Ontogeny of the Early Triassic cynodont Thrinaxodon liorhinus (Therapsida): dental morphology and replacement

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ONTOGENY OF THE EARLY TRIASSIC CYNODONT *THRINAXODON LIORHINUS* (THERAPSIDA): DENTAL MORPHOLOGY AND REPLACEMENT

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ABSTRACT—Here for the first time we use micro-computed tomography (μCT) scanning techniques to study dental replacement in the Early Triassic cynodont *Thrinaxodon liorhinus*. We analyzed five specimens ranging 37–87 mm in skull length using μCT scanning, which were supplemented by detailed anatomical analysis of 48 specimens with a basal skull length of 30–96 mm. Our results indicate that lower postcanines are more numerous and present a more complex morphology than the upper postcanines, even in the same individual; only the lower postcanines have more than three sectorial cusps and a cingular collar on the lingual margin. Complexity of the postcanines increases from the smallest individual to specimens with a skull length of 75 mm, but complexity decreases in larger specimens. Our results confirm the alternate replacement of the postcanines and the posterior migration of the postcanine series (including the loss without replacement of the anterior-most postcanines). Observations point to a posterior-to-anterior replacement wave in lower postcanines, but the evidence is not clear-cut for the upper series. The virtual extraction of functional and replacement teeth permitted us to conclude that in most of the cases the upper canines were replaced anteriorly, whereas lower canines were replaced posteriorly. The presence of two simultaneous replacements of the upper canine tooth was observed in two small juveniles, suggesting a higher rate of canine replacement at a younger age. Incisors also had a sequential replacement pattern, and more replacement teeth were present in medium-sized individuals.

INTRODUCTION

One of the key features that attracted the attention of scholars studying mammal-like therapsids and mammalian origin was their dentition. In most non-mammalian therapsids, the dentition is clearly differentiated into functional groups including incisors, canine, and postcanines. In non-mammaliaform cynodonts, the postcanines show a complex morphology, and in some cases (e.g., gomphodont cynodonts), examples of irregular occlusion between upper and lower buccolingually expanded postcanines occur (Crompton, 1972). *Thrinaxodon liorhinus*, a widespread Gondwanan cynodont from the Early Triassic, is represented by numerous specimens found in the South African Karoo Basin (Abdala and Ribeiro, 2010). This species was once considered as a hypothetical mammalian ancestor (Crompton and Jenkins, 1968; Hopson and Crompton, 1969), mainly because the postcanine morphology resembles those of the basal mammaliaform *Morganucodon*.

Thrinaxodon liorhinus, a small therapsid ranging between ca. 30 and 96 mm in basal skull length (Fig. 1), is indeed one of the best-known and most studied basal cynodonts, and the only one for which a computed tomography (CT)-scanned digital atlas of the skull has been published (Rowe et al., 1993). Studies of dental morphology and replacement in this taxon were first undertaken by Parrington (1936) using nine specimens ranging from less than 61 to 84 mm (Table 1). This contribution was followed by Crompton's (1963) detailed analysis of dental replacement in the species,

also based on nine specimens (only two of them were also part of Parrington's [1936] sample). Van Heerden (1972) presented an extensive survey on the ontogeny of *Thrinaxodon liorhinus* in which he briefly considered the dentition of the studied specimens. A study of morphological variation of the postcanine dentition was then presented by Osborn and Crompton (1973), who categorized the lower postcanine teeth into three morphotypes and compared their occurrence across different ontogenetic stages. Gow (1985) introduced new evidence and extended the range of specimen analysis by physically preparing the dentition of specimens much smaller than those studied previously (Table 1).

The recent recovery of several well-preserved specimens (e.g., Smith and Botha, 2005:fig. 4), plus the application of micro-computed tomography (μCT) scanning techniques to specimens of different size, makes this taxon conducive to renewed studies of ontogenetic change. Here we present a detailed analysis of morphological variation and replacement of the teeth of *Thrinaxodon liorhinus*. The μCT scanning of an ontogenetic series for the first time allows a detailed survey of tooth replacement in both the upper and lower postcanine series in selected specimens of different sizes, which allows exploration of the synchrony of the dental replacement in the different tooth rows of one individual. This contribution also documents the replacement pattern of the incisor teeth.

Institutional Abbreviations—AMMM, McGregor Museum, Kimberley, South Africa; **BP**, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; **BSP**, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; **CAMZM**,

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TABLE 1. *Thrinaxodon liorhinus* specimens examined in previous studies, listed in increasing size.

Parrington (1936)		Crompton (1963)		Osborn and Crompton (1973)		Gow (1985)	
Specimen	BSL (mm)	Specimen	DSL (mm)	Specimen	BSL (mm)	Specimen	SL (mm)
CAMZM T811		BP/1/1376	~30	TM 80	56	TM 4984	
CAMZM R2739	61	BSP	58	TM?		BP/1/1376	~30
CAMZM T813	65	NHMUK R3731	68	TM 80B	69	BP/1/1376a	~30
CAMZM T814		SAM-PK-K377	73	NHMUK R3731	71	TM 80	56
NHMUK R3731	71	SAM-PK-K380	78	NM 354	71	TM 80	69
CAMZM T815	69	NHMUK 511	78	SAM-PK-K?		TM 81	80
NHMUK R5480	78	SAM-PK-K378	80	TM 180	75		
CAMZM R2736		NHMUK R511a	84	NHMUK R511	84		
NHMUK R511a	84	SAM-PK-K379	86	TM 81	80		
				NHMUK 511a	86		
				TM 180	75		

Abbreviations: **BSL**, basal skull length; **DSL**, dorsal skull length; **SL**, skull length.

University Museum of Zoology, Cambridge, U.K.; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **NHMUK**, Natural History Museum, London, U.K.; **NM**, National Museum, Bloemfontein, South Africa; **SAM**, Iziko South African Museum, Cape Town, South Africa; **TM**, Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa; **UCMP**, Museum of Paleontology, University of California, Berkeley, California, U.S.A; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

MATERIALS AND METHODS

Gross Anatomical Specimens

Specimens studied are listed in Table 2. The basal skull length of this sample (Fig. 1) ranges from ca. 30 mm (SAM-PK-K8004, BP/1/1375a, b) to 96 mm (SAM-PK-K1461). The collecting localities for these specimens are part of the *Lystrosaurus* Assemblage Zone, which include the upper part of the Palingkloof Member of the Balfour Formation, the Katberg Formation, and the Harrismith Member of the Normandien Formation (Rubidge et al., 1995). Some specimens from the Iziko South African Museum (SAM-PK-K378, K379, and K380) have no information listed for specimen locality.

μCT-Scanned Specimens

Five specimens of *Thrinaxodon*, representing presumed juvenile (BP/1/5372, TM 80A) and subadult to adult (TM 180, BP/1/7199, and BP/1/5905) stages were analyzed using μCT (Table 2). Specimen TM 80A was scanned using a XTH 225 LC at DebTech (DeBeers, Johannesburg, South Africa); the skull was scanned with an isotropic voxel size of 50 μm and 66 μm for the mandible. Specimen TM 180 was scanned using a XTH 225 ST at X-Sight (Stellenbosch, South Africa), with an isotropic voxel size of 50 μm. Three-dimensional (3D) rendering of the slice data of both specimens were undertaken using the 3D visualization software Mimics (version 13.1; Materialise, Leuven, Belgium) and ScanIP (version 4.0; Simpleware, Exeter, U.K.). The entire data set for the TM 80A (skull) and TM 180 scans could not be

FIGURE 1. Lateral view of the skulls of the smallest (SAM-PK-K8004) and largest (SAM-PK-K1461) specimens of *Thrinaxodon liorhinus* in our sample. Scale bar equals 10 mm. (Color figure available online.)

TABLE 2. *Thrinaxodon liorhinus* specimens examined in this study, listed in increasing size.

Specimen	BSL (mm)	Observations
SAM-PK-K8004	~30	Lacks anterior portion of the snout
BP/1/1375a	~30	Estimated after the complete dentary
BP/1375b	~30	Same size as BP/1/1375a
TM 1486	~33	BSL 30, lacking incisor portion
BP/1/5372	37	μCT-scanned
UCMP 42878	~38	
UCMP 42877	40	
SAM-PK-K10016	42	
SAM-PK-K10017	42	
TM 4984	56	
TM 80A	56	μCT-scanned
TM 4984	56	
BP/1/4280	61	
UCMP 42865	61	
MCZ 8892	~62	
FMNH UR 156	~64	
"Cynodont B"	65	Sectioned specimen (Hopson, 1964)
CAMZM T 813	65	
SAM-PK-K1468	~65	Lacks anterior portion of the snout
SAM-PK-K10607	~67	
CAMZM T 817	~68	
CAMZM T 815	69	
CAMZM T 814	~69	Similar size to CAMZM T815
TM 80B	69	
TM 782	70	
NMQR 811	~70	Snout length ca. 30 mm
UCMP 42866	~70	
BP/1/4263	71	
NHMUK R3731	71	
NMQR C354	71	Sectioned specimen (Fourie, 1974)
SAM PK-K1498	72	
BP/1/5208	73	
UCMP 40466	74	
BP/1/7199	75	μCT-scanned
TM 180	75	μCT-scanned
SAM PK-K1499	75	Lacks anterior portion of the snout
SAM-PK-K378	~75	Tip of the snout absent
SAM-PK-K380	~76	Snout length ca. 35 mm
CAMZM T 816	78	
NHMUK R5480	78	
BP/1/1730	79	
TM 81a	80	
BP/1/1375c	81	
TM 167	81	
NHMUK R511	84	
AMMM 4283	85	
TM 5074	~85	
NHMUK R511a	86	
BP/1/5905	87	μCT-scanned
SAM-PK-K379	89	
BP/1/2824	~90	
NMQR 809	91	
USNM 22812	94	
SAM-PK-K1461	96	

Abbreviation: **BSL**, basal skull length.

imported into Mimics, and so the data were resampled in the z-direction (200 micron z-spacing in TM 80A; 100 micron z-spacing in TM 180). The mandible of TM 80A was cubic resampled to 85 μm in ScanIP.

Specimens BP/1/5372, BP/1/7199, and BP/1/5905 were μCT-scanned at the European Synchrotron Radiation Facility (ESRF; Grenoble, France) on the beamlines ID17 and ID19. The skull of BP/1/7199, enclosed in a burrow cast (BP/1/5558), was scanned on ID19 using filtered white beam (filtered with aluminium: 12 mm, copper: 8 mm, and tungsten: 0.25 mm) in half-acquisition mode and a sample-camera distance of 4 m. Five thousand projections of 0.15 s each were recorded over 360° using a 30-μm optic. Specimen BP/1/5372 was scanned on ID19 in propagation phase-contrast mode (sample-detector distance of 900 mm) using a monochromatic beam of 60 keV (double Si 111 monochromator), with 1999 projection of 0.6 s each over 360°. The projections were recorded using a 20.24 μm optic. Specimen BP/1/5905 was scanned on the beamline ID17 using an attenuation protocol and using the half acquisition mode (Carlson et al., 2011). The scan was performed using a monochromatic beam of 96 keV, 5000 projections of 0.5 s each, a sample/detector distance of 5 m, and a taper fiber optic producing isotropic pixels of 45.5 microns. Three-dimensional rendering and segmentation were performed using the software VG Studio MAX 2.1 (Volume Graphics, Heidelberg, Germany).

In all specimens, teeth and bones were segmented as separate materials. The segmentation was performed using semiautomatic 3D region growing tools. When this tool did not permit complete extraction (e.g., too low contrast between the bone and the matrix, or too high fracture level), missing parts were added slice-by-slice using manual segmentation whenever possible.

Tooth Morphology and Replacement Patterns

In most specimens, only the lateral (labial) side of the upper tooth row is visible, thus limiting the amount of information available for classification of the teeth. The entire tooth morphology can be described, however, for specimens that have been acid-prepared and/or μCT-scanned. The μCT data also allowed tooth replacement patterns to be observed because unerupted and old fragments of teeth become clearly visible.

Teeth in the mandible have previously been divided into three different tooth morphologies (A, anterior; M, middle; P, posterior) (Crompton, 1963; Osborn and Crompton, 1973). These three tooth types captured both the positional information and morphology of the teeth. A-type teeth were simple tricuspid teeth without cingular cusps, located in an anterior position in the tooth row; M-type teeth were tricuspid teeth with cingular cusps, typical of postcanines placed in the middle positions of the tooth series; and P-type teeth were the most complex, being either tricuspid or multicuspid and having cingular cusps, and located in posterior positions (Osborn and Crompton, 1973:fig. 3). A 'hybrid' MP type, which has an intermediate morphology between the M and P types and located at the posterior end of the postcanine series, was also recognized. However, after we reexamined many of these specimens, it became apparent that a new classification that accounts for the full spectrum of variability and complexity of the postcanine teeth was necessary (Fig. 2). This new classification accounts for the number of main cusps (A, bicuspid; B, tricuspid; C, multicusped), number of lingual cingular cusps (0, none; 1, one or two isolated cingular cusps; 2, multiple cingular cusps in a collar), and number of labial cusps (X, none; Y, one labial cusp; Z, two labial cusps).

There are some difficulties in numbering the postcanine (PC) teeth due to the presence of a space (diastema) between the canine and first postcanine in some specimens. This feature may occur on only one side of the jaw in an individual (e.g., BP/1/7199), possibly indicating that the first postcanine was lost on one side only. We evaluated the condition of the tooth row on both sides of the jaw to define the first postcanine. If the first postcanine was represented on one side of the tooth row and definitively lost (and not replaced) on the other side, then we labeled the first element

as 'X' and then considered the second element as homologous to the first postcanine of the other side of the jaw. This particular consideration regarding the first postcanine of the dental series was specifically used when analyzing replacement sequences in the μCT-scanned specimens.

To analyze the replacement rate and size variation in postcanine series, we did comparative measurements of the anteroposterior length (APL) of the postcanine crowns in μCT-scanned specimens using VG Studio MAX 2.1. To ensure that the measurements were similar in nature, we oriented each tooth individually in 3D space so that the elongated axis of the root was parallel to the vertical axis and the labial side of the tooth crown was parallel to the plane of the computer screen. The APL was then measured on the coronal μCT slice located at the base of the crown, where it shows its maximal anteroposterior length.

To estimate the variation in size of two successive teeth in the replacement sequence, we compared the APL from relevant elements. For instance on the sixth locus of the left mandible of TM 80A (Fig. 3A), the functional tooth is soon to be shed and its associated replacement seems to have reached its maximal anteroposterior extension; comparison of the APL of these two elements gives an estimation of the size variation occurring when a tooth is being replaced. We expressed the crown length increase in terms of percentage. Because this case was rare within our sample, we supplemented them with additional values: in both mandibles of BP/1/7199, the third postcanine (PC3) is erupting, whereas the surrounding PC2 and PC4 represent an older generation of teeth (Fig. 3B); we therefore estimated the size of the previously shed PC3, based on the measurements from PC2 and PC4, and compared these values with the size of the erupting PC3, supplementing the estimation of the percentage of postcanine increase after replacement.

Because these were the only options for measuring the increase of postcanine size after replacement, we considered the obtained values as constant throughout the life of the animal, in order to estimate the number of replacement postcanines occurring between two different stages. The variation in tooth size can be expressed as a geometric sequence. Thus, the APL after n replacement cycles is:

$$APL_n = APL_0 \times R^n$$

where APL_0 is the start value of the sequence (here obtained from the smallest individual of our study) and R is the common ratio (i.e., percentage increase). The recursive relation of the sequence permits the assessment of the number of replacement cycles that occurred between two different ontogenetic stages. We then compared the APL of the two extremes of the μCT-scanned ontogenetic series, the smallest (BP/1/5372) and the largest (BP/1/5905) specimens. This comparison takes into account the loss of anterior postcanines during ontogeny.

Because all of the replacement teeth are recognized by the presence of mineralized tissue, they are considered here as being at least in an advanced bell stage, following Luckett (1993).

RESULTS

Tooth Morphology

Incisors—*Thrinaxodon liorhinus* has four upper and three lower incisors (I). The upper incisor morphology is quite simple with a usually backwardly directed cusp that can vary from conical and pointed to broader and rounded. They usually have a broad base and, in some cases (e.g., the fourth incisor of SAM-PK-K10016), there is a gradual reduction of the size from the base to the tip of the tooth. The labial faces of the first three incisors are clearly

more rounded that of the fourth incisor (I4). In some specimens (e.g., SAM-PK-K10016, TM 80A, and TM 782), I4 is compressed mediolaterally, and resembles a small canine. However, this recurved incisor is situated far anterior to the position of the functional canine. In BP/1/7199, all four upper incisors are completely preserved and it is possible to observe that the bases are more robust in the third and fourth incisors than in the first two.

The lower incisors of *T. liorhinus* show a very broad base and the distal portion is reduced progressively to the tip. The lingual face is concave and the labial is convex, and the teeth are generally oriented somewhat anteriorly (procumbent). The third incisor (I3) can sometimes have a straighter (dorsoventral) orientation, as observed in the lower jaw of TM 81a.

Canines—The canine, for the most part, is a single functional tooth with a broad, cone-shaped morphology. The most noticeable feature in some specimens is the presence of dorsoventrally directed facets on the surface of the canine (Fig. 2A, B), which are original structures of the tooth not related with occlusion. The crowns of both the upper and lower canines are similar in shape, although the latter is slightly more slender, and there is no evidence of serrated margins on either of the functional or replacement canines. A facet on the lateral side of the root of the functional upper (BP/1/7199, TM 80A) and lower (TM 80A) canines is observed in some of the μCT-scanned specimens. The orientation of the lower canines is almost vertical, whereas the uppers are slightly directed anteriorly.

Postcanines—The number of postcanines recorded in our sample is variable from five to nine uppers, and six to nine lowers (Table 3). The posterior upper postcanine morphology is much simpler than that of the posterior lower postcanines (compare Fig. 4B, D; see also Crompton, 1963:495). There is only one specimen (SAM-PK-K378) that has labial cusps on an upper postcanine (PC6), whereas several specimens have labial cusps on the lower postcanines (Table 4). In addition, there are no upper postcanines that have more than three main cusps (type C), which is unlike the teeth in the mandible (e.g., TM 180; Table 4).

Some trends are present in both the upper and lower postcanines. If the postcanine is a bicuspid tooth (type A), it is the posterior accessory cusp that is present. The bicuspid postcanines never develop cingular or labial cusps. When cingular cusps are present in tricuspid postcanines, the anterior is the first to appear, and is much more developed and bigger than the posterior cingular cusp if both the anterior and posterior cusps are present on the cingulum.

The morphology of the upper and lower postcanines increases in complexity with age. In the upper jaw of the juvenile specimen SAM-PK-K10016, the majority of the postcanines are bicuspid and there is only one tricuspid tooth (PC7; Table 4), whereas the intermediate-sized individual TM 80A only has tricuspid postcanines in the upper jaw, with no cingular or labial cusps (Table 4). The adult individual TM 180 has the most complex postcanine morphology, with upper postcanines possessing cingular cusps, and the lower postcanines having multiple cusps as well as labial cusps (Table 4). The morphology appears to become simpler in old adults, such as in TM 5074 and BP/1/5905, which have no type C (multicusped) lower postcanines.

The ultimate (posterior-most) upper postcanine is often the smallest postcanine tooth (Table 3). This condition was observed in 10 smaller specimens of our sample (the only exception being UCMP 42865) and in 18 other specimens that range in size from subadult to adult (with basal skull lengths [BSLs] from 61 to 89 mm). However, there were 15 specimens in which a smaller ultimate upper postcanine was not observed (Table 3). The first postcanine (PC1) also tends to be smaller in size relative to the other postcanines and a bicuspid tooth (type A), even in large individuals such as BP/1/2824 (Table 4).
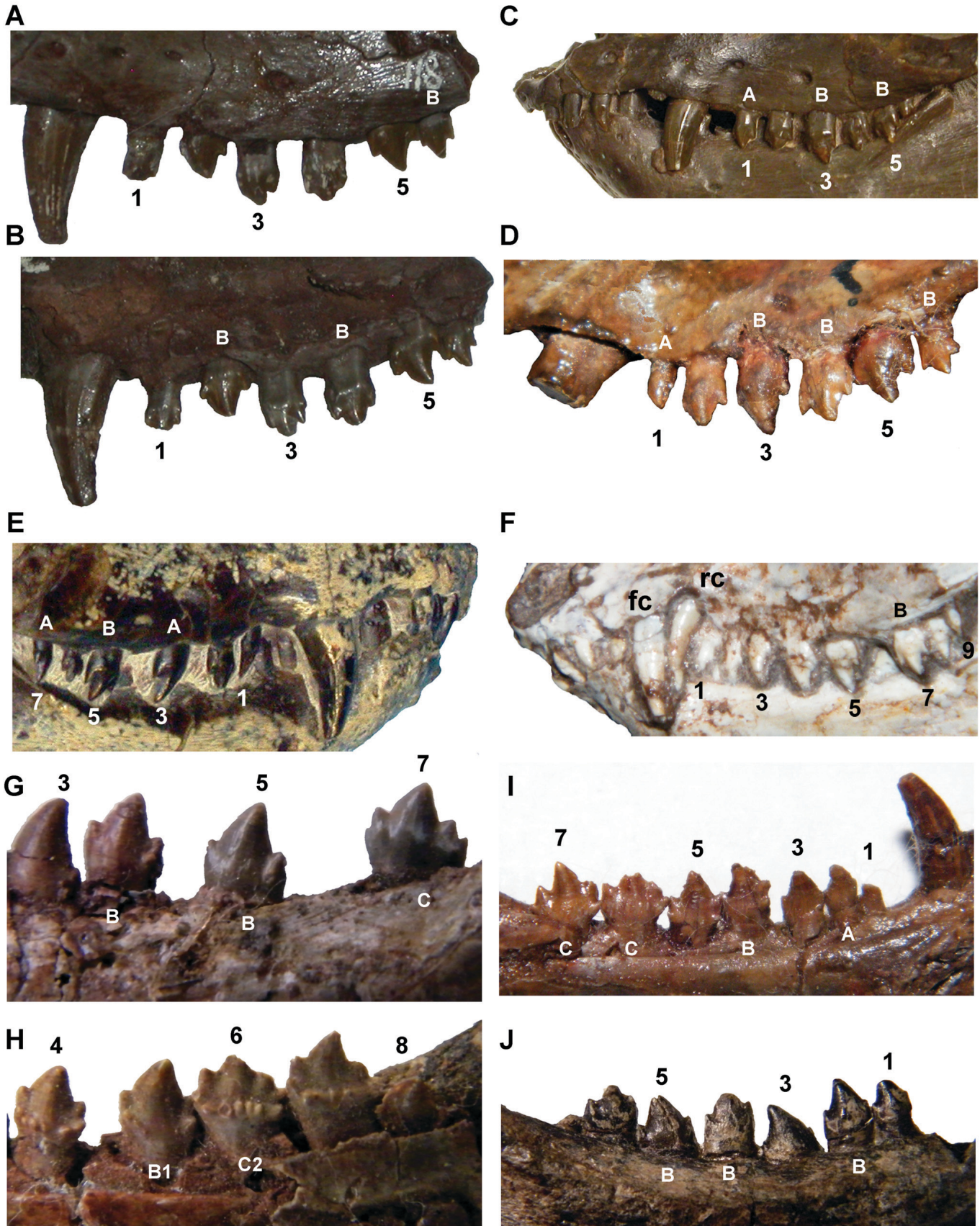
FIGURE 3. Three-dimensional rendering of the mandibular postcanines used to calculate the size variation occurring in the replacement process. **A**, posterior postcanines of the left lower jaw of TM 80A; **B**, anterior postcanines of the right lower jaw of BP/1/7199. White lines represent the maximum anteroposterior length of the crown (APL), measurements of the maximum APL were done on the coronal cross section from μCT data (not shown here); Arabic numerals indicate tooth loci. Not to scale (see also Figs. 7D, 8C). (Color figure available online.)
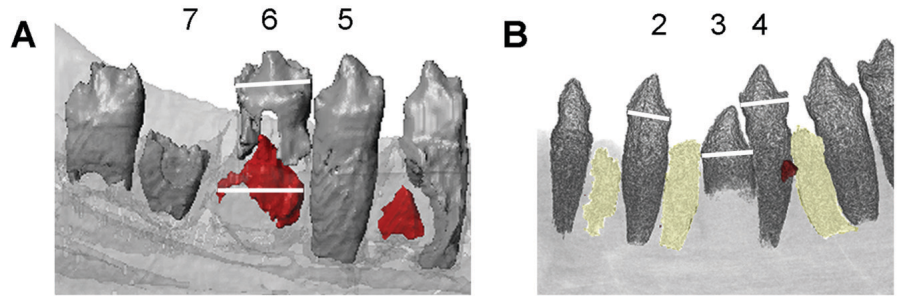
Tooth Replacement

Evidence of tooth replacement, such as the presence of replacement pits, was observed in the gross osteological specimens but it was more accurately surveyed from μCT data. Replacement teeth for incisors and postcanines are situated lingual to the functional postcanine tooth. The replacement canine is usually not erupted.

The μCT scans of several specimens offered the possibility to evaluate the replacement activity of the full dentition of the same individual. Replacement variables, such as the presence of replacement teeth and condition of the roots of functional teeth, are presented for five specimens of *Thrinaxodon*, listed in increasing ontogenetic age.

BP/1/5372 (BSL 37 mm)

Incisors—Incisor alveoli are better defined in the upper dentition. The adjacent functional incisors are separated from each other by alveolar bone walls (Fig. 6A). There is a predominance of spaces separating roots and alveolar walls, and only restricted contact between them. These spaces vary between one-third to one-fifth of the root diameter. There is a total coalescence between the alveoli of the functional and replacement teeth. Replacement of the upper I3 occurs on both sides, with the new tooth eroding the base of the functional tooth (Figs. 5A, B, 6A). On the left side, there is evidence of replacement of I1, with some erosion of the functional tooth (Figs. 5A, 6A). The second and fourth incisors on both sides lack replacement teeth.

Lower incisor alveoli are clearly separated at the ventral-most portion of the root, but they are coalescent dorsally in a way that there is contact between the roots of adjacent teeth (Fig. 6B). A marked coalescence also happens between alveoli of functional and replacement teeth, in a way that only three alveoli are recognized, having diffuse limits (Fig. 6B). Replacement is similar on both sides (Fig. 5C, D). On both mandibular rami, there is a big replacement tooth behind I1 that is eroding the base of the functional tooth, and there is a smaller replacement tooth in the second incisor (Fig. 6B). There is no evidence of replacement of the third element.

Canine—In both maxillae, there are minute replacement canines growing anteromedially to the functional ones (Figs. 5A, B, 6A). There are two alveoli accommodating the roots of the functional and of an older canine in the proximal portion that coalesces into one large alveolus more deeply. A third alveolus with an incipient replacement canine is medial to the remnant root, at the level of the palate (Fig. 5A, B). The incipient replacement canines have not eroded the root of the functional canine.

Both dentaries display replacement canines growing posteromedially to the functional teeth (Figs. 5C, D, 6B). Most of the root of the canine is separated by a reduced space from the alveolar wall, and contact between them is only observed in the anterior portion of the root. Posterior to the functional canine, there are remains of an older canine root. This old root is eroded medially by the growing replacement canine.

Postcanines—There is reduced anteroposterior space between successive alveoli that are nearly contacting each other. The alveoli are very large lateromedially and with considerable space between the root and the alveolar margin. The small last upper postcanine is encapsulated in a small alveolus, which is anteromedially connected with the large alveolus of the preceding tooth.

Only with the first lower postcanine there appears to be contact between the root and the alveolar margin, whereas in all the remaining lower teeth there are spaces between the alveoli and the roots.

In the upper right series, there are seven postcanine alveoli and six teeth preserved; PC6 is absent. The root of PC1 is closed and it does not contact the root of the functional canine. There is no evidence of postcanine replacement (Fig. 5A). Whereas the other postcanines show almost closed roots, the root of the fifth postcanine is widely open.

In the upper left series, there are seven postcanine alveoli and six teeth preserved; PC5 tooth is absent. The root of PC1 does not contact the root of the canine and there is more separation between these two teeth in comparison with those on the right side. There are three replacement teeth (Fig. 5B). Two of them are associated with PC1 and PC3, and the last one is ex situ. The latter could possibly be associated with PC6 or PC7. PC5 is lost, but on the right side the fifth tooth is erupted, yet it has an open

← FIGURE 2. Series of dentition of *Thrinaxodon liorhinus*. Left upper canine and postcanines of NMQR 811 in **A**, lateral and **B**, medial views (imaged is mirrored horizontally). **C**, left upper dentition of UCMP V 40466 in lateral view. **D**, left upper canine and postcanines of TM 4984 in lateral view. **E**, right upper dentition of CAMZM T815 in lateral view. **F**, left upper dentition of the juvenile SAM-PK-K10016. Note that the replacing upper canine is posterior to the functional one, a condition rarely observed in our sample. This specimen also shows nine upper postcanines, the largest number of these teeth in our sample. **G**, left lower postcanines of TM 180 in lateral view; **H**, right lower postcanines of TM 180 in lingual view. **I**, left lower postcanines of TM 4984 in lingual view. **J**, right lower postcanines of TM 5074 in lateral view. **Abbreviations**: **A**, bicuspid postcanine; **B**, tricuspid postcanine; **B1**, tricuspid postcanine with separated lingual cingular cusps; **C**, multicuspid (more than three cusps) postcanine; **C2**, multicuspid postcanine with lingual cingular cusps in collar; **fc**, functional canine; **rc**, replacement canine. Arabic numerals indicate postcanine positions. (Color figure available online.)

TABLE 3. Dental survey of *Thrinaxodon liorhinus* indicating the number of postcanine teeth and whether there was a size reduction of the ultimate upper postcanines. The numbers indicated are obtained via direct observation of a tooth or empty locus and are independent of the developmental sequence.

Specimen	Upper postcanines	Lower postcanines	Last upper postcanine reduced in size
SAM-PK-K8004	6	—	Present
BP/1/1375a	7-7	8-7	Present
BP/1375b	7	—	Present
TM 1486	8-8	—	?Present
UCMP 42877	7-?8	—	
UCMP 42878	7	—	
BP/1/5372[a]	7-7	8-8	Present
SAM-PK-K10016	9-9	—	Present
SAM-PK-K10017	7	7	Present
TM 4984	6-6	7-7	Present
TM 80A[a]	7-7	9-9	Present
UCMP 42865	6-6	—	Absent
TM 4984	5-6	7-7	Present
BP/1/4280	6-6	—	Present
MCZ 8892	7	—	Absent
FMNH UR 156	5-5		Present (R)
CAMZM T 813	6-6	—	Present
CAMZM T 814	6	8	Present
SAM-PK-K1468	6	6	Present
SAM-PK-K10607	7-7	—	Present
CAMZM T 817	8-7	—	Absent
CAMZM T 815	7-7	—	Present*
TM 80B	—	6-7	Absent
TM 782	5-5	—	Absent
NMQR 811	5-6	—	Present
UCMP 42866	6	—	Present
BP/1/4263	?7-?7	—	Absent
NHMUK R3731	6-6	7-7	Absent
BP/1/5208	8	—	Absent
UCMP 40466	6-6	8-7	Present
BP/1/7199[a]	7-7	8-8	Present
TM 180[a]	7-6	8-9	Absent
SAM PK-K1499	6-6	—	Absent
SAM-PK-K378	6	9	
SAM-PK-K380	6-6	—	Absent
CAMZM T 816	6-6	7	Absent
NHMUK R5480	6-7	8-8	?Present
BP/1/1730	6-6	—	
TM 81a	6-7	8-8	?Present
BP/1/1375c	6-6	—	Present
TM 167	6	—	
NHMUK R511	6-6	8-7	Present
AMMM 4283	6	—	Present
TM 5074	7-7	7-8	Present
NHMUK 511a	7-6	7-7	Absent
BP/1/5905[a]	?7	—	
SAM-PK-K379	6	—	Present
BP/1/2824	7-7	—	Absent
NMQR 809	?5	—	
USNM 22812	6-6	6-7	Absent
SAM PK-K1461	6-?7	6-7	

An asterisk (*) indicates that the penultimate and ultimate postcanines are smaller than the more anterior postcanines. For the postcanine tooth number, the first number indicates the right dentition and second number indicates the left dentition. **Abbreviation**: **R**, right dentition.
[a]μCT-scanned.

root and is out of place (see above). Therefore, we infer that the fifth upper tooth was also an almost completely developed element with an open root. The replacing teeth are quite similar in size, the third being slightly larger.

The lower left postcanine series consists of seven functional teeth, with an eighth erupting tooth. There are replacing teeth in the second, fourth, and seventh positions (Fig. 5D). The fourth re-
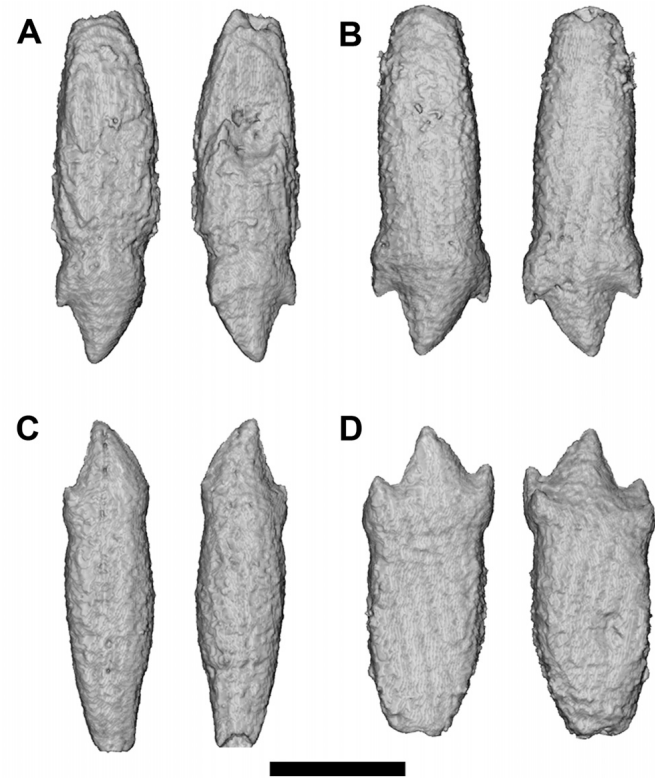

FIGURE 4. Three-dimensional rendered postcanines of *Thrinaxodon liorhinus*, BP/1/7199. **A**, labial and lingual views of the second right upper postcanine (B0X); **B**, labial and lingual views of the fifth right postcanine (B0X); **C**, labial and lingual views of the second right lower postcanine (B1X); **D**, labial and lingual views of the seventh right lower postcanine (B1X). Note that the anterior main cusp is less developed in the anterior postcanine teeth (**A**, **C**). See also Table 4 for the explanation of tooth types. Scale bar equals 3 mm.

placement tooth is the largest, but smaller than the replacement of the same tooth in the right mandibular ramus. The erupting eighth tooth, which is the ultimate tooth of the series, is slightly smaller than the replacement of the fourth but is already more complex, showing three cusps differentiated on the right side (Fig. 5C). The replacements for PC2 and PC7 are tiny. The root of PC6 is open. The condition of the replacing fourth teeth and of the eighth element is suggestive that the replacing sequence is somewhat delayed relative to that of the right postcanine row.

In the lower right postcanine series, there is a large replacement tooth in the fourth position already showing three cusps, and a tiny tooth in the seventh position. There is an erupting eighth tooth, half the size of the previous one, but with two well-defined cusps (Fig. 5C). PC6 has an open root.

TM 80A (BSL 56 mm)

Incisors—Upper incisors one and three from both sides have replacement teeth located either posteriorly (I1) or medially (I3) to the functional tooth (Fig. 7A, B). In the dentaries, only I2 has a replacement tooth, which is positioned medially to the functional tooth (Fig. 7C, D). The root of the functional incisor is eroded by the replacement tooth.

Canines—In the upper jaw, the root of the old canine is positioned anteriorly to the functional canine, and the replacement

TABLE 4. Morphological complexity of the upper and lower postcanines by order of appearance in each tooth row in specimens of *Thrinaxodon liorhinus*.

Specimen	BSL (mm)	Series	1	2	3	4	5	6	7	8	9
BP/1/1375a	~30	UR	A0X	A0X	B0X	B0X	B0X	—	—		
		UL	A0X	A0X	—	B0	B?X	B0X	E		
		LR	—	—	B0X	B0X	B0X	B0X	(?C)0X	C0X	
		LL	—	B0X	B0X-E	B0X	B1X	—	(?C)0X		
BP/1375b	~30	UL	—	—	(?A)0X	—	—	B0X	—		
TM 1486	~33	UR	?	—	B0X	—	B0X	(?B)0X	B0X	—	
		UL	—	(?A)0X	B0X	B0X	B0X	—	B0X	—	
BP/1/5372	37	UR	A0X	B0X	B0X	B0X	B0X	—	B0X		
		UL	A0X	B0X	B0X	B0X	—	B0X	B0X		
		LR	A0X	B0X	B0X	B0X	C0X	C0X	C0X	E	
		LL	A0X	B0X	B0X	B0X	C0X	C0X	C0X	E	
UCMP 42877	40	UR	(?B)X	BX	E	(?B)X	—	—	X		
SAM-PK-K10016	42	UR	AX	AX	X	AX	AX	—	BX	AX	E
		UL	AX	AX	AX	AX	AX	—	BX	E	E
SAM-PK-K10017	42	UL	—	—	A	—	—	?A	—		
		LL	—	A	A	X	B	—	—		
TM 80A	56	UR	—	B0X	B0X	B-E	B	—	B0X		
		UL	B0X	B0X	B0X	B0X	B0X	B0X	—		
		LR	—	B1X	B1X	—	B1X	B1X	B1X	B1X	E
		LL	B0X	B1X	B1X	B1	B1X	B1X	—	B1X	E
TM 4984	56	UR	(?B)0X	B0X	B0X	B0X	B0X				
		UL	A0X	B0X	B0X	B0X	B0X	B0X			
		LR	—	A0X	B(?1)X	B1X	B0X	C1X			
		LL	A0X	A0X	B0X	B1X	B1X	C(?1)X	C1X		
UCMP 42865	61	UR	AX	—	BX	(?B)X	BX	—			
		LR	(?B)X	(?B)X	BX	BX	BX	(?C)X	?		
		UL	AX	—	—	X	(?B)X	(?B)X			
BP/1/4280	61	UR	(?A)X	BX	BX	BX	BX	(?B)X			
		UL	—	BX	BX	BX	BX	(?B)X			
MCZ 8892	~62	UR	AX	E	BX	E?	BX	E	—		
FMNH UR 156	~64	UR	(?A)X	BX	BX	?X	—				
		UL	AX	—	BX	(?B)X	—				
CAMZM T813	65	UR	—	BX	E	(?C)X	AX	AX			
		UL	E	BX	(?B)X	CX	BX	—			
SAM-PK-K1468	~65	UL	AX	BX	E	BX	BX	—			
		LL	B0	A	B0	B0	B	B0			
SAM-PK-K10607	~67	UR	—	AX	AX	—	—	BX	—		
		UL	E	A	BX	BX	BX	BX	(B?)X		
CAMZM T817	68	UR	AX	—	AX	AX	—	—	—	E	
		UL	—	(?A)X	—	—	BX	(?A)X	—		
CAMZM T815	69	UR	AX	BX	BX	—	BX	BX	BX		
		UL	—	BX	E	BX	BX	BX	AX		
CAMZM T814	~69	UR	AX	AX	BX	BX	BX	BX			
		LL	—	(?B)X	BX	—	BX	BX-E	CX	(?C)X	
TM 80B	69	UR	0X	X	B0X	—	—	—			
		UL	A0X	B0X	B1X	B1X	—				
		LR	—	B1X	B1X	B1X	C1X	B1X			
		LL	B0	0X	B1X	B1X	—	—	—		
TM 782	70	UR	A0X	A0X	(?B)0X	—	(?B)0X				
		UL	—	B0X	—	B0X	B0X				
		LR	B0X	E	B1X	B1X	B2X	B2X	B1X		
		LL	B0X	B1X	B1X	B1X	B1X	B2X	B1X		
NMQR 811	~70	UR	A0X	A0X	—	(?A)0X	B0X				
		UL	(?B)0X	B0X	B0X	B0X	B0X	B(?1)X			
BP/1/4263	71	UR	—	—	—	BX	—	—	?		
		UL	—	—	—	—	(?A)X	BX	?		
NHMUK R3731	71	UR	E	(?A)1X	—	B1X	1X	E			
		UL	B0X	1X	B1X	2X	1X	E			
		LR	A0X	B0X	1X	(?B)2Z	B1Z	2X	C1X		
		LL	—	1X	B1X-E	B2Z	B1Z	C2X	1X		
BP/1/5208	73	UL	(?A)X	—	BX	—	—	BX	(?B)X	(?B)X	
UCMP 40466	74	UR	—	(?A)X	—	BX	BX	?			
		UL	(?A)X	BX	BX	BX	BX	?			
BP/1/7199	75	UR	A0X	B0X	(?B)0X	B0X	B0X	B0X	E		
		UL	A0X	B0X	B0X	B0X	B	B0X	B0X		
		LR	B0X	B1X	(?B)-E	B0X	B1X	B1X	B1X	(?A)-E	
		LL	B0X	B1X	(?B)-E	B1X	B2X	B1X	B1X	E	
TM 180	75	UR	B0X	(B?)	B1X	B1X	—	B(0?)X	E		
		UL	(A?)	—	B1X	B2X	B1X	E			
		LR	—	B1	B1	B2Y	B1X	C2Y	C2Y	E	
		LL	?1?	B1X-E	B1(?Y)	B1X	B2Y	B1Y	—	C2Z	B1-E

(*Continued on next page*)

TABLE 4. Morphological complexity of the upper and lower postcanines by order of appearance in each tooth row in specimens of *Thrinaxodon liorhinus*. (*Continued*)

Specimen	BSL (mm)	Series	1	2	3	4	5	6	7	8	9
SAM PK-K1499	75	UR	AX	BX	E	BX	BX	BX			
		UL	AX	BX	E	BX	BX	BX			
SAM-PK-K378	~75	UL	—	B1	B1X	B1X	B1X	B1Z			
		LL	B1X	B1X	B2	B1	B2Z	—	1	B2	—
SAM-PK-K380	~76	UR	E	—	E	—	—	—			
		UL	E	B1X	B1X	B1X	—	—			
CAMMZ T816	78	UR	—	—	AX	E	AX	AX			
		UL	AX	BX	X	E	BX	X			
		LL	—	—	AX	AX	BX	BX	—		
NHMUK R5480	78	UR	—	—	E	—	—	—			
		UL	—	—	E	—	—	—	—		
		LR	A	A	?A	B1X	B1X	C	?B	B1	
		LL	—	—	—	—	B1X	1X	—	(?B)X	
BP/1/1730	79	UR	—	—	(?B)X	—	—	BX			
		UL	—	BX	BX	—	—	—			
TM 81a	80	UR	E	—	—	—	B1X	—			
		UL	B0X	B0X	B1X	B1X	B1X	B(?1)X	—		
		LR	—	—	B1(?X)	1	B(?1)X	B(?1)X	—	—	
		LL	B0X	B1X	B1X	B1X	B1X	B1X	C(?1)X	(?B)1X	
BP/1/1375c	81	UR	(?A)X	—	?A	—	—	—			
		UL	—	AX	E	—	BX	—			
TM 167	81	UR	(?A)X	BX	BX	BX	(?B)X	—			
NHMUK R511	84	UR	—	—	—	—	—	—			
		UL	—	BX	B1X	—	B1X	—			
		LR	—	B0X	B1X	(?B)1X	—	B(?1)Z	B2X	B2Z	
		LL	—	—	—	B2X	B2Z	—	B2X		
TM 5074	~85	UR	—	E	—	—	X-E	1X	1X		
		UL	B0X	B1X-E	B1X	B1X	B1X-E	B1	B1-E		
		LR	B1X	B1X	B1X-E	B1X	B1Y	B2X-E	X		
		LL	—	E	B1(?X)	B1X	B1X	B2X	B1X	E	
NHMUK R511a	86	UR	—	E	—	—	—	B0(?X)	E		
		UL	—	E	B0X	B1X	B1X	(?B)0X			
		LR	A0X	B0X	R	X	B1X	X	B1X		
		LL	A0X	—	X	B0X	B1X	B1X	—		
SAM-PK-K379	89	UL	—	—	BX	BX	BX	BX			
BP/1/2824	~90	UR	—	—	—	—	—	—	BX		
		UL	AX	—	—	—	—	—	(?B)X		
USNM 22812	94	UR	—	A0X	B1X	BX	B1X	B0X			
		UL	—	—	AX	B1X	(?B)X				
		LR	—	(?B)0X	E	(?A)X	BY	—			

Postcanine morphological classes: number of main cusps (A, bicuspid; B, tricuspid; C, multicusped); number of cingular cusps (0, none; 1, one or two cingular cusps; 2, cingular cusps in collar); and number of labial cusps (X, none; Y, one labial cusp; Z, two labial cusps). A question mark between parentheses indicates a tentative score and a dash symbol indicates that the morphology could not be determined because of absence or poor preservation of the tooth. **Abbreviations**: **BSL**, basal skull length; **E**, erupting tooth; **LL**, lower left dentition; **LR**, lower right; **UL**, upper left; **UR**, upper right.

canine is situated anteromedially to the functional canine (Fig. 7A, B). The upper replacement canine did not penetrate the root of the functional canine, but only eroded its surface, leaving a distinct flat facet.

In both dentaries, the old canine root and the replacement canine are positioned posteromedially to the functional one (Fig. 7C, D). The replacement tooth eroded into the root of the functional canine.

Postcanines—In the upper left series, there is no diastema between the canine and PC1, and the root of PC1 contacts the root of the functional canine. Replacement teeth are present in the second, fifth, and seventh positions, and are similar in size (Fig. 7B). The replacement tooth of PC2 has partially eroded the root of the functional tooth. The replacement tooth for PC7 has eroded into the older, nonfunctional tooth. PC4 is not in its final position in the alveolus and has an open root.

In the upper right series, the root of a small PC1 remnant contacts the root of the functional canine. PC2, PC5, and PC7 have replacement teeth, but only the replacement of PC2 has eroded into the root of the functional tooth (Fig. 7A). All of the replacement postcanines are in the early stages of development and only have

the tip of the single main cusp developed. PC4 is in the process of erupting and it retains an open root.

Both mandibles show a similar replacement pattern (Fig. 7C, D). PC2, PC4, and PC6 have replacement teeth, which have eroded into the roots of the functional postcanines. The replacements of PC2 and PC4 are located posteromedially to the functional teeth, whereas the replacement of PC6 is below the functional tooth. The sixth replacement tooth is the largest, followed by the fourth and then the second. We interpret an open root for PC8, but this may prove to be a broken root instead. There is a tiny unerupted PC9. The main difference between the mandibular rami is the presence of an old, partially resorbed postcanine in the former first position on the right ramus (Fig. 7C).

BP/1/7199 (BSL 75 mm)

Incisors—Alveoli of the upper incisors are separated from each other; there is a limited contact between alveoli and the root, which is mostly medial and restricted to the level of the dental margin of the bone. There is evidence of strong bone resorption medially and in many cases the small alveolus of the replacement
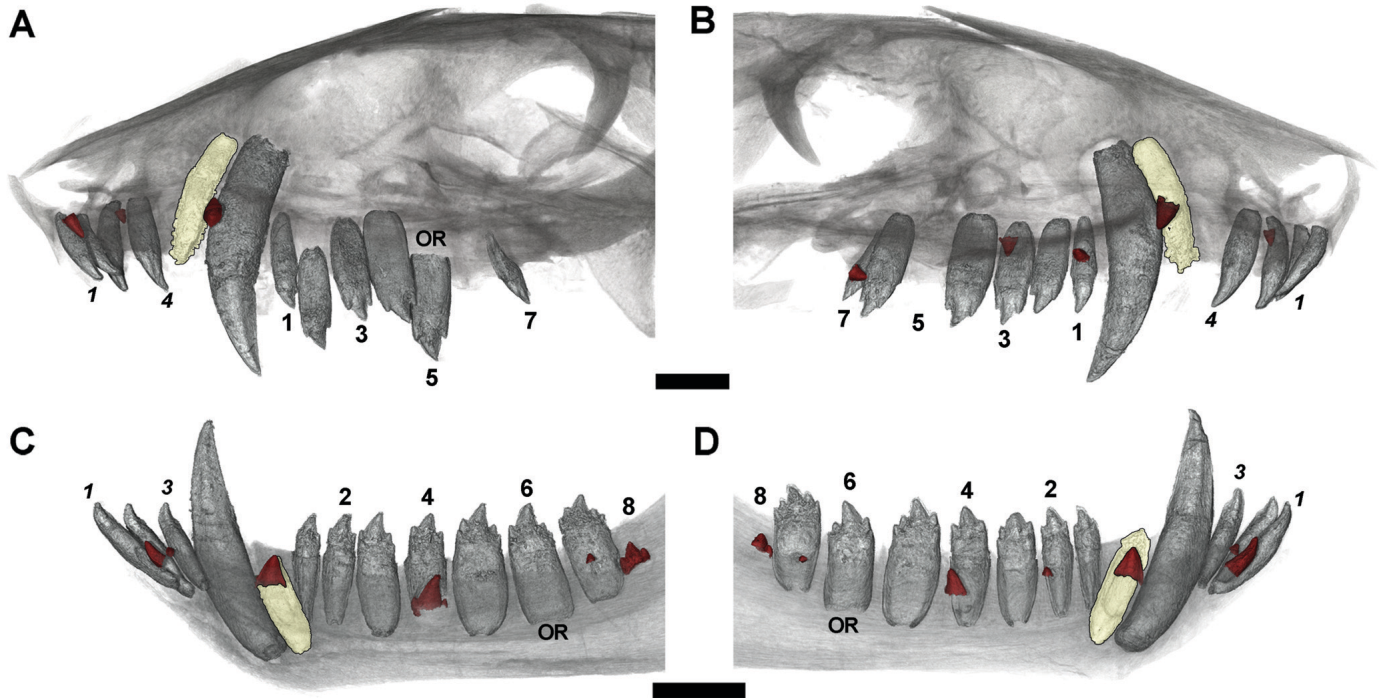
FIGURE 5. Three-dimensional rendering of tooth rows in medial view of a juvenile of *Thrinaxodon liorhinus* (BP/1/5372). **A**, upper right; **B**, upper left; **C**, lower right; **D**, lower left. Replacement teeth in red, old remnant roots in yellow. **Abbreviation**: **OR**, open roots. Arabic numerals indicate incisor (italics) and postcanine positions. Scale bars equal 2.5 mm (**A**, **B**) and 3 mm (**C**, **D**). (Color figure available online.)

is coalescent with the alveolus of the functional incisor. There are replacement teeth for the four right upper incisors and for three of the four left upper incisors (Figs. 8A, B, 9A). Replacement teeth for both I3 are by far more developed than the others (Figs. 8A, B). On the right side, the first and second replacement elements are the same size and are larger than the tiny fourth element (Fig. 8A).

Alveoli of the lower incisors are poorly defined and spaces between roots and alveolar margins are present. Incisors are not touching each other (Fig. 9B). The three left and two of the right lower incisors have replacement teeth (Figs. 8C, D, 9B). The second replacement element on both sides is remarkably large. Both I1 are associated with replacement elements, whereas the I3 of the left dentary shows a smaller replacement tooth (Fig. 9B).

Canine—Both maxillae feature a functional canine, a replacement tooth anterior to it, and the root of an older canine that is preserved anterior to both functional and replacing canines (Figs. 8A, B, 9A). As in BP/1/5372, two separated alveoli accommodate the functional and the remnant root proximally, and coalesce to one large alveolus distally. A third alveolus with a new replacement canine is medial to the remnant root, at the level of the palate (Fig. 9A). There is a space separating the root from the alveolar margin, with a limited contact near the ventral margin of the maxilla. The replacing canine on the left maxilla is slightly larger than the right. The proximal part of the older canine root has been etched, whereas the right older root is more complete. There is clear bone deposition taking place on the former pulp cavity of the old canine root.
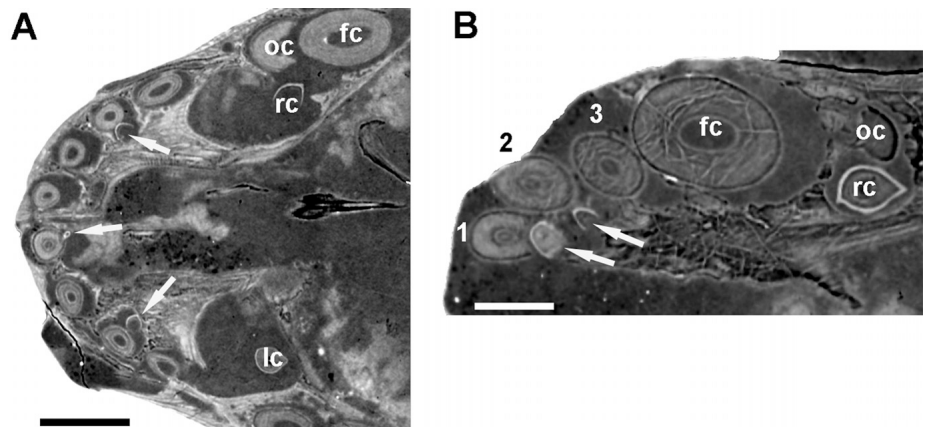

FIGURE 6. Virtual horizontal cross-section of **A**, upper and **B**, lower jaws of a juvenile of *Thrinaxodon liorhinus* (BP/1/5372). **Abbreviations**: **fc**, functional canine; **lc**, lower canine; **oc**, old canine; **rc**, replacement canine. Arrows indicate replacement incisors. Arabic numerals indicate lower incisor positions. Scale bars equal 2 mm (**A**) and 1 mm (**B**).
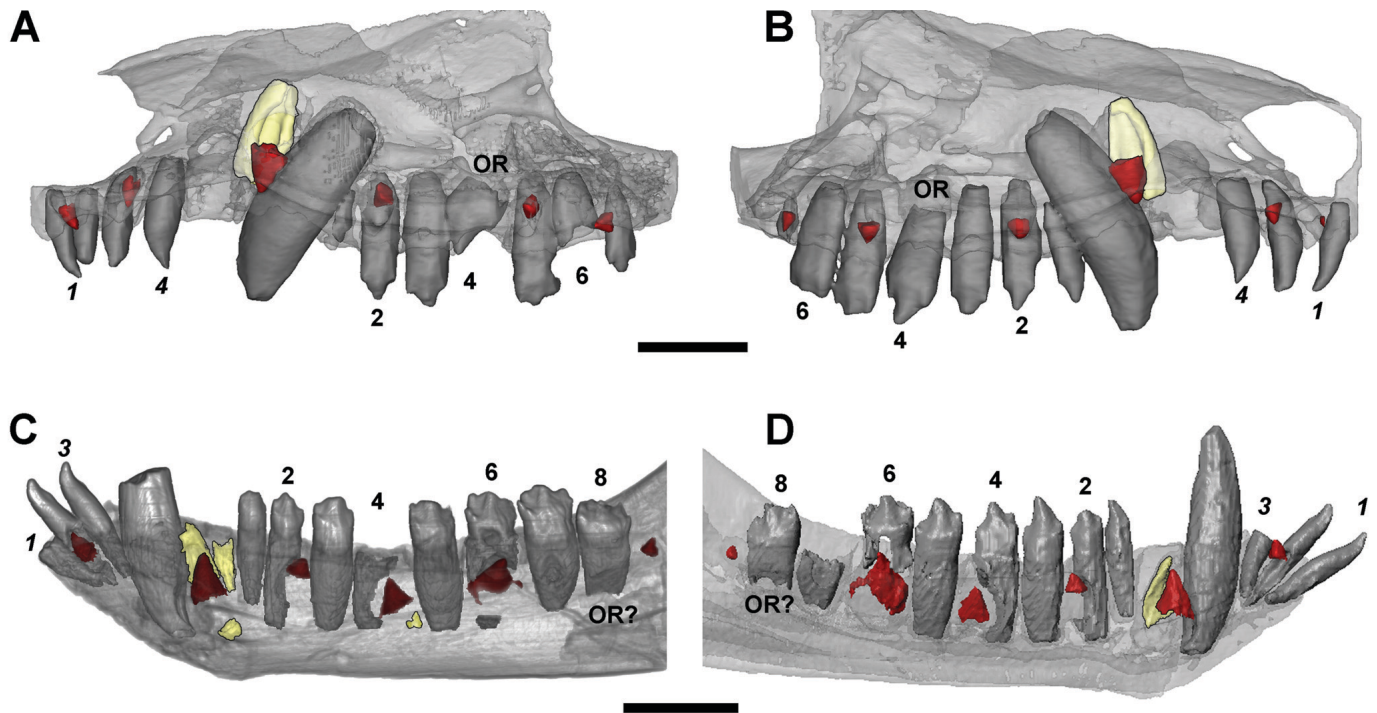
FIGURE 7. Three-dimensional rendering of tooth rows in medial view of a juvenile of *Thrinaxodon liorhinus* (TM 80A). **A**, upper right; **B**, upper left; **C**, lower right; **D**, lower left. **Abbreviation**: **OR**, open root. Replacement teeth in red, old remnant roots in yellow. Arabic numerals indicate incisor (italics) and postcanine positions. Scale bars equal 5 mm. (Color figure available online.)

In the dentaries, there are two alveoli distally that coalesce in one large alveolus. The replacing canines are almost erupted behind the functional ones (Figs. 8C, D, 9B). There is a large space between the root and the alveolar margin laterally and slight contact between these elements medially. In the left dentary, there is a root remnant lateral to the canine replacement tooth (Fig. 8D).

Postcanines—In the upper left series, there is no diastema between the canine and the first postcanine ('X'; Fig. 8B), and the root of this postcanine almost contacts the root of the functional canine. There are replacement elements for the PC1, PC2, PC4, PC5, and PC6 (Fig. 8B). The largest replacement tooth is the first, followed by similarly sized replacement teeth in the fourth and sixth positions. The tiny replacement tooth in the fifth position is the smallest.

In the upper right series, there is a small space between the canine and PC1. The PC2, PC4, and PC6 have replacing elements (Fig. 8A). The fourth replacing tooth is the largest followed by the sixth and finally the second. PC7 is erupting and has an open root.

The first lower postcanines on both sides are clearly connected to the bone, because it is difficult to differentiate between the bone and the teeth. Both PC6 have a large replacement tooth, and and they are also connected to bone. Remaining postcanines show spaces between the alveolar margin and their roots.

In the lower left series, the third tooth is erupting. Replacement teeth are represented in the fourth, sixth, and seventh positions (Fig. 8D). PC8 is erupting and is larger than the replacement teeth. The sixth replacement tooth is the most developed, whereas both fourth and seventh replacement teeth are tiny. Root remnants of former postcanines are present posterior to PC1, PC2, and PC4 (Fig. 8D).

In the lower right series, as observed in the left tooth row, the third tooth is erupting and has an open root. PC4 and PC6 have replacement teeth (Fig. 8C), whereas PC8 is erupting. As in the left side, the newly erupted PC8 is larger than the sixth replacement tooth, which is larger than the fourth. Remnants of old roots are present posterior to the PC1, PC2, and PC4 (Fig. 8C).

TM 180 (BSL 75 mm)

Incisors—On the right side of the upper jaw, only the second functional incisor has a replacement tooth, whereas all four upper incisors on the left side have replacement teeth (Fig. 10A, B). The upper left replacement teeth of I1 and I3 have eroded into the roots of the functional incisors, and these replacement teeth are more developed than those for I2 and I4. In both the right and left upper jaws, there is a remnant of an older root anterolateral to I2.

In the left and right mandibular rami, I1 has a replacement tooth positioned posterior to the functional one (Fig. 10C). The replacement for the third left element is placed medially. None of these replacement teeth have eroded into the functional incisors. On both sides of the mandible, there is a fragment of an old incisor near the anterior edge of the first tooth, and near the lateral edge of the third incisor. In the right mandibular ramus, there is a root remnant, anterior to the functional canine, which is interpreted to be that of an old incisor.

Canine—In the upper jaws, the old canine root is positioned anterior to the functional one, and the replacement tooth is situated anteromedially to the functional canine (Fig. 10A, B). The replacement canine did not erode into the root of the functional canine, although there is a flat facet on the root of the functional
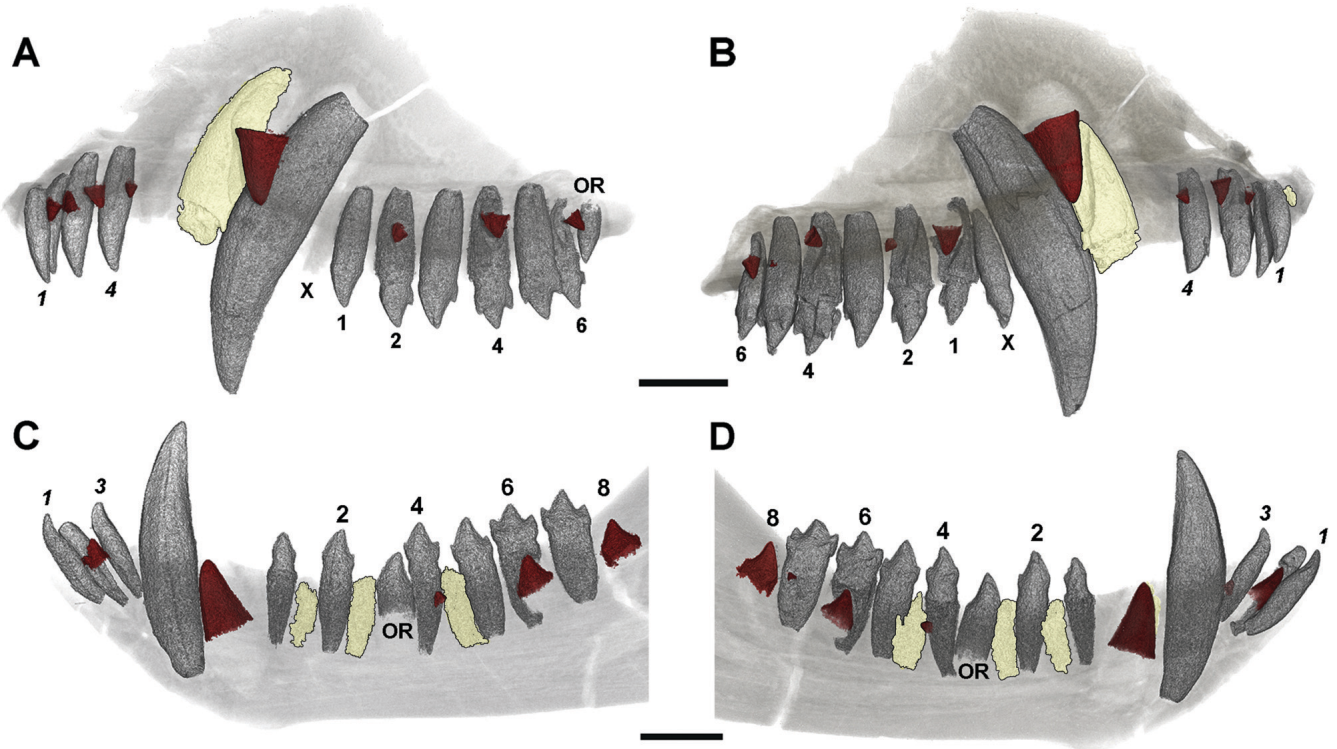
FIGURE 8. Three-dimensional rendering of tooth rows in medial view of a subadult specimen of *Thrinaxodon liorhinus* (BP/1/7199). **A**, upper right; **B**, upper left; **C**, lower right; **D**, lower left. **Abbreviations**: **OR**, open root; **X**, position that indicates a shed PC1 that is homologous with the PC1 on the other side of the jaw. Replacement teeth in red, old remnant roots in yellow. Arabic numerals indicate incisor (italics) and postcanine positions. Scale bars equal 5 mm. (Color figure available online.)

canine dorsal to the replacement canine (Fig. 10A). The replacement canine instead eroded into the root of the old canine tooth (Fig. 10A, B).

Although the right lower functional canine is not fully developed (no root) and is in the process of erupting (Fig. 10C), the left lower canine is fully erupted and has a long root. The right lower erupting canine has eroded into the root of the old canine, which is located posteriorly.

Postcanines—In the upper left series, the diastema is larger than on the right side of the upper jaw, and the definitive loss of a former tooth, indicated as 'X' (Fig. 10B), is interpreted for the left tooth row. The root of PC1 does not contact the root of the functional canine, but it has eroded into its old root that is located laterally (Fig. 10B). In position 2, the small replacement tooth has partially eroded the medial edge of the PC2 root. PC2 also has a fragment of an old root that is partially resorbed. The root of PC4 is completely eroded on its medial edge by the large replacement tooth (Fig. 10B). This replacement tooth is well developed, with an anterior accessory cusp fully visible. There is a root remnant located between PC4 and PC5, and it appears to be a remnant of an old PC5. The PC6 is a developing tooth that is located in the medial replacement pit (there is no alveolus that could contain a
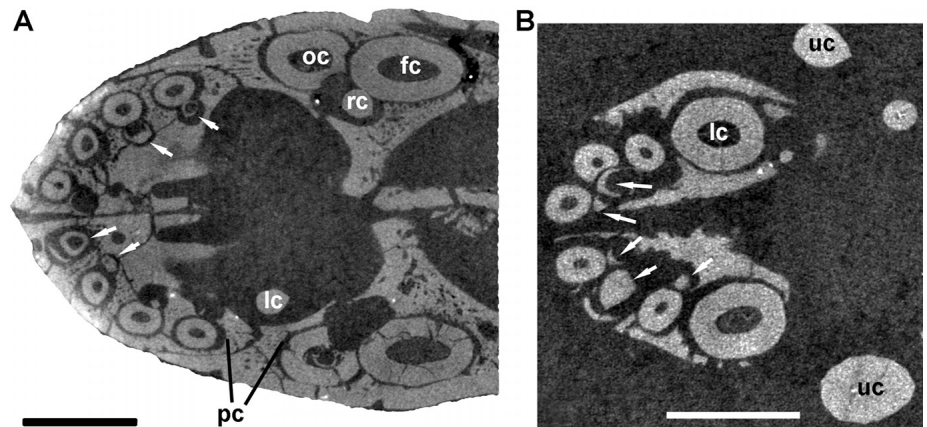

FIGURE 9. Virtual horizontal cross-section of a subadult specimen of *Thrinaxodon liorhinus* (BP/1/7199). **A**, upper jaw and **B**, lower jaw. **Abbreviations**: **fc**, functional canine; **lc**, lower canine; **oc**, old canine; **pc**, paracanine fossa; **rc**, replacement canine; **uc**, upper canine. Arrows indicate replacement incisors. Scale bars equal 10 mm.
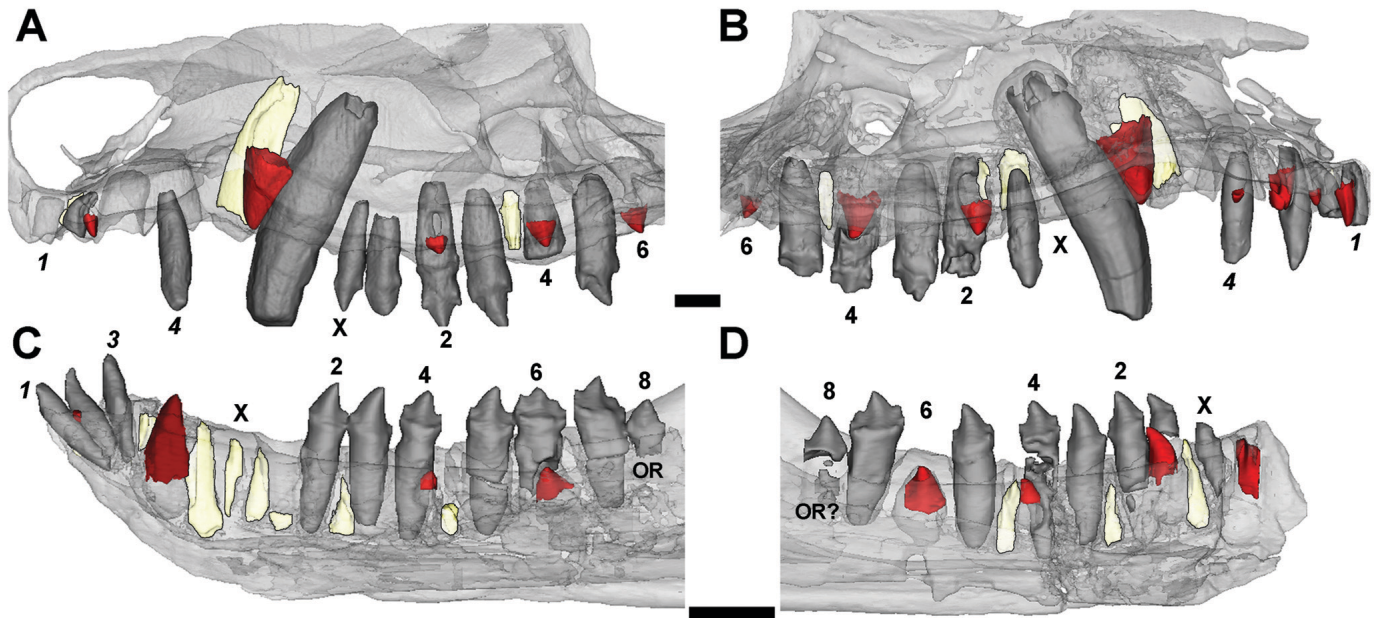
FIGURE 10.   Three-dimensional rendering of tooth rows in medial view of a subadult specimen of *Thrinaxodon liorhinus* (TM 180). **A**, upper right; **B**, upper left; **C**, lower right; **D**, lower left. **Abbreviations**: **OR**; open root; **X**, postcanine in the process of being shed (or already shed) without replacement, excluding the locus of the next replacement sequence. In **D**, the anterior part of the left mandibular ramus is not shown because it is attached to the right ramus, and the anterior-most tooth in red is a fragment of the replacement canine. Replacement teeth are in red, old remnant roots in yellow. Arabic numerals indicate incisor (italics) and functional postcanine positions. Scale bars equal 2.5 mm (**A**, **B**) and 5 mm (**C**, **D**). (Color figure available online.)

functional tooth); this is similar to the condition of the right PC6 (compare Fig. 10A, B). The posterior replacement tooth (PC4) is more developed than the anterior replacement tooth (PC2).

In the upper right series, the first postcanine is labeled 'X' (Fig. 10A) because it is interpreted to be homologous with the first already shed and not replaced tooth that would have present in the larger diastema of the left series (Fig. 10B). The root of this first tooth does not contact the root of the functional canine (Fig. 10A). The medial edges of the roots of PC2 and PC4 are eroded by replacement teeth. The posterior replacement tooth (PC4) is more developed than the anterior replacement tooth (PC2). The developing PC6 is starting to erupt. There is a remnant of a tooth root located between PC3 and PC4 (Fig. 10A).

In the lower left series, the first postcanine ('X'; Fig. 10D) appears to be in the process of being resorbed into the jaw because the interface between the jaw bone and tooth is indistinct in the coronal μCT slices. An old tooth fragment, located between PCX and PC1, is eroded on its posterior edge; therefore, it may represent the old PC1. There is a replacement tooth located medial to PC1, and a fragment of an old, partially resorbed tooth situated between PC2 and PC3 and also between PC4 and PC5 (Fig. 10D). The medial edge of PC4 root is eroded by a replacement tooth. The anterior replacement tooth (PC1) is more developed than the posterior replacement tooth (PC4). PC6 is in the process of erupting: the tip of the tooth has not yet eroded the alveolar margin, but the tooth is visible in the replacement pit (Fig. 10D).

In the lower right series, the identities of the postcanine tooth positions posterior to the functional and the old canine remnant are not clear due to the presence of three other roots fragments embedded within the diastemal region of the mandible (Fig. 10C). The anterior-most fragment is situated within an alveolus that has been infilled with bone ('X'; Fig. 10C), and it is likely a remnant of PC1 because it is not eroded on its anterior edge like the adja-

cent old canine. Additional evidence is that on the left mandibular ramus, the first postcanine (PCX) is undergoing resorption and that the right side shows slightly more advanced resorption of PC1 and infilling of the tooth socket. The other two posteriorly situated fragments associated with an open alveolus (Fig. 10C) are considered to be part of an old postcanine, hereby labeled as PC1 according to our requirements for numbering postcanines (see Materials and Methods, above). PC3 is eroding into the old root located between PC2 and PC3. A small replacement tooth is eroding into the root of PC4, whereas the sixth element has a larger replacement tooth eroding into its root. PC8 is in process of erupting and has an incomplete root.

BP/1/5905 (BSL 87 mm)

Incisors—Only I4 of the left premaxilla is preserved in situ, and is associated with an incipient replacement tooth (Fig. 11B). In the dentary, there are three left and two right incisors preserved, but no replacement teeth are observed (Fig. 11C, D).

Canine—In the maxillae, both functional canines are being replaced by teeth erupting immediately anterior to them (Fig. 11A, B). Unlike the smaller specimens described previously above, the remains of older canines roots are not present. However, because the canine roots are crushed inside the canine sockets, the lack of root remnants might be due to poor preservation.

Both dentaries lack a replacement canine (Fig. 11C, D). However, the roots of both canines are severely damaged, making it difficult to determine the replacement more precisely. There are remnant roots of an old canine anterior to the functional canine on both sides.

Postcanines—In the upper right series, the poorly preserved postcanine series shows only an incipient replacement tooth between the fifth and sixth positions (Fig. 11A).
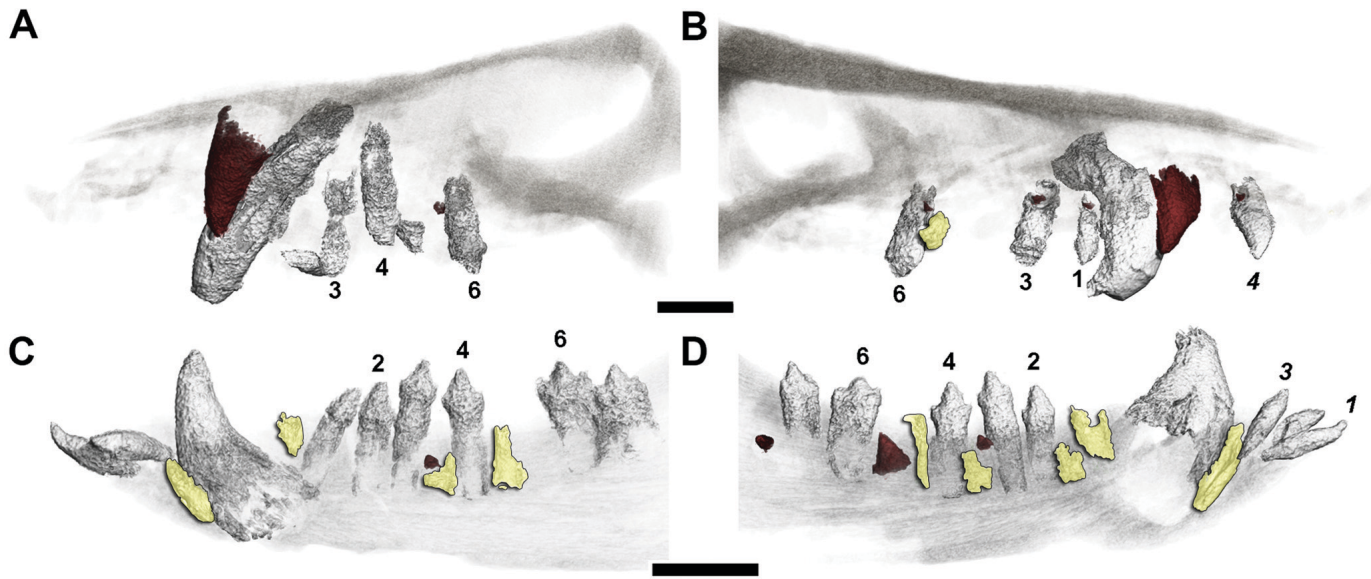
FIGURE 11. Three-dimensional rendering of tooth rows in medial view of an adult specimen of *Thrinaxodon liorhinus* (BP/1/5905). **A**, upper right; **B**, upper left; **C**, lower right; **D**, lower left. Replacement teeth in red, old remnant roots in yellow. Arabic numerals indicate incisor (italics) and postcanine positions. Scale bars equal 6 mm (**A**, **B**) and 7 mm (**C**, **D**). (Color figure available online.)

In the upper left series, only PC1, PC3, and PC6 are present, the first two are associated with incipient replacement teeth that are similar in size (Fig. 11B), whereas a third replacement tooth is placed between the fifth and sixth positions.

In the lower right series, a single incipient replacement tooth is visible between the PC3 and PC4 (Fig. 11C). There are remnants of older teeth anterior to PC1, and posterior to both PC3 and PC4.

In the lower left series, two replacement teeth and a newly erupting PC8 are visible (Fig. 11D). The anterior-most replacement tooth is located in a position between PC3 and PC4. The fifth replacement tooth is the most developed, already showing a posterior accessory cusp. There are four remnants of roots: in the first tooth position, anterior to the deep portion of the root of PC2, between PC3 and PC4, and also posterior to PC4.

Quantitative Assessment of Postcanine Replacement

Comparison of the anteroposterior length (APL) of the lower PC6 (APL = 2.4 mm) and its associated replacement tooth (APL = 2.67 mm) in TM 80A reveals that the increase in the replacement tooth size is ca. 12%. We measured on both sides of the mandible of BP/1/7199 the variation between PC3 and PC2 (16% and 13% of increase) and between PC3 and PC4 (15% and 5% of increase), giving an average of 12.25%.

The results obtained for the number of replacement cycles is not consistent and varies from three to 14 in the upper series and from three to six in the lower (Table 5). The values indicate three or four replacements for the anterior-most postcanine on both the upper and lower dentitions; four or five replacements for the third lower postcanine; six or seven replacements for the third upper and second lower postcanines, and 13 or 14 for the fifth upper postcanine (Table 5). Because the APL measurements to do this analysis were obtained from elements in the anterior and central portions of the lower dentition (see Fig. 3), we assume that the number of estimated replacements is more accurate for these portions of the dental series. In addition, the 13 or 14 replacements estimated for the fifth upper postcanine are indeed influenced by the fact that the

APL of the fifth tooth of BP/1/5905 was compared with the seventh (ultimate and smaller) element of BP/1/5372. Thus, the use of the tiny crown (PC7 in BP/1/5372) to calculate the ratio for the geometric sequence will result in an overestimation of the number of replacements.

TABLE 5. Maximum length of the postcanine crown (in mm) of the smallest (BP/1/5372; BSL = 37 mm) and largest (BP/1/5905; BSL = 87 mm) μCT-scanned specimens of *Thrinaxodon liorhinus*.

Postcanine locus	BP/1/5372	BP/1/5905	Percentage of difference	Number of replacements
UP				
1	0.78	X		
2	1.11	X		
3-1	1.15	1.74	51%	3–4
5-3	1.33	2.86	115%	6–7
7-5	0.65	3	362%	13–14
LP				
1	0.8	X		
2	0.89	X		
3-1	1.22	1.87	53%	3–4
4-2	1.14	2.43	113%	6–7
5-3	1.54	2.63	71%	4–5
6-4	1.5	2.87	91%	5–6

We assumed that the two first anterior postcanines in BP/5905 were lost (see also Figs. 14, 15) and thus the homologous tooth loci were compared here. The percentage of difference indicates how much larger the homologous tooth is in the larger specimen BP/1/5905. Using the value of 12% as indicating one tooth replacement after evidence gathered from TM 80A and BP/1/7199 (see Materials and Methods), we indicate the possible number of times the postcanine was replaced in the dental locus. With the exception of the first two teeth of BP/1/5372, only the postcanines preserved in both specimens are presented here. **Abbreviations**: **BSL**, basal skull length; **LP**, lower postcanines; **UP**, upper postcanines; **X**, loss of postcanine.

DISCUSSION

Tooth Morphology and Number

Anterior Teeth—The formula of four upper and three lower incisors in *Thrinaxodon liorhinus* is one of the most consistent in non-mammaliaform cynodonts. This formula is present in basal Permian cynodonts and is retained by the vast majority of Early–Middle Triassic cynodonts (Hopson and Barghusen, 1986; Abdala, 2007). An increase in the incisor number is observed in the Late Permian *Procynosuchus* (see cladogram in Fig. 16) and *Dvinia*. From the Upper Triassic to the Jurassic, there are trends towards the reduction in the number of incisors, a condition represented in advanced traversodontids (e.g., *Exaeretodon*), the tritheledontid *Pachygenelus*, and in all tritylodontids (see Fig. 15). In contrast, basal Mammaliaformes such as *Sinoconodon* and *Morganucodon* show an increase in the number of incisors.

The ultimate upper incisor in some immature specimens of *Thrinaxodon liorhinus* (e.g., SAM-PK-K10016, TM 80A, and TM 782) morphologically resembles the canine, mostly because the anteroposterior orientation of the long edge of the tooth is similar to that of the canine. This condition is also represented in the traversodontid *Menadon*, where the last two upper incisors are caniniforms (Kammerer et al., 2008). The last incisor of *T. liorhinus* may have functioned for prey capture but also, as is typical of canines, for retention of prey items (Ungar, 2010).

Our extensive survey of *Thrinaxodon liorhinus* specimens representing all ontogenetic stages revealed only one case of double canines (see Fig. 2F). It is interesting that this occurred in a juvenile, and that the double canine is only observed on one side of the tooth row, suggesting that the other side was more advanced, the old canine being already lost. Gow (1985:12) stated that there could be "shift of dominance with age from the anterior to the posterior canine," although he was unsure why this switch occurred. The evidence provided by this juvenile specimen suggests that at some early stage, the retention time of the functional canine was extended. This seems to be particularly the case when the replacement upper canine is erupting posteriorly to the functional one, which is rarely the case in this taxon.

Postcanines—The number of postcanines recorded in our sample varied from five to nine uppers and six to nine lowers (Table 3). The smallest number of upper postcanines is represented in TM 782, in which both sides show five elements. An inordinate number of nine upper postcanines was observed in SAM-PK-K10016 (Fig. 2). This seems to be an exceptional case because similar-sized specimens such as SAM-PK-K10017 have seven postcanines, the same number observed in smaller specimens such as BP/1/5372. The majority of specimens (27) indicate that the typical number of upper postcanines in the species is six (Table 3).

The smallest number of mandibular postcanines is six, as observed in gross view of SAM-PK-K1468 and on only one side of the mandible in specimens TM 80B and NHMUK R3731 (Table 3). Variations of seven or eight postcanines are almost equally distributed in our sample (nine specimens with seven postcanines and nine with eight postcanines), and both should be considered as the typical number of lower postcanines in *Thrinaxodon*. Nine is the largest number of lower postcanines, which was observed in the adult specimen SAM-PK-K378 and in the juvenile μCT-scanned TM 80A. On the left side of TM 180, there are also nine lower postcanines, but the first one (PCX) is in process of being shed without replacement (Fig. 10D).

The simple anterior postcanines (type A) with a high, slightly curved backward main cusp and tiny or absent accessory cusps were probably used in conjunction with the anterior dentition in capturing, retaining, and killing the prey. The complex 'triconodont-like' postcanines (type B or C) from the middle and posterior portions of the tooth row with well-developed accessory

cusps and a cingulum were indeed used to puncture and tear food, and to reduce food item size before swallowing (Crompton, 1974; Lucas and Peters, 2000). The postcanine morphology of *T. liorhinus* suggests shearing between the upper and lower teeth, whereas the presence of a cingulum has been considered as important in the cynodont *Procynosuchus* for tearing off cuticles of insects (Kemp, 2005). The posterior lower postcanines of *T. liorhinus* are very similar to those of the mammaliaform *Morganucodon* (Crompton and Jenkins, 1968; DeMar, 1972), but a major difference between these taxa is the lack of wear facets in the postcanines of *T. liorhinus*, indicating the absence of dental occlusion between upper and lower postcanines (Crompton, 1974). This condition is most likely linked with the alternate multiple replacements of the postcanines in *Thrinaxodon*.

The upper postcanines of *Thrinaxodon*, independent of ontogenetic age, are simpler (with the maximum complexity consisting of a tricuspid tooth that lacks a cingular collar) than the lower postcanine morphology. A similar condition was also noted for *Prozostrodon brasiliensis* (formerly *Thrinaxodon brasiliensis*; see Abdala and Giannini, 2002:fig. 8; Bonaparte and Barberena, 2001).

Multicusped lower postcanines appear to be linked with the age of the individual. They are present in specimens with a BSL up to 80 mm (e.g., TM 81a), whereas in larger specimens the maximum complexity of lower postcanines is only a tricuspid tooth. A maximum of four multicusped lower postcanines is observed in the tiny specimen BP/1/5372, whereas in larger specimens that have multicusped postcanines, there is only one or two of these complex teeth in each dental row. Usually multicusped teeth are located posteriorly in the series (from the fifth to eighth positions). The only exception is, again, the juvenile BP/1/5372, in which both mandibular PC3 are multicusped.

The lingual cingulum is a feature that is associated with the postcanine morphology of *Thrinaxodon*. We defined two kinds of cingula, the most simple is composed of cingular cusps that do not form a collar around the tooth, and the more complex have a collar formed by a series of cingular cusps. The collared cingulum is only present on lower postcanines. The smallest specimen that shows a cingular collar is SAM-PK-K378 (BSL >68 mm) and the largest is TM 5074 (BSL = ∼85 mm). In some cases, collared cingula are present on PC3, but this complex morphology is more commonly observed on PC5 and PC6. There is only one case of a collared cingulum for a PC7 and three cases for a PC8 (Table 4).

Five specimens showed development of labial cingular cusps. There is a single case of the presence of this cingulum on an upper postcanine: the left PC6 of SAM-PK-K378. Labial cusps on the lower postcanines are represented in specimens ranging from 68 to 85 mm of basal skull length. In five specimens, the PC5 in one hemimandible has a labial cingulum. TM 180 represents an extreme case with six teeth having a labial cingulum.

During early ontogeny, the morphology of the upper and lower postcanines increases in complexity, but this decreases in older adults (e.g., NHMUK R511a). It is interesting to note some variations in the morphology of similar-sized individuals. In BP/1/7199, there are no multicusped lower postcanines (Table 4), in contrast with the similar-sized TM 180 that not only has multicusped posterior lower postcanines, but these teeth show the most complex morphology of all the dental series in our sample. We interpret this as an individual variation of TM 180 because this complexity is not duplicated in any of the other sampled specimens.

Dental Replacement

Although evidence is not clear-cut, osseous connection of the postcanine root with the alveolus seems to be represented (or at least is more common) in functional postcanines where there is replacement activity, either manifesting in the form of presence of
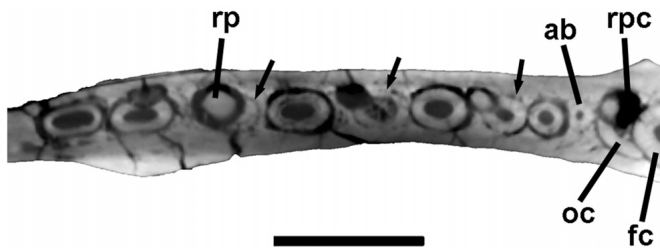
FIGURE 12. Virtual horizontal cross-section of right lower postcanine row of TM 80A. **Abbreviations**: **ab**, alveolus of the former first postcanine infilled by bone; **fc**, functional canine; **oc**, old canine; **rp**, replacement post-canine; **rpc**, replacement cavity of the canine; **uc**, upper canine. Arrows indicate osseous connection of roots of functional postcanines that have replacement activity. Scale bar equals 50 mm.

a replacement cavity or as a replacement tooth (Fig. 12). Our observations show that replacement of the teeth generally starts with erosion of the root of the functional tooth, separating the crown from the proximal portion of the root. The crown of the tooth is then lost, but the uneroded part of the root remains in the jaw. This root remnant is eventually resorbed, but a portion of it may persist for long periods of time and there is evidence that the relative position of the teeth have changed during growth of the skull and jaws (e.g., specimen TM 180 has a remnant of a postcanine root that occurs between PC3 and PC4 on the upper right side, and between PC4 and PC5 on the upper left and on both mandibles; Fig. 10). Although these root remnants are quite rare in incisor alveoli, they have been clearly observed adjacent to some of the upper and lower canines of μCT-scanned specimens. Remnants of postcanine roots were noticed in the larger specimens TM 180, BP/1/7199 (only in the mandible), and BP/1/5905.

Incisors—Only a brief description of incisor replacement, limited to recognition of the existence of replacement in some incisors, was presented by Hopson (1964) and Gow (1985). Here for the first time, we provide evidence of the timing and pattern of incisor replacement in *Thrinaxodon*. Timing between replacements of successive adjacent teeth appears slower for the smaller juveniles BP/1/5372 and TM 80A (Figs. 5, 7), which only have replacement in first and third positions, whereas larger specimens BP/1/7199 and TM 180 show replacement activity associated in nearly all of the incisors. There is evidence of alternate replacement for the incisor series (e.g., left upper of BP/1/5372; right and left uppers of TM 80A; and left upper and both lowers of BP/1/7199 and TM 180). In addition, a definite synchrony is clear, not only in the replacement loci between left/right dentitions (e.g., I1 and I2 on both sides of the mandible show replacement in BP/1/5372), but also in the degree of development of the replacement elements in left/right homologous positions.

Canines—The μCT-scanned specimens allowed observation of the canine replacement activity that could not be fully understood from direct (gross) observation of fossils. In addition, at least 17 exhaustively prepared specimens in our sample (see also Crompton, 1963; Gow, 1985) show replacement activity at different ages.

In four of the μCT-scanned specimens, it is clear that all the replacement canines (upper/lower, left/right) show a similar degree of development (Figs. 5, 7, 8, 10), whereas in BP/1/5905 only the upper postcanines show replacements, which are in a roughly similar degree of development (Fig. 11A, B). This evidence suggests that there is a common switch that starts the development of these teeth in the individual.

As previously noted (Hopson, 1964; Gow, 1985), the canine replacement pattern differs in the skull and the mandible. In the mandible, the replacement canine develops posteriorly to the functional tooth, whereas in the cranium, the replacement canine usually develops anteriorly (see Fourie, 1974:fig. 33A). Although this pattern is confirmed by the majority of the studied specimens, some specimens show a different pattern for the upper canine replacement. For instance, three small specimens BP/1/1375a, TM 1486, and SAM-PK-K10016 show an upper replacement tooth that is posterior to the functional canine. In TM 1486, an additional smaller replacement bud is located medially against the root of the functional canine (as described by Gow, 1985). In the juvenile SAM-PK-K10016, the replacement canine on the left side is positioned posterior to the functional canine (Fig. 2F), whereas on the right only one functional canine is visible. This specimen shows retention of the old functional canine so that on one side it appears to have two canines, a condition common in some basal therocephalians (Kermack, 1956; Van den Heever, 1980). Fourie (1963, 1974:392–393) also observed a single case of a posterior replacement of an upper canine in *Thrinaxodon*, and suggested an "alternation of consecutive generations of functional canines between the anterior and posterior halves of the alveolus."

In all the μCT-scanned specimens, there are root remnants of an old upper canine, which was partially eroded by the development of the functional canine and, also, in some cases, by the new replacing one (Figs. 7A, B, 8A, B). In all these cases, the root remnants are located anterior to the functional canine (see also Fourie, 1974:fig. 33A).

None of the μCT-scanned specimens directly show a posterior replacement of the upper canine, but it is interesting to note that the old canine root remnants are situated anterior to the root of the functional canine, suggesting a migration of the erupting tooth. This migration appears to be supported by differences in relative locations of the upper canines in BP/1/2824. In that specimen, the recently erupted right canine is located more posteriorly along the jaw than the left one. We interpret that the canine was recently replaced only on the right side, whereas the functional left canine was not recently replaced. This evidence also suggests a forthcoming posterior migration of the newly erupted canine (see also discussion of postcanine replacement below). This hypothesis of canine migration was also proposed by Osborn and Crompton (1973:4–5) for the lower canines.

In the lower jaw, remnants of the old canine are observed in all μCT-scanned *Thrinaxodon* specimens. In most cases, they are located posterior to the functional canine, with the exception of BP/1/5905, which shows remnants of old canines anterior to the functional lower canine, and a tiny tooth fragment in the right lower jaw of TM 180 is also interpreted as an old canine remnant. However, due to the poor preservation of the functional canine roots of BP/1/5905 (Fig. 11C, D), these remnants could also represent displaced fragments of the functional canine. A lateral facet on the root of the functional lower canine, produced by activity of the erupting canine, is observed in TM 80A (Fig. 7C).

In the mandible, a diastema is absent between the last incisor and the functional canine, whereas in the skull, this space is present and is where the paracanine fossa is located (e.g., Fig. 9A). There is a reduced diastema or none between the upper canine and first postcanine, and in some cases, the root of the first upper postcanine is very close to or even in contact with the canine root (Figs. 5A, 7A, B).

From our survey, it appears that the rate of replacement of the canine is relatively higher in juveniles, with two cases that show two replacement teeth occurring at the same time, suggesting a short time separating the successive replacements. We measured in BP/1/5372 the anteroposterior length (APL) of the roots of the

remnants and functional canines from the skull and the mandible (Fig. 13). In the skull, the APL of the remnant is 58% that of the functional canine (0.77 vs. 1.42 mm; Fig. 13A), whereas in the mandible, it reaches 69% (0.82 vs. 1.19 mm; Fig. 13B). These percentages are intended for providing a rough estimation of the proportional difference between successive canines, because we are unsure about the precise homology of the points measured in these teeth.

Postcanines—Before we discuss postcanine replacement patterns gleaned from our studied specimens, we first need to review the postcanine replacement theories previously proposed for *Thrinaxodon liorhinus*.

Crompton (1963) interpreted that postcanine tooth replacement in *T. liorhinus* had an alternate pattern based on the Zahnreihen theory of Edmund (1960, 1962, 1969; see also DeMar, 1972, 1973), which proposed an explanation for the pattern of tooth replacement in living and extinct reptiles. This theory accounts for the pattern of tooth replacement in reptiles as the result of an impulse passing along the margin of the dental lamina and initiating a tooth germ at regular intervals (Edmund, 1962, 1969). The new bud grows and moves away (i.e., dorsally in the dentary and ventrally in the maxilla) from the dental lamina as the impulse progressed posteriorly, initiating another dental bud. The tooth series produced by an impulse is a Zahnreihe. This process would imply that replacement in animals with continuous growth throughout life is not a by-product of tooth wear but a controlled mechanism to avoid having adjacent teeth absent from the tooth series at the same time (Berkovitz, 2000). Crompton (1963; see also Hopson, 1964) interpreted the postcanine replacement sequence in *T. liorhinus* as being formed by impulses traveling posteriorly in the jaws and proposed that after the migration of the first impulse posteriorly through two and a half tooth positions, the next impulse started at the first position. This process will result in a posterior-to-anterior wave of development of alternate teeth (see Crompton, 1963:fig. 13). In addition to this, Crompton (1963) was able to recognize that the postcanine series had a posterior migration, with loss of anterior elements and addition of posterior ones. The sequence interpreted by Crompton (1963) from his sample (skulls of 36–89 mm in length) includes six Zahnreihen, and the loss of at least three anterior postcanines in the posterior migration of the series. Osborn and Crompton (1973), in a study focused on the lower postcanines, proposed that replacement in *T. liorhinus*, although polyphyodont, was limited in comparison with living reptiles. They then interpreted this condition as a first step in evolution of non-polyphyodont dentitions and considered that the simpler pattern of the last postcanines in larger animals illustrated reduced activity of the dental lamina in adult *T. liorhinus*. They speculated that a new-born *T. liorhinus* would develop the earliest 'strongly cusped' postcanines (i.e., our C type) at positions 3 and 4 (representing the end of the series in the specimen) and that only these complex postcanines would have been present in small, younger specimens. Osborn and Crompton (1973) replaced the Zahnreihen model with the 'tooth families' model in which there is a localized control that is repeated in each individual tooth position (Osborn, 1970, 1973, 1975). The area in which a dental bud is produced generates an inhibition zone, which will prevent initiation of new teeth in the vicinity of the forming bud (Osborn, 1975, 1977; Westergaard, 1983). The replacement sequence in the tooth families model is linked with the morphology of the teeth in each dental position so that it will change from a more complex to less complex morphology (from P type to M type and finally to A type in Osborn and Crompton's [1973] morphological classification of the postcanines).
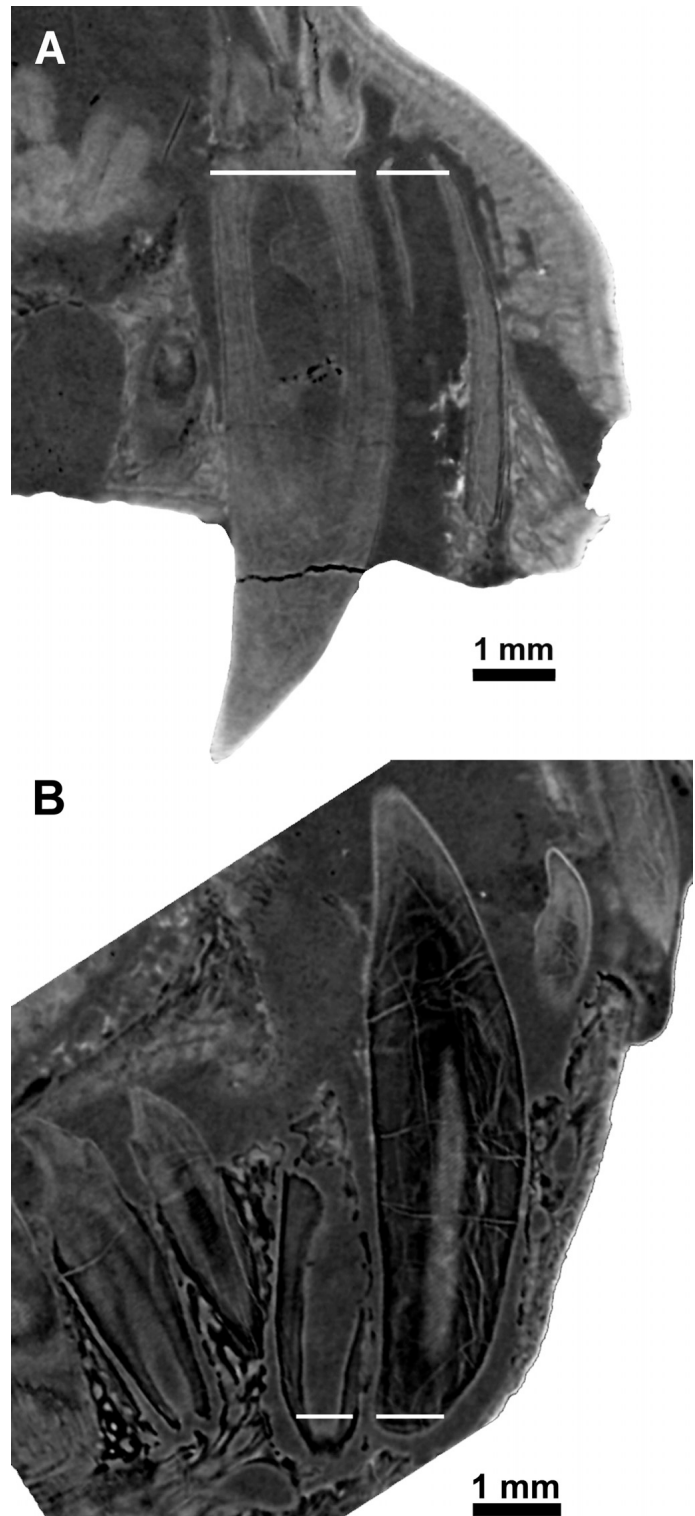

FIGURE 13. Virtual sagittal cross-section of **A**, upper and **B**, lower canines of a juvenile *Thrinaxodon liorhinus* (BP/1/5372). White lines indicate where the root lengths of functional and old remnant canines were measured. Measurements were done on the coronal cross section from μCT data (not shown here).

A

	1	2	3	4	5	6	7	8	9
BP/1/5372 37mm	▽		▽		OR	?▽			
TM 80A 56mm	X	▽		OR	▽		▽		
BP/1/7199 75mm	X	X	▽	▽		▽	▽	▽	
TM 180 76mm	X	X	▽		▽		▽	▽	

B

	1	2	3	4	5	6	7	8	9	10
BP/1/5372 37mm		*△		*△		OR*	△	△		
TM 80A 56mm	X		*△		*△		*△		?OR*	△
BP/1/7199 75mm	X			△	*△		*△	△	*△	
TM 180 75mm	X	△			*△		*△		△	
BP/1/5905 87mm	X	X			*△		*△			△

FIGURE 14. Interpretation of replacement sequences in μCT-scanned specimens of *Thrinaxodon liorhinus*. **A**, upper postcanines; **B**, lower postcanines. Triangles indicate presence of replacement postcanines (variation in size and thickness represent degree of development of the replacement elements); **X** represents lost anterior teeth (X in gray indicates that the loss of the postcanine is restricted to one side of the dental series of the specimen); **OR** indicates the presence of open roots in the erupted tooth; **?** indicates that the replacement tooth is out of place and its original location is not known. Asterisk identifies posteroanterior replacement sequence.

The results of our studies shows that the smallest specimen BP/1/5372 replaced its upper postcanines in the odd-numbered positions (PC1, PC3, and PC5, the last already erupted but having an open root; Fig. 14A); in the lower dentition, replacement activity is widespread occurring in even-numbered positions (left PC2 and PC4; right PC4; left and right PC6 with open roots). In addition, the lower odd-numbered series has a tiny replacement in PC7. From this early age, lower postcanines are more numerous than uppers (eight vs. seven; Fig. 14A, B), a trend that will remain during the ontogeny of the species (see Table 3). A close comparison of the replacement patterns (position and degree of development) in the lower jaws of BP/1/5372 reveals some aspects of replacement synchrony: the small replacement tooth from the second left position has no counterpart on the right mandible (Fig. 5C, D), suggesting an advanced replacement timing for the left element. Conversely, the erupting PC8 and replacement teeth from the fourth position show a higher degree of morphological differentiation on the right side (compare Fig. 5C, D). These observations indicate that even when there is general synchrony in the replacement sequence, each position will have some independence in the timing of the development of the replacement tooth.

The skull of the immature specimen TM 80A shows the upper canine root intersecting the root of PC1 on both sides (Fig. 7A, B), which indicates that the latter will be shed and not replaced. This condition predicts that TM 80A would have had six upper postcanines during the next stage of growth. Contrary to BP/1/5372, replacement activity in the anterior upper postcanines of TM 80A occurred in even-numbered positions (PC2 and PC4; Fig. 7A, B). However, the posterior portion of the upper postcanines of TM 80A show similarities with BP/1/5372 in the presence of replace-

ment activity on PC5 (represented by a tooth with an incomplete root in BP/1/5372). In the lower dentition of TM 80A, the replacement sequence is similar to that observed on the left side of BP/1/5372, with replacement in second, fourth, and sixth positions. However, considering the loss of the anterior tooth of the series, the replacements in TM 80A would correspond to the third, fifth, and seventh positions of the mandibular series of BP/1/5372. In addition, TM 80A shows evidence of a new tooth (ninth position) at the end of the lower dental row.

In the upper dentition of BP/1/7199, the postcanine replacements on the right side are more advanced than on the left side: (1) there is the loss of PC1 without replacement ('X'; Fig. 8A, B); (2) the complete eruption of PC1; and (3) presence of PC7 on the right side (Fig. 8A, B). Replacement of the upper postcanines occurs in even-numbered positions (PC2, PC4, and PC6). The same situation is represented in the maxillae of TM 180, in which the left PC1 is lost without replacement ('X'; Fig. 10B) and the replacement sequence is in the same positions as that of BP/1/7199.

In the lower dentition of TM 180, there is clear evidence of the loss of the first postcanine. On the right mandibular ramus, there is osseous infilling of the anterior-most postcanine alveolus, whereas the element in the homologous position on the left side is in process of being resorbed and shed without replacement ('X'; Fig. 10C, D). Replacement of PC1 is occurring on the left side, with the functional tooth soon to be shed and, similar to BP/1/7199, replacement occurs in the even-numbered PC4, PC6, and PC8, with the last as a new erupting element (Fig. 10C, D). In both mandibular rami, the posterior replacement tooth is clearly more developed than the anterior one, confirming a posterior-to-anterior replacement wave. Both TM 180 and BP/1/7199 show
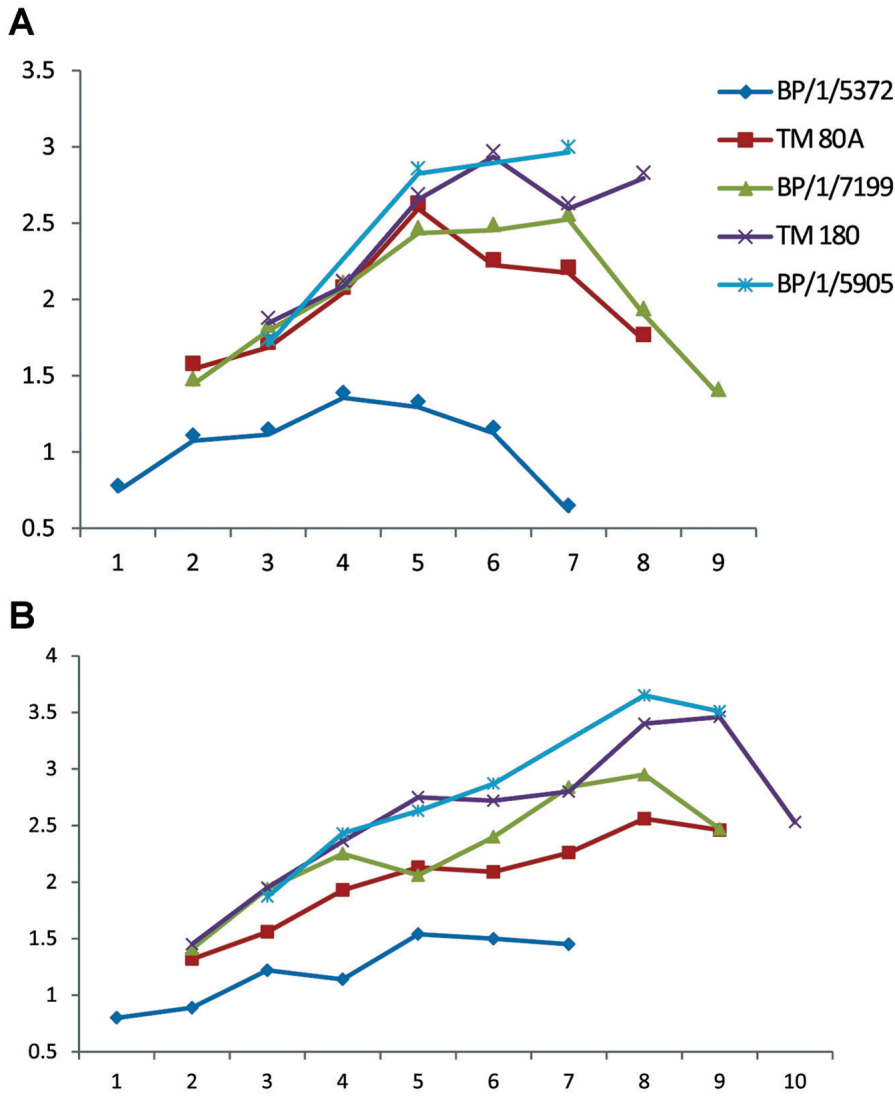
FIGURE 15. Replacement of postcanine teeth in *Thrinaxodon liorhinus*. **A**, upper postcanines; **B**, lower postcanines. Y-axis indicates crown length (in mm) in the five μCT-scanned specimens and X-axis is the dental locus. The values represent averages if teeth from both sides are preserved or a single value when only the tooth of one side is represented. Note: (1) complete separation of smallest specimen (BP/1/5372) from remaining specimens both in upper and lower series; (2) superposition of postcanine sizes of the anterior postcanines (more clear in upper ones) in the four largest specimen plotted. Only three upper postcanines of the largest specimen BP/1/5905 are plotted (see also Table 5). (Color figure available online.)

remnants of old postcanines in the lower jaw, but only TM 180 has remnants in the upper jaw between PC3/PC4 on the right side and between PC4/PC5 on the left. Old tooth remnants of lower postcanines are observed in the anterior and central portions of the tooth row in both specimens, suggesting that migration of the dental series is occurring in the anterior half of the lower dentition.

In the largest specimen, BP/1/5905, the preservation is poor, but it is possible to observe tiny replacements for PC1, PC3, and anterior to PC6 (Fig. 11B). A tiny replacement tooth is erupting between the third and fourth positions on both mandibular rami. On the left side, there is a well-developed replacement for PC5 and the development of the ultimate tooth, PC8 (Fig. 11D).

Replacement teeth develop medially to the functional ones in the upper jaw and posteromedially in the lower jaw (Figs 5, 7, 8, 10, and 11). Replacement of upper postcanines can be ascribed to the iguanid method of replacement originally proposed by Edmund (Rieppel, 1978; Kline and Cullum, 1984; Delgado et al., 2003), whereas replacement in the lower postcanines follows the model of the intermediate pattern of Rieppel (1978; see also Del-

gado et al., 2003). Replacement starting posterior to the center of the functional tooth was interpreted as a mechanism that would provide necessary space for larger teeth during the growth of the animal (Kline and Cullum, 1984). Both upper and lower postcanines show posterior migration of the dental series, which would also allow increasing space for replacement teeth, but only the lower postcanine series has replacement teeth that start their development posteromedially to the functional tooth, which suggests a comparatively longer increase in space for the lower dentition. Three μCT-scanned specimens (TM 80A, BP/1/7199, and TM 180) show a loss of the anterior postcanine without replacement and evidence of posterior migration of the canine. This evidence clearly indicates a posterior migration of the postcanine row, as new teeth are added posteriorly (see Crompton, 1963). Another line of evidence of this posterior migration is represented by the root remnants of old postcanines that are located between functional postcanines (Figs. 8C, D, 10), indicating that teeth of the new series moved posteriorly in relation to the postcanine row of the previous stage. It is interesting to note that there are more remnants of old roots between the functional teeth in the mandible than in the
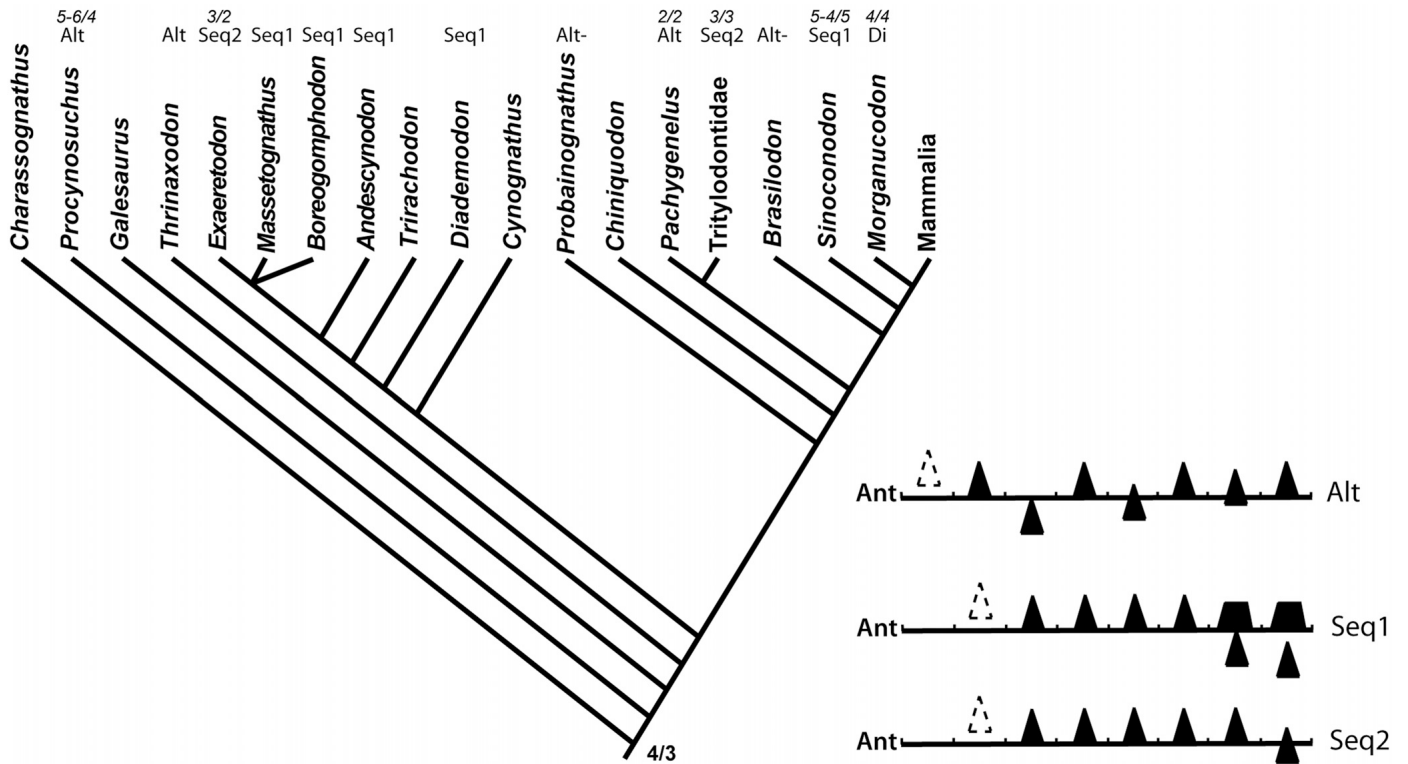
FIGURE 16. Cladogram of cynodonts showing selected taxa with number of incisors and type of postcanine replacement for each taxon. Phylogeny based on Abdala (2007), Kammerer et al. (2008), Sues and Hopson (2010), and Liu and Olsen (2010). *Brasilitherium* is considered a synonym of *Brasilodon* following Liu and Olsen (2010). Variation of the synapomorphic condition of cynodonts (4/3 incisors at the base of the cladogram) is shown in italics for terminal taxa, in which x/x denotes upper/lower incisor number. Incisor number in tritylodontids is after *Oligokyphus*, considered one of the most basal tritylodontids by Clark and Hopson (1985). **Abbreviations**: **Ant**, anterior; **Alt**, alternate postcanine replacement pattern; **Alt-**, alternate postcanine replacement pattern, with termination of replacement during the life of the individual; **Di**, diphiodonty; **Seq1**, postcanine replacement pattern that includes posterior migration of the postcanine series (with loss of anterior tooth and addition of posterior ones) and replacement of teeth (e.g., the sectorial posterior teeth in juveniles of *Andescynodon* were replaced by gomphodont postcanines, the only type of postcanines represented in the adult of this taxon); **Seq2**, migration of the tooth row series, without evidence of postcanine replacement.

skull (Figs. 8, 10, 11). This perhaps indicates slower resorption of old teeth in the mandible.

Our observations confirm an alternate sequence of postcanine replacement previously proposed for *Thrinaxodon liorhinus* (Parrington, 1936; Crompton, 1963; Osborn and Crompton, 1973; Gow, 1985). This pattern is observed between two to four alternate positions in most specimens (Fig. 14). The direction of the replacement sequence as described by Crompton (1963), i.e., replacement wave going from back to front, is clear for mandibular sequences, but it is not clear-cut for the upper dentition (Fig. 14). A posterior-to-anterior sequence of replacement is also observed in the lower dentition BP/1/7199 (Fig. 8C, D). The upper left series of this specimen seems to have three different replacement waves: one represented by the well-developed replacement of the first tooth, another with replacement in the even-numbered sequence formed by PC2, PC4, and PC6 (the two posterior elements more developed than the anterior one), and the third that appears to start with a tiny replacement in the fifth position (Fig. 8B). For both upper and lower postcanines, the replacement is more or less synchronized on the left and right sides.

Considering the evidence provided by the largest μCT-scanned specimen (BP/1/5905), it is clear that tooth replacement continued to occur in old individuals, indicating that the growth in *Thrinaxodon liorhinus* was continuous until the final stages of life.

A similar condition is represented in the basal mammaliaform *Sinoconodon*, where replacement teeth are also present late in the ontogeny, but are clearly different of the replacement in other basal mammaliaforms, such as *Morganucodon* and *Hadrocodium*, in which diphyodont replacement is recognized (Luo et al., 2004).

Quantitative Changes in Postcanine Crown during Ontogeny

As mentioned above, evidence from TM 80A and BP/1/7199 (Fig. 3) allowed the estimation of the proportional increase between crown lengths of successive teeth. In their computer simulation model for lower (non-mammalian) tetrapods, Bolt and DeMar (1986) proposed a growth increment of 5% or less each time the tooth is replaced. This contrasts with the ca. 12% presented in this study, but the model of Bolt and DeMar (1986) disallowed translating dentitions (i.e., loss of anterior teeth and addition of posterior ones), a phenomenon that is indeed represented in *Thrinaxodon*, and in most if not all non-mammaliaform cynodonts (see below).

Our analyses using crown size (APL) shows that differences in postcanine size are notably larger between the smallest (i.e., youngest) specimen BP/1/5372 (BSL = 35 mm), which is clearly isolated from remaining specimens with skull size ranging from 56 to 87 mm, in both upper and lower rows (Fig. 15A, B). Another trend observed is that anterior homologous teeth in

specimens larger than BP/1/5372 tend to be of a similar size, whereas size differentiation in posterior homologous loci is more marked. This trend is common to both upper and lower postcanine series, but is more conspicuous in the uppers (Fig. 15A, B).

The variations of postcanine size between the smallest and largest μCT-scanned specimens (35–87 mm) in locus interpreted as homologous (e.g., PC1 of BP/1/5905 and PC3 of BP/1/5372; Table 5) ranges from 51% to 362% for upper postcanines and from 53% to 113% in the mandibular rami. The increase of 362% is indeed an outlier resulting from the presence of a reduced last upper postcanine in several specimens of *T. liorhinus* (see below). Thus, this value resulted from the contrast of the exceptionally small last PC7 of BP/1/5372 with PC5 of BP/1/5905. The following percentage of 115%, comparing variation between PC3 and PC5, is close to the maximum percentage recorded for the lower postcanines.

Considering the increase in size from the PC3 of BP/1/5372 to the PC1 of BP/1/5905 (both located at an homologous locus) (Table 5), we interpret three to four replacement cycles for both upper and lower series. The third upper postcanine and seventh lower postcanine loci of BP/1/5905 had six to seven replacements. Four to five replacement cycles are interpreted for the third locus of the lower jaw of BP/1/5905 (corresponding to fifth locus of BP/1/5372) and five to six replacements for the fourth locus of the lower jaw of BP/1/5905. It is important to remark that the calculations of number of replacements are estimated considering a constant replacement rate. However, we should stress that length variation in postcanines crowns is larger between smaller specimens (i.e., very young), indicating that the growth ratio of these elements is larger in younger ages. Replacement numbers in the jaws of *Thrinaxodon* are quite reduced in comparison with polyphyodont reptiles such as *Heloderma suspectum* and *Iguana iguana*, which replace their teeth four and five/six times per tooth position per year, respectively (Edmund, 1969; Kline and Cullum, 1984). On the contrary, three to fourth replacements were interpreted for the nine anterior pleurodont teeth of *Agama agama* (Cooper et al., 1970), a condition closer to the number of replacements we estimated for *Thrinaxodon*.

Summary of Postcanine Replacement in Non-mammaliaform Cynodonts

Replacement of the postcanines has been well studied in *Thrinaxodon liorhinus*, which has a multiple alternating replacement sequence (Parrington, 1936; Crompton, 1963; Osborn and Crompton, 1973; Gow, 1985; this study). A very active alternating replacement was interpreted in the specimen of the Late Permian basal cynodont *Procynosuchus* studied by Kemp (1979). In the lower jaw, *Procynosuchus* shows replacement activity posterior to the PC4, and at least an odd replacement wave in the posterior dentition of the left lower jaw (including PC9, PC11, and PC13; Kemp, 1979:fig. 4). A reduction of the frequency of dental replacement, in comparison with that of *Thrinaxodon*, was inferred by Crompton and Jenkins (1979) for the sectorial-toothed cynodont *Probainognathus*, in which all postcanines of adult individuals show heavy wear (Romer, 1970). An alternate pattern is described for the Late Triassic cynodonts *Brasilodon* and *Brasilitherium* with evidence of posterior migration of the postcanine series, and of cessation of replacement in one specimen of *Brasilodon*, which shows the entire postcanine series strongly worn out (Martinelli and Bonaparte, 2011). An interesting point highlighted by these authors is the presence of tongue-and-groove-like arrangement on the crown of some lower postcanines of these taxa, even though there is no mesiodistal junction between the teeth. Therefore, structures that will help secure adjacent teeth appear before the acquisition of a diphyodont dentition (Martinelli and Bonaparte, 2011). Alternate replacement of postcanines is also interpreted

in the sectorial cynodonts *Pachygenelus* (Gow, 1980; Crompton and Luo, 1993:figure 4.14) and *Diarthrognathus* (Gow, 1980:476), both members of Tritheledontidae, a group phylogenetically close to Mammaliaformes (Fig. 16). A peculiar non-alternating pattern was described by Shapiro and Jenkins (2001) for the sectorial and double-rooted postcanines of *Mitredon*. However, the evidence is restricted to a partial lower jaw, but it is clear that replacement is happening along the entire dental row (in PC2, PC5, and PC6).

Contrary to the alternate 'reptilian' replacement, gomphodonts and tritylodonts exhibit a sequential replacement (Fig. 16), with loss of anterior postcanines and addition of new ones at the end of the series (Crompton, 1955, 1972; Goñi, 1986; Abdala et al., 2002; Luo et al., 2004; Jasinoski and Chinsamy, 2012). In this type of replacement, the postcanine tooth row migrates posteriorly and shows a clear difference between the badly worn-out anterior teeth and the new posterior elements of the series (Fig. 16). In the gomphodont cynodont *Diademodon*, there is also a posterior migration of the tooth row (Fourie, 1963), but the postcanine series in this taxon is heterogeneous, with simple conical anterior teeth and buccolingually expanded gomphodont teeth in the middle and sectorial posterior teeth, which are represented in all ontogenetic stages (Crompton, 1963). Several interpretations were proposed to explain the replacement pattern for the complex dentition of *Diademodon* (Crompton, 1963; Fourie, 1963; Ziegler, 1969; Hopson, 1971; Osborn, 1974). It is clear that in order to maintain the heterogeneity in the postcanine dentition, there was replacement of postcanines of different crown morphology (i.e., anterior gomphodont tooth replaced by conical and anterior sectorial by gomphodont) during the migration of the series, whereas new sectorial elements erupted at the end of the row. In addition, some traversodont cynodonts, such as *Andescynodon* and *Massetognathus*, have sectorial teeth at the end of the postcanine series in juveniles that are replaced by gomphodont teeth in adults in which there is no presence of sectorial teeth (Goñi, 1986; Liu and Sues, 2010). Slightly different from the previous pattern appears to be the postcanine replacement in the Laurasian traversodontid *Boreogomphodon* in which posterior sectorial teeth are present in juveniles and in one large adult. In this case, two generations of posterior sectorial postcanine are interpreted in this taxon (Liu and Sues, 2010). The condition in the traversodontid *Exaeretodon* and in tritylodontids is represented by a posterior migration of the series (loss of anterior and addition of posterior teeth), without evidence of tooth-by-tooth replacement (Fig. 16). Anteroposterior sequential replacement of the postcanines is also known in the basal mammaliaform *Sinoconodon*, with deciduous premolars replaced only once and then lost in older specimens and the posterior molars having at least one replacement in adults (Crompton and Luo, 1993; Zhang et al., 1998; Luo et al., 2004). In other basal mammaliaforms, such as *Morganucodon* and the docodont *Haldanodon*, there is a mammalian replacement with a diphyodont anterior and monophyodont posterior dentition (Greenwald, 1988; Luo et al., 2004).

Reduction of the Ultimate Upper Postcanine in Cynodonts

In juveniles and in some subadults and adults of *Thrinaxodon liorhinus*, the ultimate upper postcanine (usually the sixth) is remarkably smaller relative to the penultimate postcanine (Table 3), and in some cases, it is similar in size to the first postcanine of the series. This is not the only cynodont in which the ultimate upper postcanine of the series tends to be considerably smaller. The Middle Triassic cynodont *Probainognathus* also usually has the ultimate postcanine reduced in size (see Romer, 1970:fig. 2; Abdala, 1996; F.A., pers. observ., 1998). This differentiation in size is also more pronounced in juveniles and subadults of the taxon, whereas in adults there is variation in the presence of this tooth (F.A., pers. observ., 1998). Other forms having a pattern of small

ultimate upper postcanines are cf. *Probainognathus* from the Upper Triassic of Argentina (Bonaparte and Crompton, 1994), *Lumkuia fuzzi* from the Middle Triassic of South Africa (Hopson and Kitching, 2001), and the basal mammaliaforms *Morganucodon* from the Lower Jurassic of the U.K. and China (Kermack et al., 1981) and *Hadrocodium* from the Lower Jurassic of China (Luo et al., 2001:fig. 1C). The first two taxa are represented by one specimen each, and they are considered to have been juveniles. Finally, in the basal mammaliaform *Sinoconodon*, it is clear that the small ultimate postcanine in juveniles is replaced by a larger tooth in the adult (Luo et al., 2004). The reduction of the last upper postcanine in *Thrinaxodon* was also noted by Osborn and Crompton (1973:12), who interpreted the reduction in size as well as the simpler tooth morphology in the anterior and posterior postcanines as evidence of senescence of the tooth lamina. However, the reduction in size in the ultimate postcanine is typical only of the upper tooth row, and considering that it is consistently observed in juveniles, we disagree with the hypothesis of senescence of the dental lamina to explain this feature.

CONCLUSIONS

The extensive survey in the dentition of *Thrinaxodon liorhinus* indicates that the average adult dental formula is 4/3, 1/1, 6/7–8. There is evidence of alternate incisor replacement and some synchrony in the replacement activity between the left and right incisor teeth. Timing between the replacements of successive incisors appears slower for the smaller specimens BP/1/5372 and TM 80A, with replacements in the first and third upper positions, whereas the larger specimens BP/1/7199 and TM 180 show replacement activity associated with nearly all incisors. Eruption of new canines in the lower jaw was consistently posterior to the functional canine and typically anterior to the functional upper canine, although two small specimens had upper canines erupting posterior to the functional canines. In one of these small specimens, the functional canine was retained until the eruption of its replacement was almost complete. The rate of canine replacement appears to be very high during the lifetime of an individual because replacement was observed in all the μCT-scan specimens (ranging 37–87 mm in skull length). This is corroborated by the presence of replacement canines observed in replacement pits in several gross anatomical specimens of different ages.

The crowns of the lower postcanines are clearly more complex than those of the upper postcanines, which lack a lingual collar cingulum. Maximum complexity in the postcanine series is attained in TM 180 with a skull length of 75 mm. Larger specimens show a trend toward simplification of the morphology of the postcanine crowns. The ultimate upper postcanine is markedly smaller than the preceding postcanines in a large number of the sampled specimens, sometimes having a size similar to the upper PC1. This is common in all specimens ranging from 30 to 56 mm, and in 18 specimens larger than 56 mm (in contrast to 14 specimens lacking it). Replacement in the postcanine series is alternated, and evidence presented here suggests a posterior to anterior direction of the replacement waves for the lower dentition, whereas the direction is not clear-cut in the case of the upper postcanine series. There is clear evidence of a posterior mobility of the postcanine series, with loss of the anterior-most tooth and addition of new postcanines at the end of the series. The replacement is more or less synchronized on the left and right sides of the postcanine series, although one side of the tooth series might be slightly more advanced relative to the other. This slight asynchrony results in some individuals losing their first postcanine (which will not be subsequently replaced) on one side, whereas on the other side the old first tooth is not yet shed.

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