Tooth Histology of the Parareptile Soturnia caliodon from the Upper Triassic of Rio Grande do Sul, Brazil

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Tooth histology of the parareptile *Soturnia caliodon* from the Upper Triassic of Rio Grande do Sul, Brazil

SERGIO FURTADO CABREIRA and JUAN CARLOS CISNEROS

A histological analysis of the dentition of the small procolophonid parareptile *Soturnia caliodon* reveals detailed information concerning tooth implantation and replacement for this taxon. The presence of acrodont tooth implantation is verified, which contradicts current models for procolophonid dentition. A heterogeneous enamel layer, that reaches large thickness on the cusps, and a broad secondary dentine are also recorded. These structures provide a very stable occlusal morphology that extends the useful life of the teeth. During the process of replacement, old teeth were not pushed out but reabsorbed. The evidence indicates that *Soturnia caliodon* had a very low rate of tooth replacement which constitutes a valuable adaptation for its high-fibre herbivorous niche.

Introduction

Procolophonids are the most successful clade of parareptiles, being notable for developing several specializations for herbivory (Reisz and Sues 2000; Cisneros 2008) which played an important role for the survival of this group during more than 50 million years until the end of the Triassic. Some of these adaptations, such as the acquisition of transversely expanded molariforms, evolved in procolophonids independently and earlier than in other tetrapod lineages of the Triassic such as cynodonts, therocephalians or trilophosaurids. Despite the significant role of the dentition through the evolutionary history of the group, our knowledge of procolophonid tooth histology is basically restricted to some comments on the enamel of *Procolophon trigoniceps* based on SEM analysis (Sander 1999). The recently described *Soturnia caliodon* (Cisneros and Schultz 2003) is the only Gondwanan member of the Leptopleuroninae, a very characteristic clade of procolophonids that dominated during the Late Triassic (Sues et al. 2000; Fraser et al. 2005; Cisneros 2008). New material of this species is used here to provide a description of the tooth histology of a procolophonid.

Institutional abbreviation.—UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Other abbreviation.—EJL, enamel-dentine junction layer.

Material and methods.—Specimen UFRGS PV1112T (Fig. 1A) consists of a partial left maxilla and pterygoid, bearing the second incisiform (I2) and well preserved first and second molariforms (M1–M2), and a partial mandible in occlusion with two complete molariforms (m1–m2). UFRGS PV1112T was collected from the type locality, a exposure of the Caturrita Formation in the Municipality of Faxinal do Soturno (29°33’27’’ S, 53°26’56’’ W), Rio Grande do Sul, Brazil. The local fauna at Faxinal do Soturno is considered to be early Norian in age (Rubert and Schultz 2004; Bonaparte and Sues 2006; Langer et al. 2007). Tooth and related bone tissues were studied through the use of a polarized light microscope, which allows detailed observation of the internal structure and organization of elements. The specimen was embedded in polystyrene resin, and posteriorly ground down using a diamond grinding wheel. Several photographs were taken, during successive stages of wear, using a digital camera through a petrographic microscope equipped with polarized light.

Results

Enamel.—The tooth enamel of *Soturnia caliodon* is aprismatic (Figs. 1E–G, 2A, B, E). In the region of the cusps, “crystallites” (sensu Carlson 1990) are virtually perpendicular to the enamel-dentine junction layer (Fig. 2A) and are oriented in a straight line towards the enamel surface with no evidence of abrupt changes in direction or decussation. In the region between the apex and the cervix, the crystallites lie slightly oblique to the EJL, showing very weak sigmoid curvatures (Fig. 2B) pointing towards the enamel surface. Enamel crystallites are parallel to one another and lack inter-prism sheaths.

No structural features that could suggest more intra-structural enamel complexity were found, such as incremental lines or other internal structures. This pattern is characteristic of aprismatic enamel (Carlson 1990). Tooth enamel partially covers the external surface, from the cusps to a level close to the cervix, where part of the root bulb dentine is exposed. Tooth crowns show considerable variation of enamel presence and thickness. The molariforms possess a thick and well distributed enamel on its apical surface (maximum thickness ~260 μm), but it becomes progressively thinner towards the cervical region, disappearing completely before reaching the cervix (Fig. 1F).

Dentine.—The dentine walls are thick and the crown pulp cavities are notably broad. Older teeth possess thick dentary walls and exhibit a volume reduction of the pulp cavity, which is associated with occlusal wear surfaces. Primary dentine from the most apical regions of the crowns shows roughly straight dentinal tubules

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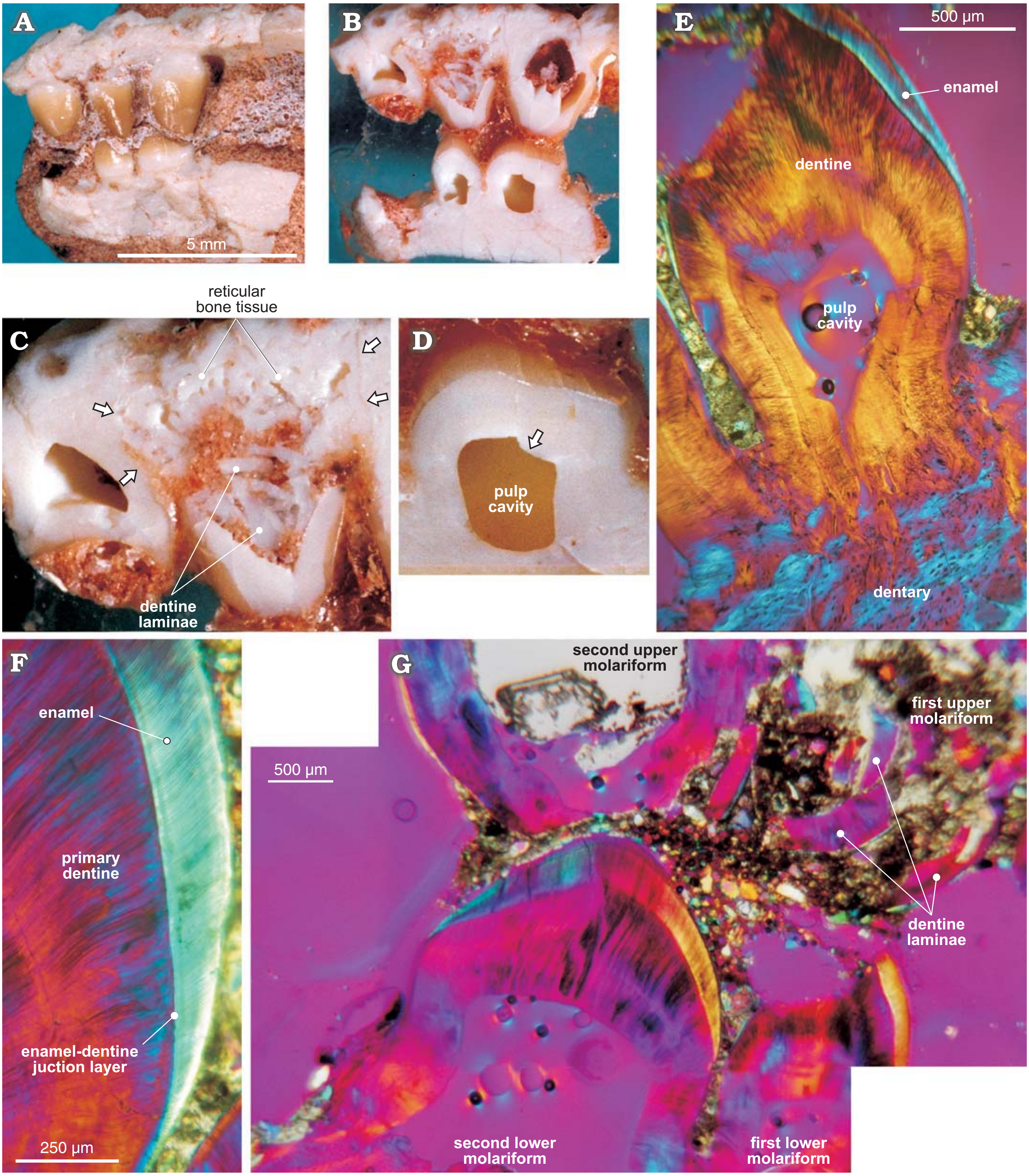

Fig. 1. The procolophonid *Soturnia caliodon* Cisneros and Schultz, 2003, UFRGS PV1112T, from the Norian (Upper Triassic) Caturrita Formation of Rio Grande do Sul, Brazil. Partial left maxilla and mandible, before preparation (**A**), and during initial stages of preparation (**B**). **C**. I2 (to the left) and M1 (to the right), showing the limits of tooth morphogenetic fields (indicated by arrows), reticular bone tissue, fragmentary dentine, indicating tooth resorption in M1. **D**. A pronounced secondary dentine pulp deposition (indicated by an arrow) in m2. **E**. m1, note that enamel is completely absent in the cervix. **F**. Portion of m2 crown, showing the transition of thick enamel in the apex (to the top) to a very thin enamel close to the cervix (to the bottom). **G**. M1, M2, m1 and m2. Note remnant dentine fragments in most of M1. A–D in labial view, anterior is to the left. E–G in lingual view and under polarized light.

(Fig. 2A, E), whereas dentine in the cervical regions shows slightly more irregular tubules (Fig. 2C). Approximately three incremental lines within the dentine are observed in all teeth (Fig. 2C). These lines are interpreted as an evidence of variation in dentine apposition in ectothermic vertebrates (Carlson 1990). Due to the fact that these incremental lines are strongly outlined in *Soturnia* we think that they reflect a very important event during the development of the individual. We suggest that they are a result of physiological stimuli produced by the beginning of mastication at an early morphogenetic stage, as it is generally observed in mammals (Berkovitz et al. 2002). Thus, these incremental lines represent a division between primary and secondary dentine. The secondary dentine pulp deposition is pronounced both in the occlusal wear areas that form "basins" (Cisneros and Schultz 2003: figs. 2a, 3b) in the maxillary molariforms and under cusps, making the internal walls of some pulp cavities to become irregularly thick, as can be seen in M2 (Fig. 1D).

The outline of each tooth resembles a bulb (Figs. 1E, 3) with an expanded root base forming a short dentine pedicle that is anchored in compact cortical bone and fixed by attachment bone tissue (Figs. 1E, 2D, F). There are no true roots; the teeth are fixed only through short pedicles on the tooth bearing bone walls.

Tooth implantation.—Teeth are situated on compact cortical bone tissue of intramembranous origin. Most bone cell lacunae, which have an elongated shape, are oriented anteroposteriorly along the dentary (Fig. 2F), suggesting that the osseous lamellae were oriented also in this way. Bone cell lacunae possess different shapes when associated with a dental pedicle, indicating different stages of osteogenesis. Elongated bone cell lacunae indicate a more mature bone and low cell synthesizing rates. Globular bone cell lacunae that are associated with numerous vascular canals indicate bone tissue with high remodelling activities (Enlow 1969; Francillon-Vieillot et al. 1990).

Vascular canals for nutrient delivery can be seen extending to the thin pulp cavity that is located within the pedicle (Fig. 2F) and to the actual pedicle base. The external walls of the dentinary pedicle are largely covered by a non-organized and heavily vascularized bone tissue, that we recognize as attachment bone tissue which provides greater tooth adherence. As it can be observed, this model of tooth implantation is typically acrodont as the teeth do not have true root cylinders. These tooth pedicles are merely short extensions of the cervix, bearing irregular dentinary projections, confined within lamellary bone and attachment bone. There is no evidence of alveolar structures (sockets), cementum or periodontal membrane in the dentition of *Soturnia*.

Tooth replacement.—Significant osteological variations, which are interpreted as representing tooth replacement processes were observed in only one of the five teeth that underwent histological preparation. Both the base and the cervix walls of M1 (Fig. 1B, C) feature irregular bone trabeculae and fragmentary dentine. This osseous arrangement suggests that the bone had a large number of irregularly anastomosed vascular canals, a pattern that is compatible to that seen in reticular bone tissue (Enlow 1969; Francillon-Vieillot et al. 1990). This bone pattern is strongly suggestive that a process of osseous resorption and remodelling was taking place in this region at the time of death, very likely related to the process of future odontogenesis. A vertical line of strong discontinuity within the ossification pattern (Fig. 1B, C, see arrows) can be traced between the tooth implantation pedicles of the second and third maxillary molariforms, and less marked discontinuities outline the bases of all teeth and their supporting bone regions. Restriction of this process of bone activity and resorption to M1 indicates that these lines represent the limits of tooth morphogenetic fields that are responsible for induction and control of the odontogenetic developmental processes. Similar discontinuity lines were noted in the mandible of the procolophonid *Libognathus sheddi* by Small (1997: fig. 3) who described them as "replacement pits". Furthermore, the pulp cavity shows irregularly arranged fragmentary dentine laminae (Fig. 1G) also separated by matrix. The presence of these dentine remains confirms that the dentinary walls were suffering a resorption process, probably under the influence of the dentinoclasts. This process will end in a complete removal of the tooth cylinder. This would create an empty tooth locus, a condition that likely anticipates a replacement process.

Discussion

Three basic models of tooth implantation have been proposed for procolophonids: acrodonthy (Broom 1905), protothecodonthy (Broili and Schröeder 1936, also referred as "subthecodonthy") and ankylothecodonthy (Sues and Olsen 1993). Acrodonthy can be briefly defined as the condition when a tooth is fused to the surface of the bone without a socket (Peyer 1968). Protothecodonthy and ankylothecodonthy are models usually described as being characterized by the fusion of tooth roots to alveolar structures through attachment bone, with larger roots (and consequently, larger sockets) distinguishing the ankylothecodont condition (see discussion in Small 1997). Several authors (e.g., Gow 1977; Li 1983; Sues and Olsen 1993; Small 1997) classify procolophonid dentition as being either protothecodont or ankylothecodont. Besides *Soturnia*, the tooth implantation and replacement of two other leptopleuronine procolophonids have been described: *Libognathus sheddi* (Small 1997) and *Hypsognathus fenneri* (Sues et al. 2000). Small (1997) classifies the implantation of *Libognathus* as protothecodont and concludes that all procolophonids must have this pattern. In addition, this author proposes that the replacement teeth of *Libognathus sheddi* force the old teeth out. Sues et al. (2000) do not specify if *Hypsognathus fenneri* possesses a protothecodont or an ankylothecodont dentition but clearly mention the presence of roots fused to sockets. Sues et al. (2000) also propose that the new teeth of this taxon push out the old teeth as in *Libognathus*. It has to be noticed that all these observations on the dentition of procolophonids were not supported by detailed histological analysis of specimens.

Despite the ankylothecodont pattern of tooth implantation being proposed for a number of reptiles, including rhynchosaurs, trilophosaurids and prolacertiforms (Chatterjee 1974; Benton 1984), we are not aware of any histological studies supporting these models. Indeed, the development of a tooth im-

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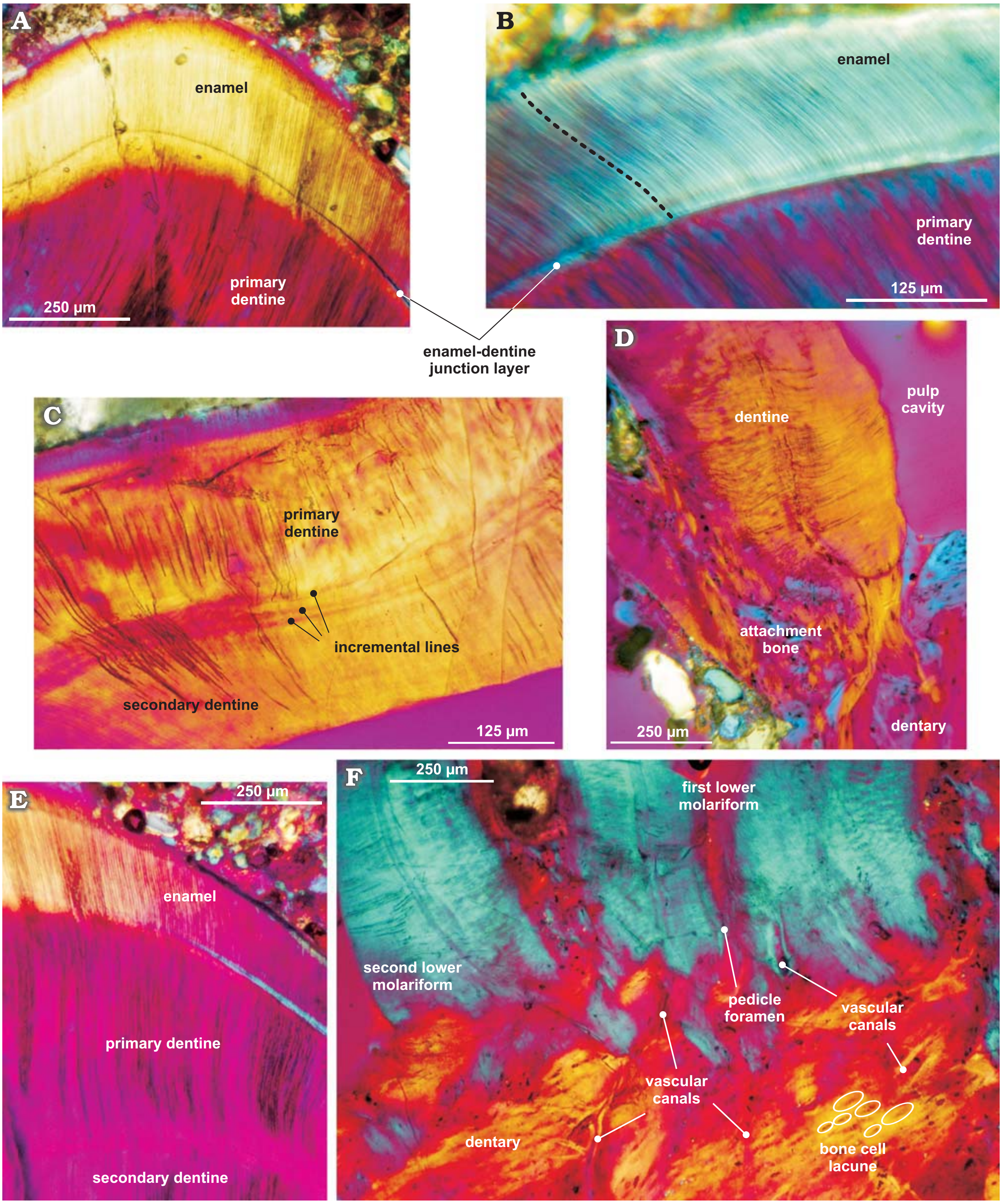

Fig. 2. The procolophonid *Soturnia caliodon* Cisneros and Schultz, 2003, UFRGS PV1112T, from the Norian (Upper Triassic) Caturrita Formation of Rio Grande do Sul, Brazil. **A**. Enamel and primary dentine from the apical region of m2. **B**. Enamel and primary dentine from the region between the apex and the cervix of m2. The slightly sigmoid curvature of the crystallites is highlighted by a dashed line. **C**. Primary and secondary dentine in the anterior portion of the cervical region of m2. Note the irregular primary dentinal tubules compared to those in the apical region (A and E). **D**. Attachment bone in the posterior region of the base of m2. **E**. Primary dentine in the apical region of m2. **F**. Tooth implantation in m1 and part of m2. Attachment bone, characterized by globular or irregular bone cell lacunae, is predominant in the reddish areas of the photograph. Dentine is shown in blue, note some small amounts of pedicle dentine within the dentary bone. Dentary bone tissue, represented in yellow and orange, showing predominance of elongated and anteroposteriorly directed bone cell lacunae. The apex is placed to the left in B and C. All photographs taken using polarized light.

plantation characterized by roots fused to sockets (both ankylothecodonthy and protothecodonthy) would necessarily be constrained to the embryological suppression of two periodontal structures: periodontal ligament and cement. These structures, together with the alveolar bone, are known to originate from the same tooth foliculum (Carlson 1990; Ten Cate 1997; Berkovitz et al. 2002). For this reason, the fusion of alveoli to roots by attachment bone—and the necessary absence of periodontal ligament and cement—would be unlikely in any tetrapod. *Soturnia caliodon*, as shown in this study, possesses a dentition that is clearly acrodont, without sockets.

As described above, the specimen studied shows one tooth, M1, apparently undergoing a substitution process. This tooth seems to be heavily worn, showing perforation of the pulp chamber. Reticular bone tissue occupies the whole basal region, and in a later stage, this element would proceed to the removal of all remnant bone and tooth tissue. After the removal of both the tooth to be substituted and the supporting bone, a new tooth element would begin its formation, eruption and fusion. The pulp degradation of a worn and perforated tooth would trace the posterior stages of resorption of a "dead tooth" and activate a new tooth germ. Thus, old teeth are not pushed out, but recycled.

The processes of tooth substitution would take place slowly during the skeletal growth of the individual, following an alternate and polyphyodont pattern. The production of secondary (physiological) dentine extends the useful life of a tooth, by precluding exposition of the pulp cavity. In this way, the functionality of the occlusal morphology is effectively maintained through the internal addition of secondary dentine, in opposition to the wearing of the occlusal basins. The heterogeneous distribution of enamel, showing a great thickness in the cusps and progressive thinning towards the occlusal basins (where it is completely absent) further preserves the occlusal morphology and expands the useful life of the teeth. By being a high-fibre herbivorous reptile *Soturnia* should be restricted to a low rate of tooth substitution. This is implied by the fact that high-fibre plant cells, being low in nutritional value and rich in cellulose, must be macerated more consistently, for more efficient digestion and absorption. The loss of one tooth would be critical for the individual, particularly for a species with a highly reduced tooth formula like *Soturnia*, with only two upper incisors and two to three molariforms. The highly resistant teeth of this taxon are consistent with a strategy of a low rate of tooth replacement. Previous authors (Ivakhnenko 1975; Gow 1977; Li 1983) had noted that tooth replacement is an extremely rare event in other procolophonid species.

We recognize that it would be premature to suggest that all procolophonids possess the same model of tooth implantation and replacement described here, especially considering the morphological diversity and different feeding habits of members of this clade (Reisz and Sues 2000; Cisneros 2008). Nevertheless, judging from the marked anatomical similarity of the dentition of procolophonids that are closely related to *Soturnia caliodon*, such as *Hypsognathus fenneri*, *Leptopleuron lacertinum*, *Libognathus sheddi*, and the unnamed Chinle Formation form (Fraser et al. 2005), it should be expected that these leptopleuronines possess the same or similar pattern of tooth implantation and substitution revealed by the Brazilian taxon. It is also worth noting that Colbert (1946) had already proposed that the dentition of *Hypsognathus fenneri* is fully acrodont.

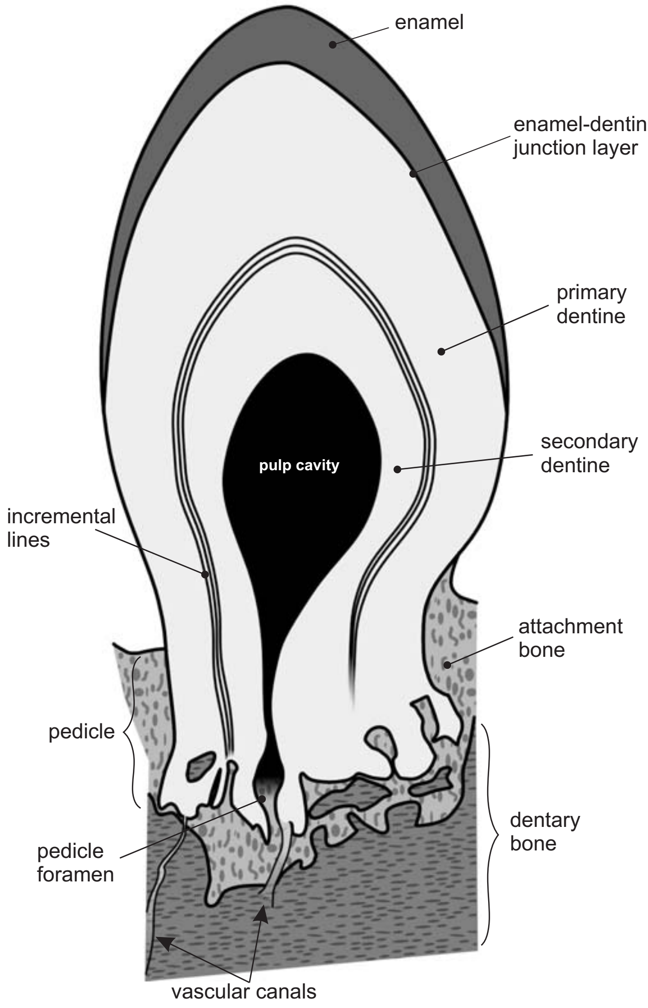

Fig. 3. The procolophonid *Soturnia caliodon* Cisneros and Schultz, 2003, from the Norian (Upper Triassic) Caturrita Formation of Rio Grande do Sul, Brazil. Reconstruction of a lower molariform tooth in parasagittal section based on m1 from UFRGS PV1112T.

Conclusions.—A histological analysis shows that the dentition of the small parareptile *Soturnia caliodon* is clearly acrodont. None of the two models of tooth implantation that are traditionally proposed for procolophonids, protothecodonthy or ankylothecodonthy, are applicable to this procolophonid, and are unlikely to be found in other parareptile taxa, due to the embryological constraints that prevent the development of these tooth patterns. The teeth of *Soturnia* possess a very stable occlusal morphology which extends their useful life and indicates a low rate of tooth replacement, necessary for the consumption of high-fibre plant material. The pattern of tooth implantation and replacement of this taxon may be applicable to other Late Triassic procolophonids but further analyses are necessary to obtain a better picture of other members of the Procolophonidae and the Parareptilia as a whole.

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