 type by Hopson (1971), departs from this morphology. Although subcircular in outline, the tooth

365 shows an important lingual projection and includes a high labial cusp and a low lingual

366 cingulum. The latter is comprised of three or more cingular cuspules linguomesially and an

367 additional cingular cuspule behind the labial cusp distally (Crompton, 1955).

368   As in the upper jaw, the lower conical postcanines increase in width distally, being

369 weakly labiolingually compressed in the first two or three teeth and subcircular in the following

370 crowns. No information on the first two conical teeth could be extracted from the specimens.

371 These lower postcanines are believed to be monocuspid like those from the cranium, and do not

372 show any cingulum. The third and fourth lower conical postcanines preserved in AM 458 are

373 proportionally wider than the upper conical postcanines of MB R1004 and BSP 1934 VIII 14

374 from the same alveoli. In AM 458, the mesial carina of conical postcanines faces linguomesially

375 whereas the distal carina is positioned distally (Figure 4I, J). Both mesial and distal carinae are

376 clearly denticulated in AM 458. The distal denticles are large and apically inclined whereas the

377 mesial denticles are low and show a widely convex external margin. Cingular cuspules are

378 visible on the linguodistal surface, at the base of the third and fourth conical postcanines of AM

379 458 (Figure 4J). A distal accessory cusp is also present at mid-crown height in the lower conical

380 teeth of SAM-PK-5877 (Figure 4K).

381 *Upper gomphodont postcanines*

382   According to Brink (1977), the number of upper gomphodont postcanines varies between

383 two (BSP 1936 II 8; Broili & Schröder, 1936; Hopson, 1971) to seven (BP/1/2522; Brink, 1963).

384 The best-preserved upper gomphodont postcanines are from the holotypic specimen SAM-PK-

385 571a, which includes in situ teeth within the maxillae (Figure 4N–O) as well as two well-

386 preserved isolated postcanines from the more distal portion of the jaw (Figure 4L–M). With a

387 CBR ranging from one to 1.7, most of the upper gomphodont postcanines are wider than the

388 lower gomphodont postcanines. Gomphodont postcanines of *Diademodon* are characterized by

389 the presence of several accessory ridges and bumps on the mesial and distal surfaces of the

390 transverse crest. The mesial and distal accessory ridges vary in length, orientation and extension

391 along the tooth row so that each gomphodont postcanine has a unique morphology along the jaw.

392 All upper postcanines, however, bear a large labial cusp longer and slightly higher than the

393 lingual cusp (Figure 4L, N). A smaller and lower yet well-demarked labiodistal accessory cusp

394 always follows the labial cusp. The mesial and distal crests of the labial cusp appear to be weakly

395 denticulated, with the largest denticles being present in the basal portion of the cusp. The lingual

396 cusp is always adjacent to a linguomesially accessory cusp, and the latter is as long and tall as

397 the lingual cusp. In the fourth right gomphodont postcanine of BSP 1934 VIII 14, the

398 linguomesial accessory cusp is in fact much longer than the lingual cusp (Figure 4P) and is

399   followed by a second shorter linguomesial accessory cusp. The presence of accessory ridges and

400   bumps on the transverse crest makes it difficult to delimit the central cusp in SAM-PK-571a,

401   which seems to be centrally positioned on the crest (Figure 4L, M). Both mesial and distal

402   margins of the upper gomphodont postcanines are delimited by one or several accessory cusps

403   forming a cingulum (Figure 4L). The size, position and height of these cingular cuspules vary in

404   each upper postcanine along the tooth row (see below). The isolated upper postcanines of the

405   holotype bear a single mesial cingular cuspule (Figure 4M) and perhaps some other minor

406   cingular cuspules, whereas the distal cingulum is made of four to five cuspules increasing in

407   height and width lingually (not clearly visible in Figure 4L, see 3d model). The distal basin is

408   longer than but as deep as the mesial basin. The root is more than twice as long as the crown and

409   bears a deep, wide and centrally positioned depression on its distal surface.

410   The upper gomphodont postcanines from the anterior half of the maxilla (Figure 4N, O)

411   follow the same pattern of ridges and cusps seen in the isolated upper postcanines, i.e., they have

412   two main labial and lingual cusps adjacent to two prominent labiodistal and linguomesial

413   cingular cuspules, respectively. The labial and lingual cusps have, however, the same height. The

414   labiodistal accessory cusp is significantly lower and shorter than the labial cusp, whereas the

415   linguomesial accessory cusp is longer and as high or higher than the lingual cusp. The transverse

416   crest of these postcanines bears accessory ridges and bumps on the mesial surface only, the distal

417   surface being smooth (Figure 4N). In one of the two in-situ upper postcanines, the mesial surface

418   shows an accessory ridge running perpendicular to the transverse crest and parallel to a second,

419   poorly marked ridge, as well as a single accessory bump on its linguomesial portion. The central

420   cusp of the transverse crest is long, low and appears to bear some poorly defined serrations on its

421   labial and lingual crests. Some portions of the mesial and distal cingula and labiomesial,

422   labiodistal, linguomesial and linguodistal ridges also show a beaded appearance and are finely

423   serrated in the three best-preserved upper postcanines. The distal basin of the distalmost

424   preserved postcanine is narrow, well defined and bounded by the distal cingulum. This basin is,

425   however, shallow and poorly defined in the preceding tooth (Figure 4N) and absent in the

426   mesialmost preserved postcanine. The mesial basin of the two first postcanines has also been

427   worn out, a feature shared with *Titanogomphodon*. Similar to the isolated upper postcanines, the

428   mesial margins of the in-situ postcanines have a single and weakly lingually deflected cingular

429   cuspule. Likewise, the distal cingulum is formed by four cingular cuspules that increase in width

430   and height lingually. Two distal cingular cuspules are seen on the linguodistal margin of the

431   preceding tooth (Figure 4N). A higher number of cingular cuspules can, however, been counted

432   on the cingula of other *Diademodon* specimens, with five, possibly six, cingular cuspules in the

433   mesial cingulum of the best-preserved right upper postcanine of NHMUK PV R3303, and five to

434   six cingular cuspules in the distal cingulum of the largest left and right upper postcanines of

435   NHMUK PV R3765. Although the width and height of the mesial cingular cuspules also increase

436   lingually in NHMUK PV R3303, the cingular cups of the distal carina decrease in size either

437   towards the center of the cingulum or sporadically along the cingulum in NHMUK PV R3765.

438   *Lower gomphodont postcanines*

439   The number of lower gomphodont postcanines appears to vary between three (juvenile

440   specimen BSP 1936 II 8; Broili & Schröder, 1936; Hopson, 1971) to five (large-sized/adult

441   specimens BSP 1934 VIII 505 and SAM-PK-177), or even possibly more. Two lower

442   gomphodont postcanines from the posterior portion of an incomplete left mandible of the

443   holotype SAM-PK-571a are also among the best-preserved lower postcanines known (Figure

444   5A–E). The best-preserved lower postcanine, which is the most distal one, is longer than wide

445   and the lingual cusp is as wide but slightly shorter and lower than the labial cusp (Figure 5A, C).

446   It is difficult to know whether accessory cusps were present. Based on the size of the cusps, the

447   linguomesial and labiodistal accessory cusps appear to be present and may not correspond to

448   cingular cuspules. These two cusps are lower and shorter than the lingual and labial cusps

449   (Figure 5A, B). It is unknown whether the lingualmost cingular cuspule of the mesial cingulum

450   is homologous to the linguomesial accessory cusp (Figure 5A, B). The mesial and distal

451   accessory ridges are prominent, higher than the low and poorly delimited transverse crest and

452   diagonally oriented from it. Three accessory ridges can be counted on the mesial surface of the

453   transverse crest and one on the distal surface (Figure 5A). A second much shorter distal ridge

454   extending linguodistally is present at the level of the distal basin. Three protuberant and well-

455   delimited mesial cingular cuspules composed the mesial cingulum whereas the distal cingulum

456   encompasses four smaller and poorly delimited cingular cuspules (Figure 5A, C). As observed in

457   some upper postcanines, the mesial and distal edges of the labial cusp are denticulated (Figure

458   5E). The second more mesial lower gomphodont postcanine is more sub-circular in outline and

459   the mesial and distal accessory ridges on the transverse crest are not so prominent. We assume

460   the presence of a labiodistal and linguomesial accessory cusps in this tooth, but the mesialmost

461   and distalmost cingular cuspules are as wide and as well-delimited as these two putative

462   accessory cusps. Both labial and lingual cusps are incomplete and it is unknown whether they

463   had the same width and height.

464   The lower gomphodont postcanines of the large majority of other more mature specimens

465   of *Diademodon* preserving the lower dentition (e.g., BMNH R3588; BSP 1934 VIII 16, 505; MB

466   R1004; GSN R321) are worn out and only the distalmost mandibular postcanines of AM 458,

467   AM 3753 and SAM-PK-5877 are complete enough to provide some information on their

468   morphology. In all specimens, the labial cusp is the largest, and is significantly longer, wider and

469   higher than the lingual cusp. The transverse crest connecting the two cusps forms a narrow ridge

470   bearing a low and poorly defined central cusp. One or two large pointed mesial cingular cuspules

471   are visible in the three specimens, mesial to the lingual cusp (Figure 5D). Based on their size,

472   these cingular cuspules may correspond to the linguomesial accessory cusps of more derived

473   gomphodonts. A wide and high centrally positioned mesial cingular cuspules is well-visible in

474   SAM-PK-5877 (Figure 5D) but worn out in AM 458 and AM 3753. The central cingular

475   cuspules are wider than the mesial cuspules directly mesial to the lingual cusp but narrower than

476   the preceding one situated on the linguomesial margin of the lower postcanine. The distal

477   cingulum, well-preserved in the left and right distalmost lower postcanines of SAM-PK-5877,

478   bears four to six well-delimited cingular cuspules (Figure 5D). These distal cingular cuspules

479   extend on the labiodistal ridge of the labial cusp in the left postcanine where they increase in

480   length mesially. As in the holotype, several accessory ridges of variable length and orientation

481   (i.e., perpendicular, diagonally oriented or parallel to the transverse crest) are present on the

482   mesial and distal surfaces of the transverse crest in SAM-PK-5877, AM 458 and AM 3753. In

483   SAM-PK-5877, one of the mesial accessory ridges reaches the largest mesial cingular cuspules

484   (Figure 5D).

485   *Transitional postcanines*

486   The transitional upper and lower postcanines, which are relatively well preserved in MB

487   R1004, SAM-PK-K177 and AM 3753, have an intermediate morphology between the distalmost

488   gomphodont and the sectorial postcanines. They are subcircular, weakly labiolingually

489   elongated, drop-shaped or oval in outline. These teeth show a large recurved cusp on the labial

490   portion of the crown homologous to the labial cusp and the main cusp of gomphodont and

491   sectorial postcanines, respectively. A lingual cingulum formed by three to five well-delimited

492   and strongly protruding cingular cuspules are also visible (Figure 5F, G). Labiodistally oriented

493   ridges connecting the main cusp to one or several of these cingular cuspules can be seen in some

494   specimens (Figure 5F). One or two distal accessory cusps are also present distal to the main cusp,

495   with the one directly mesial to the main cusp being likely homologous to the labiodistal

496   accessory cusp of gomphodont postcanines of *Diademodon* and possibly other trirachodontids

497   and traversodontids. Two transitional postcanines can be observed in the lower jaw of SAM-PK-

498   K177 (Figure 5F). Although incomplete, the main cusp of those two teeth appears to be

499   linguomesially oriented and subcircular in outline. The transitional upper postcanines (the

500   'intermediate gomphodont of Osborn 1974) were lost in some specimens of *Diademodon* such as

501   BSP 1934 VIII 14 in which they probably were replaced by gomphodont postcanines, following

502   the replacement model proposed by Hopson (1971) and Osborn (1974).

503   *Sectorial postcanines*

504   The upper and lower sectorial postcanines always bear a recurved main cusp followed by

505   a distal main cusp, or, more commonly, one distal main cusp and a smaller distal accessory cusp

506   (Figure 5H–I). The distal accessory cusp of the sectorial teeth is either of the same length or

507   slightly shorter than the distal main cusp. Some teeth also bear a minute mesial main cusp on the

508   basal third of the mesial margin of the main cusp (Figure 5H). The mesial and distal carinae of

509   the main cusp are usually denticulated along the whole crown height. The specimen BP/1/4529

510   shows the unique feature of having both mesial and distal denticles divided into two parts, i.e., a

511   large sub-denticle apically and a smaller one basally (Figure 5J, K). The distal main and distal

512   accessory cusps are also denticulated in this specimen (Figure 5J). A lingual cingulum composed

513   of six to seven cuspules is clearly present in the mesial lower sectorial teeth of AM 3753, MB

514   R1004 and SAM-PK-K177. This cingulum is, however, absent in the upper sectorial postcanines

515   of BSP 1934 VIII 14 and in the distalmost upper and lower sectorial teeth of MB R1004.

516   *Crown enamel surface texture and microstructure*

517   Histological studies of the postcanine of *Diademodon tetragonus* were done by Grine

518   (1977, 1978), Osborn & Hillman (1979) and Sander (1997b). The enamel microstructure of this

519   taxon was revealed to be prismless and columnar (the synapsid columnar enamel SCE of Sander,

520   1997b), and to include incremental lines and enamel tubules. The enamel surface texture (sensu

521   Hendrickx, Mateus & Araújo, 2015) of incisors, canines and postcanines is braided and

522   apicobasally oriented.

523   ***Titanogomphodon crassus* Keyser, 1973**

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

525   **Referred dental material:** None.

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

527   **Horizon:** Etjo Beds, upper levels of the upper Omingonde Formation.

528   **Age:** late Anisian-Ladinian?, Middle Triassic. The upper fauna from the upper Omingonde

529   Formation is correlated to that from the *Dinodontosaurus* AZ of Brazil and the Chañares

530   Formation of Argentina (Abdala & Smith, 2009; Abdala et al., 2013; Martinelli et al., 2017).

531   Given that the Chañares Formation was recently dated to the lower Carnian (Marsicano et al.,

532   2016), the upper fauna from the Omingonde Formation might also be from the lowermost part of

533   the Upper Triassic.

534   **Dental formula:** i?/? : c?/? : pc>7/? (cpc?: gpc>3: tpc1 : spc3).

535   **Dental morphology:** Keyser (1973) described the dentition of *Titanogomphodon* in relative

536   details given the poor preservation of the teeth. The holotypic specimen GSN R323 preserves the

537   distal portion of the three distalmost gomphodont postcanines as well as a transitional postcanine

538   and the first and third sectorial teeth (Figure 6).

539   *Upper gomphodont postcanines*

540   As noted by Keyser (1973), the transverse crest of the gomphodont postcanine, which

541   connects the labial and lingual cusps (both unpreserved in all gomphodont postcanines of GSN

542   R323), is slightly mesially displaced (Figure 6B). As seen in *Diademodon* upper postcanines, a

543   faint mesial accessory ridge can be observed in the distalmost gomphodont tooth (Figure 5A, C).

544   Unlike Keyser's (1973) description of the upper gomphodont postcanines, no labiodistal

545   accessory cusp or distinct cuspules forming a distal cingulum can be observed in the preserved

546   teeth (Figure 6A). Nonetheless, the damaged right mesialmost gomphodont postcanine appears

547   to show a labiomesial accessory cusp, mesial to the unpreserved labial cusp as well as a mesial

548   cingular cuspule (Figure 6D, F). Many portions of the enamel and dentine surface of this tooth

549   are, however, missing and the presence of these two accessory cusps/cingular cuspules needs to

550   be confirmed. Similar to some upper postcanines of *Diademodon* that have been worn out, and

551   unlike trirachodontid postcanines, the mesial and distal basins are absent in all preserved

552   postcanines of *Titanogomphodon*.

553   *Transitional and sectorial postcanines*

554   According to Keyser (1973), *Titanogomphodon* is diagnosed by the diagonal orientation

555   of the sectorial postcanines, of which the long axis is linguomesially oriented. Such orientation

556   of the sectorial teeth indeed contrasts with the mesiodistally oriented upper sectorial postcanines

557   of other gomphodont cynodonts such as *Diademodon*, *Langbergia*, *Trirachodon*, *Andescynodon*

558   and *Boreogomphodon*, in which the long axis is parallel to the labial margin of the upper jaw. As

559   in *Diademodon* and unlike trirachodontids, a transitional postcanine is present between the

560   gomphodont and sectorial teeth. Little information can be extracted from the transitional and

561   sectorial postcanines due to wear and the incompleteness of the crowns. No main and accessory

562   cusps, or cingular cuspules are preserved in the sectorial postcanines and only a concavity

563   centrally positioned on the lingual surface of the crown and root is present in the two sectorial

564   teeth (Figure 6A, E).

565   **Trirachodontidae Romer, 1967**

566   *Langbergia modisei* **Abdala, Neveling & Welman, 2006**

567   **Holotype:** NMQR 3255 (from Langberg), an incomplete cranium.

568   **Referred dental material:** from Goedgedacht: NMQR 3251; from Langberg: NMQR 3256,

569   BP/1/5362; from Rexford Store: NMQR 3268, BP/1/5363; from Eerste Geluk: NMQR 3280,

570   3281; from Bosrand: BP/1/5400, 5401, 5404; from Driefontein: BP/1/5666; from Moerbeidal:

571   CGP/1/33; from Palmiet Fontein: CGP/1/120; from Kaaimansgat: SAM-PK-11481.

572   **Occurrence:** (from Abdala, Neveling & Welman (2006), Table 1) Langberg 556 and

573   Driefontein, Paul Roux, Thabo Mofutsanyane District, Free State Province, South Africa;

574   Rexford Store 433, Bethlehem, Thabo Mofutsanyane District; Eerste Geluk 131, Kestell, Thabo

575   Mofutsanyane District; Goedgedacht 15, Marquard, Thabo Mofutsanyana District; Bosrand 12,

576   Senekal, Thabo Mofutsanyane District; Moerbeidal 648, Kaaimansgat 146 and Hugo's Kop 620,

577   Rouxville, Xhariep District, Free State Province, South Africa; Palmiet Fontein 94, Tarkastad,

578   Chris Hani District, Eastern Cape Province, South Africa;.

579   **Horizon:** subzone A of the *Cynognathus* Assemblage Zone (AZ), Burgersdorp Formation,

580   Beaufort Group, Karoo Supergroup.

581   **Age:** late Olenekian, Early Triassic.

582   **Dental formula:** i4/3 : c1/1 : pc7-9/8 (cpc1-2: gpc3-7?: spc2-4).

583   **Dental morphology:** The dentition of *Langbergia modisei* has been well-described by Abdala,

584   Neveling & Welman (2006). Here we provide additional information based on firsthand

585   examination of the best-preserved specimens.

586   *Incisors*

587   The mesial carina of the incisors does not seem to be denticulated, whereas the distal

588   carina is denticulated and bears around 30 denticles per 5 mm (contra Abdala, Neveling &

589   Welman, 2006; Figure 7A-C). The denticles of the first right lower incisor of NMQR 3251 have

590   a symmetrically convex external margin and are poorly delimited. They are apicobasally

591   elongated and change sporadically in size along the carina (Figure 7A, B). The largest denticles

592   are at mid-crown and the denticles do not extend up to the crown apex and the root (Figure 7A,

593   B). The distal denticles of the fourth upper incisor of NMQR 3281 and SAM-PK-11481 share the

594   same morphology, with the largest denticles at mid-crown and the basalmost and apicalmost

595   denticles extending far above the root (Figure 7C) and below the crown apex, respectively. A

596   concave surface adjacent to the distal carina is also present on the labial surface of the third?

597   right incisor in SAM-PK-11481. Based on the first and best-preserved lower incisor of NMQR

598   3280, the mesial carina faces mesially whereas the distal carina is distally, almost linguodistally

599   positioned, giving a lenticular to D-shaped cross-sectional outline at mid-crown. The distal

600   profile of the upper incisors of this specimen is sigmoid in labial view, with the basal one-third

601   and the apical two-thirds of the crown being convex and concave, respectively. The incisors are

602   apically recurved and some of them are weakly mesiodistally constricted at the cervix.

603   *Canines*

604   Both upper and lower canines of *Langbergia modisei* have denticulated carinae

605   (BP/1/5362; NMQR 3251, 3268) with a denticle density ranging from 20 to 32 denticles per 5

606   mm. In NMQR 3251 and 3268, the mesial and distal denticles of the canines do not extend to the

607   cervix basally, but do reach the crown apex in NMQR 3251. Similar to the incisors, the mesial

608   and distal denticles change sporadically in size along the carinae and have a symmetrically to

609   asymmetrically convex external margin (Figure 7F, G). The denticles of the canines tend to be

610   better delimited and mesiodistally longer than those of the incisors so that denticles are

611   apicobasally elongated and sometimes subquadrangular in shape. Despite the fact of changing

612   randomly in size, the basal and apicalmost denticles are smaller than those of the mid-crown on

613   both mesial and distal carinae. Faint longitudinal ridges delimiting mesiodistally short, flat facets

614   can be observed on the labial surface of the canines of BP/1/5362 (Figure 7H) and SAM-PK-

615   11481. In the latter specimen, the mid-crown cross-sectional outline of the upper canine is

616   roughly salinon-shaped (sensu Hendrickx, Mateus & Araújo, 2015), with a wide convex labial

617   margin showing a weakly concave labiodistal surface, and a biconcave lingual margin, of which

618   the mesial concavity is longer than the distal one (Figure 7E). A concave surface is also present

619   on the mesial and distal surfaces of the erupting right and left upper canines of NMQR 3268,

620   respectively. The cross-sectional outline of the canine of NMQR 3251 is, however, parabolic at

621   mid-crown. This indicates that there is variation in cross-sectional outline in the canines. No

622   transverse undulations could be observed on the upper and lower canines of the specimens

623   examined. The enamel surface texture of NMQR 3268 is clearly braided and curves basally close

624   to the carinae (Figure 7I).

625   *Gomphodont postcanines*

626   As noted by Abdala, Neveling & Welman (2006), the first upper and lower postcanines

627   differ in their morphology. The first upper postcanine of NMQR 3251 is significantly smaller

628   than the more distal ones, has a sub-circular cross-sectional outline and only bears a single main

629   cusp, a morphology that is similar to the conical postcanines of *Diademodon*. In NMQR 3255,

630   the first upper postcanine has an oval cross-sectional outline and is only slightly smaller than the

631   other gomphodont postcanines. Given the incomplete preservation of the first upper postcanines

632   on both sides, it is unknown whether they were monocuspid as well. The morphology of the first

633   lower postcanine appears to be more complex. It includes a main centrally positioned and a

634   slightly labially displaced cusp (Figure 7N), which is homologous to the central cusp of more

635   distal gomphodont postcanines based on its size, position and morphology. This main cusp is

636   bordered by a small apically pointed mesial accessory cusp and a low lingual cingulum formed

637   by at least three minute cingular cuspules (Figure 7N), a morphology reminiscent to that of

638   sectorial postcanines seen in diademodontids and trirachodontids. Because the distal portion of

639   this tooth is missing, it is unknown whether an accessory cusp was present distal to the main

640   cusp.

641   Unlike other trirachodontids, the upper and lower gomphodont postcanines of *Langbergia*

642   roughly share the same morphology, i.e., they are elliptical in cross-section, slightly

643   labiolingually elongated and their long axis is slightly to strongly linguomesially oriented

644   (Abdala, Neveling & Welman, 2006). This diagnosis applies to the specimens with upper and

645   lower postcanines visible in apical view (i.e., NMQR 3251 and NMQR 3255), with the exception

646   of NMQR 3268. Indeed, although the upper and lower gomphodont postcanines of NMQR 3251

647   and NMQR 3255 share a crown base ratio (CBR) varying between 1.3 and 1.45, the upper

648   gomphodont postcanines of NMQR 3268 are more labiolingually elongated, with a CBR around

649   2 in the widest teeth. Likewise, the long axis of the upper postcanines of NMQR 3268 is

650   perpendicular to the long axis of the cranium. It is unknown whether these dental differences are

651   ontogenetic, intra- or interspecific, and NMQR 3268 is here tentatively kept within the species *L.*

652   *modisei* based on the absence of a maxillary platform, a labiolingually narrow and prominent

653   central cusp, and the stratigraphic distribution of the specimen (i.e., *Cynognathus* subzone A).

654   Both upper and lower gomphodont postcanines of *Langbergia* increase in size up to the

655   penultimate tooth, which is slightly larger than the last gomphodont postcanine. The long axis of

656   the upper gomphodont postcanines is roughly parallel in all teeth in NMQR 3251, 3255 and

657   3268, with very little variation along the tooth row. In the lower postcanines, however, it changes

658   in orientation, with the long axis being strongly mesially oriented in the first two postcanines,

659   then almost parallel to the long axis of the mandibular tooth row in the last gomphodont tooth.

660   All gomphodont postcanines bear a high, wide, centrally positioned central cusp bordered

661   labially and lingually by the labial and lingual cusps, respectively (Figure 7J-M). The central

662   cusp always appears to be higher and wider than both labial and lingual cusps. It is separated

663   from these two cusps by a deep and narrow valley extending basally at a certain distance above

664   the mesial and distal basins (Figure 7L). The labial, central and lingual cusps that form the

665   transverse crest are not perfectly aligned on the same plane of elongation of the postcanine. The

666   long axis of the central cusp either follows that of the transverse crest or is diagonally oriented to

667   it (Figure 7J, K, M). Likewise, the labial cusp of the upper postcanines is significantly deflected

668   mesially from the diagonally oriented axis of the transverse cusp whereas the lingual cusp of the

669   lower postcanines is weakly deflected distally in some teeth (Figure 7J, K, M). The lingual and

670   central cusps are, however, aligned in the same plane of elongation of the postcanine while the

671   labial cusp remains mesially displaced from that plane. A cingulum formed by three to four large

672   and sometimes strongly protruding cingular cuspules delimits both the mesial and distal margin

673   of the upper and lower gomphodont postcanines in NMQR 3251 and NMQR 3255. The

674   labiomesial and linguodistal cusps are the largest accessory cusps of the cingula in the upper

675   gomphodont postcanines whereas the labiomesial, linguomesial and linguodistal are the largest

676   in the lower postcanines. Although incomplete and badly preserved, the upper postcanines of

677   NMQR 3268 do not seem to bear these large accessory cusps on the cingula. The mesial and

678   distal cingula instead comprise a large number of small cingular cuspules, as seen in *Cricodon*

679   and *Trirachodon*. Due to the incompleteness of the upper postcanines of NMQR 3268, it is

680   unknown whether the cingular cuspules extend along the whole width of the crown or are

681   restricted to a certain part of the cingulum. A similar morphology is seen in the mesial cingulum

682   of the last right upper gomphodont of SAM-PK-11481, in which the cingular cuspules also form

683   low and poorly delimited convexities. The whole morphology of this gomphodont postcanine,

684   which is strongly diagonally oriented and whose labiomesial portion is the only one not hidden

685   by the matrix, in fact departs from that seen in the gomphodont teeth of NMQR 3251, 3255 and

686   3268. The labial cusp of the crown in SAM-PK-11481 appears to form a minute projection

687   separated from the central cusp by a much wider and higher cusp. It is, however, possible that the

688   wider cusp directly adjacent to the central cusp is in fact the labial cusp, and that the small cusp,

689   which is connected to the mesial cingulum by a low ridge, corresponds to a cingular cuspule

690   mesial to the labial cusp. The cingular cuspules, however, increase in width towards the center of

691   the crown at least on the distal cingulum in this specimen. The mesial and distal basins, delimited

692   by the transverse crest and the cingulum, are deep and mesiodistally short in *Langbergia* (Figure

693   7J, K, M). As observed for the canines, the enamel texture of the gomphodont postcanines is

694   braided and apicobasally oriented.

695   *Sectorial postcanines*

696   The sectorial postcanines always include a main recurved cusp followed by one distal

697   main cusp and, in some teeth, a distal accessory cusp distally, and one or no mesial main cusp

698   (Figure 7O, P). The mesial margin of the main cusp is denticulated on the apical third of the

699   crown in BP/1/5362 (Figure 7P). The denticles are poorly defined, low, apicobasally elongated

700   projections on the carina. As in the denticles of the incisors and canines, they sporadically

701   change in size and their external margin is symmetrically to asymmetrically convex. The distal

702   main cusp is the longest whereas the distal accessory cusp is significantly smaller and sometimes

703   appears as a minute projection. The mesial main cusp is often large, projects apically and

704   strongly protrudes from the basal third of the crown (Figure 7O). The distal main cusp also

705   projects distally in some specimens. As observed by Abdala, Neveling & Welman (2006), a

706   lingual cingulum composed of five cingular cuspules is present in the second upper sectorial

707 postcanine of NMQR 3255 (Figure 7Q). The mesialmost cingular cuspule is long and followed

708 distally by two short cusps, a much longer one, and then a medium sized one. A sigmoid and

709 basally inclined cingulum formed by several minute cingular cuspules is also visible on the

710 lingual surface of the third lower sectorial postcanine of NMQR 3251. In the latter specimen, the

711 last upper sectorial crown is significantly shorter and slightly lower than the preceding one. It is

712 a tricuspid postcanine in which the main cusp, distal main cusp and distal accessory cusp projects

713 basodistally and decrease in height and length distally (Figure 7O). The distal main cusp is a

714 subtriangular prominence at mid-crown height whereas the distal accessory cusp is a minute

715 projection in the basalmost part of the crown (Figure 7O).

716 ***Cricodon metabolus* Crompton, 1955**

717 **Holotype:** UMZC T905 (from Njalila, Manda Beds, Tanzania), incomplete upper and lower

718 jaws with several loose teeth.

719 **Referred dental material:** from Avilion farm, subzone C, *Cynognathus* AZ, South Africa:

720 BP/1/5540, 5835, 6159; from Norwood farm, subzone C, *Cynognathus* AZ, South Africa:

721 BP/1/6102; from Sitwe, Ntawere Formation, Zambia: NHCC LB28; from Ruhuhu Basin, Manda

722 Beds, Tanzania: NMT RB227, NHMUK PV R36800; from Aliwal North, subzone B,

723 *Cynognathus* AZ, South Africa: NHMUK PV R3722, SAM-PK-6212, 5881*a* and *b*.

724 **Occurrence:** Stockley's bone locality B11, Njalila, Tanzania; Outcrop Z40 (Z51 according to

725 Sidor & Hopson, 2018), Ndatira River, Litumba Ndyosi District, Ruhuhu Basin, Tanzania (Smith

726 et al., 2018); Outcrops Z29, Z81, near the village of Lutimba Kuhamba, Litumba Kuhamba

727 District, Tanzania (Sidor & Hopson, 2018; Smith et al., 2018); Outcrop L23, 5 km west of Sitwe,

728 Eastern Province, Zambia; Avilion and Norwood farms, Bamboeshoek Valley, Sterkstroom,

729 Chris Hani District, Enoch Mgijima Municipality, Eastern Cape Province, South Africa; Aliwal

730 North, Joe Gqabi District, Walter Sisulu Municipality, Eastern Cape Province, South Africa.

731 **Horizon:** middle to upper Lifua Member, Manda Beds; subzones B and C of the *Cynognathus*

732 Assemblage Zone (AZ), Burgersdorp Formation, Beaufort Group, Karoo Supergroup; upper

733 Ntawere Formation.

734 **Age:** early to late Anisian, Middle Triassic.

735 **Dental formula:** i4/3 : c1/1 : pc9-10/11 (cpc0 : gpc7-9 : spc0-2).

736 **Dental morphology:** The dentition of the holotypic specimen of *Cricodon metabolus* was

737 described by Crompton (1955) and additional information was given by Abdala, Hancox &

738   Neveling (2005) and Sidor and Hopson (2018) based on referred specimens. Although Sidor and

739   Hopson (2018) recently comprehensively described the well-preserved dentition of an immature

740   *Cricodon metabolus* (NMT RB227) from Zambia, a detailed examination of the holotype and

741   referred material deposited in South Africa and England enable us to provide additional

742   information on the dental morphology of this taxon. BP/1/5540, 5835, 6102, 6159, NHMUK PV

743   R3722, R36800, SAM-PK-6212, 5881*a* (represented by a badly crushed snout and the anterior

744   portion of a mandible) and 5881*b* (preserving the left maxillary tooth row with five upper

745   gomphodont postcanines) are here tentatively referred to *Cricodon metabolus* based on the large

746   size, the low denticle density of the incisors and canines, the drop-shaped outline of the

747   distalmost upper postcanines, the step-like disposition of distalmost upper gomphodont

748   postcanines, and the long axis of lower postcanines perpendicular to the mandibular tooth row.

749   We, however, note important differences in the cranial, mandibular and dental anatomy of the

750   holotype and referred specimens NMT RB227, BP/1/6102, SAM-PK-5881 (e.g., length of the

751   diastema between the canine and the first upper/lower postcanine, morphology of the first upper

752   postcanines and last gomphodont postcanines, lateral extension of the platform marginal to the

753   dental series). If these differences could be ontogenetic, we do not exclude the possibility that

754   these referred specimens represent one or several new trirachodontid species. Conversely,

755   BP/1/5538 from the subzone C *Cynognathus* AZ of the Avilion farm (Sterkstroom District) is

756   confidently excluded from this taxon. This specimen, represented by the posterior portion of the

757   snout and orbits with the three last gomphodont and the first sectorial postcanines preserved,

758   differ from *Cricodon* by: i) longer and more ovoid upper distal gomphodont postcanines (CBR of

759   1.5 vs. CBR of 1.85 to 2.5 typical of *Cricodon*); ii) no step-like disposition of the

760   antepenultimate and penultimate upper gomphodont postcanines; iii) upper postcanines with a

761   large labiomesial accessory cusp and no distal cingulum (contra Abdala, Hancox & Neveling,

762   2005); iv) sectorial upper postcanines with a large strongly pointed and strongly apically

763   recurved main cusp and two distal accessory cusps. BP/1/5538 may also belong to a new

764   gomphodont taxon.

765   *Incisors*

766   The mesial and distal carinae of the partially erupted first left lower incisor of the

767   holotype UMZC T905 are clearly denticulated and include apicobasally elongated to

768   subquadrangular and weakly apically inclined denticles with a symmetrically convex external

769   margin (Figure 8A, B). Both mesial and distal denticles decrease in size apically and reach the

770   crown apex, although the tip of the apex remains unserrated. There are around 1.75 denticles per

771   mm (denticle density of ~9/5mm) in the basalmost erupted part of the mesial and distal carinae,

772   and 3.5 denticles per mm at the apex. The upper incisors of BP/1/6102 and BP/1/5540 share the

773   same denticle density, with 7 to 10 denticles per 5 mm in the distal carina (Figure 8C, D). This

774   contrasts with the much higher density of denticles (>20/5mm at mid-crown) on the incisors of

775   other trirachodontids. The mesial carina and denticles of BP/1/6102 are not visible and are most

776   likely covered by sediment. Only the apical denticles of the first left upper incisor can be seen on

777   the mesial carina of BP/1/5540. These mesial denticles are apicobasally elongated, have a flat

778   external margin and extend one millimeter below the crow apex. The denticles of the distal

779   carina of BP/1/6102 and BP/1/5540 also extend from the cervix to the base of the crown apex

780   (Figure 8C). In BP/1/6102, the distal denticles decrease in size apically and basally from the

781   mid-crown height, and are apicobasally elongated at mid-crown and in the apical part of the

782   crown and almost subquadrangular in the basal third of the carina (Figure 8D). On the other

783   hand, the distal denticles of BP/1/5540 are apically inclined and subquadrangular on most of the

784   carina. The denticles of the third replacing upper incisor of NHCC LB28 are more prominent

785   distally than mesially, and the distal denticles also increase in size from the apex towards the

786   base of the crown in both upper and lower incisors (Sidor & Hopson, 2018). The external margin

787   of the denticles in BP/1/5540 is symmetrically to asymmetrically convex and weakly parabolic.

788   The interdenticular space is apicobasally wide in the basal denticles and narrow in the mid-crown

789   and apical denticles in BP/1/6102 whereas it is wide in most of the denticles in BP/1/5540. The

790   distal denticles of the incisors change sporadically in size along the carina in *Cricodon*. The

791   mesial carina faces mesially whereas the distal carina is oriented linguodistally in the first two

792   and distally in the last two upper incisors. The incisors are recurved, with a strongly convex

793   mesial profile and a straight to slightly concave distal profile. Although the incisors from all BP

794   specimens referred to *Cricodon* do not seem to be constricted at the cervix, a constriction appears

795   to be present in the lower incisors of NHCC LB28, giving a spatulate outline to the crowns

796   (Sidor & Hopson, 2018). No information can be provided on the cross-sectional outline of the

797   incisors, yet the labial is convex and the lingual flat in NHCC LB28 (Sidor & Hopson, 2018).

798   The root of the incisors of this specimen are long, taper apically and have an oval cross-sectional

799   outline that is narrower mesiodistally than labiolingually (Sidor & Hopson, 2018).

800 *Canines*

801   The morphology of the canines of *Cricodon* is based on the upper and lower canines of

802 NHCC LB28, the upper canines of BP/1/6102, BP/1/5540 and NHMUK PV R3722, and the

803 lower canines of SAM-PK-5881*a*, as the canines are not preserved in the holotype (Crompton,

804 1955). As noted by Abdala, Hancox & Neveling (2005) and Sidor & Hopson (2018), both

805 carinae of the lower canine are denticulated (Figure 8E). The denticles are slightly bigger than

806 those of the incisors, with 6 to 7 denticles per 5 mm on the distal carinae at mid-crown in

807 BP/1/6102 and BP/1/5540 (Figure 8G-I), and 9 to 11 in NHCC LB28 (Sidor & Hopson, 2018).

808 The denticle density of the smaller specimens NHMUK PV R3722 and SAM-PK-5881*a* vary

809 between 12.5 and 14 denticles per 5 mm. The distal denticles are larger than the mesial ones in

810 BP/1/6102, BP/1/5540 and NHCC LB28, with a denticle density of 8.6 in the mesial carina and

811 6.8 in the distal carina in BP/1/6102 (Figure 8G, H), 8 and 6.6 denticles/5mm in BP/1/5540, and

812 9 to 11 and 15 to 19/5mm in NHCC LB28 (Sidor & Hopson, 2018). Although Sidor & Hopson

813 (2018) consider a difference in mesial and distal denticle densisty as a diagnostic feature in

814 *Cricodon*, we note, however, no size discrepancy between the mesial and distal denticles in the

815 upper and lower canines of NHMUK PV R3722 and SAM-PK-5881*a*. The denticles are

816 apicobasally elongated in the mesial and distal carinae of NHMUK PV R3722 and SAM-PK-

817 5881*a*, and apicobasally elongated to subquadrangular in the distal carina of BP/1/6102 and

818 BP/1/5540. Similar to the incisors, there is a sporadic variation in denticle size along the carina,

819 with a minute denticle followed by a much larger one in some portion of the carina. The

820 interdenticular space is particularly wide in the mid-crown denticles of the distal carina in

821 BP/1/5540 (Figure 8I). The cross-sectional outline is lenticular at mid-crown in the upper canines

822 of BP/1/6102 and NHCC LB28 (Sidor & Hopson, 2018; figure 2C), and weakly salinon-shaped

823 in the lower canine of SAM-PK-5881*a* (Figure 8F) due to the presence of concave surfaces

824 adjacent to both carinae (Figure 8E). In the latter specimen, several transverse undulations are

825 present on the lingual surface of the lower canine at mid-crown (Figure 8E). Short transverse

826 undulations ('crenulations' sensu Sidor & Hopson, 2018) are also present in the replacement

827 upper canines of NHCC LB28 (Sidor & Hopson, 2018). Unlike the postcanines, the surface

828 texture of the incisors and canines appears to be irregular and non-oriented.

829 *Upper gomphodont postcanines*

830   The morphology of the first to the fifth upper postcanines relies on specimens NHCC

831   LB28 and SAM-PK-5881*a*. In NHCC LB28, the first two postcanines are sectorial, a condition

832   only seen in the putative juvenile specimens of *Trirachodon* BP/1/4534 and 4535 among

833   Gomphodontia (Sidor & Hopson, 2018; C.H. pers. obs.). Both sectorial postcanines are

834   particularly small compared to the more distal ones, and diagonally oriented from the long axis

835   of the upper postcanine tooth row. They include a centrally positioned main cusp and a mesial

836   and distal main cusps (Sidor & Hopson, 2018). The mesial main cusp occupies one fourth of the

837   main cusp length and projects at three-fourths of the crown (Sidor & Hopson, 2018). The distal

838   main cusp is larger, longer (i.e., one half of the main cusp length) and better separated from the

839   main cusp (Sidor & Hopson, 2018). This distal main cusp also lies more basal than the mesial

840   main cusp, around one half of the crown height. A small cingular cuspule is present on the

841   lingual side of the second postcanine, basal to the mesial valley separating the main cusp from

842   the mesial main cusp. The sectorial postcanines are swollen just beneath the cusps and decrease

843   in mesiodistal length towards the root (Sidor & Hopson, 2018).

844   The upper postcanines 3 to 10 of NHCC LB28 are gomphodont, with their long axis

845   perpendicular to that of the tooth row. The postcanines increase in mesiodistal length,

846   labiolingual width and elongation up to the seventh tooth, then decrease in size and elongation

847   more distally (Sidor & Hopson, 2018). The third and fourth upper postcanines are slightly

848   smaller and shorter than those from the ninth and tenth alveoli (Sidor & Hopson 2018, table 1).

849   Likewise, postcanines eight to ten are significantly smaller than the three preceding postcanines,

850   and are labially deflected from them, so that their labiolingual width are in line with the labial

851   two thirds of postcanines five to seven. In apical view, all upper gomphodont postcanines are

852   roughly pear-shaped, with the labial third of the crown being significantly mesiodistally shorter

853   than the lingual two-thirds. Postcanines eight to ten, in fact, display a mesiodistal constriction

854   labially, at one third of the crown (Sidor & Hopson, 2018). Each upper gomphodont postcanine

855   includes a labiolingually oriented and centrally positioned transverse crest comprising a labial,

856   lingual and central cusps, all separated by shallow valleys (Sidor & Hopson, 2018). Minute

857   central accessory cusps are also present on the transverse crest, on each side of the central cusps,

858   as seen in the eighth unworn postcanine. The central cusp is labiolingually elongated and

859   lingually deflected, whereas the labial and lingual cusps are mesiodistally long and have a

860   lenticular cross-sectional outline, with their pointed extremity directed towards the central cusp

861   (Sidor & Hopson, 2018). The labial cusp, which is slightly longer than the lingual cusp, is the

862   tallest of the three cusps, whereas the lingual and central cusps share the same height (Sidor &

863   Hopson, 2018). The upper gomphodont postcanines are ringed by mesial and distal cingula,

864   which enclose shallow and short mesial and distal basins, respectively. Both cingula extend on

865   the lingual two-thirds of the crown, the labial third being devoid of cingular cuspules. The mesial

866   cingulum lies more basal than the distal one and joins the base of the labiomesial ridge of the

867   labial cusp in postcanines 3 to 5 (Sidor & Hopson, 2018). There are around six cuspules on each

868   mesial and distal cingula in postcanines 5 to 7 (eight on the mesial cingulum of the fifth

869   postcanine), with the largest cingular cuspules being in the lingual portion of the crown, adjacent

870   to the lingual cusp. Postcanines nine and ten, however, have a lower number of cingular cusps,

871   with five and three cuspules on the distal cingulum, respectively, and three and two in the

872   preserved portion of the mesial cingulum, respectively (Sidor & Hopson, 2018). Similar to the

873   more mesial postcanines, the cingular cuspules of postcanines nine and tenth are restricted to the

874   lingual portion of the cingula, with the most lingual cuspules being the largest. As seen in the

875   holotype, the enamel surface texture of the upper gomphodont postcanines is apicobasally

876   oriented and braided (Sidor & Hopson, 2018).

877   The first upper postcanine of SAM-PK-5881*a* is incomplete, worn and its labial part is

878   hidden by matrix, but clearly shows a gomphodont morphology. No mesial and distal basins can

879   be seen but they might have been worn out. The more distal upper postcanines, which are

880   relatively worn, share the same morphology and only their size and labiolingual elongation

881   increase distally. The mesial margin of the second and third upper postcanines is slightly

882   concave and follows the convexity of the distal margin of the preceding crown.

883   All isolated and in-situ upper gomphodont postcanines of the holotype UMCZ T905,

884   which belong to the distal half of the maxilla, are labiolingually expanded and ovate in outline,

885   with a CBR of 2.5, 2.3, 2 and 1.85 for the sixth, seventh, eighth and ninth left postcanines,

886   respectively. These morphology contrasts with those of the eighth to tenth upper postcanines of

887   NHCC LB28, in which CBR does not exceed 1.5 (Sidor & Hopson 2018, table 1). The long axis

888   of postcanines sixth to nine of the holotype is roughly perpendicular to the long axis of the tooth

889   row, and only the last gomphodont tooth is labiomesially oriented. A striking feature of the upper

890   tooth row of *Cricodon* is the step-like disposition of the antepenultimate and penultimate

891   gomphodont postcanines, so that each of these two teeth is at the level of the base-crown or root

892   of the preceding postcanine. This feature is also present in NHCC LB28 (Sidor & Hopson 2018,

893   figure 3A), SAM-PK-5881*b*, SAM-PK-6212 and BP/1/6102. The upper gomphodont teeth are

894   slightly mesiodistally constricted at the labial one-third of the crown, giving an asymmetrical

895   outline of the postcanine in apical view, with the labial one-third of the tooth being shorter than

896   the lingual one (Figure 8J). A similar constriction can be seen in the ninth upper gomphodont

897   postcanine. The constriction is, however, slightly more pronounced on the distal surface of the

898   eighth postcanine and particularly well-developed on the distal margin of the sixth and seventh

899   teeth. A wide concavity occupying the labial third of the crown can be seen on the distal surface

900   of these two postcanines. The upper gomphodont postcanines include a low and centrally

901   positioned transverse crest, which is straight (Figure 8J), sigmoid or weakly parabolic in outline,

902   with the concavity directed distally, in apical view. The transverse crest is made of a wide and

903   lingually displaced central cusp bordered by two prominent labial and lingual cusps. No

904   preserved upper postcanines bear fully complete labial, central and lingual cusps but the labial

905   cusp appears to be as high as the central cusp, and as high as or slightly higher than the lingual

906   cusp. As described by Crompton (1955), the labial and lingual ridge of the central cusp are

907   denticulated, with the widest denticles being close to the apex (Figure 8N). The denticles of the

908   central cusp are wide, with a weakly convex external margin. Denticles are also clearly visible

909   on the mesial, distal and central ridges of the labial and lingual cusps, being particularly

910   numerous and well-developed on the labiomesial and labiodistal ridges of the labial cusp (Figure

911   8O). Unlike the central cusp, the denticles of the mesial, distal and central ridges of the labial and

912   lingual cusps diminish in size apically. Similar to the denticles of incisors and canines, they are

913   apicobasally elongated and change sporadically in size. Their external margin is, however,

914   flattened or weakly convex (Figure 8O). The denticles on the labiomesial and labiodistal ridges

915   either extend along the whole cusp up to its apex, or are restricted to the basal half of the cusp.

916   The mesial and distal cingula of the upper postcanines bear a large number (>7) of small

917   and well-delimited cingular cuspules along most, if not all, the width of the mesial and distal

918   rims of the crown (Figure 8J, N). Unlike more mesial teeth, the distal cingulum of the ninth left

919   upper postcanine does not extend to the labial cusp. The same can be said of the mesial cingulum

920   of a loose left upper postcanine. The cingular cuspules sporadically vary in size along the crown,

921   yet the widest cuspules are found in the central and/or lingual parts of the cingulum. We counted

922   ten cingular cuspules on the mesial cingulum and seven distal in the ninth left upper gomphodont

923   postcanine, and seven cuspules in the preserved labial half of the distal cingulum of the eight left

924   upper postcanine. The preserved portion of the mesial and distal cingula of the upper

925   gomphodont postcanine sampled by Hendrickx, Abdala & Choiniere (2016) includes nine and

926   eleven cingular cuspules, respectively. Unlike to the ninth left upper postcanine, the widest

927   cingular cuspules of this isolated tooth are seen in the labial portion of the distal cingulum and in

928   the centrolabial and lingual parts of the mesial cingulum (Figure 8N). The mesial cingulum is

929   parabolic or weakly sigmoid and slopes basolabially in mesial view. The distal cingulum, on the

930   other hand, is symmetrically parabolic or biconcave. In two loose upper postcanines, the

931   denticulated labiodistal ridge of the labial cusp does not connect to the distal cingulum as the

932   lingual extremity of the latter extends on the labiodistal surface of the labial cusp, so that the

933   lingualmost distal cingular cuspules are situated apical to the labiodistal ridge.

934   The upper postcanines of the holotype and two specimens with the same specimen

935   number (SAM-PK-5881) largely follow the same morphology, yet a few differences can be

936   noted. Although the CBR of the largest upper postcanine (i.e., third right gomphodont

937   postcanine, CBR of 2.3) of SAM-PK-5881a falls within the range of values obtained in the

938   holotype, the upper postcanines of SAM-PK-5881b are more ovoid, with a CBR beyond 1.7. In

939   addition, the long axis of the last upper postcanine is not diagonally oriented in SAM-PK-5881b.

940   A deep and narrow concavity is also present in the central portion of the distal cingulum of the

941   two distalmost upper postcanines in this specimen, so that the cingulum of these crowns is

942   conspicuously biconvex (Figure 8M). The upper postcanine roots of SAM-PK-5881b, well

943   visible in mesial and labial views, are apicobasally long, three time the height of the crown in at

944   least the first gomphodont postcanine, and weakly taper apically. The cervical line separating the

945   crown from the root is roughly horizontal and particularly neat in this specimen due to the light

946   brown-orange coloring the crowns, which contrasts with the white color of the roots.

947   *Lower gomphodont postcanines*

948   As described by Crompton (1955), the upper and lower gomphodont postcanines of the

949   holotype roughly share the same morphology, but their crown base ratio is significantly lower in

950   the lower teeth, varying from 1.2 to 1.6 (Figure 8K). Similar to the upper postcanines, the first

951   lower postcanine, preserved in SAM-PK-5881a, is weakly elongated labiolingually and includes

952   a transverse crest made of labial, central and lingual cusps and ringed by the mesial and distal

953   cingula (Figure 8L). The central cusp of the lower postcanine is, however, long and wide at its

954   base and surrounded by merged mesial and distal basins, forming a subcircular groove. Three

955   cuspules are preserved on the lingual part of the mesial cingulum and four on the labial portion

956   of the distal one, and both cingula probably bore between six to eight cuspules. A mesiodistal

957   constriction is present at the cervix in the first postcanine, which is also constricted at the same

958   level on its labial surface. The morphology of the second to fifth lower postcanines of SAM-PK-

959   5881*a* follow that of the more well-preserved distal teeth of the holotype. The size and CBR of

960   these teeth increase up to the fifth lower postcanines (CBR of 1.6), then decrease more distally.

961   The transverse crest is positioned at mid-length of the crown and perpendicular to the long axis

962   of the mandible in all lower postcanines of SAM-PK-5881*a*. Only the fourth left lower

963   gomphodont tooth of this specimen preserves the distal cingulum formed by five cingular

964   cuspules, three labiolingually wide in the labial two-thirds and two small cuspules adjacent to the

965   unpreserved lingual cusp.

966   A comparative analysis of the upper and lower postcanines of the holotype provides

967   major differences between them. Similar to the postcanines of the cranium, the lower

968   gomphodont postcanines include a transverse crest composed of a labial, central and lingual

969   cusps ringed by the mesial and distal cingula. Yet, unlike the upper postcanines, large cingular

970   cuspules appear to be present linguomesially and labio- and linguodistally in the lower

971   gomphodont teeth (Figure 8K). These cuspules are most likely homologous to the putative

972   labiodistal, linguomesial and linguodistal accessory cusps of *Langbergia*. Similar to the upper

973   postcanines, the transverse crest is diagonally oriented from the long axis of the postcanine tooth

974   row in the last lower gomphodont tooth, and perpendicular to this axis in more mesial

975   postcanines, as seen in the eight right (Figure 8K) and what are assumed to be the fifth and sixth

976   left lower postcanines (n.b., Crompton (1955) interpreted these two teeth as corresponding to the

977   seventh and eight lower postcanines, yet based on their size and the height of the preserved

978   portion of the dentary, they are considered here as the fifth and sixth). Unlike the last upper

979   gomphodont postcanine, the transverse crest of the ninth lower postcanine is only mildly

980   diagonally oriented (Figure 8K). The central cusp forms a centrally positioned dome on the

981   transverse crest and, as the upper postcanines, its labial and lingual ridges are denticulated. It is

982   unknown whether the central, mesial and distal ridges of the labial and lingual cusps also bore

983   denticles in the eighth and ninth right lower gomphodont postcanines, but the mesial and distal

984   ridges of the labial cusp of the fifth? left lower postcanine is clearly serrated. The labial, central

985 and lingual cusps all share the same height in the eighth right lower postcanine, the only one

986 having these cusps complete. Unlike the upper postcanines, the labiodistal surface is angular in

987 apical view in the eighth and ninth right lower postcanines, the best preserved of the mandible,

988 with the labiodistal margin connecting to the labial surface of the crown at a slightly obtuse angle

989 (Figure 8K). The mesial and distal margins of the fifth and sixth left and right lower postcanines

990 are, however, gently convex, with no angular corner. There are ten mesial and seven distal

991 cingular cuspules on the cingula in the ninth right lower postcanine, the only lower crown

992 preserving the majority of these elements. Both cingula extend along the whole width of the

993 postcanine, and the smallest cingular cuspules are found in the central portions of the cingulum.

994 The mesial and distal cingula are badly preserved in the fifth? and sixth? left lower gomphodont

995 teeth but the labialmost cingular cusps are particularly large on both cingula. In the fifth? left

996 postcanine, the labiomesial cingular cuspule is significantly larger than the labiodistal one, and

997 strongly protrudes apically, as seen in *Langbergia*. The distal cingulum is almost complete in this

998 tooth and preserves six cingular cusps increasing in width and height lingually. Both upper and

999 lower postcanines of the holotype show a braided and apicobasally oriented enamel surface

1000 texture best visible on the mesial and distal surface of the central cusp (Figure 8N).

1001   The preserved lower gomphodont postcanines of the referred specimens NHMUK PV

1002 R36800 and NHCC LB28, on the distal portion of a mandible, have some differences with those

1003 of the holotype. As in the latter, there is a decrease in size and elongation in the distalmost

1004 postcanines of the mandible in NHMUK PV R36800, yet the last two lower gomphodont

1005 postcanines are particularly small and subcircular in outline in NHMUK PV R36800. As seen in

1006 the last lower gomphodont tooth of the holotype, the long axis of the antepenultimate lower

1007 gomphodont postcanine is slightly diagonally oriented from the labial margin of the mandible.

1008 The long axis of the two last gomphodont lower postcanines is, however, perpendicular to the

1009 long axis of the mandibular tooth row. The transverse crest of the preserved lower postcanines

1010 comprises three high subtriangular cusps, of which the central cusp is the widest, even in the

1011 subcircular postcanines. The labial, lingual and central cusps appear to share the same height.

1012 Unlike the holotype, the labiodistal margin of the lower gomphodont postcanines of NHMUK

1013 PV R36800 is not angular but smoothly convex, whereas the linguodistal surface is concave in

1014 the third and second gomphodont teeth. Six distal cingular cuspules decreasing in size toward the

1015 central part of the cingulum can be counted in the antepenultimate gomphodont postcanine.

1016   Likewise, there are at least seven mesial cingular cuspules in the last gomphodont postcanine,

1017   and their size diminishes towards the mid-width of the crown. As in the holotype, the enamel

1018   surface texture, well-visible on the surface of the central cusp of NHMUK PV R36800 is

1019   braided.

1020   Unlike the lower gomphodont postcanines of the holotype, the eighth right lower tooth,

1021   the only lower gomphodont postcanine preserved in NHCC LB28, is subrectangular in outline in

1022   apical view, with a nearly straight lingual surface and a biconvex distal margin (Sidor & Hopson

1023   2018). As seen in the ninth right lower postcanine of the holotype, the crown shows a weakly

1024   diagonally oriented transverse crest made of labial, lingual and central cusps, as well as a notch

1025   in the labiodistal corner of the crown, behind the labial cusp. The central cusp is centrally

1026   positioned on the crown and 1.5 wider than the subequal width of the labial and lingual cusps.

1027   On the transverse crest, the labial is the highest cusp and the central the lowest (Sidor & Hopson

1028   2018). The mesial and distal basins surround the transverse crest and are bounded by the cingula,

1029   respectively. The mesial cingulum is restricted to the labial two-thirds of the crown and

1030   comprises seven cingular cuspules whose width changes sporadically along the cingulum. From

1031   labial to lingual, there are three small cuspules, two large and elongate ones, and two minute

1032   cuspules on the mesial cingulum (Sidor & Hopson 2018). The distal cingulum includes a larger

1033   number of cuspules (i.e., eight or nine), with the widest cuspules located in the labial portion of

1034   the cingulum distal to the labial cusp, as seen in the holotype. The mesial basin extends from the

1035   labiomesial surface of the lingual cusp to the labialmost mesial cingular cuspules, whereas the

1036   distal basin extends from the distal side of the lingualmost distal cingular cuspule to the notch on

1037   the labiodistal surface of the crown (Sidor & Hopson 2018).

1038

1039   *Sectorial postcanines*

1040   An isolated sectorial postcanine (Figure 8P-Q) belonging to the holotype was illustrated

1041   and briefly described by Hendrickx, Abdala & Choiniere (2016). This tooth most likely

1042   represents the shearing-type crown underlying the ninth right upper postcanine described by

1043   Crompton (1955). The postcanine consists of a mesiodistally long main cusp adjacent to a poorly

1044   developed mesial main cusp, and a well-developed subtriangular and apically pointed distal main

1045   cusp. Given this morphology, we assume that this is the distalmost tooth of the sectorial tooth

1046   row, probably the tenth right upper postcanine, as suggested by Crompton (1955). The mesial

1047 and distal carinae are denticulated along the apical portion of the main cusp and the serrations

1048 extend across the apex of the cusp (Figure 8P-Q). The denticles are low, apicobasally elongated

1049 and show a symmetrically convex external margin. There is no trace of a cingulum on the labial

1050 or lingual margins of the crown.

1051   The lower sectorial postcanines partially visible in the left and right eleventh alveoli of

1052 NHCC LB28 and comprehensively describe by Sidor and Hopson (2018), provide for the first

1053 time information on the sectorial postcanines from the mandibular region of *Cricodon*. Unlike

1054 the upper postcanine of the holotype, the lower sectorial tooth is significantly longer, wider and

1055 lower. It is diagonally oriented at an angle of 45° from the rest of the jaw and includes a large

1056 subtriangular main cusp, two smaller distal and mesial main cusps, and a distal accessory cusp

1057 (Sidor & Hopson 2018). The mesial main cusp is a low but long convexity lying much lower

1058 than the distal main cusp. It is separated from the main cusp by a low valley and is slightly

1059 lingually deflected from the main and distal main cusps. The latter occupies the distal fourth of

1060 the crown and forms a low subtriangular prominence protruding vertically. It is followed by the

1061 distal accessory cusp, an even lower convexity on the distal margin of the distal main cusp.

1062 Unlike the preserved upper sectorial postcanine of the holotype, the lower sectorial tooth of

1063 NHCC LB28 includes a prominent lingual cingulum enclosing a shallow and labiolingually

1064 narrow lingual basin (Sidor & Hopson 2018). The lingual cingulum comprises five cingular

1065 cuspules, i.e., a small mesialmost one followed distally by three mesiodistally long cuspules,

1066 which increase in length distally (Sidor and Hopson 2018, figure 5F). A fifth cingular cuspule is

1067 present at the distal extremity of the cingulum but too incomplete to provide information on its

1068 size. The cingulum extends from the mesial main cusp to the distal accessory cusp, as revealed

1069 by the presence of a cingular cuspule distal to the distal accessory cusp in the left postcanine

1070 (Sidor & Hopson 2018). Two lower sectorial postcanines are also present in NHMUK PV

1071 R36800 but they are poorly preserved. The first sectorial postcanine is being replaced by a

1072 mesiodistally elongated gomphodont? postcanine with a narrow and apically pointed lingual

1073 cusp and a much longer and higher central cusp. Both lower sectorial postcanines include a large

1074 recurved main cusp bounded mesially and distally by small mesial and distal main cusps.

1075 Although the mesial main cusp of the first sectorial tooth appears to form a relatively large

1076 convexity, that of the second sectorial postcanine corresponds to a small protuberance at one

1077 third of the crown height, slightly more basal than the distal main cusp. The latter is unpreserved

1078   in the first sectorial postcanine and incomplete in the second one. Based on the preserved portion

1079   of the cusp, the distal main cusp is much longer and more prominent than the mesial main cusp

1080   in this tooth. No lingual cingulum or denticulated carinae appear to be visible in these two lower

1081   sectorial postcanines but their presence cannot be ruled out.

1082   *Crown microstructure*

1083   Hendrickx, Abdala & Choiniere (2016) recently explored the enamel and dentin

1084   microstructure in two isolated gomphodont and sectorial postcanines of the holotypic specimen

1085   of *Cricodon metabolus*. This study revealed that the enamel microstructure of this taxon is

1086   prismless and composed of discontinuous columnar divergence units (SCE). Abundant tubules

1087   and around 19 irregularly spaced striae of Retzius were also observed in the enamel layer, which

1088   is 11.5 times thicker in gomphodont postcanines (176.5 µm in average in horizontal section)

1089   compared to sectorial teeth (15.4 µm in average in horizontal section). The dentin layer of the

1090   *Cricodon* postcanine includes a large amount of tubules and approximately 100 incremental

1091   growth lines of von Ebner were counted in the gomphodont tooth.

1092   ***Trirachodon berryi* Seeley, 1894**

1093   **Holotype:** NHMUK PV R3579 (from Lady Frere, subzone B, *Cynognathus* AZ, South Africa),

1094   the mesial portion of the cranium with poorly preserved teeth.

1095   **Referred dental material:** from Burghersdorp, subzone B, *Cynognathus* AZ, South Africa: AM

1096   434 (Cragievar locality), 461 (holotype of *Trirachodon kannemeyeri*), BP/1/3775 (Cragievar

1097   locality), NHMUK PV R2807, SAM-PK-987; from Aliwal North, subzone B, *Cynognathus* AZ,

1098   South Africa: NHMUK PV R3306, R3307, R3350, R3721 (holotype of *Trirachodon browni*),

1099   SAM-PK-873 (holotype of *Trirachodon minor*), 5880; from Winnaars Baken, subzone B,

1100   *Cynognathus* AZ, South Africa: BP/1/3511, 4258, 5050, SAM-PK-12168 (= K5821), K170,

1101   K171, K7888; NMQR 1399; from Lady Frere, subzone B, *Cynognathus* AZ, South Africa: BSP

1102   1934 VIII 21, 22, 23; from Rouxville, subzone A, *Cynognathus* AZ, South Africa: BP/1/4658,

1103   4661 (Leewspuit locality), CGP/1/33 (Moerbeidal locality), SAM-PK-K10157, K10161,

1104   K10176, K10207, K10411; from Kestell, subzone A, *Cynognathus* AZ, South Africa: NMQR

1105   3279; from Bergville, subzone A, *Cynognathus* AZ, South Africa: CGP/1/79 (= CGP JNN 2000-

1106   7-2A); from unknown localities in South Africa: SAM-PK- K142, K4801, K4803, NMQR 122;

1107   from Etjo Mountain, Omingonde Formation, Namibia: GSN R327.

1108   **Occurrence:** Lady Frere, Chris Hani District, Emalahleni Municipality, South Africa;

1109   Burghersdorp, Aliwal North, and Winnaars Baken, Joe Gqabi District, Walter Sisulu

1110   Municipality, South Africa; Lemoenfontein 44 and Moerbeidal, Rouxville, Xhariep District, Free

1111   State Province, South Africa; Bergville, Thabo Mofutsanyane district, Maluti-a-Phofung

1112   Municipality, Free State Province, South Africa; western buttress of Etjo Mountain,

1113   Otjozondjupa Region, Namibia.

1114   **Horizon:** subzone A and B of the *Cynognathus* AZ, Burgersdorp Formation, Beaufort Group,

1115   Karoo Supergroup; lower? assemblage of the upper Omingonde Formation.

1116   **Age:** late Olenekian–early Anisian, Middle Triassic.

1117   **Dental formula:** i4/3 : c1/1 : pc6-12/8-9 (cpc1 : gpc4-10 : spc0-2).

1118   **Dental morphology:** The dentition of *Trirachodon* has received particularly little attention

1119   compared to other gomphodonts, and information on the dental anatomy of this taxon mostly

1120   rely on the rather limited descriptions and illustrations of Seeley (1894) and Broili & Schröder

1121   (1934). Firsthand examination of *Trirachodon* specimens with the best-preserved dental material

1122   now allows for a comprehensive description of the dentition of this taxon. Dental differences in

1123   the specimens referred to *T. berryi* and *T. kannemeyeri*, considered to be separated species by

1124   several authors (e.g., Sidor & Hopson, 2018), are also considered in the discussion.

1125   *Incisors*

1126   The incisors, well-preserved in the specimens CGP/1/79 (= CGP JNN 2000-7-2A),

1127   SAM-PK-K171, SAM-PK-12168 and BP/1/4658, have denticulated mesial and distal carinae at

1128   least in the first upper and lower incisors of SAM-PK-12168 (Figure 9A-C) and SAM-PK-K171,

1129   respectively. Mesial denticles are also visible in the third upper incisor of BP/1/4658 and an

1130   isolated upper? incisor of CGP/1/79. No denticles could be seen in the lower incisors of

1131   BP/1/4658 and 4661 and some upper and lower incisors of CGP/1/79. It is unknown whether the

1132   absence of denticles in some upper and lower incisors is a genuine condition of *Trirachodon*.

1133   The presence of unserrated canines in some specimens would, however, suggests so. The mesial

1134   denticles of SAM-PK-12168 are well-separated, apicobasally elongated and almost

1135   subquadrangular at the base of the carina (Figure 9B), whereas those of CGP/1/79 are poorly

1136   defined, particularly low and apicobasally subrectangular all along the carina. As other

1137   diademodontids and trirachodontids, they sporadically change in size and their external margin is

1138   weakly symmetrically to asymmetrically convex. Unlike *Cricodon*, which features much larger

1139 denticles, there are 6 and 10 mesial denticles per mm in the *Trirachodon* specimens SAM-PK-

1140 12168 and BP/1/4658, respectively. The largest denticles are situated apically, and given the fact

1141 that the apex and basal portions of the crown is missing, it is unknown whether the denticles

1142 reached the apex and cervix. The distal denticles of the first and second incisors of SAM-PK-

1143 12168 are incipiently developed and form poorly delimited convexities changing sporadically in

1144 size along the carina (Figure 9C). These denticles appear to extend well-above the cervix and get

1145 flared at mid-crown. Some upper and lower incisors are weakly mesiodistally constricted at the

1146 cervix, conferring a folidont (i.e., leaf-shaped) morphology to the crown. The cross-sectional

1147 outline of the upper and lower mesial incisors is D- to salinon-shaped, with the mesial carina

1148 positioned mesially and the distal carina facing linguodistally (Figure 9D, E). The incisors from

1149 the distal half of the jaw appear to have a more semi-circular cross-sectional outline, with the

1150 distal carina facing distally. Similar to *Langbergia*, a concave surface adjacent to the distal

1151 margin of the crown is visible on the labial surface of the second? upper incisor of SAM-PK-

1152 12168.

1153 *Canines*

1154   The canines of the specimens of *Trirachodon* CGP/1/79, SAM-PK-K171, 12168, K10157

1155 and BP/1/4658, 4661 and 3511 have both mesial and distal carinae denticulated. Unserrated

1156 canines are, however, present in the specimens BSP 1934 VIII 21 and 22 as well as SAM-PK-

1157 K7888. The denticles are minute, sometimes barely discernable, and always apicobasally

1158 elongated (Figure 9H). They sporadically change in size along the carina and have symmetrically

1159 to asymmetrically convex external margins. In some specimens, the denticles are incipiently

1160 developed or restricted to a small portion of the crown (e.g., BP/1/3511, SAM-PK-12168). The

1161 denticles of the canines are larger than those of the incisors, with mesial and distal denticle

1162 density ranging from three to nine denticles per mm in the canines. In BP/1/4658, the mesial

1163 carina is lingually deflected whereas the distal carina is centrally positioned on the distal margin

1164 of the crown. An apicobasally long concave surface adjacent to the distal carina is clearly present

1165 on the labial and sometimes lingual sides of the canine in BSP 1934 VIII 22, CGP/1/79, SAM-

1166 PK-K171, 12168, K10157 and BP/1/4658, 4661. A similar concave surface adjacent to both

1167 carinae on the lingual side can be seen in the lower canine of SAM-PK-K171. Transverse

1168 undulations and several faint longitudinal ridges can be observed on the labial surface of the

1169 right canine of BP/1/4661 (Figure 9F, G). Flat or mesiodistally convex surfaces meeting at acute

1170   corners are instead visible on the labial surface of one or both canines of SAM-PK-12168 and

1171   CGP/1/79. The cross-sectional outline of the incisor is elliptical, lenticular or salinon-shaped at

1172   mid-crown, indicating some important variation in cross-sectional outline in *Trirachodon*. The

1173   enamel surface texture of BP/1/4661 and CGP/1/79 is clearly braided and apicobasally oriented,

1174   curving basally adjacent to the carinae (Figure 9G). The texture of the enamel appears to be

1175   smooth in the canines of the other specimens.

1176   *Upper gomphodont postcanines*

1177   The morphology of the upper postcanines is based on the specimens BSP 1934 VIII 21,

1178   SAM-PK-K171, SAM-PK-K4801, NHMUK PV R3307 and BP/1/4658. As in *Cricodon* and

1179   *Sinognathus*, the upper postcanines are labiolingually expanded and ovate in outline. They

1180   increase in size and elongation distally up to the antepenultimate or penultimate gomphodont

1181   tooth. The first upper postcanine is the smallest and, with a CBR ranging from 1.1 to 1.6, the

1182   least labiolingually elongated of the upper gomphodont tooth row. This tooth is missing, badly

1183   preserved or in occlusion and obscured by the lower postcanines in all specimens examined first

1184   hand but CT-scan data of AM 461 provides some information on its morphology. The tooth is

1185   subconical, i.e., the crown is simple, slightly labiolingually elongated, labiolingually constricted

1186   at the cervix and bears a centrally positioned central cusp but no labial and lingual cusps nor a

1187   mesial and distal cingula.

1188   The CBR of the more distal upper postcanines varies from 1.4 to 2.4 and the outline of

1189   the crown in apical view only slightly changes along the tooth row. In BSP 1934 VIII 21 and

1190   BP/1/4658, the postcanines from the mesial half of the upper postcanines are reniform (sensu

1191   Hendrickx, Mateus & Araújo, 2015), with a weakly to strongly concave mesial margin. This

1192   outline results from the presence of a distal 'shouldering' between each tooth, which are in close

1193   contact in these two specimens. In SAM-PK-K171 and SAM-PK-K4801, the reniform outline is

1194   restricted to the third and fourth upper postcanines, yet the mesial margin is only weakly concave

1195   in the fourth tooth. Although the distal margin of the upper postcanines from the mesial half of

1196   the *Trirachodon* crown is typically convex, this distal margin is sigmoid in BSP 1934 VIII 21

1197   due to the presence of a narrow concavity on the lingual third of the distal surface of the crown.

1198   This dental feature is, however, restricted to this specimen. The more distal upper postcanines of

1199   *Trirachodon* are roughly ovate in outline, but a weak mesiodistal constriction occurs at the labial

1200   third of the crown in SAM-PK-K171, SAM-PK-K4801, and NHMUK PV R3307 (Figure 9I, K-

1201   M). This constriction, created by the presence of a concavity on the labial third/half of the distal

1202   margin of the postcanine, leads to an asymmetrical crown-shape, in which the labial third is

1203   shorter than the lingual two-thirds of the postcanine (Figure 9I, K-M). Such a concavity is

1204   particularly pronounced in the last upper gomphodont postcanines. It is, however, absent in the

1205   postcanines of BSP 1934 VIII 21 and BP/1/4658 so that the upper postcanines are

1206   subsymmetrical in shape in these two specimens (Figure 9J).

1207   As other trirachodontids, the upper postcanines of *Trirachodon* consist of a mesial and

1208   distal cingula extending on the mesial and distal rims of the crown as well as a labiolingually

1209   elongated transverse crest. The latter is made of a labial, central and lingual cusps and bounded

1210   mesially and distally by the wide mesial and distal basins, respectively (Figure 9I-K). The

1211   transverse crest is centrally positioned on the crown in the postcanines from the mesial half of

1212   the upper tooth row in BP/1/4658, SAM-PK-K171 and NHMUK PV R3307, and distally

1213   deflected in BSP 1934 VIII 21. Unlike *Cricodon*, the transverse crest runs diagonally on the

1214   crown in the distalmost gomphodont postcanines. The diagonal orientation of the transverse

1215   crest, particularly noticeable in NHMUK PV R3307, SAM-PK-K171 and SAM-PK-K4801,

1216   results from the distal deflection of the labial cusp, which points apicodistally in these specimens

1217   (Figure 9I, K-M). The central cusp is closer to the lingual cusp in most specimens, and centrally

1218   positioned on the transverse crest in SAM-PK-K4801. The central cusp is typically

1219   apicolingually inclined in distal view, so that the valley bordering the central cusp on the

1220   transverse crest is deeper between the central and labial cusps. The latter consists of a three-faced

1221   pyramidal structure, in which the edges form the labiomesial, labiodistal and labiocentral ridges.

1222   The lingual cusp shares the same shape, with a labiodistally shorter linguocentral ridge. Similar

1223   to *Cricodon*, the labiomesial and labiodistal ridges of the labial cusp are denticulated in at least

1224   one postcanine of SAM-PK-K171 and SAM-PK-K4801. The linguomesial, linguodistal,

1225   centrolabial and centrolingual ridges do not, however, appear to have serrations. The mesial and

1226   distal cingula typically bear a low number (i.e., < 6) of cingular cuspules restricted to a certain

1227   portion of the cingulum or along the whole width of the cingulum (Figure 9M-N). We counted

1228   three, four and five cingular cuspules on the mesial cingulum of the best-preserved postcanines

1229   of NHMUK PV R3307, SAM-PK-K171 and BSP 1934 VIII 21, respectively, and three to four,

1230   four, five, and six to seven distal cingular cuspules in SAM-PK-K171, BSP 1934 VIII 21, SAM-

1231   PK-K4801 and NHMUK PV R3307, respectively. The size of the cingular cuspules varies

1232   sporadically along the cingulum and does not follow any pattern along the tooth row. We,

1233   however, note that the widest cingular cuspules are often located in the middle or lingual part of

1234   the crown. When restricted to a certain portion of the postcanine, the cingular cuspules variously

1235   occupy the central, lingual or labial part of the crown. Large cingular cuspules have been

1236   observed in the labiomesial, labiodistal, linguomesial and linguodistal sides of the fully complete

1237   postcanines. Given the fact that none of these large cingular cuspules are present in all

1238   postcanines of the tooth-row, they may not be homologous to the accessory cusps of some

1239   gomphodonts. The presence of labiomesial, labiodistal, linguomesial and linguodistal accessory

1240   cusps in the upper gomphodont postcanines *Trirachodon* cannot, however, be ruled out.

1241   The morphology of the distalmost upper gomphodont postcanine of the holotype and

1242   referred specimens NHMUK PV R3579 and BSP 1934 VIII 21, respectively, which represent the

1243   specimens of *Trirachodon* with the highest number of gomphodont postcanines (i.e., 11 and 12,

1244   respectively), departs from that of the more mesial upper postcanines. In NHMUK PV R3579,

1245   the last postcanine is half the size of the preceding teeth, elliptical, long and short (CBR of 1.3)

1246   and displays a centrally positioned transverse crest ringed by the mesial and distal basins and

1247   cingula. The transverse crest includes a long and wide labial cusp, a lingually displaced central

1248   cusp and a narrow lingual cusp. The labial cusp, of which the base is preserved, was the largest

1249   and likely the highest of all three, while the central and lingual cusps appears to have the same

1250   height. The mesial cingulum seems to encompass four cingular cuspules, in which the widest,

1251   which may correspond to the labiomesial accessory cusp, is directly mesial to the labial cusp.

1252   Two particularly wide distal cingular cusps adjacent to the labial and lingual cusps may also

1253   represent the labio- and linguodistal accessory cusps of other gomphodont upper postcanines.

1254   Unlike NHMUK PV R3579, the last upper postcanine of BSP 1934 VIII 21 appears to be

1255   strongly labiolingually elongated and includes a long, high and lingually deflected central cusp

1256   and a much shorter, apically pointed labial cusp (Figure 9O). Unlike NHMUK PV R3579 and

1257   more mesial gomphodont postcanines, this tooth does not have a lingual cusp nor a distal basin

1258   and cingulum. Given that the mesial portion of the tooth is still embedded in matrix, it is

1259   unknown whether the mesial basin and cingulum were present or not. The root is twice as long as

1260   the crown at mid-width of the tooth, tapers apically and has a basolingually inclined lingual

1261   margin and sub-vertical labial border (Figure 9O). The basolingual portions of the crown and

1262   root of BSP 1934 VIII 21 also show an extensive parallelogram-shaped wear facet on its distal

1263   surface.

1264   *Lower gomphodont postcanines*

1265   Well-preserved lower gomphodont postcanines are present in SAM-PK-K171, SAM-PK-

1266   K4801 and BP/1/4658. The first postcanine, only seen in BP/1/4658 (Figure 10D), is

1267   significantly smaller than the more distal postcanines, as witnessed by the particularly small size

1268   of the alveoli in SAM-PK-K171. Its morphology does not differ from that of more distal

1269   gomphodont postcanines (Figure 10D). Similar to *Langbergia* and unlike *Cricodon*, the long axis

1270   of the lower gomphodont postcanines is linguomesially oriented and never perpendicular to the

1271   mandibular tooth row (Figure 10A-C). The linguomesial inclination of the first and last

1272   gomphodont teeth is more pronounced than the others in BP/1/4658 and SAM-PK-K171. The

1273   lower postcanines decrease in size from the middle of the mandibular tooth row in BP/1/4658, so

1274   that the last gomphodont tooth is as small as the first postcanine. As in *Langbergia* and unlike

1275   *Cricodon*, such decrease in size occurs from the penultimate lower postcanine in SAM-PK-K171

1276   and SAM-PK-K4801. The lower gomphodont postcanines share the same morphology than that

1277   of upper postcanines, yet they are symmetrical in the transverse and sagittal axes and narrower,

1278   with a CBR varying from 1.3 to 1.6 (Figure 10A-C). The central cusp is centrally positioned on

1279   the crown and occupies most of the transverse crest width. As in other trirachodontids, this cusp

1280   is bordered by the labial and lingual cusps, and the three cusps all share the same height. The

1281   mesial and distal basins are deep and both surround the dome-like central cusp mesially and

1282   distally, respectively (Figure 10A-C). The mesial and distal cingula are symmetrically concave

1283   and parabolic in shape in mesial and distal views. They include a variable number of cingular

1284   cuspules extending between the labial and lingual cusps. There are two to three and four cingular

1285   cuspules on the mesial cingulum in the best-preserved lower postcanines of SAM-PK-K171

1286   (Figure 10A, E) and SAM-PK-K4801 (Figure 10B-C), respectively, and four distal cingular

1287   cuspules in both specimens. Six to seven cingular cuspules appear to be present on the distal

1288   cingulum of the fifth right and left postcanines of BP/1/4658, respectively, while more than

1289   seven distal cuspules were present on the sixth left lower tooth. Unlike *Cricodon*, the widest

1290   cuspules typically occur in the center or labial portions of the crown. The last lower gomphodont

1291   postcanine of SAM-PK-K4801 (Figure 10C) has the peculiarity of having a particularly high

1292   transverse crest, higher than that of more mesial postcanines. The central cusp strongly protrudes

1293   apically and is higher than both the labial and lingual cusps. The distal cingulum comprises six

1294   well-separated cingular cuspules whereas the mesial cingulum includes three cuspules in its

1295   labial half (Figure 10C). The last lower postcanine of SAM-PK-K171 and BP/1/4658 share the

1296   same morphology with the other lower postcanines. The enamel texture of *Trirachodon*'s upper

1297   and lower postcanines, clearly visible on the mesial and distal surfaces of the central cusp, is

1298   braided and apicobasally oriented.

1299   *Sectorial postcanines*

1300   One or two upper and lower sectorial teeth are borne by the specimens SAM-PK-K4801,

1301   SAM-PK-K171, SAM-PK-12168, BP/1/4658, BP/1/4661, BP/1/3511, and CGP/1/79. The first

1302   right upper sectorial tooth of SAM-PK-K4801 is simpler and shorter than the second one (Figure

1303   10F). It includes a main distally positioned and recurved cusp followed mesially by a smaller

1304   mesial main cusp. This mesial main cusp is symmetrically convex and projects from the mesial

1305   surface at one third of the crown. The single or distalmost upper sectorial postcanine shares the

1306   same morphology, i.e., it comprises a main cusp, a mesial main cusp at one half of the crown and

1307   two distal cusps, the distal main and distal accessory cusps, both occupying the distal third of the

1308   crown (Figure 10F). The main cusp typically occupies the two-fifths to three-fifths of the crown

1309   length. It consists of a subtriangular, apicodistally pointed or strongly recurved (Figure 10F)

1310   projection, and its external margin is strongly parabolic and asymmetrically convex. The mesial

1311   main cusp can be minute and forms a tiny bump on the mesial surface of the main cusp, or a

1312   large, apically pointed projection similar in size or slightly longer than the distalmost accessory

1313   cusp. The distal main and distal accessory cusps are straight, decrease in size distally, and either

1314   point apically or apicodistally. The distal main cusp either forms a low, weakly pointed and

1315   mesiodistally long convexity or a high and mesiodistally short projection. No cingular cuspule

1316   were observed on the labial and lingual margin of the upper sectorial postcanines of

1317   *Trirachodon*. Variation in the morphology of the last sectorial appears to occur between the left

1318   and right sides of the cranium, as seen in SAM-PK-K4801. In this specimen, the mesial main

1319   cusp of the last upper sectorial postcanine consists of a poorly-developed bump on the right side

1320   (Figure 10F) and a large and strongly protruding projection on the left side. Likewise, the distal

1321   main cusp of this sectorial postcanine is mesiodistally short and high on the right side (Figure

1322   10F) and long and low on the left side.

1323   The morphology of the single or first lower sectorial postcanine is significantly different

1324   from that of the upper sectorial teeth. The crown is particularly wide, especially in BP/1/4658

1325   (CBR of 0.6 to 0.65). The crown consists of a large and high apically pointed main cusp

1326   bordered by two small apically projected mesial and distal main cusps (Figure 10I). The distal

1327   main cusp is larger than the mesial one in SAM-PK-K171 and BP/1/4658. The three cusps are

1328   bounded lingually by a mesiodistally concave cingulum made of minute cingular cuspules

1329   (Figure 10G). This lingual cingulum either extends along the whole length of the crown or is

1330   restricted to the mesial half of the postcanine, as seen in SAM-PK-K171. A labial cingulum is

1331   also present on the lower sectorial postcanine and occupies the whole length, as seen in the right

1332   lower postcanine of BP/1/4658 (Figure 10I), or a small portion of the distal surface of the crown

1333   only, as in SAM-PK-K4801 (Figure 10H).

1334   The second lower postcanine, only well-preserved on the left jaw of BP/1/4658 (Figure

1335   10I-J), is narrower, with an CBL of 0.54. The tooth includes a main cusp occupying slightly

1336   more than the mesial half of the crown, as well as a distal main cusp and a distal accessory cusp.

1337   No mesial main cusps appear to be present in the second left and right lower sectorial

1338   postcanines. The distal main cusp points apically and is not recurved (Figure 10I-J). The main

1339   cusp, of which only the base is visible, was likely significantly higher than the distal main cusp

1340   on the left side of the jaw. The distal main cusp of the second right sectorial postcanine is,

1341   however, much larger and probably only slightly lower than the main cusp. The distal main cusp

1342   consists of a symmetrically parabolic convexity while the distal accessory cusp is a minute and

1343   pointed projection (Figure 10I-J). A lingual cingulum bearing several minute cuspules extends

1344   along the whole length of the crown (Figure 10J). The second right lower sectorial postcanine of

1345   BP/1/4658 is significantly shorter than the preceding one (65% smaller) and is being replaced by

1346   another sectorial postcanine (Figure 10I-J). This tooth erupts distally from the second sectorial

1347   postcanine, and its morphology is reminiscent to that of the upper sectorial postcanines in that it

1348   has an apically recurved main cusp. No mesial or distal main cusps appear to be present on this

1349   erupting postcanine but they might be hidden by the matrix. The main cusp has an unserrated

1350   mesial carina twisting lingually and no cingulum is present at the base of the lingual surface of

1351   the crown (Figure 10J).

1352   *Dental morphotypes in Trirachodon berryi*

1353   As noticed by previous authors such as Sidor and Hopson (2018), two dental

1354   morphotypes of *Trirachodon* can be observed. AM 461, SAM-PK-K171, SAM-PK-12168,

1355   NHMUK PV R3307 (included in '*Cricodon kannemeyeri*' by Sidor and Hopson (2018), see

1356   Discussion below), as well as CGP/1/79, SAM-PK-K4801, BP/1/4661 and BP/1/3511, share a

1357   combination of dental features not seen in other specimens of *Trirachodon*, i.e., denticulated

1358   canines, less than ten upper postcanines comprising one or two upper and lower sectorial teeth,

1359   transversely asymmetrical distal upper gomphodont postcanines, in which the lingual half of the

1360   crown is longer than the labial one, a diagonally oriented transverse crest on the crown, and a

1361   slightly apicodistally pointed labial cusp. These specimens indeed differ from NHMUK PV

1362   R3579, BSP 1934 VIII 21 to 23 and SAM-PK-K7888 (classified among *Trirachodon berryi* by

1363   Sidor and Hopson (2018), see below), characterized by the following dental features: unserrated

1364   canines, more than nine upper postcanines, no sectorial teeth, transversely symmetrical distal

1365   upper postcanines (i.e., labial and lingual halves of the crown of the same length, apically

1366   pointed labial cusp, and non-diagonally oriented transverse crest on the crown) and last upper

1367   gomphodont postcanine being significantly smaller than the preceding tooth.

1368   It should, however, be noted that the specimen NHMUK PV R3307 does not have a

1369   sectorial postcanine on the right portion of the maxilla while a particularly low number of upper

1370   postcanines (i.e., seven) is present in this specimen. The absence of a diagonally oriented

1371   transverse crest in the upper postcanines of BSP 1934 VIII 21 could also be explained by the fact

1372   that the labial cusp of some gomphodont postcanines is worn out. All specimens classified in the

1373   morphotype of *Trirachodon berryi* do not preserve incisors and only two of them (i.e., BSP 1934

1374   VIII 21, SAM-PK-K7888) bear canines. The latter are, however, incomplete and/or badly

1375   preserved and the absence of denticles could be explained by the fact that they have been worn

1376   out from the carinae due to the advanced age of the individuals (see Discussion). We also note

1377   that BP/1/4658 appears to represent a transitional form between the dental morphotypes of *T.*

1378   *berryi* and '*T. kannemeyeri*', as this specimen includes finely denticulated canines,

1379   subsymmetrical and non-mesiodistally constricted upper gomphodont postcanines with a non-

1380   diagonally oriented transverse crest and a complete distal cingulum (present at least in the fifth

1381   right upper postcanine), penultimate and last upper gomphodont postcanines with a CBR > 2,

1382   seven upper postcanines, as well as one upper sectorial postcanines and two lower tricuspid

1383   sectorial postcanines bearing a lingual cingulum. We propose that the dental differences between

1384   these two morphotypes are ontogenetic and not interspecific, as some authors suggest, an

1385   hypothesis developed in the Discussion section.

1386   ***Sinognathus gracilis* Young, 1959**

1387   **Holotype:** IVPP V2339, an almost complete skull.

1388   **Occurrence:** Peipanching Shihpi, Wuhsiang-Yüshe area, Shanxi Province, China.

1389   **Horizon:** upper Ermaying Formation.

1390   **Age:** late Anisian, Middle Triassic.

1391   **Dental formula:** i4/2 : c1/1 : pc6/7 (cpc? : gpc5 : spc?).

1392   **Dental morphology:** The dentition of *Sinognathus gracilis*, briefly described by Young (1959)

1393   due to the lack of preparation of the skull, has received a relatively good description from Sun

1394   (1988) following a re-preparation of the postcanines teeth. Firsthand examination of the holotype

1395   provides a few additional details on the dental material of this taxon.

1396   *Incisors and canines*

1397   The incisors, poorly preserved in IVPP V2339, do not show a constriction at the level of

1398   the cervix (Figure 11A). Minute denticles can be seen at the base and apex of the distal carina of

1399   the fourth left upper incisor (Figure 11B, C). We counted eight denticles per mm on this tooth.

1400   No other incisor appears to bear serrations. The cross-section through the root base of the first

1401   left upper incisor is subcircular (Figure 11D). The root base of the left and right upper canines,

1402   the crown base of the right lower canine as well as the root, crown base and a small portion of

1403   the mesial part of the left lower canine are preserved (Figure 11E, F). None of these portions of

1404   the canines show serrations (Figure 11F) and it is unknown whether denticles are unpreserved or

1405   absent. The cross-sectional outline through the root base of the left upper canine is roughly

1406   lenticular (Figure 11G). The left lower canine is mostly projected apically, whereas the right

1407   canine appears to be weakly procumbent. The root base of the left lower canine is slightly longer

1408   than the crown base. The root is two-thirds the height of the crown and tapers basally (Figure

1409   11E).

1410   *Gomphodont postcanines*

1411   All postcanines are in occlusion. Information on their morphology can, however, be

1412   extracted from the right upper postcanines, of which the lingual portion has been prepared and is

1413   visible in medioventral view (Figure 11J-L), and from a mid-crown sagittal section through the

1414 upper and lower postcanines of the left jaw side of the skull (Figure 11H, I, N). Some parts of the

1415 labial portion of the right lower postcanines can also be seen in labial view (Figure 11M). As

1416 described by Sun (1988), the upper postcanines are labiolingually elongated and consist of a

1417 labiolingually oriented and slightly distally positioned transverse crest. The latter is apically high

1418 and comprises labial, central and lingual cusps of the same height. A small valley separates the

1419 central and lingual cusps in the best-prepared upper postcanine (Figure 11J-L). The central cusp

1420 is wide, the widest of the three cusps, and centrally located on the transverse crest. The mesial

1421 and distal ridges, visible in the sagittal cross-section through the fourth left upper postcanines,

1422 bound the mesial and distal margins of the gomphodont postcanines (Sun, 1988). These ridges

1423 are not visible in the lingual portion of the exposed upper postcanines, yet poorly preserved

1424 cingular cuspules appear to be present on what would then be the distal cingulum of the third

1425 upper postcanine (Figure 11K). A linguomesial accessory cusp may have been present in the

1426 upper gomphodont postcanine (Figure 11K). No other accessory cusps are visible in the upper

1427 postcanines. The mesial basin is longer than the distal one, and both basins are horizontal and

1428 shallow.

1429   Few details on the lower gomphodont postcanines of the holotype can be observed. They

1430 are labiolingually elongated and bear an apically high transverse crest bounded by the mesial and

1431 distal basins. Both basins are mesiodistally concave, yet the distal basin is horizontally

1432 positioned and shallow whereas the mesial basin is basally inclined and shorter. The transverse

1433 crest is slightly mesially deflected and includes labial, central and lingual cusps roughly sharing

1434 the same height. A faint mesial ridge is present at the rim of the lower postcanine. Remnants of

1435 mesial cuspules appear to be present on this ridge (Figure 11M), but future CT-data of better

1436 preserved postcanines will corroborate this information. Based on the sagittal cross-section

1437 through the left lower postcanines, no distal ridge or cingulum appears to be present.

1438   The sixth right upper postcanine was interpreted as a sectorial by Sun (1988). The crown

1439 is, however, incomplete, with the labial and central portion missing, and only an horizontal

1440 cross-section through the root can be seen in ventromedial view (Figure 11O). A closer look at

1441 the cross-sectional outline reveals that the sixth upper tooth was a gomphodont and not a

1442 sectorial postcanine. This is corroborated by the fact that the preserved portion of this crown

1443 shows a labiolingually oriented transverse crest in the middle of the crown (Figure 11O-P),

1444 whereas no sectorial postcanines bear such a ridge in gomphodont cynodonts. In addition,

1445   sectorial teeth/alveoli are typically labially positioned from the long axis of the tooth row in all

1446   gomphodont cynodonts (with the possible exception of *Beishanodon*; see discussion below), at

1447   the level of the labial half of the gomphodont postcanines. The preserved portion of the sixth

1448   upper postcanine is, however, at the same level as the lingual half of the preceding tooth (Figure

1449   11P). Based on firsthand examination of the specimen IVPP V2339, nothing support the

1450   presence of sectorial postcanines in *Sinognathus*.

1451   ***Beishanodon youngi* Gao et al., 2010**

1452   **Holotype:** PKUP V3007, an incomplete cranium.

1453   **Occurrence:** Beishan locality, Quarry-3, in Beishan Hills, northern Gansu Province, China.

1454   **Horizon:** Lower Triassic dark shales, Beishan fossil beds, Hongyanjing Formation.

1455   **Age:** late Olenekian, Middle Triassic.

1456   **Dental formula:** i4/? : c1/? : pc8/? (cpc2 : gpc7 : spc?).

1457   **Dental morphology:** The dentition of this taxon, which is only known from six upper

1458   gomphodont postcanines, has been well-described by Gao et al. (2010). Because we have not had

1459   the opportunity to examine the holotypic specimen of *Beishanodon*, we rely on Gao et al.'s

1460   (2010) text and figures to describe the dentition of this taxon.

1461   *Incisors and canines*

1462   There are four upper incisors separated from the canine by a diastema whose length

1463   corresponds to that of two incisor alveoli. As noted by Gao et al. (2010), the outline of the

1464   incisor alveoli suggest that the root and crown base of the upper incisors were particularly

1465   labiolingually expanded and slightly mesiodistally shorter, especially in the first two incisors.

1466   The canine alveoli is positioned lateroposteriorly from the paracanine fossa, and its long axis is

1467   diagonally and labiomesially oriented from that of the cranium. A short diastema of the length of

1468   the first postcanine lies between the canine and postcanines.

1469   *Upper postcanines*

1470   The postcanine tooth row is straight, extends posteriorly to the level of the anterior

1471   margin of the orbit, and its long axis is directed towards the center of the subtemporal fenestra

1472   (Gao et al., 2010). Based on the size of the alveoli, the teeth increased in width and length up to

1473   the fifth postcanine, and the two last alveoli seem to have roughly the same size. Only the four

1474   first right and the fifth and sixth left upper postcanines are preserved. The first postcanine is the

1475   smallest of the tooth row and corresponds to a conical crown with a subcircular cross-sectional
1476   outline. A large cusp lies directly labial to the apex of this tooth (Gao et al., 2010). The second to
1477   fourth postcanines are gomphodont in shape and elliptical in outline, with their long axis
1478   perpendicular to the long axis of the tooth row but linguodistally oriented from that of the skull.
1479   The CBR of the preserved teeth varies between 1.25 to 2. The gomphodont postcanine includes a
1480   labiolingually oriented, weakly distally deflected, and labiolingually curved transverse crest,
1481   with the apex of the concavity directed distally in apical view. The transverse crest is made of
1482   labial, central and lingual cusps, with the central cusp being located in the labial half of the
1483   crown, close to the labial cusp (contra Gao et al., 2010). A distal cingulum comprising up to ten
1484   cingular cuspules can be seen at the rim of the fourth right postcanine (Gao et al., 2010). The
1485   gomphodont postcanines do not seem to include any accessory cusps, and only the labiomesial
1486   and labiodistal ridges are clearly visible on the labial cusp in these teeth. It is unknown whether
1487   one or several upper sectorial postcanines were present in the distalmost portion of the tooth row,
1488   but the shape of last right alveolus, which is longer than wide, would suggest that there was a
1489   sectorial postcanine in that position.
1490
1491   ## Discussion
1492   The dentition of diademodontid and trirachodontid gomphodonts, which has one of the
1493   most complex occlusal pattern among non-mammaliaform cynodonts (Crompton, 1972), show a
1494   large variety of dental features previously unknown or undescribed. The following homologous
1495   dental characters were shown to be present and relatively common in the dentition of non-
1496   traversodontid gomphodonts: i) concave surfaces adjacent to the carinae in the incisors and
1497   canines; ii) transverse undulations, longitudinal ridges and a sporadic variation in denticles size
1498   along the carinae in the canines; iii) denticulated carinae in the incisors, canines and sectorial
1499   postcanines; iv) denticulated labial cusps, mesial and distal cingular cuspules, and a braided
1500   enamel surface texture in the gomphodont postcanines; and v) lingual and labial cingula in the
1501   sectorial postcanines. In diademodontids, we revealed the presence of denticles changing
1502   sporadically in size along the carinae in the canines, lingual cingular cuspules in the conical
1503   postcanines, denticulated labial cusp in the gomphodont postcanines and bi denticulated denticles
1504   in the sectorial postcanines in *Diademodon*, and a labiomesial accessory cusp as well as mesial
1505   cingular cuspules, in the upper gomphodont postcanines of *Titanogomphodon*. The presence of

32000

1506 these dental characters in *Titanogomphodon*, however, needs confirmation with better-preserved

1507 specimens. In trirachodontids, we described for the first time denticulated carinae in the incisors

1508 and sectorial postcanines as well as longitudinal ridges in the canines of *Langbergia*, concave

1509 surfaces adjacent to the carinae in the canines and a biconvex distal cingulum in the upper

1510 postcanines of *Cricodon*, transverse undulations and longitudinal ridges in the canines as well as

1511 labial and lingual cingular cuspules in the lower sectorial postcanines of *Trirachodon*, and

1512 denticulated incisors and no sectorial postcanines in *Sinognathus*.

1513 **The affinities of the Chinese gomphodonts**

1514 According to Gao et al. (2010), the placement of *Beishanodon* within Trirachodontidae is

1515 supported by an ovoid-elliptical outline of the upper postcanines and a long axis of the

1516 postcanine tooth row directed toward the center of the subtemporal fenestra. The upper

1517 postcanines of *Beishanodon* also share with trirachodontids a low transverse crest made of a

1518 labial, central and lingual cusps combined with a distal cingulum comprising a large number of

1519 cingular cuspules. The dentition of this taxon is nonetheless unusual for a trirachodontid in many

1520 aspects: the upper postcanine are particularly labiolingually narrow in relation to the skull length

1521 (the distance between the anteriormost point of the snout and the posteriormost point of the

1522 occipital condyles) and only *Diademodon* shares a low upper postcanine CBW/skull length ratio

1523 (Figure 12). The first conical postcanine has a large labial cusp (Gao et al., 2010), a feature

1524 absent in other gomphodont taxa. In addition, the transverse crest of the postcanines three and

1525 four is located near the distal border of the tooth, presenting an occlusal basin that resembles a

1526 traversodontid postcanine. According to figure 6A from Gao et al. (2010), the central cusp of the

1527 second right postcanine is also strongly labiodistally positioned, a feature absent in all other

1528 trirachodontids. Finally, the sectorial postcanine(s), if present, would be weakly lingually

1529 deflected from the long axis of the tooth row (Gao et al. 2010, figure 5 and 6a) whereas all

1530 gomphodont cynodonts have their sectorial postcanine labial to this axis.

1531 Although the latest cladistic analyses on gomphodont cynodonts (i.e., Liu & Abdala,

1532 2014; Sidor & Hopson, 2018) recovered *Beishanodon* and *Sinognathus* within the clade

1533 Trirachodontidae + Traversodontidae, these two taxa were recently suggested to be

1534 probainognathians by Sidor & Hopson (2018) and basal probainognathians closely related to

1535 *Aleodon brachyrhamphus* by Hopson (2014) and Hopson & Sidor (2015). Nonetheless, the

1536   dentition of *Aleodon*, the only non-tritylodontid probainognathian with labiolingually elongated

1537   and ovoid postcanines (Crompton, 1955; Abdala & Giannini, 2002; Martinelli et al., 2017),

1538   strongly differs from that of *Beishanodon* and *Sinognathus* in the following features: i) upper

1539   postcanine tooth row curved, with a long axis of the posterior portion directed towards the lateral

1540   part of the subtemporal fossa; ii) postcanines strongly protruding from the alveoli; iii) second

1541   and, in some cases, third upper postcanines subcircular and significantly smaller than the

1542   following teeth; iv) no transverse crest, central cusps or mesial and distal cingula in the

1543   postcanines; v) labial cusp significantly larger (i.e., longer, wider and higher) than the lingual

1544   'cusp' (when present) in the upper postcanines; and vi) postcanines with a wide lingual platform

1545   extending from the sectorial/labial portion of the crown. Sidor and Hopson (2018) note that the

1546   two Chinese cynodonts also share probainognathian cranial characters such as the presence of a

1547   widely bowed zygomatic arch and the absence of a parietal foramen and a zygomatic/suborbital

1548   process of the jugal, three cranial features absent in basal cynognathians (i.e., *Cynognathus*,

1549   diademodontids, trirachodontids, and basal traversodontids) according to these authors. The

1550   zygomatic arch is, however, poorly anteroposteriorly convex in *Sinognathus* (IVPP V2339),

1551   showing the same convexity than some trirachodontid specimens (e.g., NMQR 3255, CGP/1/79).

1552   In fact, the temporal fenestra of *Sinognathus* is subrectangular in dorsal view, as in *Langbergia*

1553   and *Trirachodon* and unlike *Lumkuuia*, *Chiniquodon* and *Aleodon*. If a parietal foramen is indeed

1554   present in all African trirachodontids (including the *Trirachodon* specimen AM 461; Benoit pers.

1555   comm. 2018), it is however absent in the basal traversodontids *Pascualgnathus* (MLP 65-VI-18-

1556   1; PVL 4416) and *Andescynodon* (PVL 3836, 3840; Liu & Powell, 2009). Likewise, a suborbital

1557   process of the jugal is absent in the basal traversodontid *Scalenodon* (Abdala, Neveling &

1558   Welman, 2006) and more derived forms such as *Boreogomphodon* and *Massetognathus* (Abdala,

1559   Neveling & Welman, 2006; Sues & Hopson, 2010). For those reasons, we consider both

1560   *Beishanodon* and *Sinognathus* to be confidently classified among gomphodont cynognathians.

1561   Sidor & Hopson's (2018) phylogeny recovered *Sinognathus* and *Beishanodon* among basal

1562   traversodontids, close to *Pascualgnathus*. Nevertheless, *Sinognathus* lacks the shearing planes

1563   between the outer surface of the main cusp of the lower and the inner surfaces of the main cusps

1564   of the upper postcanines characteristic of Traversodontidae. Likewise, the transverse crest of

1565   *Sinognathus* is centrally positioned on the crown, forms a low ridge and lacks the deep labial

1566   valley present in traversodontids. Consequently, this Chinese gomphodont is here confidently

1567 classified as a trirachodontid, pending a phylogenetic analysis to support this hypothesis, which

1568 will be conducted in a forthcoming contribution (Hendrickx, Abdala & Choiniere, in

1569 preparation). Finally, given the presence of a single conical postcanine, six upper gomphodont

1570 postcanines comprising a distal cingulum and a low transverse crest made of a labial, central and

1571 lingual cusps, a straight postcanine tooth row directed towards the centromedial portion of the

1572 temporal fenestra, and possibly one or two sectorial postcanines, we tentatively refer

1573 *Beishanodon* to Trirachodontidae. If correct, this reveals that diademodontids and some

1574 trirachodontids convergently evolved large skulls compared to the upper postcanine width, which

1575 remained particularly small in mature individuals.

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

1577   Two species of *Trirachodon*, *T. berryi* and '*T. kannemeyeri*', were distinguished by

1578 Seeley (1894) based on the snout expansion and the number and labiolingual elongation of the

1579 maxillary teeth. Although these two taxa were synonymized by Hopson & Kitching (1972)

1580 (along with *Trirachodon minor*, *Trirachodontoides berryi* and *Inusitatodon smithi*) and Abdala,

1581 Neveling & Welman (2006), they were considered as separate species by Kitching (1977) and

1582 more recently by Hopson & Sidor (2015) and Sidor & Hopson (2018). According to the two

1583 latter authors, *T. berryi* includes the specimens NHMUK PV R3579, BSP 1934 VIII 21 to 23 and

1584 SAM-PK-K7888, whereas the specimens AM 461, SAM-PK-K171, SAM-PK-12168 (= SAM-

1585 PK-K5821), and NHMUK PV R3307 belong to '*T. kannemeyeri*'. SAM-PK-11481 is also

1586 included in the latter taxon by Sidor & Hopson (2018), yet, as stated by Abdala, Neveling &

1587 Welman (2006), SAM-PK-11481 is here referred to *Langbergia* based on the absence of a

1588 maxillary lateral platform, the curvature of the ventral margin of the dentary, and the presence of

1589 a high central cusp separated from labial cusp by a narrow valley and strongly protruding

1590 cingular cuspules. Future CT-scanning and reconstruction of the occluded dentition of this

1591 specimen will corroborate referral to this taxon.

1592   Sidor & Hopson (2018) list the following apomorphic characters in the dentition of

1593 *Trirachodon berryi*: i) the upper gomphodont postcanines are slightly less than twice as wide as

1594 long (i.e., CBR < 2) and are transversely symmetrical in apical view; ii) the mesial and distal

1595 cingula are usually complete and typically bear small cingular cuspules; iii) the sectorial upper

1596 postcanines are absent; and iv) the last upper gomphodont postcanine is transversely expanded,

1597   and about two-thirds the transverse diameter of the preceding tooth, with reduced labial and

1598   lingual cusps. Sidor & Hopson (2018) also suggest that the dentition of '*T. kannemeyeri*' and

1599   *Cricodon* are closer than that of *Trirachodon berryi*, so that these authors propose the new

1600   combination *Cricodon kannemeyeri*. According to Sidor and Hopson (2018), shared

1601   synapomorphies between *Cricodon metabolus* and '*Cricodon kannemeyeri*' are: i) transversely

1602   expanded upper and lower gomphodont postcanines with one or two sectorial teeth at the rear of

1603   the tooth row; ii) distal upper gomphodont postcanines more than twice as wide as long (i.e.,

1604   CBR > 2) and transversely asymmetrical in apical view, with the lingual half of the crown

1605   usually being mesiodistally longer than the labial half of the crown; iii) cingular cuspules varying

1606   in size, with some being particularly large; iv) mesial and, less frequently, distal cingula often

1607   incomplete, and sometimes even absent; v) distalmost one or two postcanines sectorial and

1608   formed by three main cusps oriented mesiodistally and often with a narrow lingual cingulum.

1609   We, however, note that a single character (i.e., the presence of one or two sectorial postcanines;

1610   character 59) in Sidor & Hopson's (2018) datamatrix unites *Cricodon metabolus* and '*Cricodon*

1611   *kannemeyeri*' and differentiate them from *Trirachodon berryi*.

1612   Although Sidor & Hopson (2018) note that the mesial and distal cingula are usually

1613   complete and bear small cingular cuspules in *T. berryi*, the distal cingulum is complete and

1614   includes a large number of cingular cuspules in NHMUK PV R3307 and SAM-PK-K4801.

1615   Likewise, important variations in size in the mesial and distal cingular cuspules, which are as

1616   large as other *Trirachodon* specimens, can be noticed in BSP 1934 VIII 21. Seeley (1894) and

1617   Sidor & Hopson (2018) also observe difference in the elongation of the upper gomphodont

1618   postcanines between these species, yet the CBR of the penultimate upper gomphodont

1619   postcanine of BSP 1934 VIII 21 is 2.3 whereas the crown of SAM-PK-K171 from the same

1620   position has a CBR of 2.

1621   As stated before, we agree with Sidor and Hopson (2018) that two morphotypes can be

1622   observed among the specimens referred to *Trirachodon berryi* and '*T. kannemeyeri*' but we

1623   interpret them as ontogenetic variations. '*C. kannemeyeri*' sensu Sidor and Hopson (2018) can be

1624   considered as an younger ontogenetic stage of *T. berryi*. In adults of this sequence: i) the last

1625   sectorial postcanines were replaced by transversely symmetrical gomphodont postcanines; and ii)

1626   two to three upper gomphodont postcanines, with the last one bearing a large central cusp, and

1627   reduced labial cusp and lingual cusps (Figure 9O), were added in the distal portion of the tooth

1628   row. Such dental replacement and increase in the number of gomphodont teeth throughout

1629   ontogeny are common in gomphodont cynodonts and were observed in the closely related

1630   trirachodontid *Cricodon metabolus* (Crompton, 1955) as well as the basal traversodontids

1631   *Scalenodon angustifrons* (Crompton, 1955) and *Andescynodon mendozensis* (Goñi & Goin,

1632   1988).

1633   Given that both morphotypes of *T. berryi* and 'C. kannemeyeri' are represented by large-

1634   sized specimens with a skull of more than ten centimeters (see Abdala, Neveling & Welman

1635   (2006), Table 4; C.H. pers. obs.), this suggests that the largest specimens referred to 'C.

1636   *kannemeyeri*' were subadult/non-fully grown individuals in which: i) the maximum size was

1637   reached; and ii) the sectorial postcanines remained to be replaced by gomphodont postcanines

1638   latter in their life. Specimens classified as *T. berryi* would consequently represent fully grown,

1639   most likely old, individuals in which all sectorial postcanines were replaced by gomphodont

1640   postcanines. This hypothesis is supported by size and wear in the postcanines. All specimens

1641   belonging to *T. berryi* have skulls of more than nine centimeters (see Abdala, Neveling &

1642   Welman (2006), Table 4) and show extensive wear in the upper and lower gomphodont

1643   postcanines (e.g., NHM R3579, BSP 1934 VIII21-23; SAM-PK-K7888; Sidor & Hopson 2018,

1644   Figure 10C). On the other hand, wear is barely present or less extensive on the upper and lower

1645   gomphodont postcanines of specimens belonging to 'C. kannemeyeri' (e.g., SAM-PK-K171,

1646   NHMUK PV R3307), which includes individuals whose skull length varies from 5.2 to ten

1647   centimeters (see Abdala, Neveling & Welman (2006), Table 4; C.H. pers. obs.). An exception to

1648   this is BP/1/4658 which bears seven worn out upper and lower postcanines, and one upper and

1649   two lower sectorial teeth. As stated before, BP/1/4658 appears to represent a transitional form

1650   between the dental morphotypes of *T. berryi* and 'C. kannemeyeri' and likely belongs to a

1651   subadult individual. Consequently, all specimens previously referred to the species 'C.

1652   *kannemeyeri*' are here interpreted as younger individuals of *T. berryi*.

1653

Conclusions

1654

1655   The teeth of diademodontids and trirachodontids are morphologically complex and show

1656   particularly important positional, ontogenetic and intraspecific variations. Even the most

1657   comprehensive descriptions of the dentition of these gomphodont cynodonts have inadvertently

1658   omitted dental features that might provide taxonomic and phylogenetic information. The main

1659   differences between the dentition of diademodontids and trirachodontids include: i) the presence

1660   of a at least one transitional postcanine between gomphodont and sectorial teeth in the upper and

1661   lower tooth row; ii) one or several accessory ridges on the mesial and/or distal surfaces of the

1662   transverse crest; and iii) the absence of mesial and distal basins in some upper gomphodont

1663   postcanines in diademodontids; and i) the presence of labial and lingual cusps of the same height

1664   in the lower postcanines; ii) the absence of shearing planes between the outer surface of the main

1665   cusp of the lower and the inner surfaces of the main cusps of the upper postcanines in

1666   trirachodontids. Based on the morphology of the dentition, *Trirachodon berryi* and *T.*

1667   *kannemeyeri* more likely correspond to two morphotypes of the same species, with *T.*

1668   *kannemeyeri* representing younger individuals of *T. berryi*. The Chinese cynodonts *Sinognathus*

1669   and *Beishanodon* are here confidently reassigned to the Gomphodontia based on dental

1670   characters, with *Sinognathus* being referred to Trirachodontidae, whereas *Beishanodon* is

1671   tentatively ascribed to this clade. This study reveals the importance of describing the dentition of

1672   gomphodonts comprehensively and providing as much information as possible on the

1673   morphological varation of the complete dentition as well as crown ornamentations and surface

1674   texture, with the goal of enhancing the identification of isolated gomphodont teeth and clarifying

1675   the phylogenetic position of gomphodont taxa, an objective that we wish to tackle in subsequent

1676   contributions.

1677

Acknowledgements

1679   The cynodont material was examined in several institutions of South Africa, Namibia,

1680   Germany, the UK, Argentina, and China and access to the material was possible thanks to

1681   Johann Neveling (CGP), Helke Mocke (GSN), Mathew Lowe (UCMZ), Sandra Chapman

1682   (NHMUK), Gertrud Rößner and Femke Holwerda (BSPG), Zheng Fang (IVPP), Elize Butler and

1683   Jennifer Botha-Brink (NMQR), Zaituna Erasmus (SAM), Bernard Zipfel and Sifelani Jirah

1684   (ESI). We are particularly thankful to Helke Mocke (GSN) for giving us access to unpublished

1685   material. We also thank Christian Kammerer (NCSM) and Christian Sidor (University of

1686   Washington) for taking for us and sharing photos of the dentition of *Diademodon* and *Cricodon*,

1687   Christian Sidor for sharing an unpublished manuscript describing new material of *Cricodon* from

1688   Zambia, and Mike Day (NHM) and Johann Neveling (CGP) for providing information on the

1689   locality and horizon on some specimens. We would like to express our utmost thanks to José

1690   Eduardo Camargo Martínez for allowing us to use his artwork for the black silhouettes of

1691   cynodonts. Our thanks finally go to the Agustín Martinelli, Christian Sidor and Kirstin Brink for

1692   their helpful comments and suggestions, which considerably improved the quality of this

1693   manuscript. C. H. dedicates this work to O. Mateus.

1694

1695   References

1696   Abdala F. 1996. Redescripción del cráneo y reconsideración de la validez de *Cynognathus minor*

1697   (Eucynodontia-Cynognathidae) del Triásico Inferior de Mendoza. *Ameghiniana* 33:115–

1698   126.

1699   Abdala F. 1999. Elementos postcraneanos de *Cynognathus* (Synapsida-Cynodontia) del Triásico

1700   Inferior de la Provincia de Mendoza, Argentina. Consideraciones sobre la morfología del

1701   húmero en cinodontes. *Revista Española de Paleontología* 14:13–24.

1702   Abdala F., Barberena MC., Dornelles J. 2002. A new species of the traversodontid cynodont

1703   *Exaeretodon* from the Santa Maria Formation (Middle/Late Triassic) of southern Brazil.

1704   *Journal of Vertebrate Paleontology* 22:313–325. DOI: 10.1671/0272-

1705   4634(2002)022[0313:ANSOTT]2.0.CO;2.

1706   Abdala F., Damiani R., Yates A., Neveling J. 2007. A non-mammaliaform cynodont from the

1707   Upper Triassic of South Africa: a therapsid Lazarus taxon? *Palaeontologia Africana*

1708   42:17–23.

1709   Abdala F., Gaetano LC. 2018. The Late Triassic record of cynodonts: Time of innovations in the

1710   mammalian lineage. In: Tanner LH ed. *The Late Triassic World*. Topics in Geobiology.

1711   Springer International Publishing, 407–445.

1712   Abdala F., Giannini NP. 2002. Chiniquodontid cynodonts: systematic and morphometric

1713   considerations. *Palaeontology* 45:1151–1170. DOI: 10.1111/1475-4983.00280.

1714   Abdala F., Hancox PJ., Neveling J. 2005. Cynodonts from the uppermost Burgersdorp

1715   Formation, South Africa, and their bearing on the biostratigraphy and correlation of the

1716   Triassic *Cynognathus* Assemblage Zone. *Journal of Vertebrate Paleontology* 25:192–

1717   199. DOI: 10.1671/0272-4634(2005)025[0192:CFTUBF]2.0.CO;2.

1718   Abdala F., Jasinoski SC., Fernandez V. 2013. Ontogeny of the Early Triassic cynodont

1719   *Thrinaxodon liorhinus* (Therapsida): dental morphology and replacement. *Journal of*

1720   *Vertebrate Paleontology* 33:1408–1431. DOI: 10.1080/02724634.2013.775140.

1721   Abdala F., Marsicano CA., Smith RMH., Swart R. 2013. Strengthening Western Gondwanan

1722   correlations: A Brazilian Dicynodont (Synapsida, Anomodontia) in the Middle Triassic

1723   of Namibia. *Gondwana Research* 23:1151–1162. DOI: 10.1016/j.gr.2012.07.011.

1724   Abdala F., Neveling J., Welman J. 2006. A new trirachodontid cynodont from the lower levels of

1725   the Burgersdorp Formation (Lower Triassic) of the Beaufort Group, South Africa and the

1726   cladistic relationships of Gondwanan gomphodonts. *Zoological Journal of the Linnean*

1727   *Society* 147:383–413. DOI: 10.1111/j.1096-3642.2006.00224.x.

1728   Abdala F., Ribeiro AM. 2003. A new traversodontid cynodont from the Santa Maria Formation

1729   (Ladinian-Carnian) of southern Brazil, with a phylogenetic analysis of Gondwanan

1730   traversodontids. *Zoological Journal of the Linnean Society* 139:529–545. DOI:

1731   10.1111/j.1096-3642.2003.00096.x.

1732   Abdala F., Sa-Teixeira AM. 2004. A traversodontid cynodont of African affinity in the South

1733   American Triassic. *Palaeontologia Africana* 40:11–22.

1734   Abdala F., Smith RMH. 2009. A Middle Triassic cynodont fauna from Namibia and its

1735   implications for the biogeography of Gondwana. *Journal of Vertebrate Paleontology*

1736   29:837–851. DOI: 10.1671/039.029.0303.

1737   Battail B. 1983. La phylogénie des cynodontes gomphodontes. *Acta Palaeontologica Polonica*

1738   28:19–30.

1739   Battail B. 2005. Late Triassic traversodontids (Synapsida: Cynodontia) in southern Africa.

1740   *Palaeontologia Africana* 41:67–80.

1741   Battail B., Surkov MV. 2000. Mammal-like reptiles from Russia. In: Benton MJ, Shishkin MA,

1742   Unwin DM, Kurochkin EN eds. *The Age of Dinosaurs in Russia and Mongolia*.

1743   Cambridge: Cambridge University Press, 86–119.

1744   Bordy E., Sciscio L., Abdala F., McPhee B., Choiniere J. 2017. First Lower Jurassic vertebrate

1745   burrow from southern Africa (upper Elliot Formation, Karoo Basin, South Africa).

1746   *Palaeogeography,   Palaeoclimatology,   Palaeoecology*   468:362–372.   DOI:

1747   10.1016/j.palaeo.2016.12.024.

1748   Brink AS. 1955. A study on the skeleton of *Diademodon*. *Palaeontologia Africana* 3:3–39.

1749   Brink AS. 1963. Two cynodonts from the Ntawere formation in the Luangwa valley of Northern

1750   Rhodesia. *Palaeontologia Africana* 8:77–96.

1751   Brink AS. 1977. A model of tooth replacement in the "mammal-like reptile" *Diademodon*. *South*

1752   *African Journal of Science* 73:138.

1753   Brink KS., Reisz RR. 2014. Hidden dental diversity in the oldest terrestrial apex predator

1754   *Dimetrodon*. *Nature Communications* 5:1–9. DOI: 10.1038/ncomms4269.

1755   Broili F., Schröder J. 1934. Beobachtungen an wirbeltieren der Karrooformation. IX. Uber den

1756   Schadel von *Gomphodontosuchus* Seeley. *Sitzungsbericht der Bayerischen Akademie der*

1757   *Wissenschaften* 1:115–182.

1758   Broili F., Schröder J. 1936. Beobachtungen an Wirbeltieren der Karrooformation. XXII. Ein

1759   neuer Galesauride aus der *Cynognathus*-Zone. *Sitzungsbericht der Bayerischen Akademie*

1760   *der Wissenschaften*:269–282.

1761   Broom R. 1905. 6. On some points in the anatomy of the theriodont reptile *Diademodon*.

1762   *Proceedings of the Zoological Society of London* 75:96–102. DOI: 10.1111/j.1469-

1763   7998.1905.tb08366.x.

1764   Broom R. 1913. On evidence of a mammal-like dental succession in the cynodont reptiles.

1765   *32*:465–468.

1766   Chatterjee S. 1982. A new cynodont reptile from the Triassic of India. *Journal of Paleontology*

1767   56:203–214.

1768   Cohen KM., Finney SC., Gibbard PL., Fan J-X. 2018. The ICS international chronostratigraphic

1769   chart. *Episodes* 36:199–204.

1770   Crompton AW. 1955. On some Triassic cynodonts from Tanganyika. *Proceedings of the*

1771   *Zoological Society of London* 125:617–669. DOI: 10.1111/j.1096-3642.1955.tb00620.x.

1772   Crompton AW. 1963. Tooth replacement in the cynodont *Thrinaxodon liorhinus*. *Annals of the*

1773   *South African Museum* 46:479–521.

1774   Crompton AW. 1972. Postcanine occlusion in cynodonts and tritylodontids. *Bulletin of the*

1775   *British Museum (Natural History). Geology* 21:29–71.

1776   Crompton AW., Jenkins FA. 1968. Molar occlusion in late triassic mammals. *Biological Reviews*

1777   43:427–458. DOI: 10.1111/j.1469-185X.1968.tb00966.x.

1778   Cuvier G. 1805. *Leçons d'Anatomie Comparée: La Première Partie des Organes de la*

1779   *Digestion*. Crochard.

1780   Fauchard P. 1728. *Le Chirurgien Dentiste, ou Traité des Dents*. Chez Jean Mariette.

1781   Flynn JJ., Parrish JM., Rakotosamimanana B., Ranivoharimanana L., Simpson WF., Wyss AR.

1782   2000. New traversodontids (Synapsida: Eucynodontia) from the Triassic of Madagascar.

1783   *Journal of Vertebrate Paleontology* 20:422–427. DOI: 10.1671/0272-

1784   4634(2000)020[0422:NTSEFT]2.0.CO;2.

1785   Fourie S. 1963. Tooth replacement in the gomphodont cynodont, *Diademodon*. *South African*

1786   *Journal of Science* 59:211–213.

1787   Gaetano LC., Mocke H., Abdala F. 2018. The postcranial anatomy of *Diademodon tetragonus*

1788   (Cynodontia, Cynognathia). *Journal of Vertebrate Paleontology* 0:e1451872. DOI:

1789   10.1080/02724634.2018.1451872.

1790   Gao K-Q., Fox RC., Zhou C-F., Li D-Q. 2010. A new nonmammalian eucynodont (Synapsida:

1791   Therapsida) from the Triassic of Northern Gansu Province, China, and its biostratigraphic

1792   and biogeographic implications. *American Museum Novitates*:1–25. DOI: 10.1206/649.1.

1793   Godefroit P. 1999. New traversodontid (Therapsida: Cynodontia) teeth from the Upper Triassic

1794   of Habay-la-Vieille (southern Belgium). *Paläontologische Zeitschrift* 73:385–394. DOI:

1795   10.1007/BF02988049.

1796   Godefroit P., Battail B. 1997. Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern

1797   France). *Geodiversitas* 19:567–631.

1798   Goñi RG., Goin FJ. 1988. Morfología dentaria y biomecánica masticatoria de los cinodontes

1799   (Reptilia, Therapsida) del Triásico Argentino; I, *Andescynodon mendozensis* Bonaparte

1800   (Traversodontidae). *Ameghiniana* 25:139–148.

1801   Gow CE. 1978. The advent of herbivory in certain reptilian lineages during the Triassic.

1802   *Palaeontologia Africana* 21:133–141.

1803   Grine FE. 1977. Postcanine tooth function and jaw movement in the gomphodont cynodont

1804   *Diademodon* (Reptilia; Therapsida). *Palaeontologia Africana* 20:123–135.

1805   Grine FE. 1978. Postcanine dental structure in the mammal-like reptile *Diademodon*

1806   (Therapsida; Cynodontia). *Proceedings, Electron Microscopy Society of Southern Africa*

1807   8:123–124.

1808   Groenewald GH., Welman J., Maceachern JA. 2001. Vertebrate burrow complexes from the

1809   Early Triassic *Cynognathus* Zone (Driekoppen Formation, Beaufort Group) of the Karoo

1810   Basin,   South   Africa.   *Palaios*   16:148–160.   DOI: 10.1669/0883-

1811   1351(2001)016<0148:VBCFTE>2.0.CO;2.

1812   Hammer WR. 1995. New therapsids from the upper Fremouw Formation (Triassic) of

1813   Antarctica.   *Journal   of   Vertebrate   Paleontology*   15:105–112.   DOI:

1814   10.1080/02724634.1995.10011210.

1815   Haughton SH. 1924. A bibliographic list of pre-Stormberg Karroo Reptilia, with a table of

1816   horizons. *Transactions of the Royal Society of South Africa* 12:51–104.

1817   Hendrickx C., Abdala F., Choiniere JN. in preparation. Evolutionary transformations in the

1818   dentition of gomphodont cynodonts.

1819   Hendrickx C., Abdala F., Choiniere J. 2016. Postcanine microstructure in *Cricodon metabolus*, a

1820   Middle Triassic gomphodont cynodont from south-eastern Africa. *Palaeontology*

1821   59:851–861. DOI: 10.1111/pala.12263.

1822   Hendrickx C., Choiniere J., Abdala F. in preparation. Dental morphology in Traversodontidae

1823   (Cynodontia: Gomphodontia).

1824   Hendrickx C., Mateus O., Araújo R. 2015. A proposed terminology of theropod teeth

1825   (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology* 35:e982797. DOI:

1826   10.1080/02724634.2015.982797.

1827   Hillson S. 2005. *Teeth: Second Edition*. New York: Cambridge University Press.

1828   Hopson JA. 1964. Tooth replacement in cynodont, dicynodont and therocephalian Reptiles.

1829   *Proceedings of the Zoological Society of London* 142:625–654. DOI: 10.1111/j.1469-

1830   7998.1964.tb04632.x.

1831   Hopson JA. 1971. Postcanine replacement in the gomphodont cynodont *Diademodon*. *Zoological*

1832   *Journal of the Linnean Society* 50:1–21.

1833   Hopson JA. 1984. Late Triassic traversodont cynodonts from Nova Scotia and southern Africa.

1834   Hopson JA. 1985. Morphology and relationships of *Gomphodontosuchus brasiliensis* von Huene

1835   (Synapsida, Cynodontia, Tritylodontoidea) from the Triassic of Brazil. *Neues Jahrbuch*

1836   *für Geologie und Paläontologie, Monatshefte* 1985:285–299.

1837   Hopson JA. 2005. A juvenile gomphodont cynodont specimen from the *Cynognathus*

1838   Assemblage Zone of South Africa: implications for the origin of gomphodont postcanine

1839   morphology. *Palaeontologia Africana* 41:53–66.

1840   Hopson JA. 2014. The traversodontid cynodont *Mandagomphodon hirschsoni* from the Middle

1841   Triassic of the Ruhuhu Valley, Tanzania. In: Kammerer CF, Angielczyk KD, Fröbisch J

1842   eds. *Early Evolutionary History of the Synapsida*. Vertebrate Paleobiology and

1843   Paleoanthropology. Springer, 233–253.

1844   Hopson JA., Kitching JW. 1972. A revised classification of cynodonts (Reptilia; Therapsida).

1845   *Palaeontologia Africana* 14:71–75.

1846 Hopson JA., Sidor CA. 2015. A juvenile specimen of the trirachodontid *Cricodon metabolus*
1847   from the Luangwa Basin of Zambia: implications for tooth replacement in gomphodont
1848   cynodonts and for trirachodontid systematics. *75th Annual Meeting Society of Vertebrate*
1849   *Paleontology, Dallas, Texas, USA. (October 14-17, 2015), Program and Abstracts*:147.

1850 Hopson JA., Sues H-D. 2006. A traversodont cynodont from the Middle Triassic (Ladinian) of
1851   Baden-Württemberg (Germany). *Paläontologische Zeitschrift* 80:124–129. DOI:
1852   10.1007/BF02988972.

1853 Illiger JKW. 1811. *Prodromus Systematis Mammalium et Avium: Additis Terminis Zoographicis*
1854   *Utriusque Classis, Eorumque Versione Germanica*. Salfeld.

1855 Ivakhnenko MF. 2011. Permian and Triassic Therocephals (Eutherapsida) of Eastern Europe.
1856   *Paleontological Journal* 45:981–1144. DOI: 10.1134/S0031030111090012.

1857 Kammerer CF., Flynn JJ., Ranivoharimanana L., Wyss AR. 2008. New material of *Menadon*
1858   *besairiei* (Cynodontia: Traversodontidae) from the Triassic of Madagascar. *Journal of*
1859   *Vertebrate Paleontology* 28:445–462. DOI: 10.1671/0272-
1860   4634(2008)28[445:NMOMBC]2.0.CO;2.

1861 Kammerer CF., Flynn JJ., Ranivoharimanana L., Wyss AR. 2012. Ontogeny in the Malagasy
1862   traversodontid *Dadadon isaloi* and a reconsideration of its phylogenetic relationships.
1863   *Fieldiana Life and Earth Sciences*:112–125. DOI: 10.3158/2158-5520-5.1.112.

1864 Kemp TS. 1980. Aspects of the structure and functional anatomy of the Middle Triassic
1865   cynodont *Luangwa*. *Journal of Zoology* 191:193–239.

1866 Keyser AW. 1973. A new Triassic vertebrate fauna from South West Africa. *Palaeontologia*
1867   *Africana* 16:1–15.

1868   Kitching JW. 1977. The distribution of the Karoo vertebrate fauna. Johannesburg: Bernard Price

1869   Institute for Palaeontological Research, University of the Witwatersrand.

1870   Langer MC., Ferigolo J. 2013. The Late Triassic dinosauromorph *Sacisaurus agudoensis*

1871   (Caturrita Formation; Rio Grande do Sul, Brazil): anatomy and affinities. *Geological*

1872   *Society, London, Special Publications* 379:353–392. DOI: 10.1144/SP379.16.

1873   Liu J. 2007. New traversodontid materials from North Carolina, United States and the taxonomy,

1874   phylogeny of Traversodontidae (Synapsida: Cynodontia). Ph.D. Dissertation Thesis. New

1875   York, New York: Columbia University.

1876   Liu J., Abdala F. 2014. Phylogeny and taxonomy of the Traversodontidae. In: Kammerer CF,

1877   Angielczyk KD, Fröbisch J eds. *Early Evolutionary History of the Synapsida*. Vertebrate

1878   Paleobiology and Paleoanthropology. Springer Netherlands, 255–279.

1879   Liu J., Powell J. 2009. Osteology of *Andescynodon* (Cynodontia: Traversodontidae) from the

1880   Middle Triassic of Argentina. *American Museum Novitates*:1–19. DOI: 10.1206/606.1.

1881   Liu J., Ramezani J., Li L. 2018. High-precision temporal calibration of Middle Triassic

1882   vertebrate biostratigraphy: U-Pb zircon constraints for the *Sinokannemeyeria* Fauna and

1883   *Yonghesuchus*. *Vertebrata PalAsiatica* 56:16–24.

1884   Liu J., Sues H-D. 2010. Dentition and tooth replacement of *Boreogomphodon* (Cynodontia:

1885   Traversodontidae) from the Upper Triassic of North Carolina, USA. *Vertebrata*

1886   *PalAsiatica* 48:169–184.

1887   Lucas SG., Estep JW., Heckert AB., Hunt AP. 1999. Cynodont teeth from the Upper Triassic of

1888   New Mexico, USA. *Neues Jahrbuch fur Geologie und Palaontologie-Monatshefte*

1889   1999:331–344.

1890   Marsicano CA., Irmis RB., Mancuso AC., Mundil R., Chemale F. 2016. The precise temporal

1891   calibration of dinosaur origins. *Proceedings of the National Academy of Sciences*

1892   113:509–513. DOI: 10.1073/pnas.1512541112.

1893   Martin RE. 1999. *Taphonomy: a process approach*. Cambridge, England; New York: Cambridge

1894   University Press.

1895   Martinelli AG. 2010. On the postcanine dentition of *Pascualgnathus polanskii* Bonaparte

1896   (Cynodontia, Traversodontidae) from the Middle Triassic of Argentina. *Geobios* 43:629–

1897   638. DOI: 10.1016/j.geobios.2010.03.006.

1898   Martinelli AG., de la Fuente M., Abdala F. 2009. *Diademodon tetragonus* Seeley, 1894

1899   (Therapsida: Cynodontia) in the Triassic of South America and its biostratigraphic

1900   implications. *Journal of Vertebrate Paleontology* 29:852–862. DOI:

1901   10.1671/039.029.0315.

1902   Martinelli AG., Kammerer CF., Melo TP., Neto VDP., Ribeiro AM., Da-Rosa ÁA., Schultz CL.,

1903   Soares MB. 2017. The African cynodont *Aleodon* (Cynodontia, Probainognathia) in the

1904   Triassic of southern Brazil and its biostratigraphic significance. *PloS one* 12:e0177948.

1905   Martinelli AG., Soares MB., Schwanke C. 2016. Two new cynodonts (Therapsida) from the

1906   Middle-Early Late Triassic of Brazil and comments on South American

1907   probainognathians. *PloS One* 11:e0162945. DOI: 10.1371/journal.pone.0162945.

1908   Martínez RN., Fernández E., Alcober OA. 2013. A new non-mammaliaform eucynodont from

1909   the Carnian-Norian Ischigualasto Formation, northwestern Argentina. *Revista Brasileira*

1910   *de Paleontologia* 16:61–76.

1911   McGraw-Hill 2003. *Dictionary of Bioscience*. New York, New York: McGraw-Hill Professional

1912   Publishing, McGraw-Hill Companies, The Distributor.

1913 Melo TP. 2014. Sobre a presença de *Menadon besairiei* (Synapsida: Traversodontidae) na zona-
1914   associação de *Santacruzodon*, triássico superior da supersequência Santa Maria, Brasil.
1915   Master Thesis Thesis. Porte Alegre, Rio Grande do Sul, Brazil: Universidade Federal do
1916   Rio Grande do Sul. Instituto de Geociências. Programa de Pós-Graduação em
1917   Geociências.

1918 Melo TP., Abdala F., Soares MB. 2015. The Malagasy cynodont *Menadon besairiei*
1919   (Cynodontia; Traversodontidae) in the Middle–Upper Triassic of Brazil. *Journal of*
1920   *Vertebrate Paleontology* 35:e1002562. DOI: 10.1080/02724634.2014.1002562.

1921 Melo TP., Martinelli AG., Soares MB. 2017. A new gomphodont cynodont (Traversodontidae)
1922   from the Middle–Late Triassic *Dinodontosaurus* Assemblage Zone of the Santa Maria
1923   Supersequence, Brazil. *Palaeontology* 60:571–582. DOI: 10.1111/pala.12302.

1924 Niu Y., Liu C., Shi GR., Lu J., Xu W., Shi J. 2018. Unconformity-bounded Upper Paleozoic
1925   megasequences in the Beishan Region (NW China) and implications for the timing of the
1926   Paleo-Asian Ocean closure. *Journal of Asian Earth Sciences*. DOI:
1927   10.1016/j.jseaes.2018.06.019.

1928 Oliveira TV., Soares MB., Schultz CL., Rogrigues CN. 2011. A new carnivorous cynodont
1929   (Synapsida, Therapsida) from the Brazilian Middle Triassic (Santa Maria Formation):
1930   *Candelariodon barberenai* gen. et sp. nov. *Zootaxa* 3027:19–28.

1931 Osborn JW. 1974. On tooth succession in *Diademodon*. *Evolution* 28:141–157.

1932 Osborn JW., Hillman J. 1979. Enamel structure in some therapsids and Mesozoic mammals.
1933   *Calcified Tissue International* 29:47–61.

1934 Ottone EG., Monti M., Marsicano CA., de la Fuente MS., Naipauer M., Armstrong R., Mancuso
1935   AC. 2014. A new Late Triassic age for the Puesto Viejo Group (San Rafael depocenter,

1936   Argentina): SHRIMP U–Pb zircon dating and biostratigraphic correlations across

1937   southern Gondwana. *Journal of South American Earth Sciences* 56:186–199. DOI:

1938   10.1016/j.jsames.2014.08.008.

1939   Owen R. 1840. *Odontography; or, A treatise on the comparative anatomy of the teeth; their*

1940   *physiological relations, mode of development, and microscopic structure, in the*

1941   *vertebrate animals*. London, H. Baillière.

1942   Pacheco CP., Martinelli AG., Pavanatto AEB., Soares MB., Dias-da-Silva S. 2018. *Prozostrodon*

1943   *brasiliensis*, a probainognathian cynodont from the Late Triassic of Brazil: second record

1944   and improvements on its dental anatomy. *Historical Biology* 30:475–485. DOI:

1945   10.1080/08912963.2017.1292423.

1946   Peecook BR., Steyer JS., Tabor NJ., Smith RMH. 2018. Updated geology and vertebrate

1947   paleontology of the Triassic Ntawere Formation of northeastern Zambia, with special

1948   emphasis on the archosauromorphs. *Journal of Vertebrate Paleontology* 37:8–38. DOI:

1949   10.1080/02724634.2017.1410484.

1950   Ranivoharimanana L., Kammerer CF., Flynn JJ., Wyss AR. 2011. New material of *Dadadon*

1951   *isaloi* (Cynodontia, Traversodontidae) from the Triassic of Madagascar. *Journal of*

1952   *Vertebrate Paleontology* 31:1292–1302. DOI: 10.1080/039.031.0619.

1953   Rauhut OWM., Werner C. 1995. First record of the family Dromaeosauridae (Dinosauria:

1954   Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan).

1955   *Paläontologische Zeitschrift* 69:475–489. DOI: 10.1007/BF02987808.

1956   Reisz RR., Sues H-D. 2000. Herbivory in late Paleozoic and Triassic terrestrial vertebrates. In:

1957   Sues H-D ed. *Evolution of Herbivory in Terrestrial Vertebrates*. New York: Cambridge

1958   University Press, 9–41.

1959   Romer AS. 1967. The Chañares (Argentina) Triassic reptile fauna. III. Two new gomphodonts,

1960   *Massetognathus pascuali* and *M. teruggii. Breviora* 264:1–25.

1961   Rubidge BS. 2005. 27th Du Toit Memorial Lecture Re-uniting lost continents - Fossil reptiles

1962   from the ancient Karoo and their wanderlust. *South African Journal of Geology* 108:135–

1963   172. DOI: 10.2113/108.1.135.

1964   Sander PM. 1997a. Prismless enamel in amniotes: terminology, function, and evolution. In:

1965   Koenigswald W v., Sander PM eds. *Tooth Enamel Microstructure*. Rotterdam;

1966   Brookfield, VT: CRC Press, 92–106.

1967   Sander PM. 1997b. Non-mammalian synapsid enamel and the origin of mammalian enamel

1968   prisms: the bottom-up perspective. In: Koenigswald W v., Sander PM eds. *Tooth Enamel*

1969   *Microstructure*. Rotterdam; Brookfield, VT: CRC Press, 41–62.

1970   Sander PM. 1997c. Teeth and jaws. In: Currie PJ, Padian K eds. *Encyclopedia of Dinosaurs*. San

1971   Diego, California: Academic Press, 717–725.

1972   Sander PM. 1999. The microstructure of reptilian tooth enamel: terminology, function, and

1973   phylogeny. *Münchner Geowissenschaftliche Abhandlungen, Reihe A* 38:1–102.

1974   Schwenk K. 2000. *Feeding: Form, Function and Evolution in Tetrapod Vertebrates*. Academic

1975   Press.

1976   Seeley HG. 1894. Researches on the structure, organization, and classification of the fossil

1977   Reptilia. Part IX., Section 3. On *Diademodon. Philosophical Transactions of the Royal*

1978   *Society of London. B* 185:1029–1041.

1979   Seeley HG. 1895. Researches on the structure, organization, and classification of the fossil

1980   Reptilia. Part IX., Section 4. On the Gomphodontia. *Philosophical Transactions of the*

1981   *Royal Society of London. B* 186:1–57.

1982   Seeley HG. 1908. Additional evidence as to the dentition and structure of the skull in the South

1983   African fossil reptile genus *Diademodon. Proceedings of the Zoological Society of*

1984   *London* 78:611–617. DOI: 10.1111/j.1469-7998.1908.tb07394.x.

1985   Sidor CA., Hopson JA. 2018. *Cricodon metabolus* (Cynodontia: Gomphodontia) from the

1986   Triassic Ntawere Formation of northeastern Zambia: patterns of tooth replacement and a

1987   systematic review of the Trirachodontidae. In: *Vertebrate and Climatic Evolution in the*

1988   *Triassic Rift Basins of Tanzania and Zambia. Society of Vertebrate Paleontology Memoir*

1989   *17. Journal of Vertebrate Paleontology 37(6, Supplement)*. 39–64.

1990   Smith JB., Dodson P. 2003. A proposal for a standard terminology of anatomical notation and

1991   orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology* 23:1–12.

1992   Smith RMH., Sidor CA., Angielczyk KD., Nesbitt SJ., Tabor NJ. 2018. Taphonomy and

1993   paleoenvironments of Middle Triassic bone accumulations in the Lifua Member of the

1994   Manda Beds, Songea Group (Ruhuhu Basin), Tanzania. *Journal of Vertebrate*

1995   *Paleontology* 37:65–79. DOI: 10.1080/02724634.2017.1415915.

1996   Smith R., Swart R. 2002. Changing fluvial environments and vertebrate taphonomy in response

1997   to climatic drying in a Mid-Triassic rift valley fill: The Omingonde Formation (Karoo

1998   Supergroup) of Central Namibia. *PALAIOS* 17:249–267. DOI: 10.1669/0883-

1999   1351(2002)017<0249:CFEAVT>2.0.CO;2.

2000   Smith JB., Vann DR., Dodson P. 2005. Dental morphology and variation in theropod dinosaurs:

2001   Implications for the taxonomic identification of isolated teeth. *The Anatomical Record*

2002   *Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology* 285A:699–736.

2003   DOI: 10.1002/ar.a.20206.

2004   Soares MB., Martinelli AG., Oliveira TV. 2014. A new prozostrodontian cynodont (Therapsida)

2005   from the Late Triassic *Riograndia* Assemblage Zone (Santa Maria Supersequence) of

2006   Southern Brazil. *Anais da Academia Brasileira de Ciências* 86:1673–1691.

2007   Spielmann JA., Lucas SG. 2012. Tetrapod Fauna of the Upper Triassic Redona Formation East-

2008   central New Mexico: The Characteristic Assemblage of the Apachean Land-vertebrate

2009   Faunachron: Bulletin 55. *New Mexico Museum of Natural History and Science* 55:1–119.

2010   Sues H-D., Hopson JA. 2010. Anatomy and phylogenetic relationships of *Boreogomphodon*

2011   *jeffersoni* (Cynodontia: Gomphodontia) from the Upper Triassic of Virginia. *Journal of*

2012   *Vertebrate Paleontology* 30:1202–1220. DOI: 10.1080/02724634.2010.483545.

2013   Sues H-D., Hopson JA., Shubin NH. 1992. Affinities of ?*Scalenodontoides plemmyridon*

2014   Hopson, 1984 (Synapsida: Cynodontia) from the Upper Triassic of Nova Scotia. *Journal*

2015   *of Vertebrate Paleontology* 12:168–171. DOI: 10.1080/02724634.1992.10011447.

2016   Sues H-D., Olsen PE., Carter JG. 1999. A Late Triassic traversodont cynodont from the Newark

2017   Supergroup of North Carolina. *Journal of Vertebrate Paleontology* 19:351–354. DOI:

2018   10.1080/02724634.1999.10011146.

2019   Sun A. 1988. Additional study on *Sinognathus gracilis* (Cynodontia; Reptilia). *Vertebrata*

2020   *Palasiatica* 26:173–180.

2021   Tatarinov LP. 2002. Gomphodont cynodonts (Reptilia, Theriodontia) from the Middle Triassic of

2022   the Orenburg region. *Paleontological Journal* 36:176–179.

2023   Valencio DA., Mendía J., Vilas JF. 1975. Palaeomagnetism and K-Ar ages of triassic igneous

2024   rocks from the Ischigualasto-Ischichuca Basin and Puesto Viejo Formation, Argentina.

2025   *Earth and Planetary Science Letters* 26:319–330. DOI: 10.1016/0012-821X(75)90007-2.

2026   Watson DMS. 1911. XL.—The skull of *Diademodon*, with notes on those of some other

2027   Cynodonts. *Annals and Magazine of Natural History* 8:293–330. DOI:

2028   10.1080/00222931108693034.

2029   Watson DMS. 1913. I.—On a new cynodont from the Stormberg. *Geological Magazine* 10:145–

2030   148. DOI: 10.1017/S0016756800126032.

2031   Wynd BM., Peecook BR., Whitney MR., Sidor CA. 2018. The first occurrence of *Cynognathus*

2032   *crateronotus* (Cynodontia: Cynognathia) in Tanzania and Zambia, with implications for

2033   the age and biostratigraphic correlation of Triassic strata in southern Pangea. *Journal of*

2034   *Vertebrate Paleontology* 37:228–239. DOI: 10.1080/02724634.2017.1421548.

2035   Young C. 1959. Note on the first cynodont from the *Sinokannemeyeria* faunas in Shansi, China.

2036   *Vertebrata PalAsiatica* 3:124–132.

2037   Ziegler AC. 1969. A theoretical determination of tooth succession in the therapsid *Diademodon*.

2038   *Journal of Paleontology* 43:771–778.

2039

2040   Figure captions

2041   Figure 1. Phylogeny and geographic and stratigraphic distribution of cynodont clades. **A**, Tree
2042   topology based on the results of the cladistic analyses of Liu & Abdala (2014) for cynognathians
2043   and Martínez, Fernandez & Alcober (2013) and Martinelli, Soares & Schwanke (2016) for
2044   probainognathians. *Titanogomphodon*, considered to be a close relative of *Diademodon* by
2045   Keyser (1973) and Martinelli, de la Fuente & Abdala (2009), is placed among Diademodontidae.
2046   Node 1, Eucynodontia; Node 2, Probainognathia; Node 3, Cynognathia; Node 4, Gomphodontia;
2047   Node 5, Diademodontidae; and Node 6, Trirachodontidae. Arrows indicate that the clades extend
2048   beyond the Lower Jurassic. **B**, Stratigraphic distribution of Diademodontidae (in yellow) and
2049   Trirachodontidae (in blue-purple), with *Diademodon* in pale yellow, *Titanogomphodon* in dark
2050   yellow, *Langbergia* in pale blue, *Cricodon* in blue sky, *Trirachodon* in dark blue, *Sinognathus* in
2051   light purple and *Beishanodon* in dark purple. Stratigraphic extension of geological units based on

2052   Liu et al. (2018) for the Ermaying Formation, Gao et al. (2010) and Niu et al. (2018) for the

2053   Hongyanjing Formation, Rubidge et al. (2005) for the *Cynognathus* Assemblage Zone, Wynd et

2054   al. (2018) for the Manda Beds and the Upper Omingonde, Ntawere and Fremouw formations,

2055   and Ottone et al. (2014) for the Río Seco de la Quebrada Formation. Stars denote the U-PB

2056   geochronologic ages of 243.53 Ma from Liu et al. (2018) for the upper Ermaying Formation in

2057   China, and 235.82 Ma from Ottone et al. (2014) for the Rio Seco de la Quebrada Formation in

2058   Argentina. Wavy lines indicate unconformities and diagonal lines formational interfingering,

2059   whereas dashed lines, indicates an unclear relationship to the geologic time scale. Age of the

2060   Triassic stage limits based on Cohen et al. (2018). **Abbreviations**: **CAZ**, *Cynognathus*

2061   Assemblage Zone; **E**, Early Triassic; **Fm**, Formation; **M**, Middle Triassic; **Ma**, million years;

2062   **Pr.**, Province. Ottone et al.'s (2014) hypothesis refers to the Carnian dating for levels of the Río

2063   Seco de la Quebrada Formation. Black silhouettes credit: Sergey Meleshin (*Sinognathus*), José

2064   Eduardo Camargo Martínez (all others), used with permission.

2065

2066   Figure 2. Dental terminology used in this study. **A-B**, *Diademodon* rostrum in **A**, palatal and **B**,

2067   labial views; **C**, **F**, idealized right upper gomphodont postcanine in **C**, apical and **F**, distal views

2068   (based on the upper gomphodont postcanine of *Scalenodon angustifrons* by Hopson, 2005;

2069   modified); **D**, **G**, idealized left lower gomphodont postcanine in **D**, apical and **G**, distal views

2070   (based on the lower gomphodont postcanine of *Scalenodon angustifrons* by Hopson, 2005;

2071   modified); **E**, upper right gomphodont postcanine of *Menadon besairiei* (UA 10601) in apical

2072   view; **H**, upper right gomphodont postcanine of *Diademodon tetragonus* (SAM-PK-571) in

2073   apical view; **I**, idealized sectorial postcanine of *Diademodon tetragonus* in lingual view (based

2074   on the second right upper sectorial postcanine of *Diademodon tetragonus* BP/1/4529); **J**, apex of

2075   main cusp of an upper sectorial postcanine of *Diademodon tetragonus* with close up on the

2076   denticles, in labial view; **K**, close up on the enamel surface texture of the second right upper

2077   sectorial postcanine of *Diademodon tetragonus* (BP/1/4529). **Abbreviations**: **c**, canine; **ca**,

2078   carina; **cap**, crown apex; **cc**, central cusp (in green); **cev**, central valley; **ci**, cingulum; **cic**,

2079   cingular cuspules; **clar**, centrolabial ridge; **clir**, centrolingual ridge; **co**, crown; **cos**, concave

2080   surface; **cpc**, conical postcanine; **cri**, central ridge; **cu**, cusp; **db**, distal basin; **dac**, distal

2081   accessory cusp; **dad**, distal accessory cusp; **dar**, distal accessory ridge; **dca**, distal carina; **dcc**,

2082   distal cingular cuspule; **dci**, distal cingulum (in violet); **de**, denticle; **dia**, diastema; **dmc**, distal

2083 main cusp; **dri**, distal ridge; **dv**, distal valley; **ec**, ectopterygoid; **ent**, enamel texture; **gpc**,

2084 gomphodont postcanine; **i**, incisor; **j**, jugal; **lac**, labial cusp (in red); **lacc**, labial cingular cusp;

2085 **laci**, labial cingulum (in orange); **lacr**, labiocentral ridge; **ladc**, labiodistal accessory cusp; **ladr**,

2086 labiodistal ridge; **lamr**, labiomesial ridge; **lar**, labial ridge; **lav**, labial valley; **lic**, lingual cusp (in

2087 blue); **licc**, lingual cingular cuspule; **lici**, lingual cingulum (in turquoise); **licr**, linguocentral

2088 ridge; **lidc**, linguodistal accessory cusp; **lidr**, linguodistal ridge; **limc**, linguomesial accessory

2089 cusp; **limr**, linguomesial ridge; **lir**, lingual ridge; **liv**, lingual valley; **lri**, longitudinal ridge; **mac**,

2090 mesial accessory cusp; **mar**, mesial accessory ridge; **mb**, mesial basin; **mc**, main cusp; **mca**,

2091 mesial carina; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum (in beige); **mmc**, mesial main

2092 cusp; **mri**, mesial ridge; **mv**, mesial valley; **mx**, maxilla; **pal**, palatine; **pc**, postcanine; **pcf**,

2093 postcanine fossa; **pmx**, premaxilla; **ro**, root; **se**, serration; **spc**, sectorial postcanine; **tc**, transverse

2094 crest (in yellow); **tpc**, transitional postcanine; **tun**, transverse undulation.

2095

2096 Figure 3. Dentition of non-traversodontid Gomphodontia. **A**, Upper gomphodont postcanine

2097 (SAM-PK-571a); and **B**, cranial dentition (mainly based on BSP 1934 VIII 14) of *Diademodon*

2098 *tetragonus* in apical and palatal views, respectively; **C**, last right upper gomphodont postcanine;

2099 and **D**, cranial dentition of *Titanogomphodon crassus* (GSN R322) in apical and palatal views,

2100 respectively; **E**, upper gomphodont postcanine (reconstruction based on the fourth and third left

2101 upper gomphodont teeth of NMQR 3251 and 3255, respectively); and **F**, cranial dentition

2102 (NMQR 3255) of *Langbergia modisei* in apical and palatal views, respectively; **G**, last right

2103 upper gomphodont postcanine (UMCZ T905); and **H**, cranial dentition (reconstruction based on

2104 BP/1/6102 and UMCZ T905 for the anterior and posterior portions of the cranium, respectively,

2105 and NHCC LB28 for the anterior postcanine dentition) of *Cricodon metabolus* in apical and

2106 palatal views, respectively (the dashed-line represents the lateral margin of the cranium of

2107 NHCC LB28); **I-J**, antepenultimate right upper gomphodont postcanines (NHM PV R3307,

2108 *Trirachodon* 'kannemeyeri' morphotype, and BSP 1934 VIII 21, *Trirachodon berryi*

2109 morphotype, for **I** and **J**, respectively); and **K**, cranial dentition (BP/1/4658) of *Trirachodon*

2110 *berryi* in apical and palatal views, respectively; **L**, fourth right upper gomphodont postcanine;

2111 and **M**, cranial dentition of *Beishanodon youngi* (PKUP V3007) in apical and palatal views,

2112 respectively; **N**, lower gomphodont postcanine (left anterior tooth of SAM-PK-571b); and **O**,

2113 mandibular dentition (reconstruction based on MBR 1004 for the mandible, incisor and canine

2114 morphology, SAM-PK-571b and AM 3753 for the anterior postcanine dentition, and SAM-PK-

2115 K177 for the posterior postcanine dentition) of *Diademodon tetragonus* in apical and dorsal

2116 views, respectively; **P-S**, upper sectorial postcanines of **P**, *Diademodon tetragonus* (MB R1004);

2117 **Q**, *Langbergia modisei* (NMQR 3251); **R**, *Trirachodon berryi* (SAM-PK-4801); and **S**,

2118 *Cricodon metabolus* (UMCZ T905) in labial view; **T**, lower gomphodont postcanine (third right

2119 tooth of NMQR 5251); and **U**, mandibular dentition (NMQR 3251) of *Langbergia modisei* in

2120 apical and dorsal views, respectively; **V**, lower gomphodont postcanine (last right tooth of

2121 UMCZ T905); and **W**, mandibular dentition (based on SAM-PK-5881a and UMCZ T905 for the

2122 anterior and posterior dentitions, respectively) of *Cricodon metabolus* in apical and dorsal views,

2123 respectively; **X**, lower gomphodont postcanine (antepenultimate right gomphodont tooth of

2124 SAM-PK-K4801); and **Y**, mandibular dentition (BP/1/4658) of *Trirachodon berryi* in apical and

2125 dorsal views, respectively; **Z**, lower gomphodont postcanine (sixth and antepenultimate right

2126 gomphodont tooth of SAM-PK-K171); and **α**, mandibular dentition (SAM-PK-K171) of

2127 *Trirachodon berryi* (*T. 'kannemeyeri'* morphotype) in apical and dorsal views, respectively.

2128 **Abbreviations**: **c**, canine (in orange); **cpc**, conical postcanine (in yellow); **dac**, distal accessory

2129 cusp; **dar**, distal accessory ridge; **dcc**, distal cingular cuspule; **gpc**, gomphodont postcanine (in

2130 violet); **i**, incisor (in blue); **licc**, lingual cingular cuspule; **lici**, lingual cingulum; **mar**, mesial

2131 accessory ridge; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mmc**, mesial main cusp; **pcf**,

2132 postcanine fossa; **spc**, sectorial postcanine (in green); **tpc**, transitional postcanine (in red).

2133

2134 Figure 4. Dentition of *Diademodon tetragonus*. **A**, Isolated upper incisor (first left incisor?) of

2135 BSP 1934 VIII 14, with **B**, close up on the distal denticles, in labial view; **C**, Isolated upper

2136 incisor (first or second right incisor?) of BSP 1934 VIII 14, with **D**, close up on the mesial

2137 denticles, in lingual view; **E**, Isolated canine of SAM-PK-571b, with **F**, close up on the distal

2138 denticles, in lingual? view; **G**, First to third right upper conical postcanines of MB R1004 in

2139 labial view; **H**, Fifth right upper conical postcanine of BSP 1934 VIII 14 in apicolabial view; **I**,

2140 **J**, Third and fourth left lower conical postcanines of AM 458 in **I**, labial and **J**, lingual views; **K**,

2141 Second to fourth left lower conical postcanines of SAM-PK-5877 in labial view; **L**, **M**, Isolated

2142 upper gomphodont postcanine of SAM-PK-571a in **L**, apical and **M**, mesial views; **N**, **O**, Second

2143 and third right upper gomphodont postcanines of SAM-PK-571a in **N**, apical and **O**, distal view;

2144 **P**, Fourth right upper gomphodont postcanine of BSP 1934 VIII 14 in apical view.

2145 **Abbreviations**: **cc**, central cusp; **cic**, cingular cuspules; **dac**, distal accessory cusp; **dar**, distal
2146 accessory ridge; **dca**, distal carina; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **dde**, distal
2147 denticle; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lic**, lingual cusp; **limc**, linguomesial
2148 accessory cusp; **lri**, longitudinal ridge; **mar**, mesial accessory ridge; **mca**, mesial carina; **mcc**,
2149 mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **tc**, transverse crest.
2150
2151 Figure 5. Dentition of *Diademodon tetragonus*. **A-C**, **E**, Lower gomphodont postcanine from the
2152 posterior portion of the mandible of SAM-PK-571b in **A**, apical, **B**, labial, **C**, distal views, and
2153 **E**, close up on the labial cusp of the distal postcanine,; **D**, distalmost right lower gomphodont
2154 postcanine of SAM-PK-5877 in apical view; **F**, Sixth? gomphodont, first and second transitional,
2155 and first sectorial postcanines from the left mandible of SAM-PK-K177 in apical view; **G**, First
2156 transitional and first sectorial postcanines of the right mandible of MB R1004 in apical view; **H**,
2157 Transitional, first and second left upper sectorial postcanines of MB R1004 in labial view (photo
2158 credit: Christian Kammerer); **I-K**, Second right upper sectorial postcanine of BP/1/4529, with
2159 close up on **J**, showing the first distal accessory cusp, and **K**, the mesial denticles, in labial view.
2160 **Abbreviations**: **cc**, central cusp; **dac**, distal accessory cusp; **dar**, distal accessory ridge; **dcc**,
2161 distal cingular cuspule; **dci**, distal cingulum; **dde**, distal denticle; **de**, denticle; **dmc**, distal main
2162 cusp; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lic**, lingual cusp; **licc**, lingual cingular
2163 cuspule; **limc**, linguomesial accessory cusp; **lir**, lingual ridge; **mar**, mesial accessory ridge; **mc**,
2164 main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **mmc**,
2165 mesial main cusp; **tc**, transverse crest.
2166
2167 Figure 6. Dentition of *Titanogomphodon crassus*. **A-C**, **E**. Right upper gomphodont, transitional
2168 and sectorial postcanines of GSN R322, with close up on **B**, the penultimate gomphodont, **C**,
2169 mesial accessory ridge of the distalmost gomphodont, and **E**, distalmost sectorial postcanine in
2170 apical view; **D-F**, left mesialmost preserved upper gomphodont postcanine of GSN R322 in **D**,
2171 apical and **F**, mesial views. **Abbreviations**: **lac**, labial cusp; **lamc**, labiomesial accessory cusp;
2172 **lic**, lingual cusp; **mar**, medial accessory ridge; **mcc**, mesial cingular cusp; **spc**, sectorial
2173 postcanine; **tc**, transverse cusp; **tpc**, transitional postcanine.
2174

2175   Figure 7. Dentition of *Langbergia modisei*. **A-B**, First left lower incisor of NMQR 3251, with **B**,

2176   close up on the distal carina in labial view; **C**, close up on the distal carina of the fourth left

2177   upper incisor of NMQR 3281 in labial view; **D**, **F-G**, right lower canine of NMQR 3251, with

2178   close up on the **F**, distal and **G**, mesial carina, in labial view; **E**, cross-sectional outline of the

2179   right upper canine of SAM-PK-11481 in apical view (labial and mesial sides to the top and the

2180   right, respectively); **H**, right upper canine of BP/1/5362 in labial view; **I**, centromesial portion of

2181   the erupting left upper canine of NMQR 3268 in labial view; **J**, fourth and fifth left upper

2182   gomphodont postcanines of NMQR 3251 in apical view; **K**, third left upper postcanine of

2183   NMQR 3255 in apical view; **L**, close up on the fourth left upper postcanine of NMQR 3251 in

2184   mesial view (crown upside down); **M**, third and fourth right lower gomphodont postcanine of

2185   NMQR 3251 in apical view; **N**, first left lower gomphodont postcanine of NMQR 3251 in

2186   apicodistal view; **O**, first and second right upper sectorial postcanine of NMQR 3251 in labial

2187   view; **P**, first right upper sectorial postcanine of BP/1/5362 in labial view; **Q**, second left upper

2188   sectorial postcanine of NMQR 3255 in linguomesial view. **Abbreviations**: **cc**, central cusp; **dac**,

2189   distal accessory cusp; **db**, distal basin; **dcc**, distal cingular cuspule; **dci**, distal cingulum; **dde**,

2190   distal denticle; **de**, denticle; **dmc**, distal main cusp; **lac**, labial cusp; **ladc**, labiodistal accessory

2191   cusp; **lamc**, labiomesial accessory cusp; **lic**, lingual cusp; **licc**, lingual cingular cuspule; **lidc**,

2192   linguodistal accessory cusp; **limc**, linguomesial accessory cusp; **lri**, longitudinal ridge; **mac**,

2193   mesial accessory cusp; **mb**, mesial basin; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mci**,

2194   mesial cingulum; **mde**, mesial denticle; **mmc**, mesial main cusp; **tc**, transverse crest. Elongation

2195   axes of the crown and the central cusp in green and red, respectively.

2196

2197   Figure 8. Dentition of *Cricodon metabolus*. **A-B**, First left lower incisor of UMCZ T905 in **A**,

2198   labial and **B**, labiodistal views; C-D, fourth left upper incisor of BP/1/6102, with **D**, close up on

2199   the distal denticles, in labial view; **E-F**, left lower canine of SAM-PK-5881*a*, in **E**, lingual view;

2200   with **F**, cross-sectional outline at mid-crow apical view; **G**, centromesial and **H**, centrodistal

2201   denticles of the right upper canine of BP/1/6102 in labial view; **I**, centrodistal denticles of the

2202   right upper canine of BP/1/5540 in labial view; **J**, eight? and nine? right upper gomphodont

2203   postcanines of UMCZ T905 in apical view; **K**, eight and nine right lower gomphodont

2204   postcanines of UMCZ T905 in apical view; **L**, first left lower gomphodont postcanine of SAM-

2205   PK-5881*a* in apical view; **M**, last right upper gomphodont postcanine of SAM-PK-5881*b* in

2206 distal view; **N**, last left upper gomphodont postcanine of UMCZ T905; **O**, close up on the

2207 denticles on the labiodistal ridge of an isolated left upper postcanine of UMCZ T905 in

2208 labiodistal view; **P-Q**, ninth right upper sectorial postcanine of UMCZ T905 in **P**, labial and **Q**,

2209 apical views. **Abbreviations**: **cac**, central accessory cusp; **cc**, central cusp; **cos**, concave surface;

2210 **dac**, distal accessory cusp; **db**, distal basin; **dcc**, distal cingular cuspule; **dci**, distal cingulum;

2211 **dde**, distal denticle; **de**, denticle; **dmc**, distal main cusp; **ent**, enamel surface texture; **lac**, labial

2212 cusp; **ladc**, labiodistal accessory cusp; **lic**, lingual cusp; **lidc**, linguodistal accessory cusp; **limc**,

2213 linguomesial accessory cusp; **lri**, longitudinal ridge; **mb**, mesial basin; **mc**, main cusp; **mcc**,

2214 mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **mmc**, mesial accessory

2215 cusp; **tc**, transverse crest; **tun**, transverse undulation. The red lines highlight the angular

2216 labiodistal margin of the lower postcanines.

2217

2218 Figure 9. Dentition of *Trirachodon berryi* I. **A-C**, First? left upper incisor, with close up on **B**,

2219 mesial and **C**, distal denticles of SAM-PK-12168 in labial view; **D**, first left and right upper and

2220 **E**, first right lower incisors of BP/1/4658 in apical views; **F-G**, right upper canine of BP/1/4661

2221 with **G**, close up on the centrodistal part of the crown, in labial view; **H**, distal denticles of the

2222 right lower canine of BP/1/4658 in labial view; **I**, fifth and sixth right upper gomphodont

2223 postcanines of SAM-PK-K171 ('*T. kannemeyeri*' morphotype) in apical view; **J**, tenth and

2224 eleventh left (reversed) upper gomphodont postcanines of BSP 1934 VIII 21 (*T. berryi*

2225 morphotype) in apical view; **K**, penultimate right upper gomphodont postcanine of SAM-PK-

2226 K4801 ('*T. kannemeyeri*' morphotype) in apical view; **M**, penultimate left upper gomphodont

2227 postcanine of NHMUK PV R3307 ('*T. kannemeyeri*' morphotype) in apical view; **N**, tenth left

2228 upper gomphodont postcanine of BSP 1934 VIII 21 (*T. berryi* morphotype) in apical view; **O**,

2229 partially erupted twelfth (and last) upper gomphodont postcanine of BSP 1934 VIII 21 in distal

2230 view. **Abbreviations**: **cc**, central cusp; **dac**, distal accessory cusp; **db**, distal basin; **dcc**, distal

2231 cingular cuspule; **dci**, distal cingulum; **ent**, enamel surface texture; **lac**, labial cusp; **ladc**,

2232 labiodistal accessory cusp; **lamc**, labiomesial accessory cusp; **lic**, lingual cusp; **lidc**, linguodistal

2233 accessory cusp; **limc**, linguomesial accessory cusp; **lri**, longitudinal ridge; **mb**, mesial basin; **mc**,

2234 main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **tc**, transverse crest; **tun**,

2235 transverse undulation.

2236

Figure 10. 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 basolingually 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 apicomesial 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; **dmc**, distal main cusp; **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; **mmc**, mesial main cusp.

Figure 11. 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-sectional 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.

2267   Figure 12. Comparison of skull length (i.e., distance measured from the anteriormost point of the

2268   snout to the posteriormost point of the occipital condyles) and widest upper gomphodont

2269   postcanine labiolingual width in gomphodont cynodonts, with linear regression trendlines for

2270   gomphodont taxa (in black) and *Diademodon* (in yellow). *Diademodon* I, II and III refer to

2271   specimens BSP 1934 VIII 14, MB R1004 and BSP 1934 VIII 19, respectively, *Andescynodon* I

2272   and II to specimens PVL 3836 and PVL 3894-1, *Pascualgnathus* I and II to specimens PVL

2273   4416 and MLP 65-VI-18-1, and *Massetognathus* I, II, III and IV to specimens BP/1/4245, PVL

2274   4729, PVL 4727 and PVL 4613, respectively. **Abbreviations**: **CBW**, crown base width.

Figure 1

Phylogeny and geographic and stratigraphic distribution of cynodont clades.

A, Tree topology based on the results of the cladistic analyses of Liu & Abdala (2014) for cynognathians and Martínez, Fernandez & Alcober (2013) and Martinelli, Soares & Schwanke (2016) for probainognathians. *Titanogomphodon*, considered to be a close relative of *Diademodon* by Keyser (1973) and Martinelli, de la Fuente & Abdala (2009) , is placed among Diademodontidae. Node 1, Eucynodontia; Node 2, Probainognathia; Node 3, Cynognathia; Node 4, Gomphodontia; Node 5, Diademodontidae; and Node 6, Trirachodontidae. Arrows indicate that the clades extend beyond the Lower Jurassic. **B**, Stratigraphic distribution of Diademodontidae (in yellow) and Trirachodontidae (in blue-purple), with *Diademodon* in pale yellow, *Titanogomphodon* in dark yellow, *Langbergia* in pale blue, *Cricodon* in blue sky, *Trirachodon* in dark blue, *Sinognathus* in light purple and *Beishanodon* in dark purple. Stratigraphic extension of geological units based on Liu et al. (2018) for the Ermaying Formation, Gao et al. (2010) and Niu et al. (2018) for the Hongyanjing Formation, Rubidge et al. (2005) for the *Cynognathus* Assemblage Zone, Wynd et al. (2018) for the Manda Beds and the Upper Omingonde, Ntawere and Fremouw formations, and Ottone et al. (2014) for the Río Seco de la Quebrada Formation. Stars denote the U-PB geochronologic ages of 243.53 Ma from Liu et al. (2018) for the upper Ermaying Formation in China, and 235.82 Ma from Ottone et al. (2014) for the Rio Seco de la Quebrada Formation in Argentina. Wavy lines indicate unconformities and diagonal lines formational interfingering, whereas dashed lines, indicates an unclear relationship to the geologic time scale. Age of the Triassic stage limits based on Cohen et al. (2018) . **Abbreviations**: **CAZ**, *Cynognathus* Assemblage Zone; **E**, Early Triassic; **Fm**, Formation; **M**, Middle Triassic; **Ma**, million years; **Pr.**, Province. Ottone et al.'s (2014) hypothesis refers to the Carnian dating for levels of the Río Seco de la Quebrada Formation. Black silhouettes credit: Sergey Meleshin (*Sinognathus*), José Eduardo Camargo Martínez (all

others), used with permission.

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-PK-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); **cev**, central valley; **ci**, cingulum; **cic**, cingular cuspules; **clar**, centrolabial ridge; **clir**, centrolingual ridge; **co**, crown; **cos**, concave surface; **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; **dmc**, distal main cusp; **dri**, distal ridge; **dv**, distal valley; **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; **lav**, labial valley; **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; **liv**, lingual valley; **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); **mmc**, mesial main cusp; **mri**, mesial ridge; **mv**, mesial valley; **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.

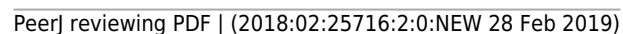



Figure 3

Figure 3. Dentition of non-traversodontid Gomphodontia.

A, Upper gomphodont postcanine (SAM-PK-571a); and **B**, cranial dentition (mainly based on
BSP 1934 VIII 14) of *Diademodon tetragonus* in apical and palatal views, respectively; **C**, last
right upper gomphodont postcanine; and **D**, cranial dentition of *Titanogomphodon crassus*
(GSN R322) in apical and palatal views, respectively; **E**, upper gomphodont postcanine
(reconstruction based on the fourth and third left upper gomphodont teeth of NMQR 3251
and 3255, respectively); and **F**, cranial dentition (NMQR 3255) of *Langbergia modisei* in
apical and palatal views, respectively; **G**, last right upper gomphodont postcanine (UMCZ
T905); and **H**, cranial dentition (reconstruction based on BP/1/6102 and UMCZ T905 for the
anterior and posterior portions of the cranium, respectively, and NHCC LB28 for the anterior
postcanine dentition) of *Cricodon metabolus* in apical and palatal views, respectively (the
dashed-line represents the lateral margin of the cranium of NHCC LB28); **I-J**, antepenultimate
right upper gomphodont postcanines (NHM PV R3307, *Trirachodon 'kannemeyeri'*
morphotype, and BSP 1934 VIII 21, *Trirachodon berryi* morphotype, for **I** and **J**, respectively);
and **K**, cranial dentition (BP/1/4658) of *Trirachodon berryi* in apical and palatal views,
respectively; **L**, fourth right upper gomphodont postcanine; and **M**, cranial dentition of
Beishanodon youngi (PKUP V3007) in apical and palatal views, respectively; **N**, lower
gomphodont postcanine (left anterior tooth of SAM-PK-571b); and **O**, mandibular dentition
(reconstruction based on MBR 1004 for the mandible, incisor and canine morphology, SAM-
PK-571b and AM 3753 for the anterior postcanine dentition, and SAM-PK-K177 for the
posterior postcanine dentition) of *Diademodon tetragonus* in apical and dorsal views,
respectively; **P-S**, upper sectorial postcanines of **P**, *Diademodon tetragonus* (MB R1004); **Q**,
Langbergia modisei (NMQR 3251); **R**, *Trirachodon berryi* (SAM-PK-4801); and **S**, *Cricodon
metabolus* (UMCZ T905) in labial view; **T**, lower gomphodont postcanine (third right tooth of

NMQR 5251); and **U**, mandibular dentition (NMQR 3251) of *Langbergia modisei* in apical and dorsal views, respectively; **V**, lower gomphodont postcanine (last right tooth of UMCZ T905); and **W**, mandibular dentition (based on SAM-PK-5881a and UMCZ T905 for the anterior and posterior dentitions, respectively) of *Cricodon metabolus* in apical and dorsal views, respectively; **X**, lower gomphodont postcanine (antepenultimate right gomphodont tooth of SAM-PK-K4801); and **Y**, mandibular dentition (BP/1/4658) of *Trirachodon berryi* in apical and dorsal views, respectively; **Z**, lower gomphodont postcanine (sixth and antepenultimate right gomphodont tooth of SAM-PK-K171); and **ɑ**, mandibular dentition (SAM-PK-K171) of *Trirachodon berryi* (*T*. 'kannemeyeri' morphotype) in apical and dorsal views, respectively.

Abbreviations: **c**, canine (in orange); **cpc**, conical postcanine (in yellow); **dac**, distal accessory cusp; **dar**, distal accessory ridge; **dcc**, distal cingular cuspule; **gpc**, gomphodont postcanine (in violet); **i**, incisor (in blue); **licc**, lingual cingular cuspule; **lici**, lingual cingulum; **mar**, mesial accessory ridge; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mmc**, mesial main cusp; **pcf**, postcanine fossa; **spc**, sectorial postcanine (in green); **tpc**, transitional postcanine (in red).

A mar
dar
cpc

C mar

Labial cusp
Central cusp
Lingual cusp

E mcc
i
c

G dcc
pcf
spc

I

J

L

B gpc
tpc

D tpc

F spc

H spc

K

M

N mar
dar

P dmc
dac
mc

Q dmc
dac
mc
mmc
mc

T

V mcc
dcc

X

Z

O mmc
licc
tpc
lici

R dac

S dmc
mmc
mc

U

W

Y

α

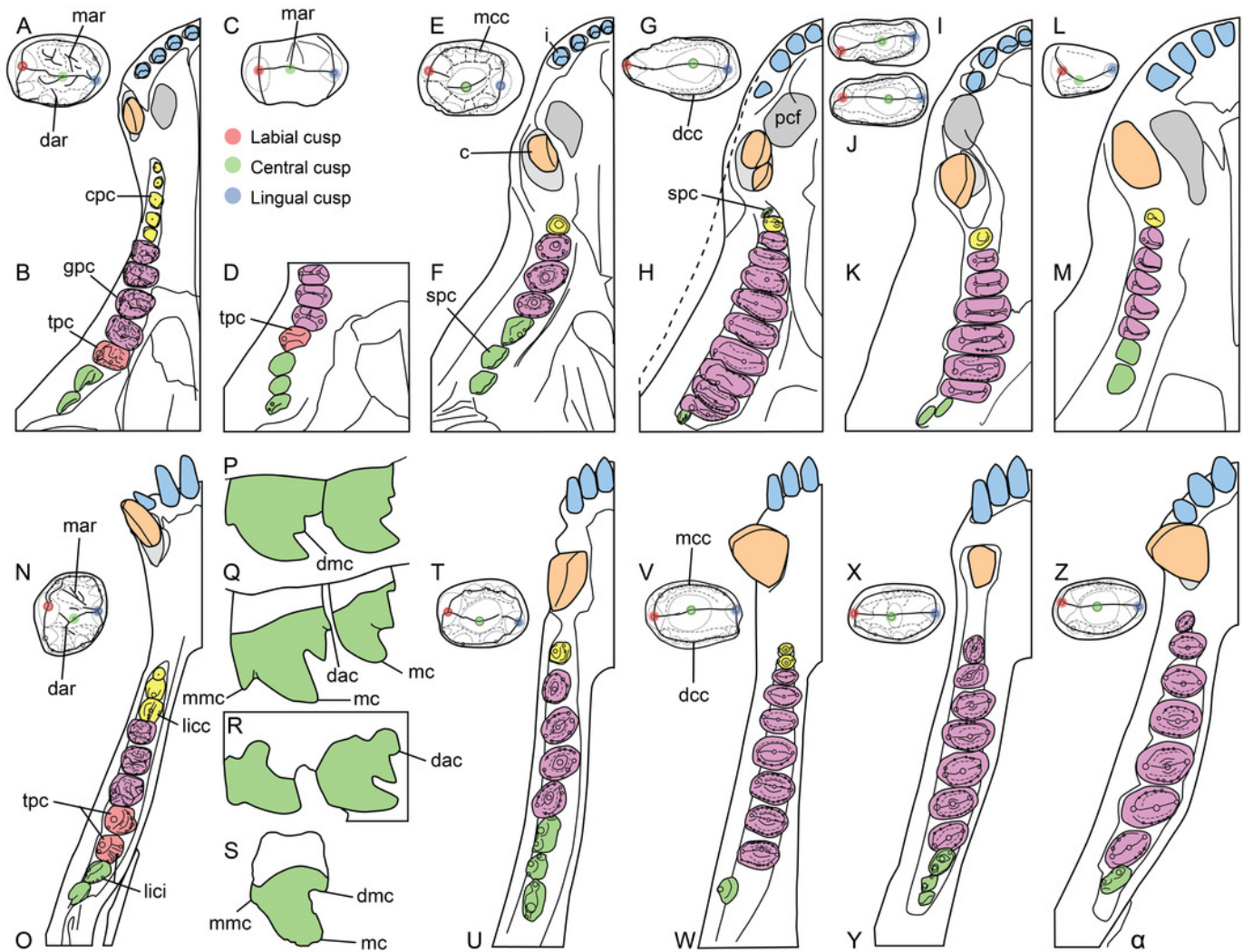



Figure 4

Dentition of *Diademodon tetragonus*.

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 MB 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.

Diademodon tetragonus

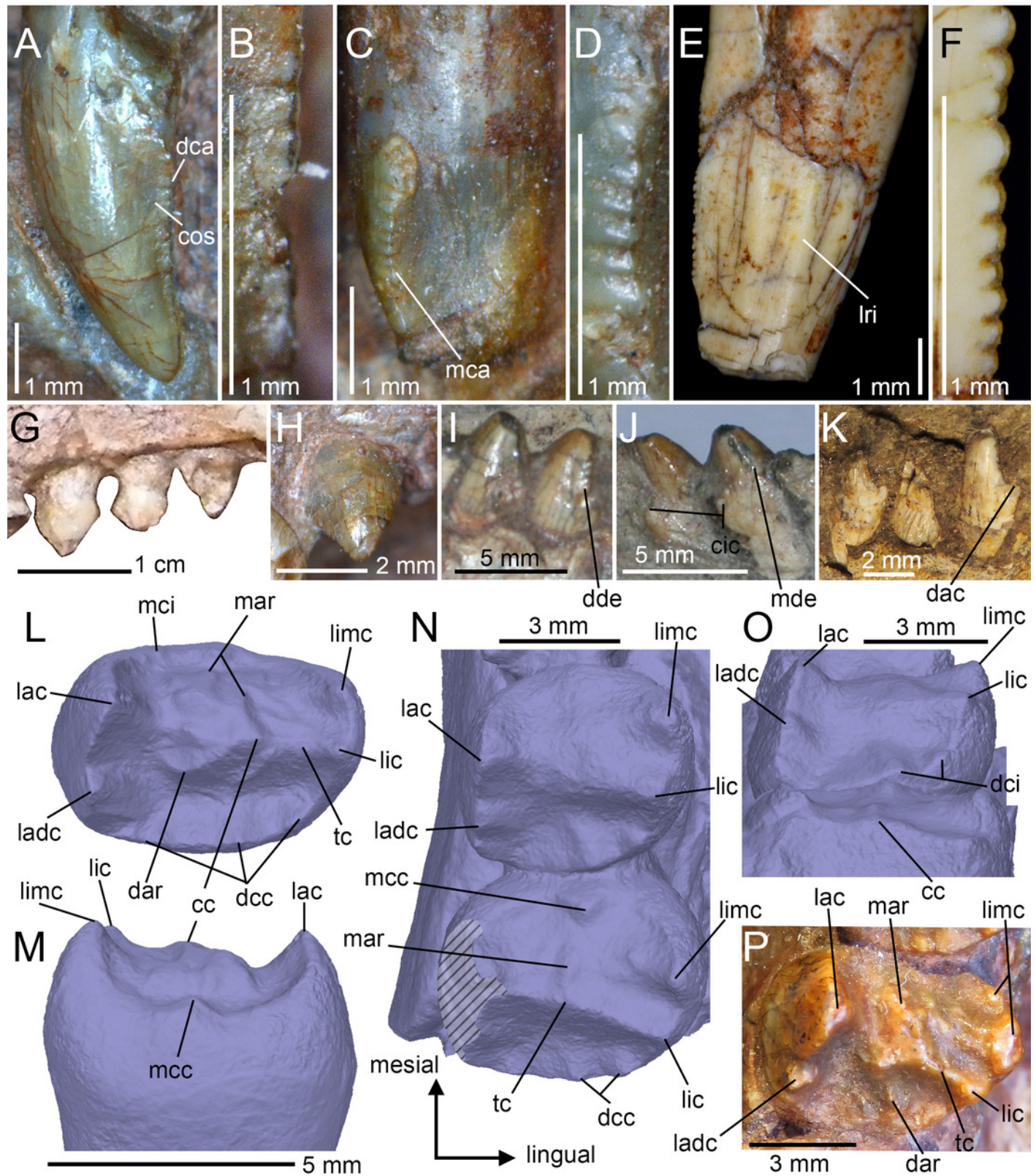



Figure 5

Dentition of *Diademodon tetragonus*

A-C, **E**, Lower gomphodont postcanine from the posterior portion of the mandible of SAM-PK-571b in **A**, apical, **B**, labial, **C**, distal views, and **E**, close up on the labial cusp of the distal postcanine,; **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**, Transitional, first and second left upper sectorial postcanines of MB R1004 in labial view (photo credit: Christian Kammerer); **I-K**, Second right upper sectorial postcanine of BP/1/4529, with close up on **J**, showing the first distal accessory cusp, and **K**, the 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; **dmc**, distal main cusp; **lac**, labial cusp; **ladc**, labiodistal accessory cusp; **lic**, lingual cusp; **licc**, lingual cingular cuspule; **limc**, linguomesial accessory cusp; **lir**, lingual ridge; **mar**, mesial accessory ridge; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **mmc**, mesial main cusp; **tc**, transverse crest.

Diademodon tetragonus

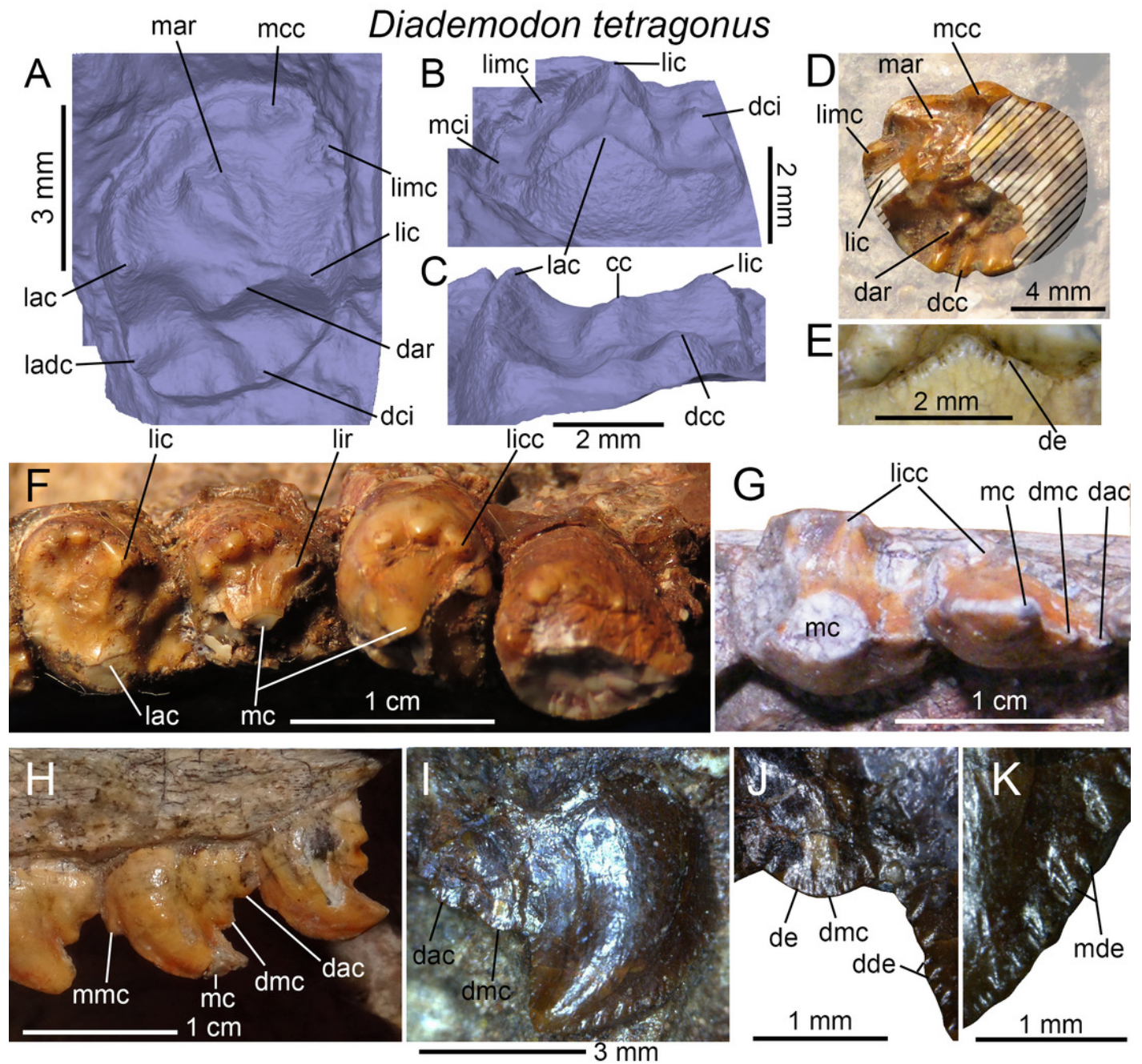



Figure 6

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

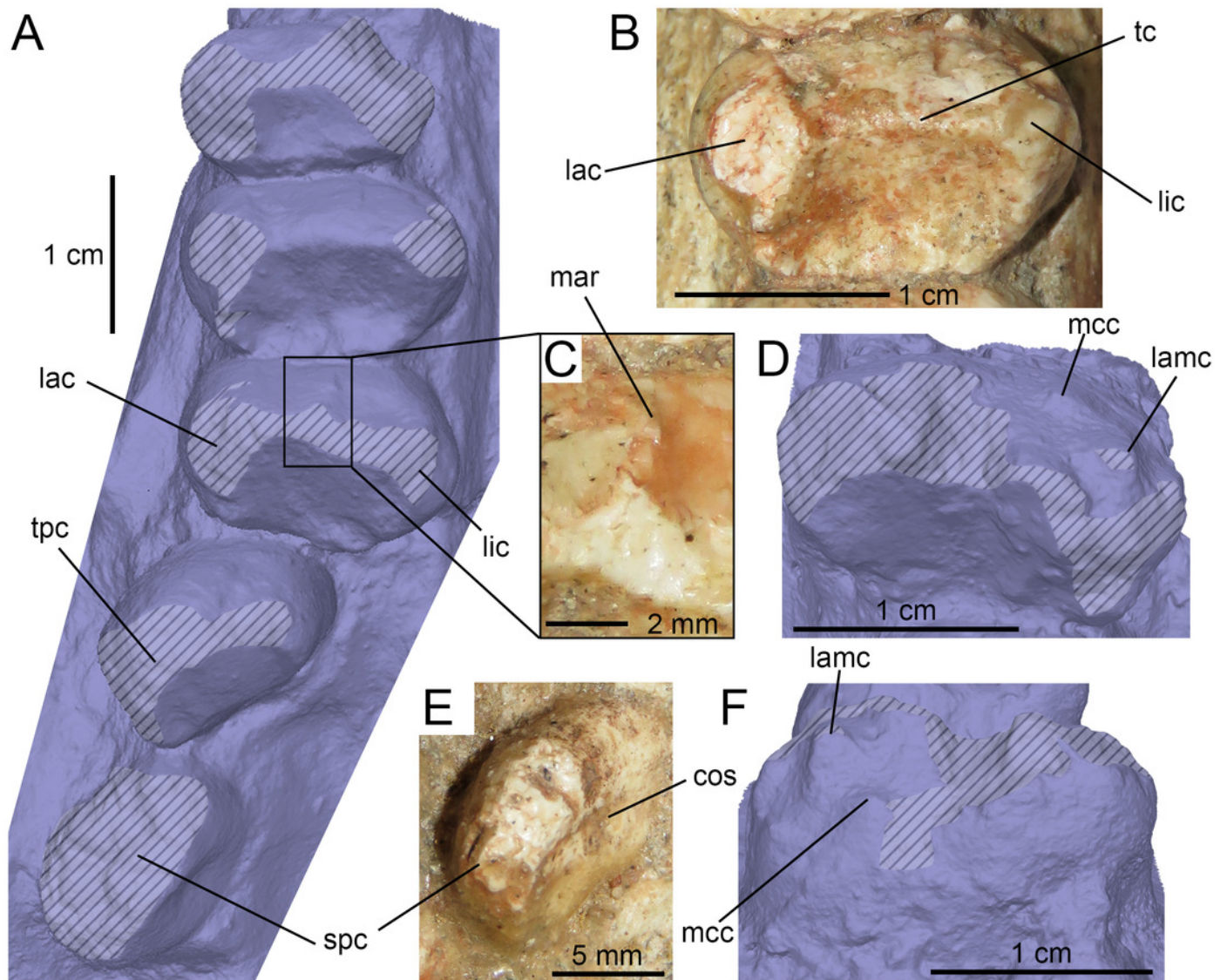



Figure 7

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-sectional outline of the right upper canine of SAM-PK-11481 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**, centromesial 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; **K**, third left upper postcanine of NMQR 3255 in apical view; **L**, close up on the fourth left upper postcanine of NMQR 3251 in mesial view (crown upside down); **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; **dmc**, distal main cusp; **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; **mmc**, mesial main cusp; **tc**, transverse crest. Elongation axes of the crown and the central cusp in green and red, respectively.

Langbergia modisei

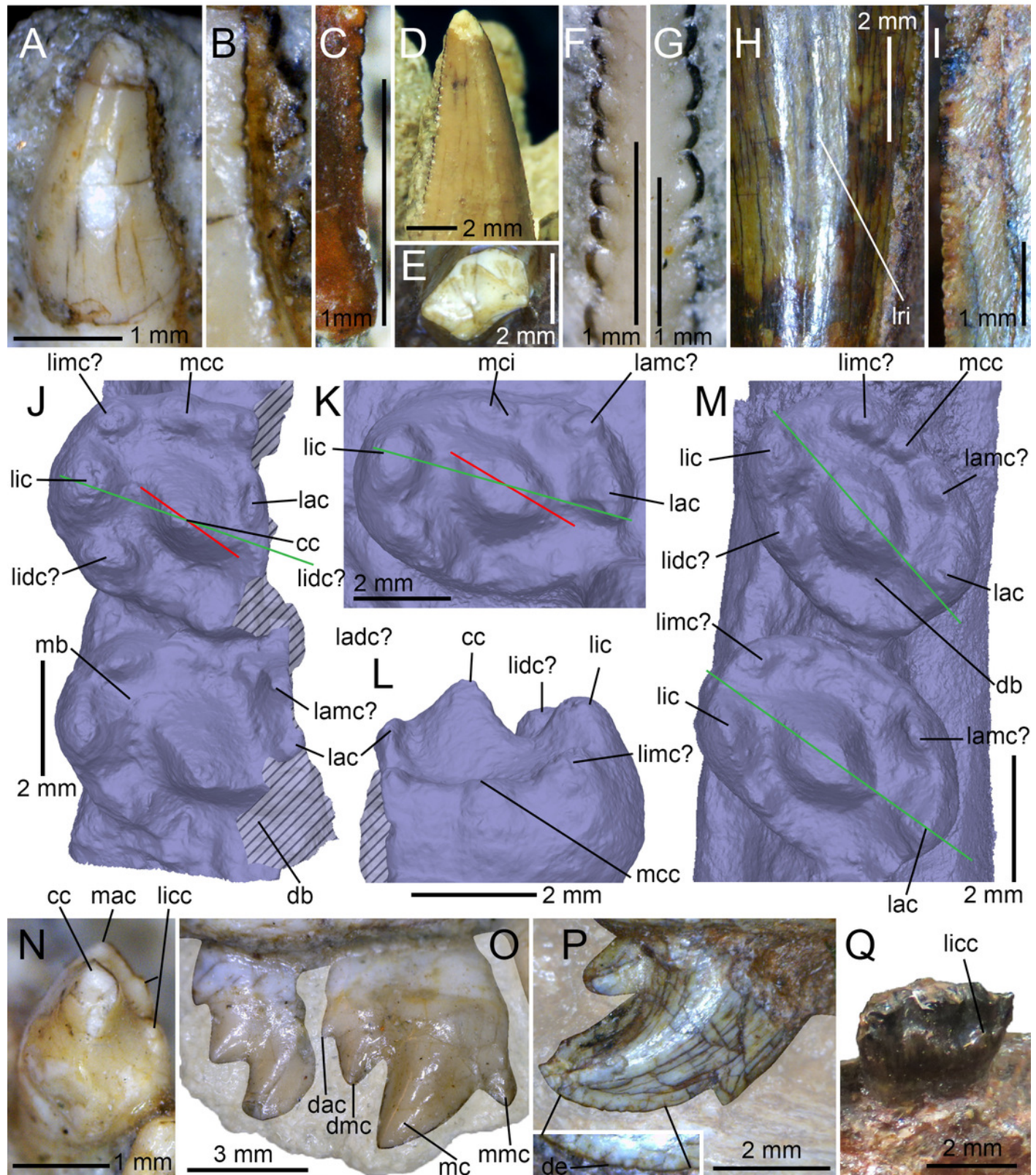



Figure 8

Dentition of *Cricodon formosus*

Dentition of *Cricodon metabolus*. **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-5881*a*, in **E**, lingual view; with **F**, cross-sectional outline at mid-crow apical view; **G**, centromesial and **H**, centrodistal denticles of the right upper canine 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-5881*a* in apical view; **M**, last right upper gomphodont postcanine of SAM-PK-5881*b* in distal view; **N**, last left upper gomphodont postcanine of UMCZ T905; **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; **dmc**, distal main cusp; **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; **mb**, mesial basin; **mc**, main cusp; **mcc**, mesial cingular cuspule; **mci**, mesial cingulum; **mde**, mesial denticle; **mmc**, mesial accessory cusp; **tc**, transverse crest; **tun**, transverse undulation. The red lines highlight the angular labiodistal margin of the lower postcanines.

Cricodon metabolus

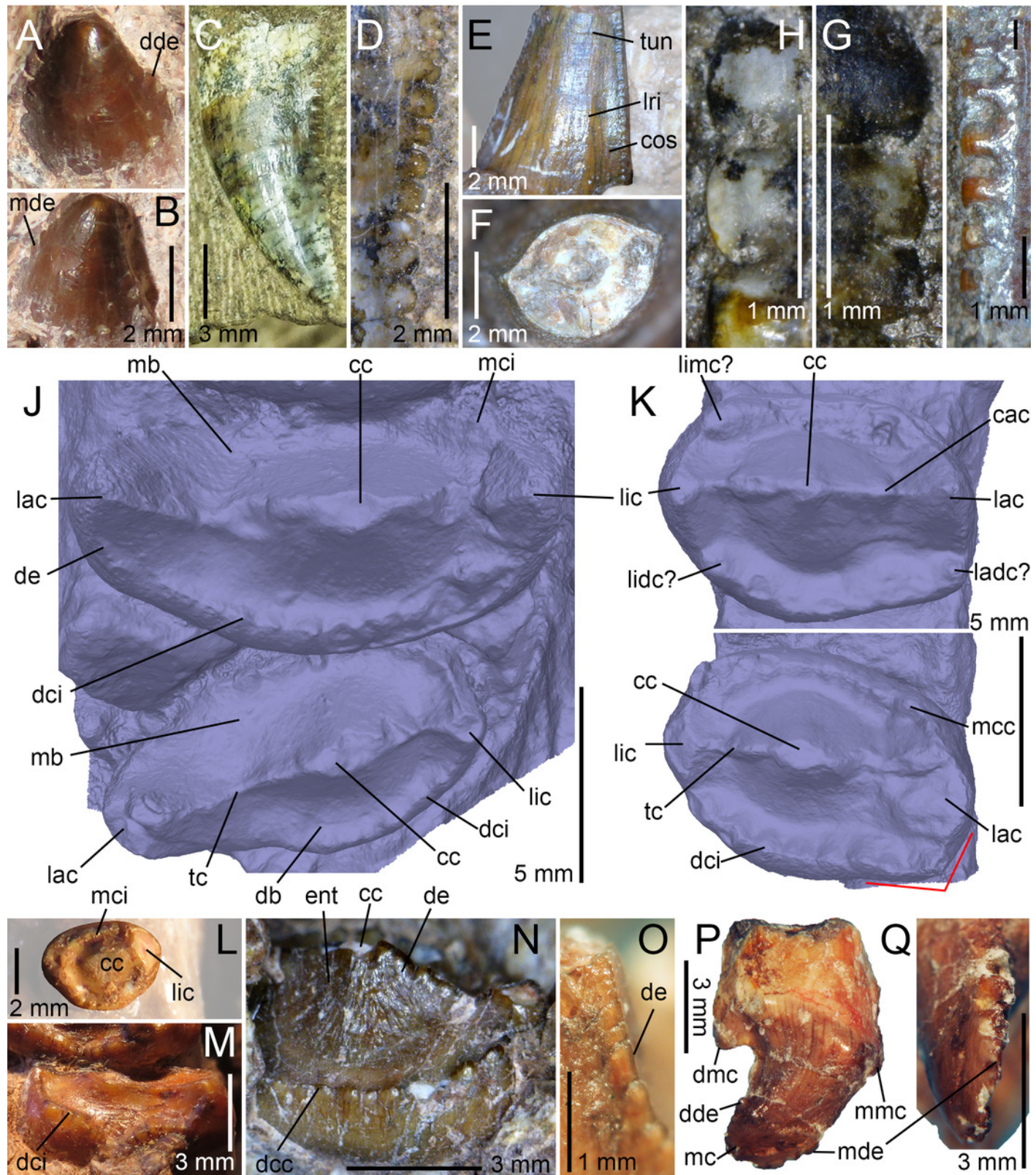



Figure 9

Dentition of *Trirachodon berryi*

A-C, First? left upper incisor, with close up on **B**, mesial and **C**, distal denticles of SAM-PK-12168 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 centrodistal 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

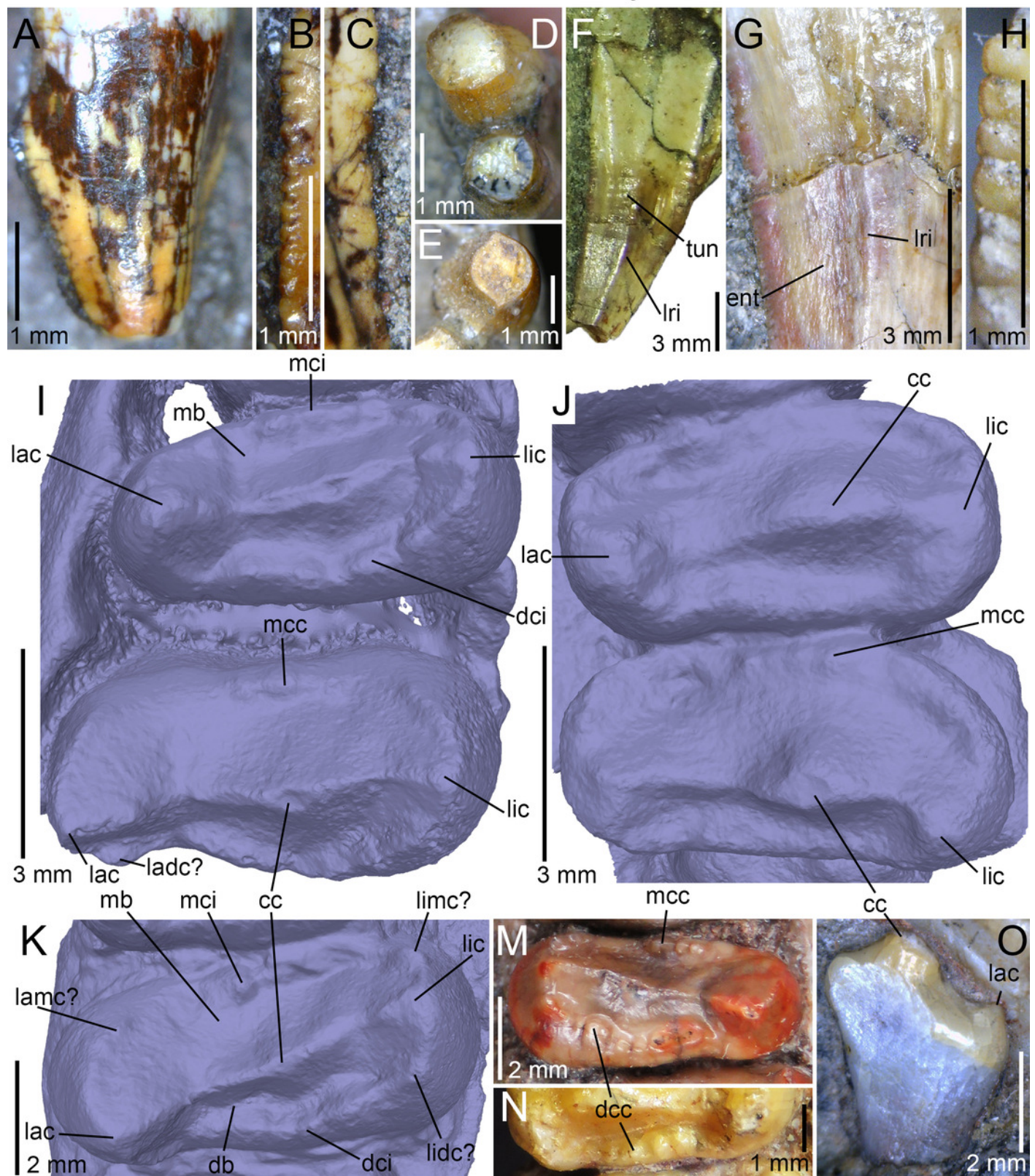



Figure 10

Dentition of *Trirachodon berryi*

A, fifth and sixth right lower gomphodont postcanines of SAM-PK-K171 in apical view; **B**, penultimate and **C**, ultimate (and basolingually 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 apicomesial 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; **dmc**, distal main cusp; **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; **mmc**, mesial main cusp.

Trirachodon berryi

Figure 11

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-sectional 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

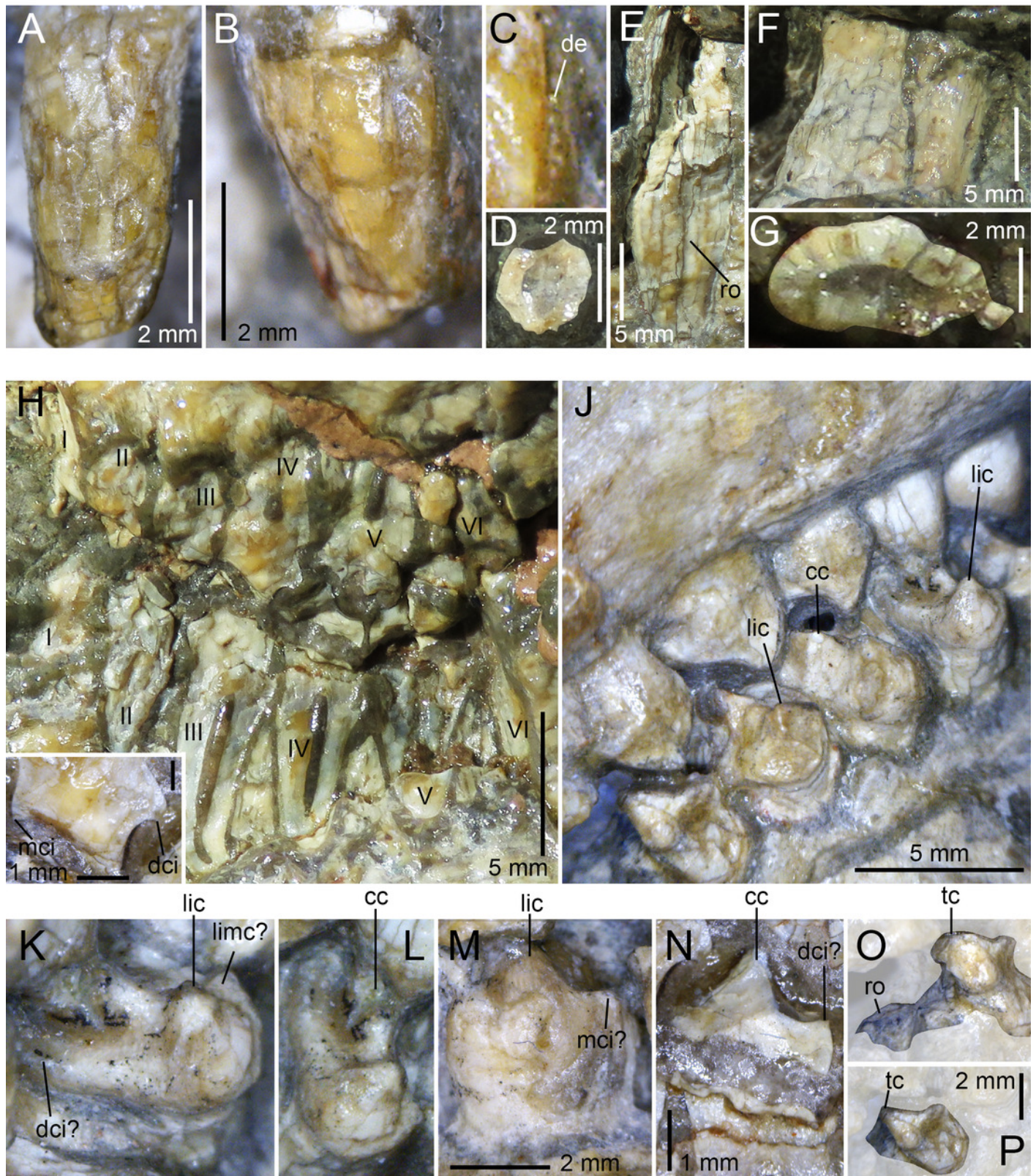
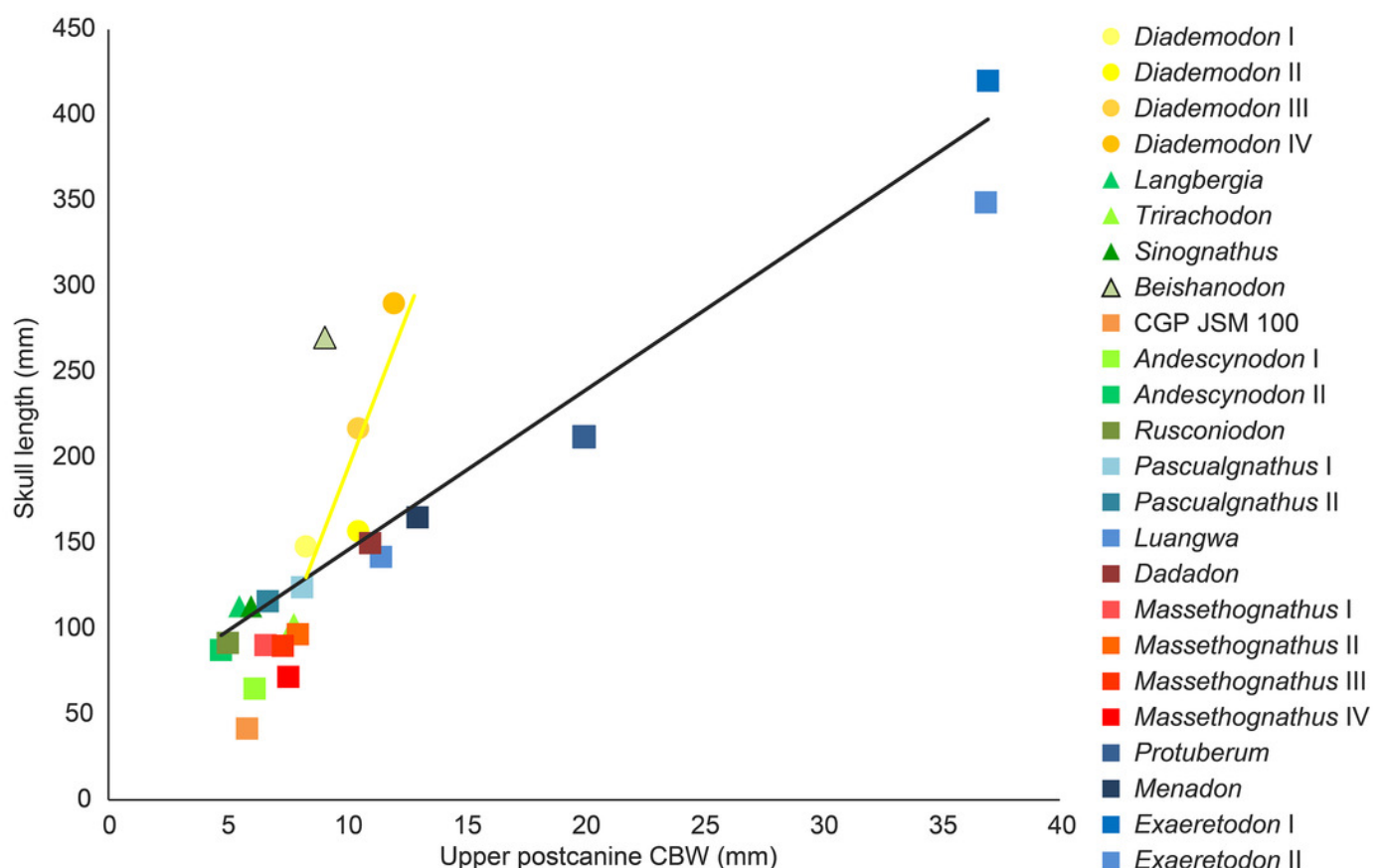



Figure 12

Comparison of skull length and widest upper gomphodont postcanine labiolingual 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, *Andescynodon* I and II to specimens PVL 3836 and PVL 3894-1, *Pascualgnathus* I and II to specimens PVL 4416 and MLP 65-VI-18-1, and *Massetognathus* I, II, III and IV to specimens BP/1/4245, PVL 4729, PVL 4727 and PVL 4613, respectively. **Abbreviations**: **CBW**, crown base width.

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

Specimens with the best-preserved dentition are underlined, and holotypic specimens are in bold.

1   Table

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

3   Specimens with the best-preserved dentition are underlined, and holotypic specimens are in bold.

Taxa	Specimens
Diademodon tetragonus	**SAM-PK-571**, 4002, 5877, 6216, 6218, 6219, 11265, K175, K177, K180, K183, ?K4660, ?K4661, K5223, K5266, K8971, K9968, K9969; AM 458, 3753; BP/1/2522, 3639, 3756, 4529, 4669, 4677; BSP 1934 VIII 14, 15, 16, 19, 20, 505; MB R1004; NHMUK PV R3303, R3588, R3765; GSN R321, RK3
Titanogomphodon crassus	**GSN R323**
Langbergia modisei	**NMQR 3255**, 3251, 3256, 3268, 3280, 3281; BP/1/5362, 5363; SAM-PK-11481
Cricodon metabolus	**UMZC T905**; BP/1/5540, 5835, 6102, 6159; NHMUK PV R3722, K36800; SAM-PK-6212, K5881*a, b*
Trirachodon berryi	**NHMUK PV R3579**, R2807, R3306, R3307, R3350, R3721; AM 434, 461; BP/1/4258, 4658, 4661; BSP 1934 VIII 21, 22, 23; CGP INN 2000-7-2A, CGP unnumbered; NMQR 1399; SAM-PK-987, 5880, K142, K170, K171, K4801, K4803, K5821 (=12168?), K7888, K10157, K10161, K10176, K10207, K10411
Sinognathus gracilis	**IVPP V2339**