

美国北卡罗来纳州上三叠统北方阔齿兽 (犬齿兽类:横齿兽科)的齿系和牙齿替换¹⁾

刘俊¹ Hans-Dieter SUES²

(1 中国科学院古脊椎动物与古人类研究所,脊椎动物进化系统学重点实验室 北京 100044)

(2 美国史密森学会国立自然历史博物馆古生物部 华盛顿特区 20013–7012)

摘要:描述了产自美国北卡罗来纳州上三叠统横齿兽类北方阔齿兽新材料的牙齿。基于牙齿的特征,尤其是犬后齿的形态,这些标本被暂归入杰斐逊北方阔齿兽 *Boreogomphodon jeffersoni*; 不过它们的下阔齿型犬后齿前横脊一般有两个而不是3个齿尖。根据牙齿大小、直接替换情况,推测阔齿型齿从后部萌发,从前部脱落。这个类群仅有一代阔齿型犬后齿;至少有一代,可能是两代裂齿型犬后齿。

关键词:美国北卡罗来纳州,上三叠统,横齿兽科,北方阔齿兽,齿系

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DENTITION AND TOOTH REPLACEMENT OF *BOREOGOMPHODON* (*CYNODONTIA*: *TRAVERSODONTIDAE*) FROM THE UPPER TRIASSIC OF NORTH CAROLINA, USA

LIU Jun¹ Hans-Dieter SUES²

(1 Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044, China liujun@ivpp.ac.cn)

(2 Department of Paleobiology, National Museum of Natural History, Smithsonian Institution Washington D. C. 20013–7012, USA)

Abstract The teeth of new specimens of the traversodontid cynodont *Boreogomphodon* from the Upper Triassic of North Carolina are described. Based on dental features, especially the postcanine morphology, the North Carolina specimens are tentatively referred to *Boreogomphodon jeffersoni*, although their lower gomphodont postcanines typically have two rather than three cusps on the anterior transverse ridge. Based on the tooth size, direct replacement on all available specimens, the gomphodont teeth were shed anteriorly and added posteriorly. Only one generation of gomphodont teeth, at least one and possibly two generations of sectorial postcanines were present.

Key words North Carolina, USA; Upper Triassic; Traversodontidae, *Boreogomphodon*; dentition

1 Introduction

Cynodonts are an important component of Triassic tetrapod faunas (Abdala and Ribeiro, 2010) and are frequently one of the dominant groups in abundance. At the end of the Olenekian

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(Subzone A of the *Cynognathus* Assemblage Zone) (Hancox et al., 1995), one particular clade, Gomphodontia, appeared in fossil record and developed complex dentitions with buccolingually expanded (gomphodont) postcanines (Crompton, 1972; Abdala et al., 2006).

One group of gomphodont cynodonts, Traversodontidae, are the most diverse family of Triassic cynodonts and formed a major element of tetrapod communities in Gondwana during the Middle and early Late Triassic (Rogers et al., 2001). By contrast, they are less common in the Northern Hemisphere (Sues and Hopson, 2010). In North America, three genera and species have been named and referred to Traversodontidae: *Arctotraversodon plemmyridon* (Hopson, 1984; Sues et al., 1992), *Boreogomphodon jeffersoni* (Sues and Olsen, 1990), and *Plinthogomphodon herpetairus* (Sues et al., 1999).

The first specimens referred to *Boreogomphodon jeffersoni* were collected from the Tomahawk Creek Member of the Vinita Formation (Upper Triassic; Carnian) in the Richmond Basin of the Newark Supergroup in Chesterfield County, Virginia. They were initially reported by Sues and Olsen (1990) and recently described in detail (Sues and Hopson, 2010).

The remains of *Plinthogomphodon herpetairus* were part of the gut content of a partial skeleton of a rauisuchian archosaur. They include a partial snout, a complete left coracoid, and a left humerus from the “Lithofacies Association II” (Upper Triassic; Norian) of the Deep River Basin of the Newark Supergroup in North Carolina (Sues et al., 1999; Sues and Hopson, 2010).

In recent years, a diverse and well-preserved tetrapod assemblage has been discovered in the Pekin Formation of Chatham County, North Carolina (Olsen et al., 2001; Sues et al., 2001). This assemblage is dominated by small traversodontid cynodonts. Although traversodontid fossils are abundant, they represent only a single taxon and can be referred to *Boreogomphodon*.

The dentition of traversodontids is rich in phylogenetic information, and our current knowledge of the phylogeny of this group is largely built on dental characters (Abdala and Ribeiro, 2003; Kammerer et al., 2008; Sues and Hopson, 2010). In this study, we will describe the dentition of the material from North Carolina and assess its phylogenetic relationships based on dental features.

In traversodontids, the pattern of tooth replacement has only been studied in detail in *Scalenodon angustifrons* (Crompton, 1955), *Andescynodon mendozensis* (Goñi, 1986; Goñi and Abdala, 1989), and *Boreogomphodon jeffersoni* (Sues and Hopson, 2010). The ontogenetic series is poorly known for most traversodontid taxa. The rich material from North Carolina now provides an additional growth series for studying tooth replacement in traversodontids.

Institutional Abbreviations: CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; NCSM, North Carolina Museum of Natural Sciences, Raleigh, North Carolina; UNC, Department of Geology, University of North Carolina, Chapel Hill, North Carolina; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC; VMNH, Virginia Museum of Natural History, Martinsville, Virginia.

2 Systematic paleontology

Cynodontia Owen, 1861

Eucynodontia Kemp, 1982

Traversodontidae Huene, 1936

***Boreogomphodon* Sues & Olsen, 1990**

***Boreogomphodon jeffersoni* Sues & Olsen, 1990**

(Figs. 1–11)

Material NCSM 11466, partial right dentary with (gomphodont) postcanines 1–3; NCSM 15295, partial snout with incisors and canines; NCSM 16292, partial skull with incisors, canines, and incomplete postcanines; NCSM 16297, partial skull with postcanines, and dentaries; NCSM 16358, left dentary with canines, gomphodont postcanines 1–3, and sectorial postcanine 4; NCSM 16364, isolated left lower postcanine tooth; NCSM 18300, partial skull with two incisors, right canine, right gomphodont postcanines 1–3 and sectorial postcanines 4–5, incomplete left postcanines 1–3, and dentaries with incisors, left canine, left postcanines 1–3, 5 and right postcanines 1–4; NCSM 19587, isolated right lower postcanine tooth; NCSM 20660, incomplete left dentary with canine and postcanines 1–2; NCSM 20662, partial left dentary with postcanines 2, 5; NCSM 20692, incomplete dentaries; NCSM 20698, nearly complete skull with partial postcranial skeleton; NCSM 20700, partial left dentary with sectorial postcanine; NCSM 20704, partial right dentary with gomphodont postcanines 1–3 and sectorial postcanine 4; NCSM 20712, anterior portion of skull with at least three left incisors, gomphodont postcanines 1–3, sectorial postcanines 4–5, incomplete left dentary with gomphodont postcanines 2–3, sectorial postcanines 4–5, and incomplete right dentary; NCSM 21370, nearly complete skull with almost complete dentition, and some postcranial elements; NCSM 21371, nearly complete skull with almost complete dentition.

Horizon Pekin Formation, Newark Supergroup; Upper Triassic (upper Carnian or lower Norian).

Locality Merry Oaks Quarry, Triangle Brick Company, Chatham County, North Carolina.

2.1 Description of dentition

We will first describe the general morphology of the postcanines and then discuss the variation seen in individual specimens.

As in *Boreogomphodon jeffersoni* from Virginia, the postcanines of the new specimens from North Carolina include both gomphodont and sectorial postcanines. The morphology of upper gomphodont postcanines is almost identical to that of specimens from Virginia whereas that of lower gomphodont teeth is slightly different. The sectorial postcanines also show minute differences among the specimens from the two samples.

The following description of the morphology of postcanine teeth is based mainly on NCSM 20712. The postcanines of this specimen are slightly worn and some additional features present in unworn postcanines of other specimens have been added.

Upper gomphodont teeth (Fig. 1) In crown view, the upper gomphodont tooth is nearly triangular because the anterior ridge is very short; its buccolingual width is greater than its anteroposterior (mesiodistal) length. The lingual ridge is slightly convex, the buccal one is nearly straight, and the distal one is concave. The concave area is the ‘shoulder’ for the slightly convex mesial margin of the posterior neighboring tooth. The buccal portion of the tooth forms a sharp ridge extending in an anterior and slightly lingual direction, on which a principal cusp, the buccal cusp, is the highest point on the crown; a minor cusp, the anterobuccal cusp, is only slightly separated from it on the anterior slope of the ridge. The two cusps are nearly confluent on worn tooth crowns. The buccal ridge has a nearly vertical lingual surface that forms the outer border of a deep basin. This basin occupies much of the crown, with its greatest depth close to the anterior border. The lingual border also forms a descending ridge, which is much weaker than the buccal ridge; its apex is the principal lingual cusp. The anterior ridge is short and low. Immediately lateral to the lingual cusp is a slightly lower central cusp, which forms a slightly anteriorly inclined, deeply V-shaped notch with the principal buccal cusp. The deepest point on the posterior ridge is nearly on the same horizontal plane as the anterior ridge. No cingulum is present on the anterior or posterior side of the tooth crown. There is no posterior accessory cusp.

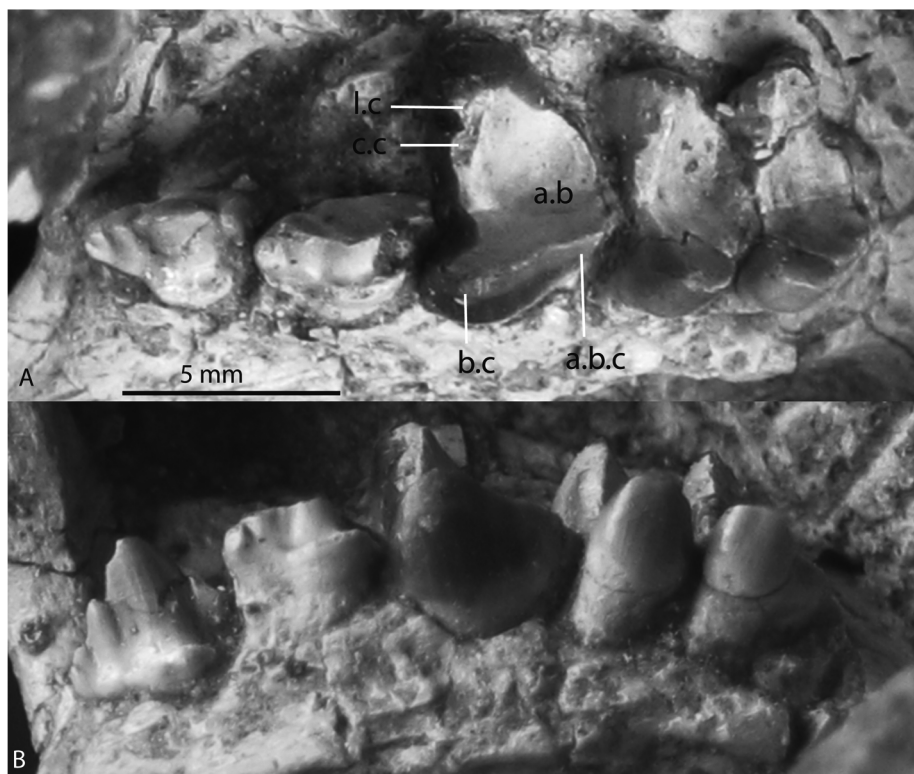


Fig. 1 Left upper postcanines of *Boreogomphodon jeffersoni*, NCSM 20712

A. occlusal view; B. labial view; anterior is right

Abbreviations: a. b. anterior basin; a. b. c. anterobuccal cusp; b. c. buccal cusp; c. c. central cusp; l. c. lingual cusp

In *Boreogomphodon jeffersoni* from Virginia, the upper gomphodont postcanines show some variation in the presence of a posterior cingulum and posterobuccal accessory cusp (Sues and Hopson, 2010).

Lower gomphodont teeth (Fig. 2) Although the upper gomphodont postcanines of the specimens from North Carolina are virtually identical to those of *Boreogomphodon jeffersoni* from Virginia, the lower postcanines show differences. In the Virginia specimens, the transverse wall is generally formed by three rather than two anterior cusps; however, only two cusps are present on some small teeth. In the North Carolina specimens, the transverse wall is almost always formed by two anterior cusps; three anterior cusps are only occasionally present (e. g., NCSM 19587) (Fig. 3).

The tooth crowns are subquadrangular in occlusal view; the buccal margin of the crown is longer anteroposteriorly (mesiodistally) than the lingual margin. The anterior portion forms a high transverse wall, partially divided into two cusps, of which the buccal one is slightly higher and wider. On postcanines with three anterior cusps, the buccal one also has the greatest height and transverse width; the central cusp is much lower than the lingual and buccal cusps, the cusps forming a concave transverse wall (Fig. 3). The posterior face of the anterior transverse wall descends steeply into the smoothly concave, shallow basin. The basin is surrounded by a continuous ridge on the buccal, mesial, and distal sides, but is open on the lingual side. The buccal ridge extends backwards, connecting the anterior and posterior buccal cusp. Its outer

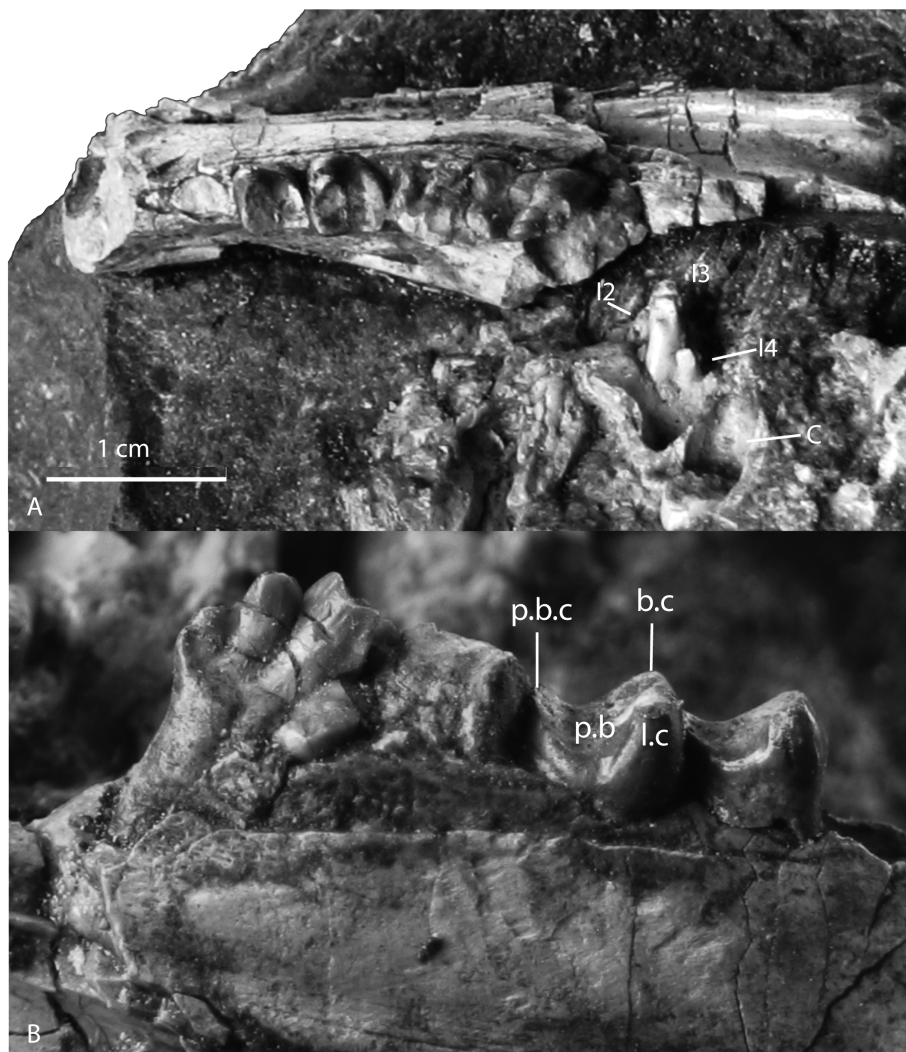


Fig. 2 *Boreogomphodon jeffersoni*, NCSM 20712

A. left upper incisors and canine, and lower postcanines in occlusal view; B. left lower postcanines in medial view
Abbreviations as in Fig. 1 plus C. canine; I. incisor; p. b. posterior basin; p. b. c. posterobuccal cusp

surface is more or less vertical. The buccal ridge is usually worn down to a slightly raised rim.

As on the larger gomphodont postcanines from Virginia, a short cingulum bearing a prominent buccal accessory cusp extends along the anterior face of the anterior wall of NCSM 19587, a relatively small tooth (Fig. 3B). Other lower gomphodont teeth show slight swellings in this region.

Upper sectorial teeth (Fig. 1) The crown is triangular in labial and lingual views. Three major cusps and some cuspules are aligned mesiodistally. The central cusp occupies more than one-third of the length of the crown and is the tallest of the three cusps. The other two cusps lie mesial and distal to the central cusp, and two cuspules are situated distal to the posterior cusp. Some vertical striations are visible on the buccal surface of the cusps. The lingual surface is slightly convex whereas a cingulum is present on the buccal surface below the cusps. Most cusps are obliterated by wear, with only the bases remaining.

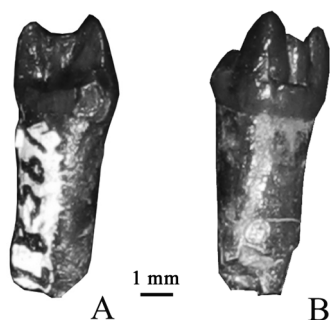


Fig.3 Right lower postcanine of *Bo-reogomphodon jeffersoni*, NCSM 19587
A. posterior view;
B. anterolingual view

Lower sectorial teeth (Fig.2) Similar to the upper sectorial teeth, the lower sectorials each have three principal cusps and at least two posterior cusps. On small teeth, the relative size of cusps differs from that on larger teeth; a cuspsule can be similar in size to the smallest principal cusp. The anterior cusp is located at approximately a right angle to the two more posterior cusps in crown view. The lingual surface of the crown is concave and its buccal surface is convex. There is no cingulum on either the buccal or lingual side of the crown. Wear on the lower sectorials is confined to the buccal side.

2.2 Dentition of individual specimens

Specimen NCSM 20712 (Figs. 1, 2) This specimen consists of anterior portion of the skull that was split into dorsal and palatal portions, much of the left dentary, and small part of the right dentary. The upper dentition is nearly completely preserved, but only the left tooth row is fully exposed; the lower dentition is only represented by the posterior four postcanines. The height of the dentary below the first postcanine is about 15 mm.

Three incisors are exposed on the left premaxilla. The middle one is the largest. The distal incisor is much smaller than the other two; its crown has been worn and has an oblique wear facet. The canine is much larger than the incisors, with a buccolingual diameter of 4 mm and a mesiodistal diameter of 5 mm. No serrations are developed on the cutting edges. The diastema between the canine and first postcanine is 4.3 mm long. The anterior three upper postcanines are gomphodont and the posterior two are sectorial. On the gomphodont postcanines, the posterolingual corner is clearly worn; only on the third postcanine the two cusps in this position still can be recognized. On the first sectorial postcanine, the lingual side of the crown is worn into a smooth plane, whereas the second postcanine is only slightly worn, indicating that it had only been erupted for a short time.

The lower postcanine tooth row comprises three gomphodont and two sectorial teeth. The first postcanine is not preserved, and the cusps on the fourth are missing. A distinct wear facet is present on the buccal side of the second postcanine.

Specimen NCSM 15295 This specimen preserves the anterior part of a snout with some incisors and canines. The canine is 4.8 mm in mesiodistal diameter. The diastema between the canine and the first postcanine is 4.1 mm long. The first postcanine alveolus is about 5.6 mm wide but only 3.7 mm long.

Specimen NCSM 21371 (Fig.4) This specimen is a nearly complete skull with occluding mandible. The skull is 50 mm long; the height of the dentary below the first postcanine is 10 mm. The incisors and canines of the dentary and the postcanine teeth of the maxilla are exposed from the buccal side, and the postcanines of the dentary are exposed in lingual view.

There are three lower incisors on each side. Their crowns have smooth cutting edges. On the left side, the first and second incisors are similar in size, and the third is slightly smaller; on right side, the second incisor is smaller than the first, and the third appears to have recently erupted. The second left incisor is broken; a small tooth similar in size to the third right incisor is erupting under the crown of a functional tooth. It shows that the replacement incisor absorbed the root of its predecessor, and the functional tooth remained unaffected for some time after the replacement tooth started erupting. The enamel surface of incisor crowns is smooth with vertical ridges, and their cutting edges lack serrations or denticles. The canines have a mesiodistal diameter of 2.6 mm, compared to 1.6 mm for the largest incisor.

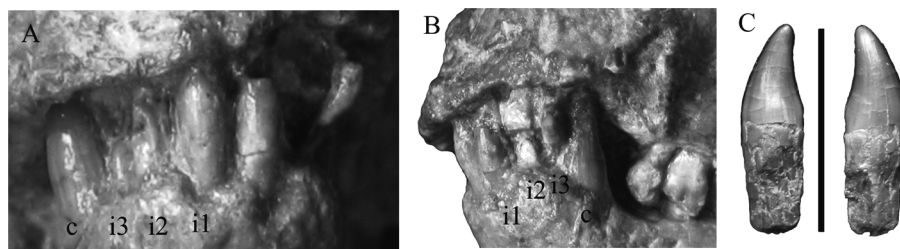


Fig. 4 *Boreogomphodon jeffersoni*, NCSM 21371

A, B. lower incisors and canine in labial view; C. isolated upper canine; scale bar equals 1 cm

Four upper postcanines are exposed on right side and five on left side. On both rows the last element is sectorial and the remaining gomphodonts. Two buccal cusps are clearly separated by a shallow notch on the buccal surface.

Specimen NCSM 21370 (Fig. 5) This specimen consists of a nearly complete skull with mandible and partial postcranial skeleton. The skull is approximately 60 mm long. The height of the dentary is 14 mm below the first postcanine.



Fig. 5 Left upper postcanines of *Boreogomphodon jeffersoni*, NCSM 21370, in labial view

The number of upper incisors is uncertain because the anterior end of the premaxilla is not preserved. The canines are moderately developed. The canine-postcanine diastema is 5 mm long on each side. Four upper postcanines are exposed on both sides, including three gomphodonts and one sectorial. The shallow notch on the buccal side disappears on the first postcanine but is present on the more posterior postcanines. The postcanine tooth measures approximately 4.3 mm in mesiodistal length for the first through the third. The dentary bears three incisors, of which the first is the largest and the third is the smallest.

Specimen NCSM 20698 This specimen has a complete skull with mandible in occlusion. The skull is approximately 60 mm long. Only the upper incisors, the left upper canine, and part of left postcanine tooth row are exposed. Four left and three right incisors are visible. The third one is the largest, with a crown height of 4.5 mm on the left side; the others are tiny, with crown heights of less than 2 mm. A 3-mm-long diastema is present between the fourth incisor and the canine. The enamel surfaces of canines and incisors bear vertical striations.

Specimen NCSM 18300 (Fig. 6) This specimen includes a partial skull with associated dentaries. The right upper dentition is almost complete, while both sets of lower postcanines are almost completely preserved. The height of the dentary below the first postcanine is approximately 12 mm.

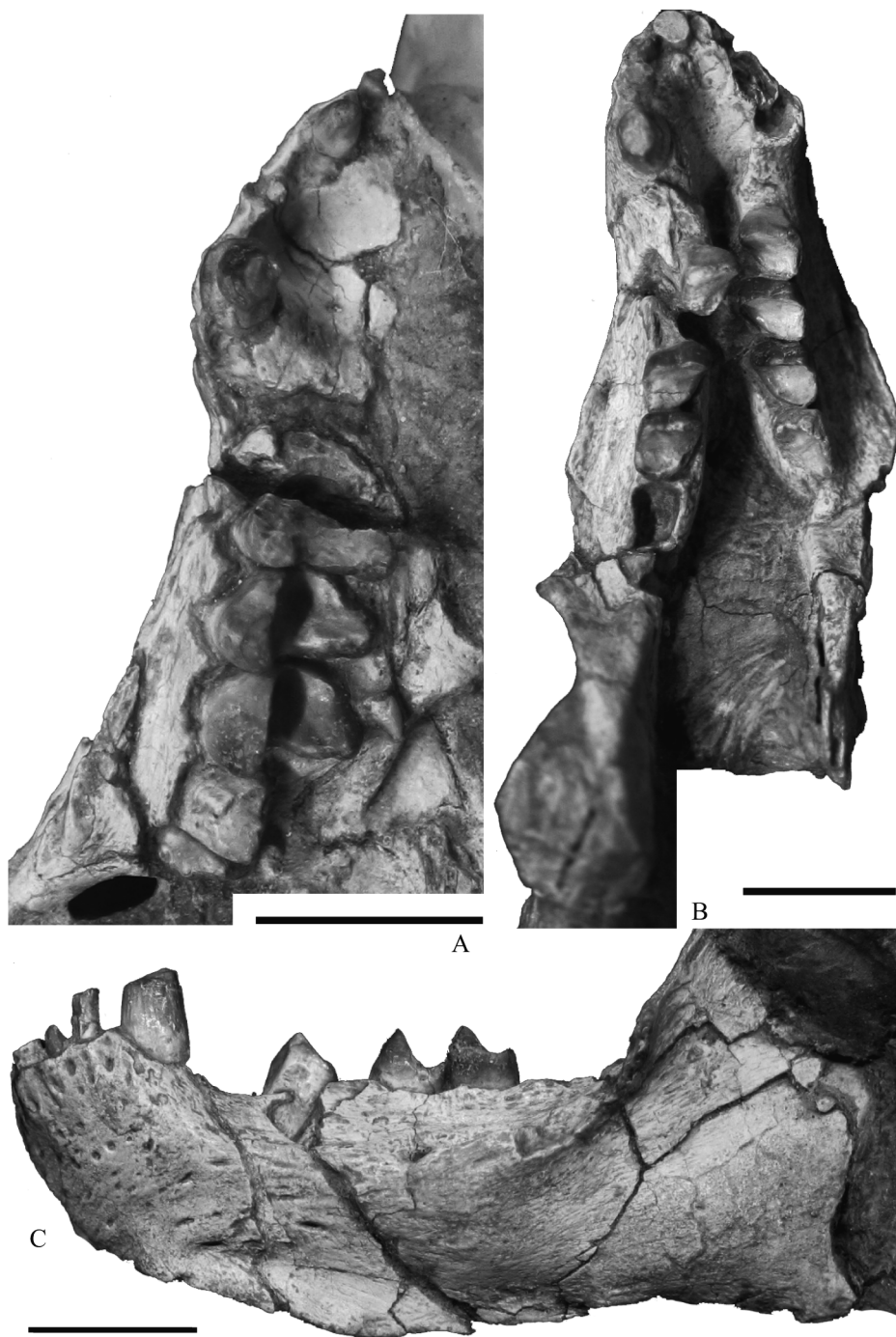


Fig. 6 *Boreogomphodon jeffersoni*, NCSM 18300

A. right upper postcanines in occlusal view; B. lower jaw in occlusal view; C. left lower dentary in lateral view; scale bars equal 1 cm

Two incisors are preserved in the right premaxilla. The canine is 3 mm in buccolingual diameter and 4 mm in mesiodistal diameter; it is separated from the postcanines by a 4-mm-long

diastema. The three gomphodont postcanines increase in size posteriorly while the degree of tooth wear decreases. The cusps of the first sectorial postcanine are almost worn down. The last postcanine (second sectorial tooth) is confined to a small space between the preceding tooth and subtemporal fossa, and is newly erupted. Its cusps are nearly aligned in a transverse direction, so it would have subsequently rotated to a mesiodistal direction.

Three left lower incisors are preserved, although their crowns are for the most part missing. The first one is slightly larger than the third one, whereas the second one is a newly erupted with an almost complete crown. No distinct diastema separates the incisors from the canine on the dentary, but the diastema between the canine and postcanines is longer (5 mm) than the mesiodistal diameter of the canine (4 mm). Four gomphodont postcanines and one empty alveolus are preserved on the left dentary, whereas there are only four gomphodont postcanines on the right dentary. No sectorial tooth is present in the mandible. The last postcanine on the left side is about half size of the anterior teeth.

Specimen NCSM 16297 (Fig. 7) This specimen consists of a partial skull with dentaries. Five right and three left upper postcanine teeth are exposed. These teeth are approximately 10 mm in total height, in which the root is at least double the height of the crown. The third postcanine is nearly vertical, while the anterior teeth are inclined forwards and the posterior teeth are inclined backwards. The roots are closely spaced.

Specimen NCSM 16292 This specimen is a skull partially exposed in ventral view. The length from the tip of the snout to the ventralmost point of the pterygoid is 65 mm; the corresponding distance is 33 mm in specimen NCSM 21371. It is the largest among the known specimens of this species.

At least three upper incisors are partially preserved on right side, in which the third is the largest. The canine is large, with a mesiodistal diameter of 6.4 mm. Only the bases of the crowns are preserved for all postcanines. On the left side, the bases are transversely expanded, indicating that the teeth were gomphodont. The buccolingual width of the last two gomphodont teeth is approximately 9 mm. A small, triangular base of a crown behind the gomphodont teeth possibly represents a small sectorial tooth similar to that in the holotype of *Plinthogomphodon herpetairus* (Sues et al., 1999). On the right side, the anterior three teeth appear to be gomphodont, the fifth could be a sectorial tooth, but the nature of the fourth is uncertain. The diastema between the canine and the postcanines is about 7.4 mm long on the right side and at least 6 mm on the left side.

Specimen NCSM 20700 (Fig. 8) This specimen is the smallest specimen of our sample. It comprises both dentaries with only the first and fourth (last) postcanine teeth present in the left dentary. The diastema between the canine and the first postcanine is about 1.5 mm. The last postcanine is a sectorial, with a length of 3.3 mm. The first postcanine is shaped like the principal cusp of a sectorial tooth, 1.5 mm in mesiodistal length; it might represent a simple tooth similar to the small first postcanine in some other traversodontid specimens (e. g., *Andescynodon*, PVL 4390; *Massetognathus* MCZ 4267). Based on the shape of the alveoli, no gomphodont teeth were present in the second and third position.

Specimen NCSM 20692 This small specimen comprises the anterior part of left and

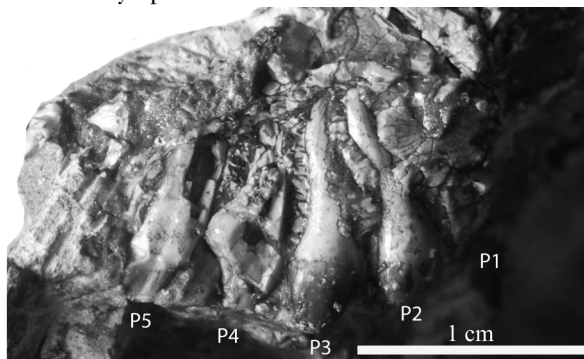


Fig. 7 Right upper postcanines (P) of *Boreogomphodon jeffersoni*, NCSM 16297, in lateral view, showing the roots

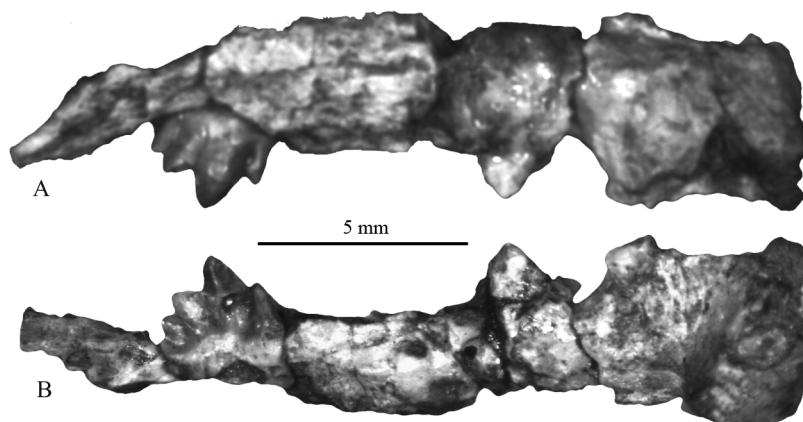


Fig. 8 Left lower jaw of *Boreogomphodon jeffersoni*, NCSM 20700
A. lateral view; B. medial view

much of the horizontal ramus of the right dentary. The height of the dentary below the third postcanine is about 8 mm. The number of incisors is unsure. The mesiodistal diameter of the canine is only 2.6 mm. A 4-mm-long diastema is present between the canine and the first postcanine. Four postcanine alveoli are preserved, the first containing the root of its tooth. The measurements in Table 1 are based on the alveoli.

Table 1 Measurements of postcanines of *Boreogomphodon jeffersoni* specimens from North Carolina (mm)

NCSM No.	20712(l)		21371		18300(r)		16297(r)		16292(r)		20692(r)		20662(l)		20704(r)		20660(l)	
	W	L	L(l)	L(r)	W	L	W	L	W	L	W	L	W	L	W	L	W	L
PC1	5.6	3.8	2.0		7.1	4.5	6.1	3.8	8.0	4.2								
PC2	5.7	3.4	2.7	2.9	7.2	4.7	6.5	4.0	8.4	5.0								
PC3	6.3	4.5	3.0	3.2	7.3	5.0				4.9								
PC4	2.9	4.5	3.5	3.5		4.1			5.5	5.0								
PC5		4.4	3.5	3.5					3.4	5.6								
pc1					3.7	4.3					2.2	2.6	3.5	4.4	>4.5	4.4	4.7	
pc2	3.6	3.5			4.2	4.4					2.5	2.6	3.8	4.5	4.7	4.8	4.7	5.1
pc3	3.9	4.1			3.9	4.8					2.6	3.3			4.9	4.9	4.2	5.4
pc4		4.5			3.6	4.9												
pc5	2.4	5.0													6.0			

Abbreviations: l. left; r. right; L. mesiodistal crown length; W. buccolingual crown width; PC. upper postcanine; pc. lower postcanine.

Specimen NCSM 16358 (Fig. 9) This small specimen is a left dentary with almost all teeth. The height of the dentary below the first postcanine is about 12 mm. The canine is a large tooth with a crown height of 9 mm. It is flattened buccolingually, with a convex buccal and a concave lingual surface. A tooth preserved anterior to this canine is similar in shape to the canine but is more slender; it has a height of more than 11 mm. It is probably a replaced canine. The diastema between the canine and first postcanine is 5.8 mm long. The mesiodistal length of the first, second and third postcanines is 3.2, 3.8, and 4.0 mm, respectively. The fourth postcanine is a sectorial, which is placed higher on the lower jaw than the more anterior postcanines.

Specimen NCSM 11466 (Fig. 10) This specimen is the anterior part of a right dentary with three postcanines. The height of the dentary below the first postcanine is about 12 mm. An incomplete markedly procumbent incisor is 1.3 mm in diameter and 4 mm high above the alveolus. The canine is broken. The diastema is about 6 mm long. The mesiodistal length of the first, second, and third postcanines is 4.2, 4.2, and 3.9 mm, respectively. The roots are strongly curved backwards, especially that of the second postcanine. The roots of anterior two postcanines lie closely together but are well separated from the root of the third one.

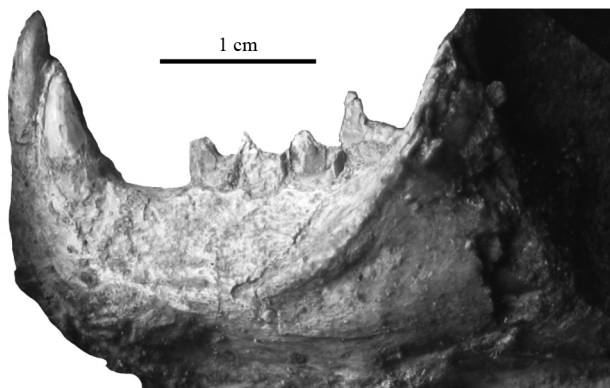


Fig. 9 Left lower jaw of *Boreogomphodon jeffersoni*, NCSM 16358, in lateral view, showing the replacement of canine

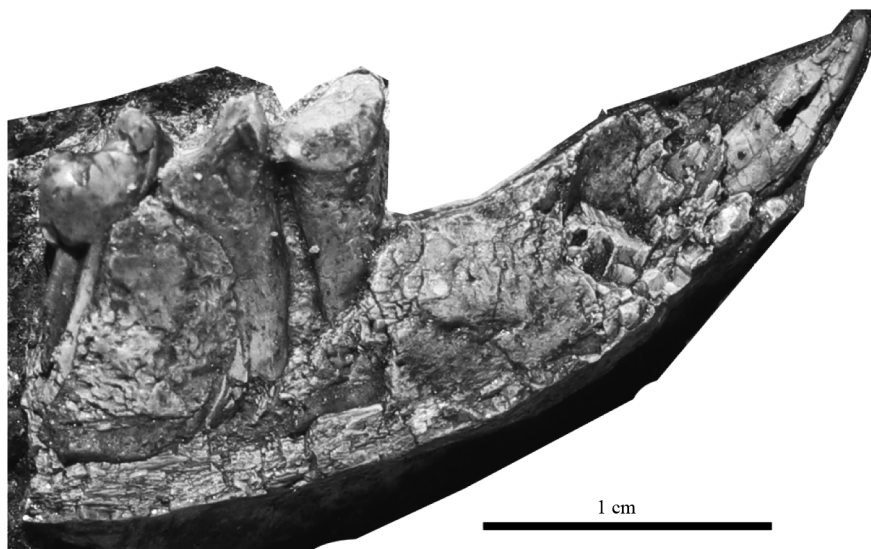


Fig. 10 Right lower jaw of *Boreogomphodon jeffersoni*, NCSM 11466, in lateral view, showing the roots

Specimen NCSM 20662 This specimen is a left dentary with two postcanines. It is about 60 mm in length from the anterior end to the posterodorsal corner of the dentary. The third and fourth postcanines are missing, and the first is represented only by its root. The shape of the fourth alveolus is similar to that of the third one, indicating a gomphodont tooth in this position. The buccal ridge of the second postcanine was eroded. The fifth postcanine is a partially erupted sectorial. The diastema is approximately 6.6 mm long.

Specimen NCSM 20704 (Fig. 11) The specimen is the posterior part of a right dentary with four postcanine teeth. The dentary is 13 mm in height below the first postcanine. The anterior portion of the first postcanine and the anterolingual corner of the second one were damaged during the preparation. The fourth postcanine has a sectorial crown. The alveoli of the fourth and the fifth are narrow and elongated, and this indicates they were previously occupied by sectorial teeth. So a sectorial tooth was replaced by another sectorial in the fourth tooth position.

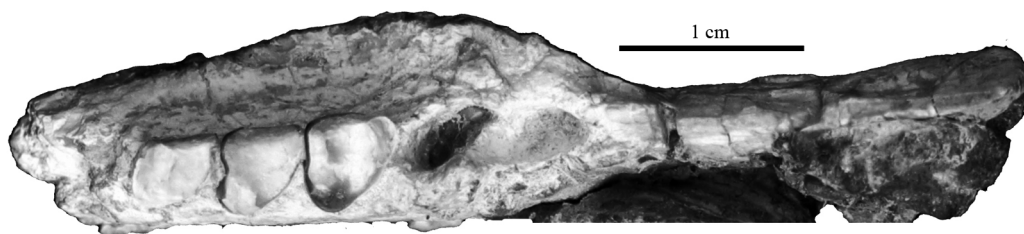


Fig. 11 Right lower jaw of *Boreogomphodon jeffersoni*, NCSM 20704, in occlusal view, showing the erupting tooth in fourth alveolus

Specimen NCSM 20660 This specimen is an incomplete left dentary with canine and two postcanine teeth. The height of the dentary is 14 mm in below the first postcanine. The crown of the canine is missing; its broken base is 4.5 mm in mesiodistal and 3.8 mm in buccolingual diameter. A diastema of about 6 mm is present between the canine and the first postcanine. The anterior two postcanines are gomphodont teeth; the shape of the third alveolus indicates a gomphodont tooth in this position. A small fragment in the anterobuccal portion of the third alveolus is probably a piece of the tooth.

Because all these specimens come from the same horizon and locality and because their postcanines share the same crown morphology they are considered the growth series of a single species. The attributes of the different types of teeth are summarized below:

Incisors Four upper incisors and three lower incisors are present. The upper third incisor is the largest. No serrations are present on the cutting edges of the incisor crowns. No replacement pits as in *Thrinaxodon* are present (Crompton, 1963), but the replacing incisor is preserved in specimen NCSM 21371. The replacing tooth developed while its predecessor was still functional, similar to the situation of *Scalenodon angustifrons* (Crompton, 1955). It is impossible to determine the order of replacement for the functional incisors and the number of replacement generations in the available material.

Canine Although canine replacement is only visible in NCSM 16358 in the sample under study, the upper and lower canines must have been replaced multiple times during life. This is indicated by the variation in the mesiodistal diameter of the canines. For example, the mesiodistal diameter of the upper canine ranges from 2.6 mm in NCSM 21371 to 6.4 mm in NCSM 16292.

Postcanines The number of postcanine teeth shows little variation in the material from North Carolina. Most specimens have five upper and lower postcanines; the smaller specimens have three gomphodont teeth and two sectorials and the larger specimens have four gomphodont teeth and one sectorial. The dentary reaches the stage of four gomphodont teeth much earlier than the maxilla. The last sectorial tooth is usually partially erupted. Occasionally, there are four or six postcanines, or all postcanines are gomphodont teeth as in NCSM 18300. Tooth occlusion also occurred between gomphodont and sectorial teeth. Postcanine tooth rows are often asymmetrical between the left and right side and between the upper and lower dentitions.

3 Comparison and discussion

3.1 Phylogenetic position of North Carolina traversodontid material

Two traversodontid species have previously been described from Virginia and North Carolina: *Boreogomphodon jeffersoni* (Sues and Olsen, 1990) and *Plinthogomphodon herpetairus* (Sues et al., 1999).

The specimens from North Carolina are almost identical to *Boreogomphodon jeffersoni* in up-

per postcanine morphology, although they lack the posterior cingulum found in some of the specimens from Virginia. The lower postcanines show some differences: the lower gomphodont postcanines of the North Carolina specimens typically have two cusps on the anterior transverse ridge whereas this cusp configuration is only found on some small lower postcanines from Virginia. Even lower postcanines with three anterior cusps slightly differ from those from Virginia in that the central cusp is much lower. However, we interpret these differences as intraspecific rather than interspecific variation. Assessment of a taxonomic distinction between the material from North Carolina and Virginia must await completion of the study of the cranial material.

The holotype of *Plinthogomphodon herpetairus* (UNC 15576) is poorly preserved; most of its teeth are broken. The newly erupted last left upper postcanine slightly differs from the upper postcanines of *Boreogomphodon jeffersoni*: it has a posterior cingulum, two anterior cusps on the buccal margin, and the central cusp is situated more anteriorly (Sues et al., 1999). However, a posterior cingulum is also present on some of the larger gomphodont postcanines of *Boreogomphodon jeffersoni* (Sues and Hopson, 2010). When the cingulum is present, the central cusp appears to be placed more anteriorly. Only one anterobuccal cusp is visible in the Virginia material, but this part of the crown is often worn. Even if only one anterobuccal cusp is present in *Boreogomphodon*, the number of anterobuccal cusps can vary within a given taxon, such as demonstrated for *Luangwa drysdalli* (Abdala and Sa-Teixeira, 2004). Thus, it is questionable whether *Plinthogomphodon herpetairus* can be distinguished from *Boreogomphodon jeffersoni* on the basis of postcanine features. The holotype of *Plinthogomphodon herpetairus*, which is similar in size as NCSM 16292, has four gomphodont and one sectorial functional postcanines in the right maxilla and six gomphodont and one sectorial postcanines on the left side. Another difference between these two specimens is in the diastema: in *Plinthogomphodon* there is no apparent diastema between the upper canine and the first postcanine, whereas in NCSM 16292, of similar size, diastemas are represented on both sides. *Plinthogomphodon herpetairus* has one unique feature: a sectorial replacement tooth preserved in the second postcanine alveolus. However, an anterior sectorial postcanine has not been observed in any other traversodontids, and this could be an individual anomaly. *Plinthogomphodon herpetairus* is clearly closely related to *Boreogomphodon jeffersoni* and may well be referable to the latter genus.

3.2 Tooth replacement pattern

The material of *Boreogomphodon jeffersoni* from Virginia was interpreted as juvenile in nature in part because of the retention of sectorial postcanines (Sues and Hopson, 2010). No sectorial postcanine teeth are known in adult specimens of most traversodontid taxa, such as *Exeretodon* (Bonaparte, 1962), *Luangwa* (Brink, 1963; Kemp, 1980; Abdala and Sa-Teixeira, 2004), and *Pascualgnathus* (Bonaparte, 1967). Sectorial postcanines are present in juveniles of *Andescynodon* (Goñi, 1986) and *Massetognathus* (personal observation on MCZ specimens) but only gomphodont postcanines are present in adults of *Andescynodon* (Goñi, 1986; Goñi and Goin, 1987) and *Massetognathus* (Romer, 1967). However, sectorial postcanines are retained even in the largest specimens from North Carolina, which reached a skull length of 100 mm. Thus, it is possible that the presence of sectorial postcanines even in adult specimens is a feature of *Boreogomphodon*, as in trirachodontids such as *Langbergia* and *Trirachodon* (Abdala et al., 2006), rather than a dental indicator of immaturity.

The specimens examined here have a wide range of size variation: the smallest dentary (NCSM 20700) measures approximately 30 mm in length whereas one large dentary is over 60 mm long (NCSM 20662) and the largest skull (NCSM 16292) exceeds 100 mm in length. As the postcanines have closed roots, this implies that the skull and new teeth continued to grow throughout life.

It is well established that the enamel surface of a tooth is fully formed before a tooth

erupts, and thus the size and cusp pattern of a fully erupted tooth do not show further change except due to wear over time (Zhang et al., 1998). One interpretation for teeth of different size or shape but occupying corresponding positions of different-sized specimens is that these teeth have undergone replacement. Another possible interpretation is that the corresponding position is not exactly the same in specimens of different sizes, as teeth may be added posteriorly and lost anteriorly, as was demonstrated in several traversodontid cynodonts. Although little direct evidence of postcanine replacement has been observed, different types of teeth and differences in postcanine sizes in small and large specimens clearly indicate such replacement.

The number of postcanines slightly varies among the specimens studied. Typically, four functional postcanine teeth are present. In specimen NCSM 21371, the left tooth row has one more anterior tooth, but this tooth was already lost on the right side. Our sample shows that teeth were added at the posterior end of the postcanine tooth row during growth. This was also the case in other cynodonts, e. g., *Thrinaxodon* (Crompton, 1963), *Diademodon* (Fourie, 1963), and *Scalenodon* (Crompton, 1955).

If the tooth position is identical in different tooth rows, the general pattern of replacement is that a smaller postcanine is replaced by a larger tooth of the same type except of the eventual replacement of sectorial by gomphodont postcanines (Fig. 12A), as showed by the erupting sectorial tooth of the fourth alveolus in specimen NCSM 20704. If this model is valid, at least three generations of successive teeth were present at each tooth locus because the size of teeth increased with the skull growth. It requires the loss of last postcanine during ontogeny of NCSM 18300. No direct (vertical) replacement of gomphodont teeth has been observed, and there is no evidence for the loss of last postcanine.

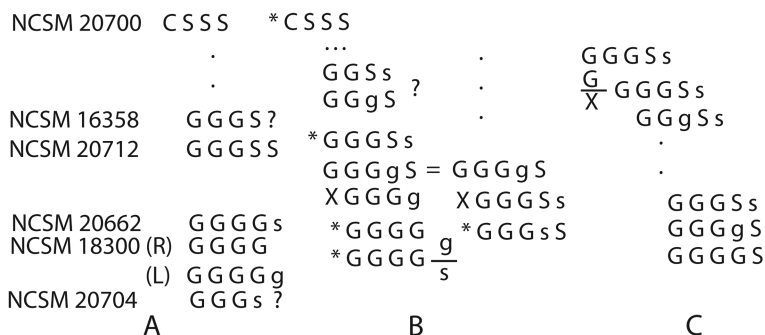


Fig. 12 Models to explain tooth patterns observed in North Carolina specimens

A. specimens ordered by lower gomphodont tooth size (NCSM 16358 and 20712 are similar in size of gomphodont teeth; NCSM 20662, 18300 and 20704 are similar in size of gomphodont teeth), and arranged in corresponding tooth positions; B. preferred model for the lower postcanine tooth replacement; C. part of the model for the upper postcanine tooth replacement

Abbreviations: C. conical tooth; G. gomphodont tooth; S. sectorial tooth; upper case indicates fully functional tooth; lower case indicates erupting tooth or newly erupted tooth; X indicates the lost tooth on anterior region; star indicates that type of dentition is observed in specimens; question mark indicates unsure

Specimen NCNM 21371 shows that gomphodont teeth were added posteriorly and lost anteriorly. This is reflected by the degree of wear on the crowns of gomphodont teeth, which progressively decreases towards the posterior end of the tooth row, indicating that only sectorial teeth were replaced. In all available specimens, the posterior gomphodont tooth is generally slightly larger than the one immediately in front. In this way, continued increase in tooth size could be accommodated during growth. A sectorial postcanine is eventually replaced by a gomphodont successor, but there are possibly two generations of sectorial teeth (right side of Fig. 12B). As specimen NCSM 20704 shows, a sectorial can replace another sectorial tooth.

The basic pattern of tooth replacement is the same for upper and lower postcanines, but all upper tooth rows have sectorial teeth whereas this is not the case for all lower tooth row, and thus the detailed tooth succession is slightly different as shown in Fig. 12. Based on this model, the total number of gomphodont teeth on the maxilla is estimated as less than 20 (around 15) during the growth series shown by NCSM 21371 and NCSM 16292.

If gomphodont teeth are lost anteriorly, the diastema between the canine and the first post-canine should increase in length. However, this is not true for the specimens studied here (Table 2). The diastema does increase in length with skull growth, but it only has a length equivalent to one or two cheek teeth. One possible explanation is backward migration of canine; another is the anterior migration of postcanine teeth as in some tritylodontids (Cui and Sun, 1987). The strongly curved root in NCSM 11466 (Fig. 10) suggests that the postcanine teeth moved forward in their alveoli. Only when the crown shifts forwards, the root anchored in alveolus will be forced to curve rather than remain vertical.

Table 2 Measurements of distema size between canine and first postcanine (D) and mesiodistal length of the first postcanine (P) in *Boreogomphodon jeffersoni* (mm)

Specimen No.	D (U)	P (U)	Specimen Number	D(L)	P (L)
NCSM 20712	4.3	2.8	NCSM 20700	1.5	1.5
NCSM 15295	4.1	3.7	NCSM 20692	4	2.6
NCSM 16292	7.4	4.2	NCSM 16358	5.8	3.2
NCSM 21370	5	4.3	NCSM 11466	6	4.2
NCSM 18300	4	4.5	NCSM 18300	5	4.3
			NCSM 20662	6.6	4.4
			NCSM 20660	6	5

Abbreviations: U. upper jaw; L. lower jaw.

The mode of tooth replacement is deduced from the change in tooth size, the evidence of replacement, and the degree of wear. Gomphodont teeth are lost anteriorly and added posteriorly; they also migrated forward within the jawbone. Only one generation of gomphodont teeth is present and two generations of sectorial postcanines were represented during the life of *Boreogomphodon*.

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