

A CYNODONT FROM THE UPPER TRIASSIC OF EAST GREENLAND: TOOTH REPLACEMENT AND DOUBLE-ROOTEDNESS

MICHAEL D. SHAPIRO¹ AND FARISH A. JENKINS, JR.¹

ABSTRACT. A new genus and species of cynodont from the Upper Triassic Fleming Fjord Formation of East Greenland possesses double-rooted postcanine teeth and a nonalternate pattern of tooth replacement. The specimen represents an addition to the known diversity of Early Mesozoic taxa with multi-rooted dentitions (tritylodontids, *Sinoconodon* sp., haramiyids, morganucodontids, *Meurthodon gallicus*), and casts doubt on traditional interpretations of the interdependency of reduced tooth replacement patterns and teeth with multiple roots.

INTRODUCTION

The Upper Triassic Fleming Fjord Formation of Jameson Land, East Greenland, preserves a diverse fossil vertebrate fauna that includes mammals, theropod and prosauropod dinosaurs, plagiosaurid and cycloosaurid amphibians, turtles, aetosaurs, phytosaurs, and pterosaurs (Jenkins et al., 1994, 2001). Mammals are represented primarily from the upper Tait Bjerg Beds and include *Kuehneotherium*, cf. *Brachyzostrodon*, and the haramiyid *Haramyavia clemmenseni* (Jenkins et al., 1994, 1997). We describe here an additional component of the fauna, a cynodont that bears double-rooted teeth, the only known specimen of this taxon. A comparable form of Late Triassic age is *Meurthodon gallicus* (Russell et al., 1976; Sigogneau-Russell and Hahn, 1994; Godefroit and Battail, 1997), represented by isolated teeth from Rhaetic deposits in France, but this taxon differs in significant details.

The following abbreviations of institutional names are used: IRSNB, Institut

royal des Sciences naturelles de Belgique, Brussels; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MGUH, Geological Museum, University of Copenhagen; and MNHP, Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris.

SYSTEMATIC PALEONTOLOGY

Order Therapsida Broom, 1905

Infraorder Cynodontia Owen, 1861

Family incertae sedis

Mitredon cromptoni new genus and species

Etymology. The generic term refers to the highly peaked primary cusps, a combination of English mitre, the high-peaked ecclesiastical headdress, from Greek *mitra*, turban, and Greek *odous* (*odon*), tooth. The specific name honors A. W. Crompton for his important contributions to our understanding of the paleobiology and evolution of cynodonts.

Holotype. MGUH VP 3392, MCZ field number 11/G95 (Figs. 1A, B), a partial left dentary bearing an incomplete alveolus mesially, three unerupted postcanine teeth, roots of four other (erupted) postcanines, and an empty tooth crypt distally.

Horizon. Uppermost dolostone of Tait Bjerg Beds, Ørsted Dal Member of the Fleming Fjord Formation.

Locality. 71°32.929'N, 22°55.450'W, north of Ærenprisdal at its confluence with Pingel Dal, Jameson Land, East Greenland.

¹ Department of Organismic and Evolutionary Biology, and Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

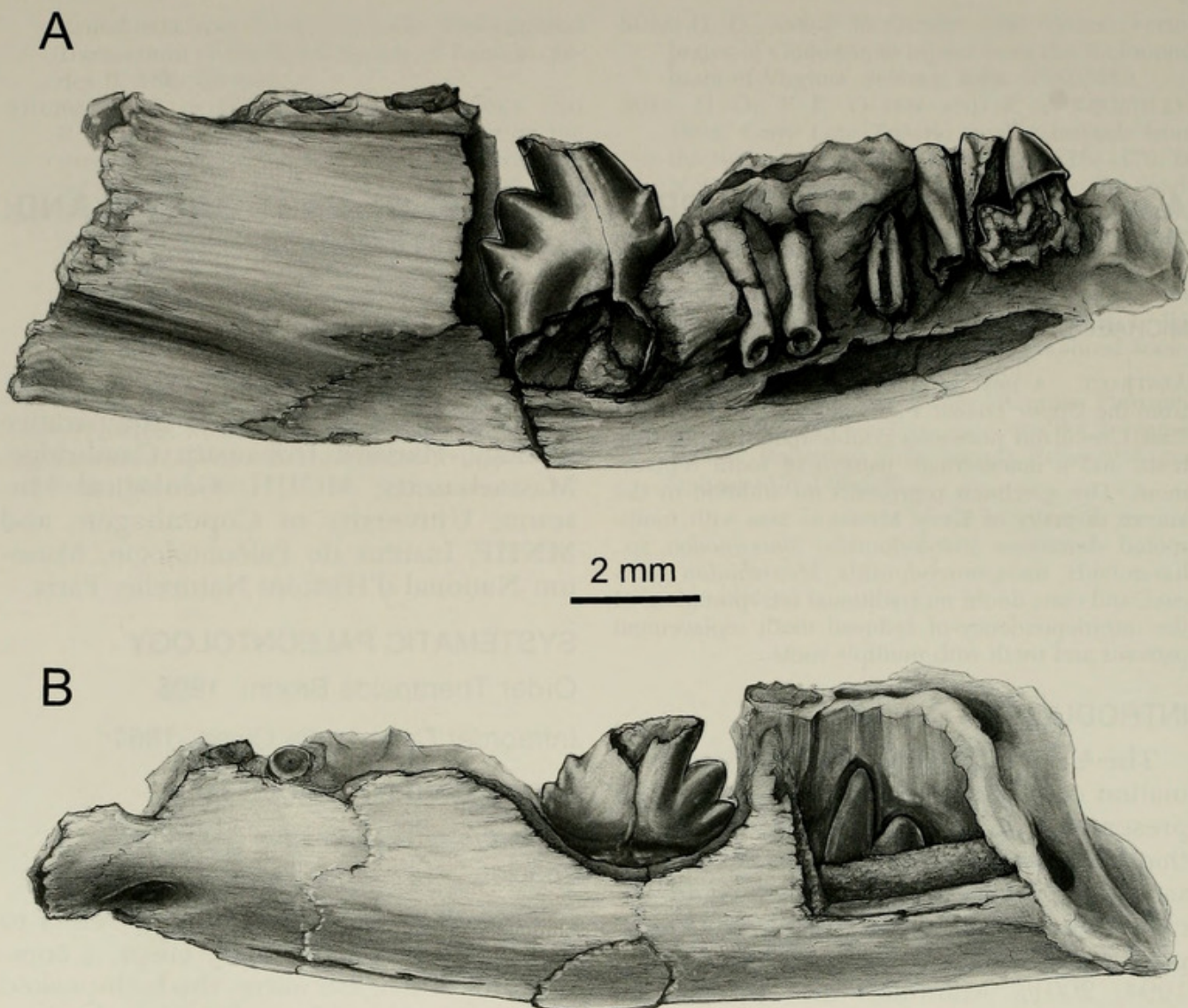


Figure 1. Left dentary of *Mitredon cromptoni*, MGUH VP 3392, in (A) lingual view and (B) occlusolabial view. In occlusolabial view, the mandibular canal is visible distally as a filled cast through a window cut in the labial aspect of the jaw; the canal obscures the basal crown of Pc_6 .

Age. Late Triassic (?Norian–Rhaetic; Jenkins et al., 1994).

Diagnosis. Cingular cusps on postcanine teeth absent or lost, a derived character shared with galesaurid cynodonts, *Cynognathus*, and *Probelesodon* (Hopson and Kitching, 1972; Hopson and Barghusen, 1986). Differs from Therioherpetidae (Bonaparte and Barberena, 1975) and other nonmammalian cynodonts in possessing bifurcate postcanine tooth roots (likely convergent with multirooted tritylodontids) and lacking alternate tooth replacement. Characters shared with “chiniquodonts” are crowns of lower postcanines

with laterally compressed cusps arranged in a longitudinal row and clearly separated from each other (Bonaparte and Barberena, 1975; Sigogneau-Russell and Hahn, 1994). A feature shared with *Meurthodon gallicus* (Russell et al., 1976; Sigogneau-Russell and Hahn, 1994) and some “chiniquodonts” (Kemp, 1982) is a recurved cusp *a* (following the nomenclature of Crompton and Jenkins, 1968); that is, the mesial crest is longer and more horizontal than the distal crest, which is shorter and more vertically oriented. A derived feature shared with *Meurthodon*, *Sinoconodon*, and Mammaliaformes (*sensu* Wible, 1991)

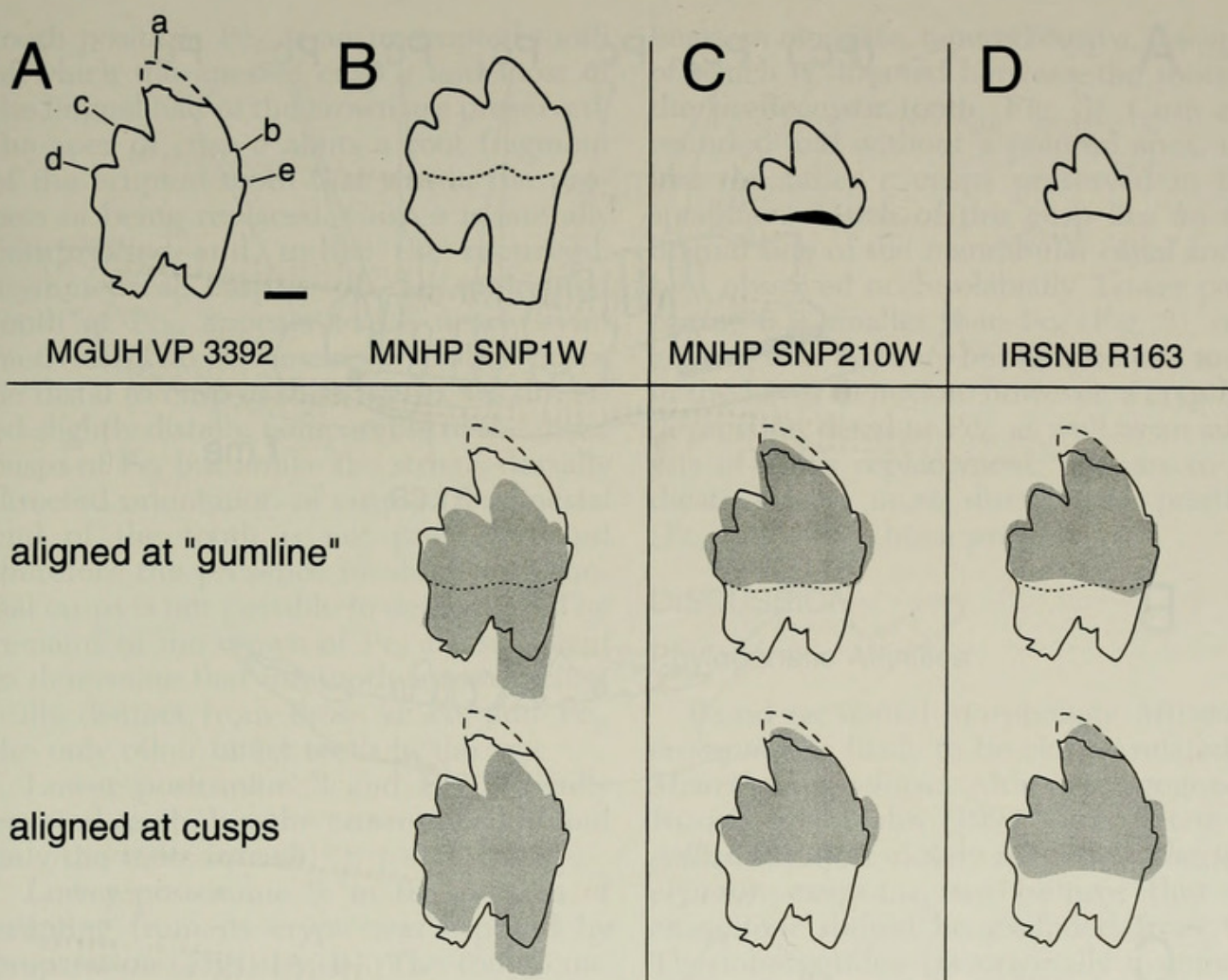


Figure 2. Comparison between (A) Pc_5 of *Mitredon cromptoni*, MGUH VP 3392, (B) the type specimen of *Meurthodon gallicus*, and (C, D) two isolated teeth referred to *Meurthodon gallicus*. Specimens MNHP SNP210W and IRSNB R163 were selected for comparison in addition to the type specimen for their gross similarity to MGUH VP 3392. In each column (B, C, and D), a *Meurthodon* tooth (shaded) is compared to Pc_5 of *Mitredon* (outline) in two ways to minimize the effects of size and completeness on morphologic comparison between specimens. First, the middle row depicts comparisons based on alignment of two teeth at the inferred gumline. Second, in the bottom row, cusps are aligned as closely as possible. Although the alignment of MGUH VP 3392 at the "gumline" with IRSNB R163 and with the cusps of MNHP SNP1W reveal overall similarities in shape, all specimens referred to *Meurthodon* lack a cusp *e*. Cusp *b* of Pc_5 in *Mitredon* is also substantially smaller than the corresponding structure in *Meurthodon*. Cusp designations in (A) after Crompton and Jenkins (1968). MNHP SNP1W redrawn from Sigogneau-Russell and Hahn (1994); MNHP SNP210W and IRSNB R163 redrawn from Godefroit and Battail (1997). For top row, scale bar = 1 mm.

is roots of lower postcanine teeth bifurcate, a character once considered diagnostic of Mammalia (e.g., Crompton and Jenkins, 1979). Distinguished from *M. gallicus* by the presence of a cuspule mesial to cusp *b* (on Pc_5); a mesiodistally longer cusp *a* (if the type specimen of *M. gallicus* and Pc_5 of *Mitredon cromptoni*, new genus and species, are scaled to the same mesiodistal length at the crown-cervical junction, the mesiodistal length of cusp *a* is approximately 60% total mesiodistal crown length

in the latter, and only 40% in the former; Fig. 2); and the absolute mesiodistal length of Pc_5 is 20% smaller than that of the type specimen of *M. gallicus* (3.5 mm versus 4.2 mm). None of the three lower teeth of MGUH VP 3392 closely resembles the single isolated tooth of the type specimen of *M. gallicus* (Russell et al., 1976; Sigogneau-Russell and Hahn, 1994) nor other isolated teeth that Godefroit and Battail (1997) subsequently referred to that taxon (Fig. 2).

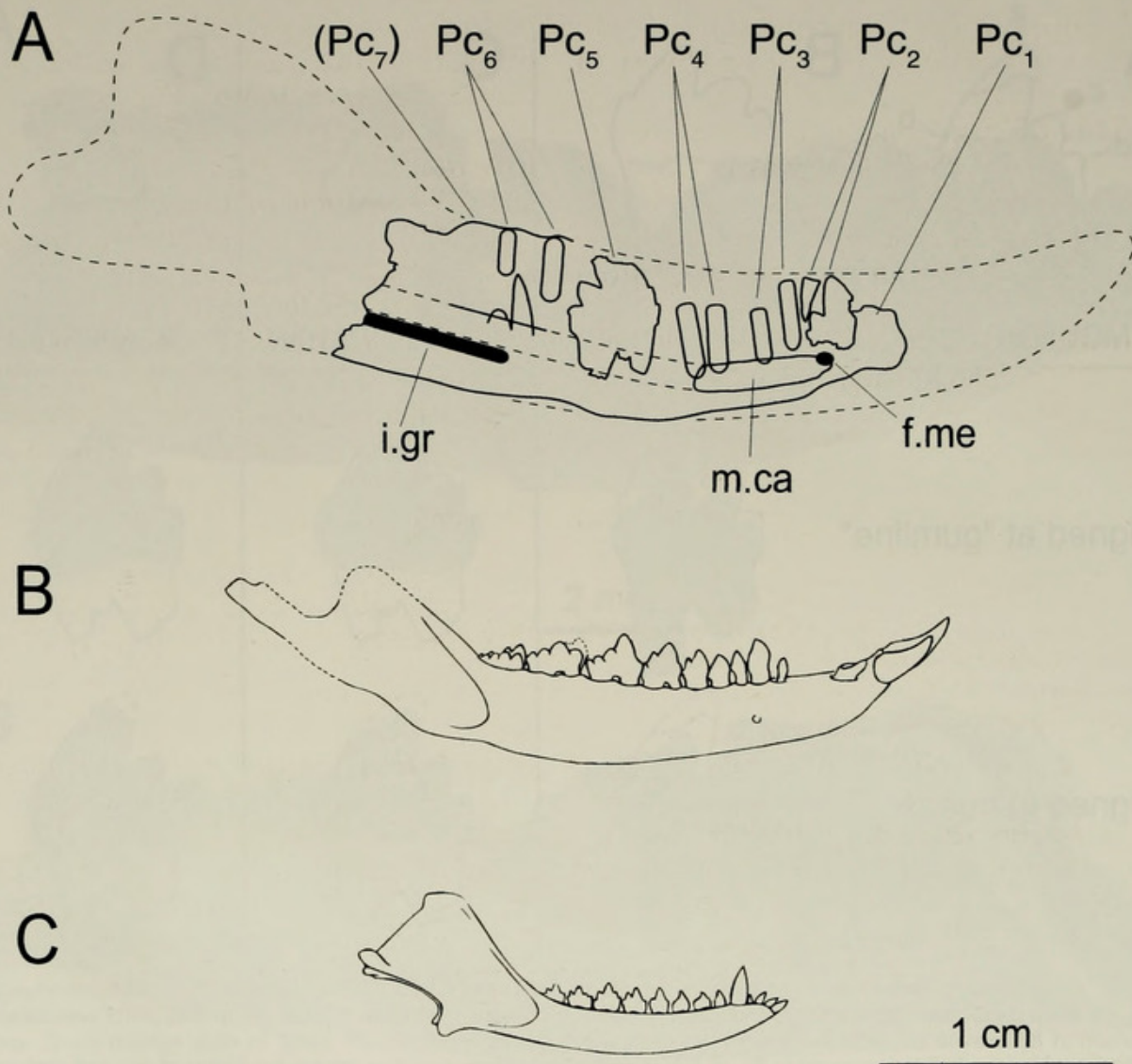


Figure 3. *Mitredon cromptoni* and contemporaneous Greenlandic mammals. (A) Schematic reconstruction of the left lower jaw of *Mitredon cromptoni*, MGUH VP 3392. Lower jaws of the Late Triassic mammals (B) *Haramiyavia* (redrawn from Jenkins et al. [1997]) and (C) *Morganucodon* (redrawn from Hopson [1994], in Bonaparte and Crompton [1994]). Abbreviations: Pc, post-canine tooth; i.gr, internal dentary groove; f.me, mental foramen; m.ca, mandibular canal.

DESCRIPTION

Lower Jaw

The specimen is a partial left dentary, slightly convex along its ventral margin, and missing the anterior and posterior ends of the ramus; erupted teeth had broken off postmortem, but several unerupted teeth are preserved within the ramus. Although the total number of postcanine teeth is uncertain, the seven tooth positions are here referred to as Pc₁ (most mesial) through Pc₇ (most distal) (Fig. 3). The mental foramen is situated ventral and la-

bial to Pc₂. An internal groove extends longitudinally along the inferior, lingual aspect of the dentary, indicating the presence of postdentary bones. The mandibular canal is exposed through breakage on the lingual aspect of the jaw between Pc₂ and Pc₄ (Fig. 1A). The canal passes to the labial side of Pc₅ and is preserved in cross section at the break across the posterior end of the specimen (Fig. 1B).

Teeth

Lower postcanine 1 is indicated by a partially preserved alveolus. In the next

tooth position, Pc_2 , is an unerupted tooth of which the apex of cusp *a* and most of the lingual half of the crown are preserved; the apex of cusp *a* abuts a root fragment of the erupted tooth that was in the process of being replaced. Cusp *a* is laterally compressed and, unlike the recurved, asymmetrical cusp *a* of the unerupted tooth at Pc_5 , appears to be nearly symmetrical. Two successively smaller cusps lie distal to cusp *a*; their apices are directed slightly distally, comparable to the distal cusps of Pc_5 but unlike the strictly dorsally directed orientation of cusp *a*. The mesial end of the tooth is not preserved and therefore the presence or absence of mesial cusps is not possible to determine. The remains of the crown of Pc_2 are sufficient to determine that the tooth is morphologically distinct from those at Pc_5 and Pc_6 , the only other intact teeth in the jaw.

Lower postcanine 3 and Pc_4 are fully erupted teeth, but the crowns are lost and only the roots remain.

Lower postcanine 5, in the process of erupting from its crypt, was exposed by preparation (Figs. 1A, B). The tooth consists of a nearly complete crown bearing five cusps, and the upper parts of two roots. Mesial cusps *b* and *e* are the smallest and cusp *a* is the largest, the latter rising 2.55 mm from the base of the crown to the point at which the apex is broken. Cusps *c* and *d* are successively smaller and more distally directed than *a*. Cusp *d* supports a distinct cuspule on its lingual surface; in an examination of a cast of *Meurthodon gallicus*, J. A. Hopson (personal communication) observed a "very faint swelling" in a similar position.

Both a functional and a replacement tooth are present at the Pc_6 position. The functional tooth is preserved only by a pair of roots that straddle cusp *a* of a replacement tooth beneath. The fully divided roots are visible as ovoid cross sections at their broken surfaces in occlusal view. The replacement tooth, exposed by preparation but partially obscured in labial view by a cast of the mandibular canal (Fig. 1B),

bears an elongate, tapered cusp *a*, the apex of which is directed between the roots of the predecessor tooth (Fig. 3). Cusp *c* is rounded and without a pointed apex, unlike the other *c* cusps preserved in this specimen. Much of this cusp lies on the lingual side of the mandibular canal and is best observed occlusolabially. Lower postcanine 6 is smaller than Pc_5 (Fig. 3), suggesting that Pc_6 may be the ultimate tooth in the lower dentition; however, a cryptlike depression distal to Pc_6 , as well as an analysis of tooth replacement, appears to indicate that a more distal tooth position (Pc_7) may have been present.

DISCUSSION

Phylogenetic Affinities

Based on dental morphology, *Mitredon cromptoni* is likely to be closely related to *Meurthodon gallicus*. Although Sigogneau-Russell and Hahn (1994) interpreted *M. gallicus* is most closely related to *Therioherpeton cagnini*, we believe that *M. cromptoni* should be excluded from the Therioherpetidae (as originally diagnosed by Bonaparte and Barberena, 1975) on the basis of the bifurcate postcanine tooth roots and the nonalternate pattern of tooth replacement (but see below discussion of root variability in early Mesozoic cynodonts). Inasmuch as *M. gallicus* also has fully bifurcate postcanine tooth roots (unlike the incipiently double-rooted condition of *T. cagnini*, in which the cross section of the single root is in the shape of a figure 8; Bonaparte and Barberena, 1975), the inclusion of this taxon in the Therioherpetidae is questionable as well.

Mitredon cromptoni might be considered a chiniquodontid cynodont, but unresolved taxonomic issues at the familial and suprafamilial levels, as well as the incompleteness of the present specimen, make such an assignment problematic. Most taxa referred to "chiniquodonts" (Chiniquodontidae or Chiniquodontoidea) exhibit alternate tooth replacement and postcanines with three to four cusps that

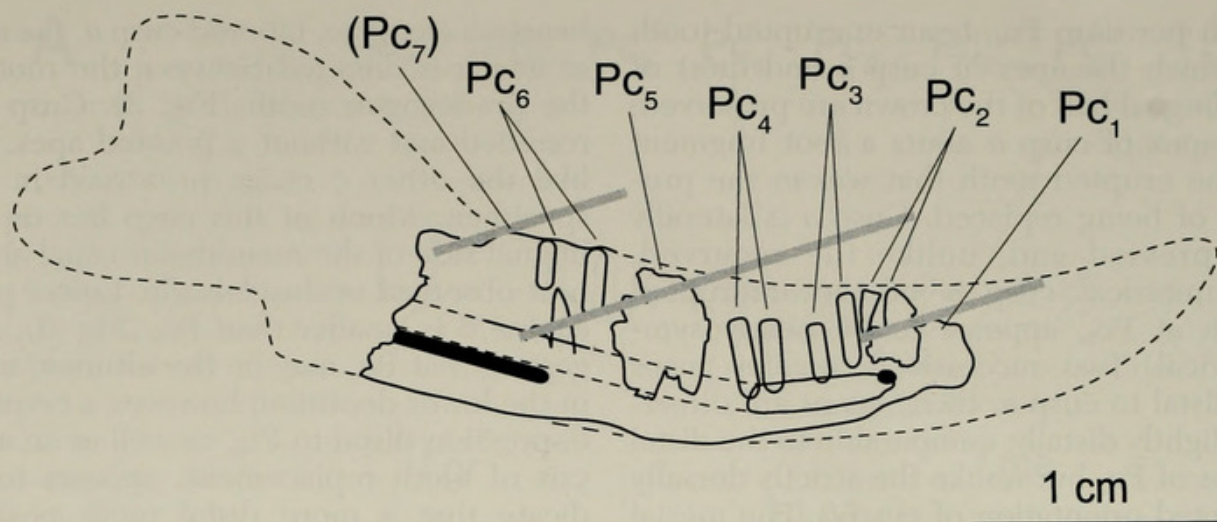


Figure 4. Schematic reconstruction of the left lower jaw of *Mitredon cromptoni*, MGUH VP 3392. Most reptiles and many cynodonts exhibit a tooth replacement pattern characterized by tooth eruption in every second tooth position. This alternate replacement pattern results from narrow spacing between *Zahnreihen* (teeth in a developmental replacement series; Hopson, 1980). As spacing between *Zahnreihen* increases, two or more teeth in a single *Zahnreihe* may be fully erupted and functional in the tooth row. Each tooth in a single *Zahnreihe* potentially may have a different crown morphology, and thus increased spacing between *Zahnreihen* may yield a heterogeneous tooth row. The dentition of *M. cromptoni* is represented by three *Zahnreihen* (heavy, shaded lines). The first *Zahnreihe* is comprised of erupting Pc_2 and probably Pc_1 (represented by an empty alveolus). The second is comprised of the erupted Pc_2 (root fragment), functional Pc_3 and Pc_4 (pairs of roots), and erupting Pc_5 and Pc_6 . The roots of Pc_6 are part of the most distal *Zahnreihe*.

are labiolingually compressed and mesio-distally aligned, features that are either primitive for cynodonts or widely distributed (e.g., in galesaurids and cynognathids; Bonaparte and Barberena, 1975). Although Sigogneau-Russell and Hahn (1994: 204) assert that the teeth of "chiniquodonts" are easily distinguished from those of mammals and other therapsids, they also note that "chiniquodont" dentitions have yet to be studied in depth and therefore the "problem of subdivision of the Chiniquodontoidea into families has yet to be resolved."

Mitredon cromptoni also shares some similarities with the Early Jurassic *Sinoconodon*, which also has double-rooted teeth and likely replaced the molariform teeth (Crompton and Sun, 1985; Crompton and Luo, 1993). The postcanine teeth of *Sinoconodon*, which have four mesio-distally aligned cusps, resemble the teeth of *M. cromptoni* in lateral profile. In *Sinoconodon* postcanine teeth do not occlude, nor do upper and lower postcanines have a consistent relationship to one another; the single jaw of *M. cromptoni*, from

which the erupted, functional teeth have been lost postmortem, does not permit an assessment of these features. In view of these uncertainties, we are reluctant to attempt a more precise taxonomic placement of *M. cromptoni*.

Tooth Replacement

Mitredon cromptoni possesses a lower postcanine dentition with at least three variants of crown structure. Differences in the teeth of *M. cromptoni* appear to represent different tooth replacement families, or *Zahnreihen*, comparable to those described for the cynodont *Thrinaxodon liorhinus* (Parrington, 1936; Crompton, 1963c; Osborn and Crompton, 1973; Fig. 4). However, tooth replacement in *M. cromptoni* is not comparable to the alternate pattern seen in *T. liorhinus* and allied forms. Furthermore, new generations of teeth erupt in the same sagittal plane as do previous ones (Pc_2 and Pc_6 erupt directly below the intact roots of preceding teeth; Figs. 1, 4), not in a more lingual plane as in *T. liorhinus*.

Although the number of crown variants

in each replacement series cannot be determined, we would interpret tooth replacement and variation in *Mitredon cromptoni* as representing three *Zahnreihe* (Fig. 4). The most mesial *Zahnreihe* consists of Pc_1 and the erupting Pc_2 . The next *Zahnreihe* begins mesially with the root remnant of the functional tooth at the Pc_2 position. The functional teeth at positions Pc_{3-4} (represented only by roots) are part of this second *Zahnreihe*, as probably also are the replacement teeth at positions Pc_{5-6} . The last tooth in the most distal *Zahnreihe* (and thus the most distal tooth in the dentition) always erupts de novo, in a position not previously occupied by another tooth. Lower postcanine 6, which is undergoing replacement, therefore cannot be the ultimate tooth in the lower dentition of *M. cromptoni* and we would expect to see another erupting distal tooth in a more complete (and perhaps ontogenetically older) specimen. Indeed, a shallow crypt occurs distal to the roots of the functional tooth at Pc_6 , evidence of yet another tooth position. The erupted Pc_6 and the potential tooth distal to it represent the most distal *Zahnreihe*.

Functional Stability of the Tooth Row and Multirooted Teeth

Before the discovery of *Mitredon cromptoni*, the fossil record appeared to provide evidence for the coevolution of stable patterns of occlusion and multirooted teeth, with the possible implication of a functional relationship. In the primitive condition, exemplified by *Thrinaxodon* and many other cynodonts, alternate replacement of single-rooted teeth resulted in continual disruption of the tooth row, and in any case there was little, if any, occlusion in the strict sense (tooth-to-tooth contact). More derived lineages (e.g., tritylodontids, *Sinoconodon*, morganucodontids, and haramiyids) developed replacement strategies to promote stability of the tooth row and, in most cases, possessed double- or multirooted postcanine teeth. An exception is the gomphodont cynodont

Diademodon, which maintained single-rooted teeth but promoted stability within the tooth row by losing teeth mesially and adding teeth distally (Crompton, 1963a; Hopson, 1971). Tritylodontids (with up to six roots on postcanine teeth in *Oligokyphus*) and *Sinoconodon* (in which postcanines may be single- or double-rooted) possessed tooth replacement patterns comparable to that of *Diademodon*, but with a reduced number of teeth in each *Zahnreihe*. Tritylodontids did not replace mesial teeth but instead added nonreplacing, "gomphodont" teeth de novo at the distal end of the row (Hopson, 1971). Similarly, *Sinoconodon* lost anterior postcanines and added small distal teeth, which were subsequently replaced by a second generation of larger ones as jaw size increased (Crompton and Luo, 1993). Thus, *Sinoconodon* neither followed the typical "mammalian" diphyodont tooth replacement pattern nor possessed true molars (that is, *Sinoconodon* did not bear teeth that erupted de novo distally in the tooth row and were not replaced by subsequent generations of teeth).

Morganucodon was among the first mammals to possess a dentition that included true molars. Available fossils do not reveal how many times (or in what order) *Morganucodon* replaced generations of deciduous teeth, but dental wear patterns suggest that the positional relationships between upper and lower postcanine teeth were relatively consistent (Crompton and Jenkins, 1968). Fixed dental relationships were also promoted by interlocking anterior and posterior accessory cusps, maintaining alignment of the molars. Similarly, the occlusal interlocking of cusps and basins on upper and lower molariforms of the haramiyid *Haramiyavia clemmense* (Jenkins et al., 1997) would have required ontogenetic stasis of the tooth row. Although the exact sequence of tooth replacement cannot be ascertained for either of these mammalian taxa, their occlusal configurations are evidence that relatively precise relations were maintained between

upper and lower dentitions throughout ontogeny.

However, *Mitredon cromptoni* has a double-rooted postcanine dentition but lacks ontogenetic stasis in the lower tooth row. The tooth replacement pattern of *M. cromptoni* clearly does not retain the alternate pattern of *Thrinaxodon*, nor are teeth exclusively lost mesially and added distally, as in gomphodonts, tritylodontids, and *Sinoconodon*. Instead, *M. cromptoni* replaces mesial and distal postcanines simultaneously and thus compromises the stability of the tooth row. Of the teeth represented in MGUH VP 3392, the second and fifth were being replaced and likely lacked functional predecessors at the time of death. Thus, of the five tooth positions represented by replacement teeth or functional roots, only the third, fourth, and sixth postcanines were occupied by functional teeth. The low number of functional postcanines in MGUH VP 3392 contrasts sharply with the "uninterrupted molari-form series" of mammals and gomphodont cynodonts (Hopson, 1971: 17).

The Origins of Multirooted Teeth

Teeth with multiple roots have traditionally been regarded as part of the functionally interdependent, coevolved complex of the mammalian masticatory system, which includes such diagnostic features as a dentary-squamosal jaw joint and unilateral mastication (e.g., Crompton, 1963a,b; Barghusen and Hopson, 1970; Kühne, 1973; Crompton and Parker, 1978; Crompton, 1989). However, several fossil taxa challenge the notion that "mammalian" characters are limited to the Mammalia. For example, Shubin et al. (1991) noted that unilateral occlusion may have originated not with the Mammaliaformes but with the common ancestor of trithelodontids and mammalianomorphs, or may have evolved independently in the Mammaliaformes. Likewise, the presently known structural diversity of roots within taxa, as well as the phylogenetic distribution of multirooted teeth, provide evi-

dence that this character evolved independently more times than previously recognized. In *Morganucodon* and *Kuehneotherium*, premolar and molar roots range from incompletely divided to widely divergent; root shape also varies, from straight with a blunt or bulbous terminus, to those that are curved and tapered (Parrington, 1971, 1978). Root morphology in *Sinoconodon* also varies: some premolars (Zhang et al., 1998) and molars of *Sinoconodon* are fully divided, but at least one example is known where the two roots are confluent beneath the crown, and are only narrowly separated distally (Luo, 1994, fig. 6.6). Cui and Sun (1987) document extensive variability among tritylodontids, which until recently were the only known Early Mesozoic cynodont clade (other than mammals) with multirooted teeth. In some taxa (e.g., *Yunnanodon*) the roots are completely separated, whereas in others (*Oligokyphus* and *Lufengia*) transverse sheets of dentine connect root pairs. *Bienotherium* exhibits differences in the degree of root separation along the upper postcanine row, with unseparated roots mesially and fully separated roots distally. In general, the number of roots in tritylodont teeth varies with the number of cusps (Cui and Sun, 1987). Finally, to this spectrum of variation may be added *Mitredon cromptoni*. With a sectorial crown morphology and a tooth replacement pattern that is comparable to no known mammal, *M. cromptoni* is best interpreted as a cynodont with double-rooted teeth.

CONCLUSIONS

Advanced cynodonts may potentially exhibit a mosaic of "mammalian" and "non-mammalian" characteristics. *Mitredon cromptoni*, *Meurthodon gallicus*, tritylodontids, and mammals all possess postcanine teeth with multiple roots. Previous analyses (e.g., Sues, 1985; supported by Wible, 1991) point to an independent evolution of this character in tritylodontids. Hence, if *M. cromptoni* and *Meurthodon gallicus* are indeed "chiquodonts" (no

recent analyses place chiniquodonts as the sister taxon of mammals), then multiple-rooted postcanines may have evolved up to three separate times in cynodonts (following the phylogenetic hypotheses of Hopson, 1994; Hopson and Kitching, 2001). This character would no longer be useful in the diagnosis of Mammaliaomorpha (Rowe, 1988) or Mammaliaformes (Wible, 1991). Alternately, double-rootedness may have evolved only once, in the Mammaliaformes (Wible, 1991; Hopson and Kitching, 2001). In this scenario, *Mitredon* and *Meurthodon* would fall within the Trithelodontidae + Mammaliaformes clade, closer to mammaliaforms than to trithelodontids.

Double-rootedness did not necessarily evolve in concert with tooth row stasis during synapsid evolution. *Mitredon cromptoni* has double-rooted teeth but retains a tooth replacement pattern uncharacteristic of taxa with precise occlusion and a functionally uninterrupted postcanine tooth series.

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