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Authors: Pretto, Flávio A., Cabreira, Sérgio F., and Schultz, Cesar L.

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Tooth microstructure of the Early Permian aquatic predator *Stereosternum tumidum*

FLÁVIO A. PRETTO, SÉRGIO F. CABREIRA, and CESAR L. SCHULTZ

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A histological investigation of the feeding apparatus of a *Stereosternum* specimen revealed a great number of adaptations in the structure and insertion of teeth, to deal with breakage risks. The tooth wall is composed of different layers of dentine, varying in orientation and composition. This mixed arrangement may have increased tooth resistance to lateral tension. The tooth insertion also involves more than one mechanism. The teeth are located inside shallow tooth sockets and are held in place by a tripartite periodontium (composed of alveolar bone, cementum and possibly soft periodontal tissue) and accessory structures, here termed anchorage trabeculae (mainly composed of cementum). Fully grown teeth are ankylosed to the bottom of the tooth socket. The recognition of alveolar bone and cementum (and the possible presence of a soft periodontal ligament) reinforces the idea that these tissues were widespread among Amniota, not being exclusive to mammals and archosaurs. The adaptations identified here reinforce the hypothesis that *Stereosternum* was an active aquatic predator.

Key words: Amniota, Mesosauridae, *Stereosternum tumidum*, histology, tripartite periodontium, Permian.

Flávio A. Pretto [flavio_pretto@yahoo.com.br] and Cesar L. Schultz [cesar.schultz@ufrgs.br], Universidade Federal do Rio Grande do Sul, Instituto de Geociências, Setor de Paleovertebrados, Av. Bento Gonçalves, 9500 – Bloco J, Prédio 43127, Campus do Vale, Agronomia−Porto Alegre, Rio Grande do Sul, Brazil, CEP 91540-000;
Sérgio F. Cabreira [sergio.cabreira@terra.com.br], Universidade Luterana do Brasil, Museu de Ciências Naturais, Av. Farroupilha 8001−Canoas, Rio Grande do Sul, Brazil, CEP 92425-900.

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Introduction

Mesosaurids were early parareptiles (Tsuji and Müller 2009) that showed a great number of structural adaptations to life underwater. Examples are the paddle-like limbs, long rostrum, laterally depressed tail, and bone pachyostosis (Gervais 1864; Osborn 1903; Ricqlès 1969, 1974; Araújo 1976; Timm and Araújo-Barberena 1996; Modesto 2006, 2010). Mesosaurid fossils are collected abundantly in Lower Permian strata (Artinskian; Santos et al. 2006) from the Irati and Mangrullo formations in South America and from the Whitehill Formation in southern Africa (Oelofsen and Araújo 1987; Piñeiro 2004). Three genera are currently recognized in the family Mesosauridae: *Mesosaurus tenuidens* Gervais, 1864, *Stereosternum tumidum* Cope, 1886, and *Brazilosaurus sanpauloensis* Shikama and Ozaki, 1966. As is common in recent works (Modesto 1999, 2006, 2010), only the generic names will be adopted in the text, given that mesosaurid taxa are monotypic.

Previous interpretations of the feeding behavior of mesosaurids, as also for most descriptions of the group, were based mainly on *Mesosaurus* specimens. MacGregor (1908) proposed that *Mesosaurus* preyed on small fish and aquatic insect larvae, a hypothesis supported by Bakker (1975). However, Modesto (2006) argued that the teeth of *Mesosaurus* would not have been resistant enough to pierce through the prey's flesh. Additionally, according to that author, the hypothesis that *Mesosaurus* was a filtering predator (Romer 1966; Carroll 1982; Chiappe and Chinsamy 1996) is biased by an erroneous interpretation (Huene 1941) of tooth number for the taxon (Modesto 2006).

The reconstruction of the skull of *Mesosaurus* (Modesto 2006) supports the idea that the animal was a predator. It probably used its marginal teeth as an imprisoning device to capture single prey, rather than as a strainer as in baleen whales. The diet of *Mesosaurus*, according to Modesto (2006), may have been notocaridid crustaceans (e.g., *Liocaris*), abundant in the same sediments (Vieira et al. 1991).

Despite the differences in the dentition of *Stereosternum* and *Brazilosaurus* when compared to *Mesosaurus*, there has been little interest in investigating possible differences in

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feeding behavior. *Stereosternum* has shorter teeth, a condition even more evident in *Brazilosaurus*, which suggests a different foraging strategy.

Histological analysis of the mesosaurid dentition was attempted by Araújo (1976), but she was unable to achieve good results owing to problems with the sectioning techniques, which greatly damaged the teeth. By overcoming these problems, we present here a detailed histological description of the dentition of *Stereosternum*. It should be noted that mesosaurids also possess teeth in some of the bones that constitute the palate. Aspects concerning these teeth are not discussed here, because no palatal material was made available for analysis. The scarcity of *Brazilosaurus* fossils also precluded investigation of this taxon.

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

Other abbreviations.—ab, alveolar bone; bc, bone cell lacunae; ce, cementum; cs, crenulated surface of the pulp-dental boundary; db, dentary bone; dw, dentine wall; es, empty tooth socket; idt, imprisoned dentine tubule; igd, interglobular dentine; mc, meckelian channel; od, orthodentine; odt, orthodentine tubule; pl, inferred location of periodontal ligament; tr, anchorage trabecula; vc, vascular canalicle; vd, vasodentine.

Material and methods

The specimen UFRGS-PV-0378-P (Fig. $1A_1$) was collected in the Passo do São Borja outcrop, southern Brazil (30º27'33'' S, 54º42'58'' W, datum SAD 69) and consists of an isolated, partial left dentary assigned to *Stereosternum* (Lavina et al. 1991). This identificartion is supported by the observed tooth length, as discussed in the "tooth description" section below.

The preparation of thin sections follows the methodology described in Cabreira and Cisneros (2009): the specimen was first embedded in polystyrene resin, and ground down with a diamond grinding wheel, until the desired thickness was obtained. Successive stages of grinding were documented with photographs.

Results

Dentary

The dentary fragment measures 182 mm, and lacks its posterior extremity. The lateral surface of the bone is devoid of any ornamentation except for a large concentration of small pores (Fig. 1A), grouped mainly in its anteriormost region. These cavities become smaller and less numerous posteriorly, and stop occurring at the point of the third visible tooth. There are at least 17 preserved tooth sockets, and eight of them still bear teeth.

Empty sockets alternate with tooth-bearing sockets (Fig. $1A_1$, B_1, B_2) in a pattern that resembles the alternation of long and short teeth described by Modesto (1999). Although the dental replacement mechanism cannot be properly observed in this analysis, the empty tooth sockets suggest that replacement teeth, probably the shorter teeth described by Modesto (1999) were only loosely attached to the jaw, being easily discarded during the decay processes (Edmund 1960; Peyer 1968). The first grinding stages (Fig. $1B_1$) revealed that the bottom of the empty sockets is dorsally concave. The socket walls are very thin, which explains why many of them are externally broken. The initial preparation also exposed part of an ample meckelian groove (Fig. $1B_1$), which progresses in a rostral direction, constituting the dentary meckelian channel.

Tooth

The mesosaurid dentition is homodont, with numerous dentary elements. Although the mean tooth width does not change, the mean tooth length is statistically different among mesosaurid taxa (Araújo 1976), thus having taxonomic utility. *Brazilosaurus* possesses shorter teeth, *Stereosternum* shows teeth of a medium length (about six times the width), and *Mesosaurus* has the longest teeth (about twelve times the width). Rossmann (2002) argued that even skulls of juvenile specimens of *Mesosaurus* have teeth longer than *Stereosternum* specimens of the same skull length. Finally, Modesto (2006) reported a tooth length equivalent to five tooth positions in *Mesosaurus*, contrasting with a length of three tooth positions in *Stereosternum*. By measuring the crown height of its longest tooth (Figs. $1A_1$, 2A), the specimen UFRGS-PV-0378-P is thereby identified as *Stereosternum*.

Marconato and Bertini (2002) recognized a pattern of longitudinal striation on the external surface of *Mesosaurus* and *Stereosternum* teeth, also with taxonomic importance. Yet, this feature is only visible using SEM, and therefore it was not observed in the specimen described here, which was investigated using only light microscopy.

Externally, the teeth of *Stereosternum* are elongated and slightly curved posteriorly. The tooth width gradually decreases, forming a sharp crown apex. In longitudinal section (Fig. 2A), it is possible to observe a thick pulp cavity that occupies a great part of the tooth's internal volume. The histological organization of the tooth comprises several layers of dentine, in some parts covered by a coat of enamel (Fig. 2A, B). The tooth base is externally covered by a thin layer of cementum.

Enamel.—The enamel layers form a thick cap in the crown apex (Fig. 2A, B), but become progressively thinner towards the tooth base, being absent in the basalmost portion. There is no clear enamel-dentine junction. It is possible that the externalmost layers of dentine were impregnated by enamel proteins, thus masking the boundary between the two tissues, as reported in extant squamates (Delgado et al. 2005). This also could have caused some dentine tubules to be imprisoned in the mineralized matrix (Fig. 2B).

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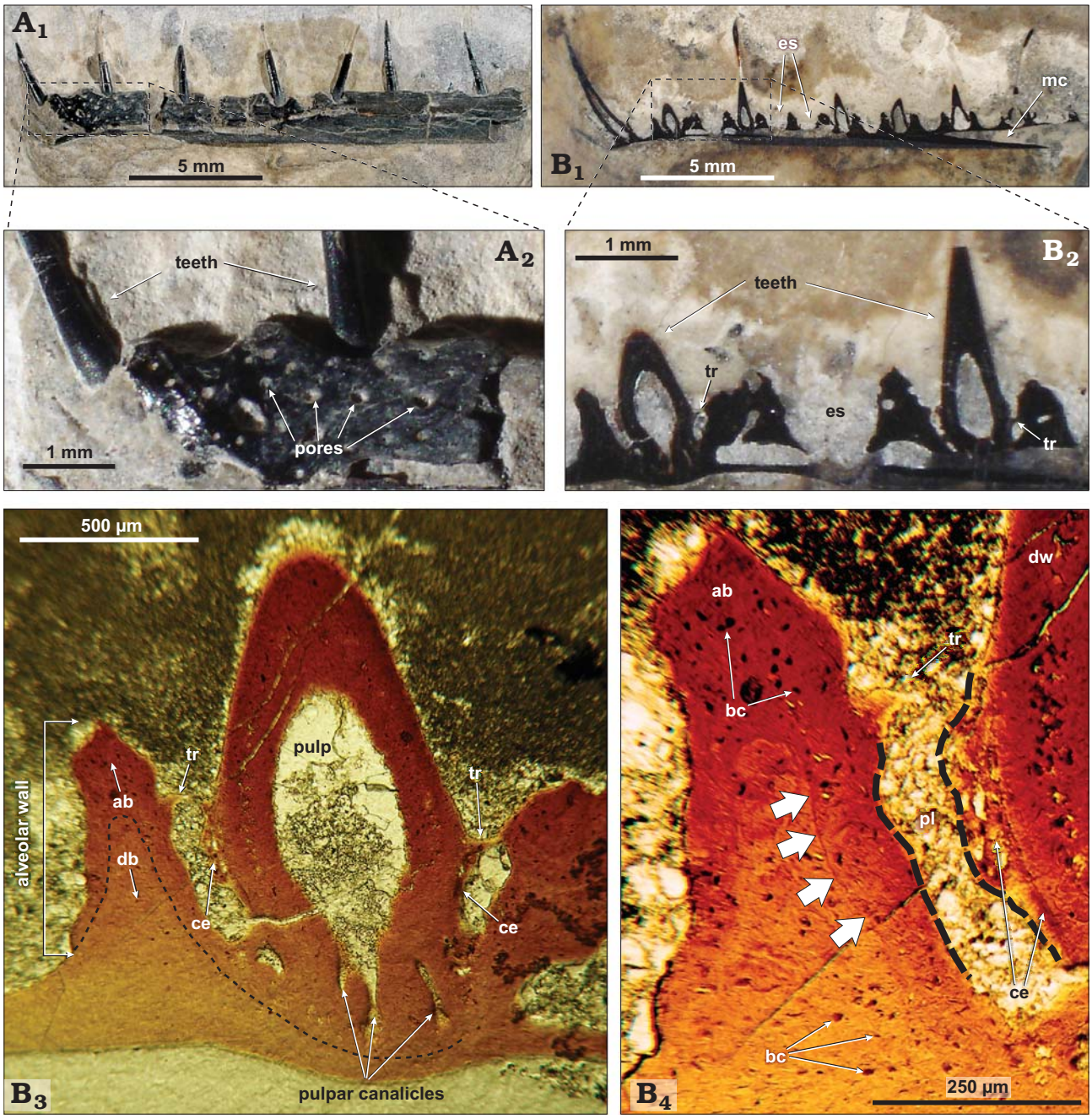


Fig. 1. Mesosaurid parareptile *Stereosternum tumidum* Cope, 1886 from Passo do São Borja outcrop, Irati Formation, Lower Permian of the Paraná Basin. **A**. UFRGS-PV-0378-P. Lateral view of the partial left dentary (A_1), before abrasion. The rostral portion is to the left. Enlarged partial view (A_2), highlighting some of the pores of the anterior region of the dentary. **B**. UFRGS-PV-0378-P. Partial abrasion of specimen (B_1), showing the alternation of empty and tooth-bearing sockets Arrows indicate two consecutive empty sockets that break the alternate pattern. The partially exposed meckelian cavity is also indicated. Detail (B_2), some anchorage trabeculae are indicated. Thin section of the anterior tooth from B_2 (B_3), shown in oblique cut. Dashed line indicates the boundary between alveolar bone and dentary bone. Two trabeculae are also pointed. At the base of the tooth, some canalicles are indicated, connecting the pulp cavity with the dentary bone. Enlarged view (B_4) of the alveolar wall indicated in B_3. Large white arrows point to the boundary between the alveolar bone and the dentary bone. The space between the alveolar bone and the cementum layer that covers the tooth base is indicated between dashed lines, and was supposedly filled in life with soft periodontal ligament. Abbreviations: ab, alveolar bone; bc, bone cell lacunae; ce, cementum; db, dentary bone; dw, dentine wall; es, empty tooth socket; mc, meckelian channel; pl, inferred location of periodontal ligament; tr, anchorage trabecula.

Dentine.—The dentine cylinder of *Stereosternum* is an astonishingly complex set of histological variation, which is represented by the arrangement of diverse dentine patterns. In the crown apex, under the enamel cap, a large coat of orthodentine is identified, with dentine tubules radiating from the pulp cavity (Fig. 2B).

However, in a segment from the tooth base to about half the tooth height (Fig. 2A, C), the dentine cylinder shows

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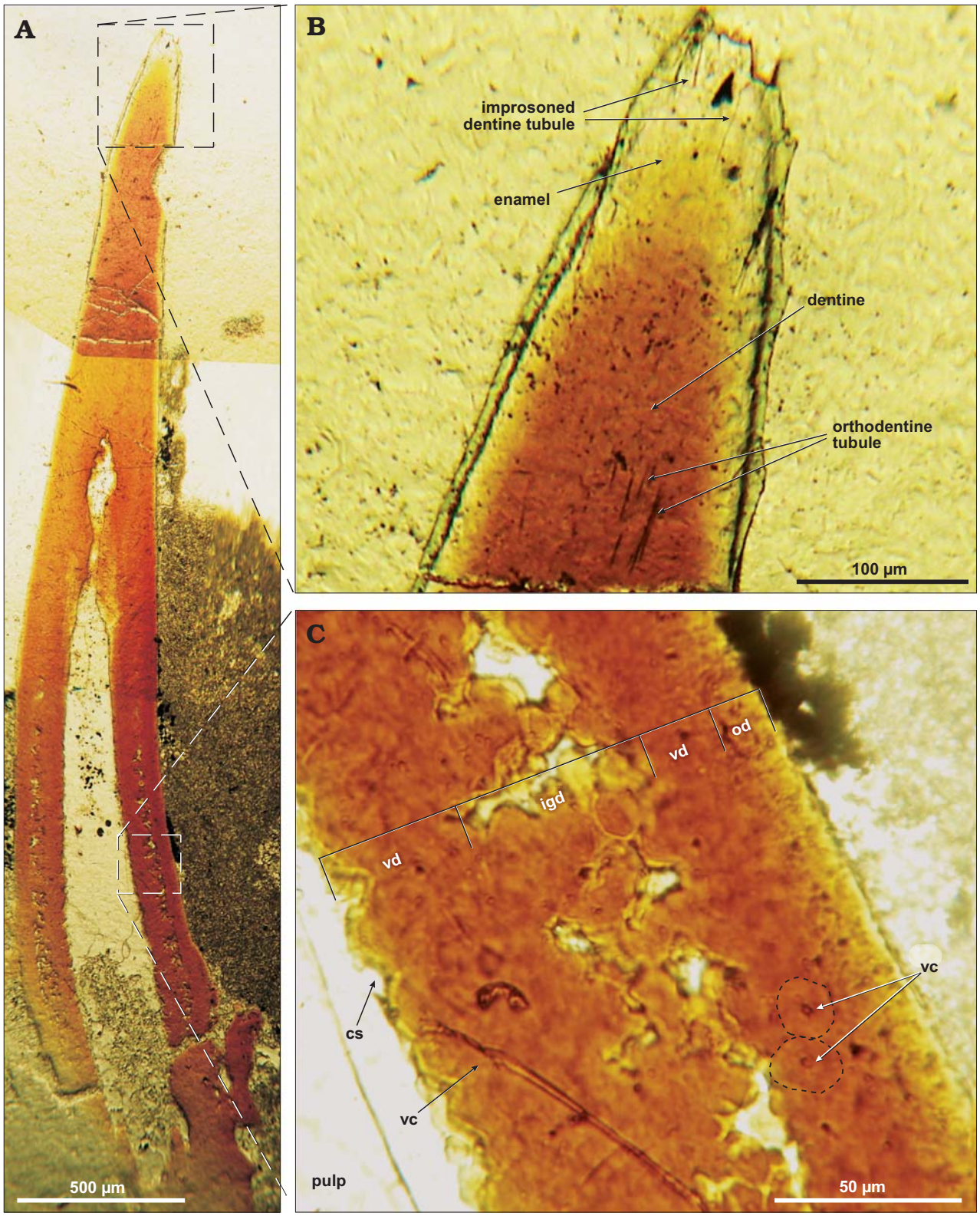


Fig. 2. Mesosaurid pararreptile *Stereosternum tumidum* Cope, 1886 from Passo do São Borja outcrop, Irati Formation, Lower Permian of the Paraná Basin; UFRGS-PV-0378-P. **A**. Composite photograph of a longitudinal cut of the anteriormost preserved tooth. **B**. Closer view of the distal extremity of the same tooth. The enamel layer is visible in a lighter color. Some dentinary tubules are indicated. **C**. Closer view of a section of the base of the same tooth, indicating the mixed composition of the dentinary wall. The crenulated boundary surface between the dentinary wall and the pulp is shown. Dashed lines indicate two denteons, and some vascular canalicles are also noted. Abbreviations: cs, crenulated surface of the pulp-dental boundary; igd, interglobular dentine; od, orthodentine; vc, vascular canalicle; vd, vasodentine.

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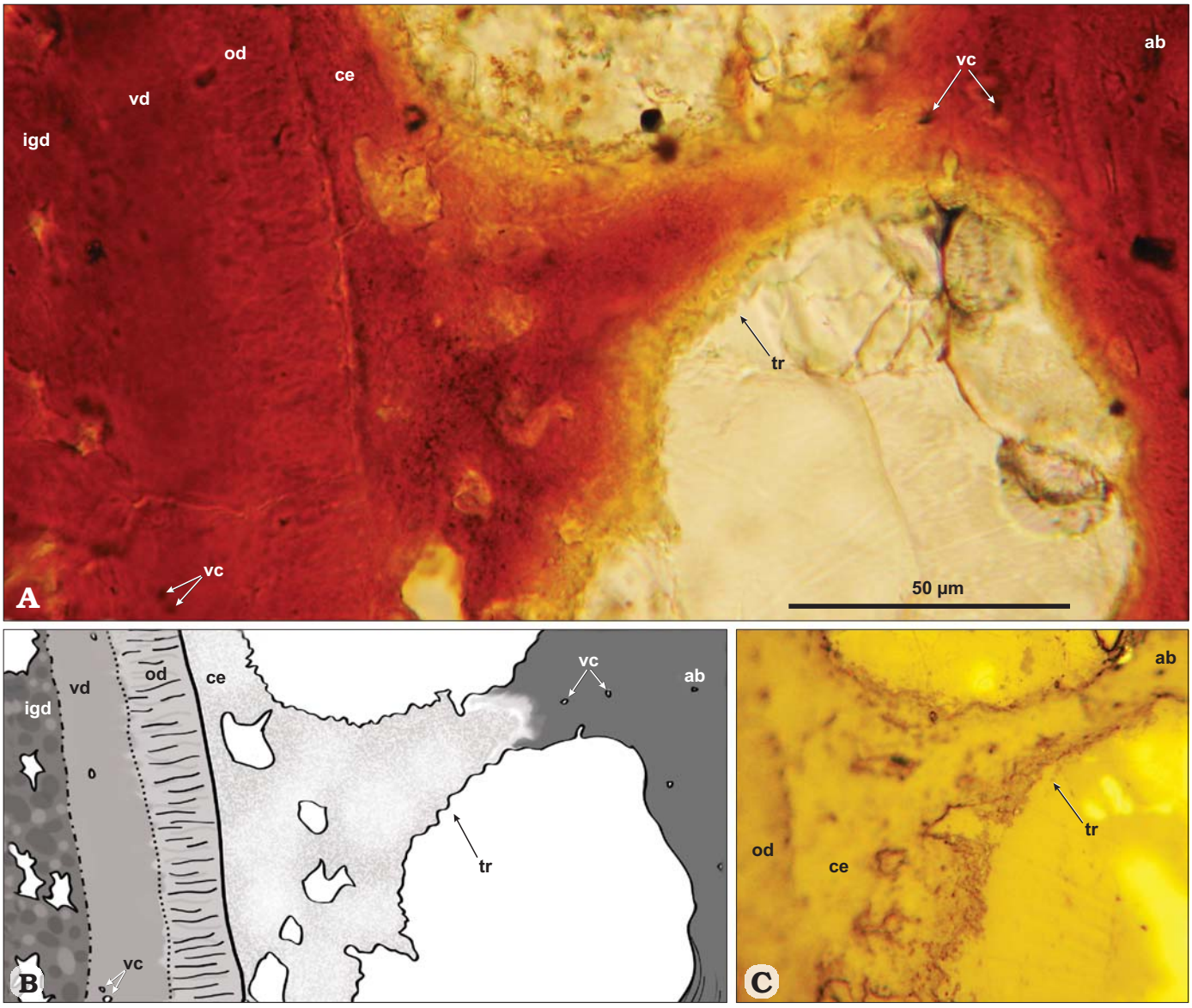


Fig. 3. Mesosaurid parareptile *Stereosternum tumidum* Cope, 1886 from Passo do São Borja outcrop, Irati Formation, Lower Permian of the Paraná Basin; UFRGS-PV-0378-P. **A**. Close view of the tooth attachment complex (the tooth wall is at the left). An anchorage trabecula is indicated, partly composed of avascular cementum and partly of alveolar bone. It is also possible to individualize the layers of orthodentine, externalmost vasodentine and interglobular dentine (at the right). **B**. Schematic drawing of A. **C**. Detail of an anchorage trabecula, viewed in reflected light optical microscopy. Abbreviations: ab, alveolar bone; ce, cementum; igd, interglobular dentine; od, orthodentine; tr, anchorage trabecula; vc, vascular canalicle; vd, vasodentine.

a different histological organization. The external wall is composed of a fine layer of orthodentine (Figs. 2A, C, 3), which constitutes the first product of the dental papilla (Peyer 1968; Carlson 1990). Internal to this layer, three distinct dentine strata are recognized. Adjacent to the external orthodentine layer is a vasodentine layer, characterized by vascular channels of diminutive diameter associated with the dentine matrix (Peyer 1968; Carlson 1990; Francillon-Vieillot et al. 1990; Sire et al. 2009). Around these vases, concentric layers of dentine are deposited, forming denteons (Figs. 2C, 3), an arrangement analogous to a primary osteon, which is why the tissue is sometimes termed osteodentine, but with a matrix composed of dentine instead of bone. The numerous vascular channels run in different directions, possibly associated with variations in the orientation of the dentine tubules.

More internally, beyond the vasodentine sheet, a layer of loosely concentrated denteons (Fig. 2C) is surrounded by a poorly mineralized interstitial matrix, indicated by empty spaces. This histological disposition of dentine characterizes the interglobular dentine: empty interglobular areas, which were composed of uncalcified dentine during life, are bounded by semiglobular projections of calcified dentine (Peyer 1968).

Internally, between the interglobular dentine layer and the pulp cavity, a second, internalmost stratum of vasodentine can be identified (Fig. 2C). Some of the blood vessels trapped in the vasodentine layer are seen connecting the den-

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tine wall with the pulp cavity, in invaginations of the crenulated pulp-dentine boundary surface (Fig. 2C). The blood vessels ran from the pulp cavity to the external vasodentine layer, reaching most of the dentine wall.

Cementum.—A thin sheet covering the wall of the tooth base is interpreted as cementum (Figs. $1B_3$, B_4, 3). This is a spongy layer of mineralized tissue, resembling the cementum layer described by Luan et al. (2009) in mosasaur material, but the limited resolution in imaging precluded visualization of fibers associated with the mineralized matrix. The cementum of *Stereosternum* resembles the thin layer that externally covers the globular dentine of *Captorhinus* (Ricqlés and Bolt 1983), which was originally described as atubular dentine, but has recently been reinterpreted as cementum (Maxwell et al. 2012).

Some regions of the cementum layer of *Stereosternum* show some lacunae, a morphological feature compatible with the avascular "cellular cementum" (sensu Caldwell et al. 2003). At some points, the cementum layer extends toward the layer of alveolar bone, forming a trabecular-like structure, here termed anchorage trabecula (Figs. $1B_3$, B_4, 3), linking the tooth to the alveolar wall. Most of the trabecula appears to be cementum, although alveolar bone possibly contributed to make part of its structure.

Alveolar bone.—The alveolar bone is a layer (Figs. $1B_3$, B_4, 3) that coats the internal surface of the alveolus. It has an embryological origin distinct from the jaw bone, and the contact between these two structures can be readily seen with light microscopy. Additionally, the alveolar bone layer can be differentiated from the underlying jaw bone by the size and quantity of bone cell lacunae. In the alveolar bone, these structures are larger, if compared to the bone cell lacunae of the tooth-bearing element. They are also highly concentrated, especially towards the apex of the alveolar wall and near the anchorage trabeculae, a condition that suggests higher cellular activity associated with bone growth and/or remodelling. Although larger than the bone cell lacunae of the jaw bone, the lacunae of the alveolar bone do not reach the size seen in the highly vascularized bone of attachment of other early amniotes. There is indeed no evidence of bone of attachment in *Stereosternum*.

Tooth insertion.—The teeth of *Stereosternum* show an uncommon pattern of insertion for parareptiles. The teeth are inserted in sockets, and dental ankylosis is observed in fully grown teeth (Figs. $1B_1$–B_3, 2A). Passing posteriorly along the tooth row, the preserved teeth seem to show progressively fewer signs of fusion with the dentary bone (Fig. $1B_1$).

The thin layer of cementum is separated from the alveolar bone by a noticeable empty space, a gap, supposed to have been filled with soft periodontal ligament, that acted as an anchor between the tooth and the jaw bone. The cementum, alveolar bone and soft periodontal ligament characterizes the periodontal tripartite arrangement typical of thecodont insertion. In extant thecodonts such as crocodilians and mammals, these three tissues are derived from the dental follicle (Nanci 2008), and the same origin is inferred for the attachment tissues of *Stereosternum*. Finally, the anchorage trabeculae, composed of cementum and also likely of alveolar bone, act as an additional structure to hold the teeth in place.

Only fully grown teeth show dental ankylosis. Its mechanism is difficult to establish in light microscopy, as well as the tissues involved in the process. The dentine layers of the tooth base interact with the underlying bone, most likely alveolar bone, as in *Varanus* (Maxwell et al. 2011a). With the tooth ankylosis, the main pulp canal was enclosed, although small canalicules still ran through the dentary bone, connecting it to the pulp cavity (Fig. $1B_3$). Through these canals, blood vessels and nerves communicated with the pulp, providing nourishment to the fully grown tooth and allowing sensory responses.

Given that the roots of developing teeth remain open, they would have attached to the jaw only by cementum/alveolar bone interaction, mediated by the soft periodontal ligament and the projections of cementum that formed the anchorage trabeculae. This last structure is a new feature for parareptiles.

The accommodation of teeth inside the alveoli, coupled with tooth ankylosis, is characteristic of the ankylothecodont insertion pattern. *Stereosternum*, however, modified it by adding anchorage trabeculae of mineralized tissue as an accessory attachment structure.

Tooth replacement.—The tooth-bearing sockets and empty sockets alternate almost perfectly, although two empty sockets can occur side by side (Fig. $1B_1$). Assuming that the empty sockets were occupied by erupting teeth in life and that the anteriormost teeth show increased stages of ankylosis, it is suggested that the replacement pulse occurred anteroposteriorly in *Stereosternum*, in a quasi-alternate polyphyodont pattern. No erupting teeth could be analyzed in thin section, however.

Discussion

Previous studies in amniote tooth histology.—There have been several studies of tooth microstructure and of the histology of the tooth attachment complex in fossil amniotes, but work on parareptiles has been largely restricted to the highly specialized dentition of the procolophonids. For example, Cabreira and Cisneros (2009) discussed the dentition of the leptopleuronine procolophonid *Soturnia*, addressing some microstructural and physiological adaptations, such as the deposition of secondary dentine, and a slow rate of tooth replacement, related to a high-fiber herbivorous diet.

Among early eureptiles, a detailed discussion on the structure and insertion of the teeth of *Captorhinus* was presented by Ricqlès and Bolt (1983). The massive bulk of orthodentine, slightly folded at the tooth base, would increase the surface for tooth insertion, regarded as subthecodont by the

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authors, or protothecodont, according to MacDougall and Modesto (2011). The occurrence of dentine folding, or plicidentine, among captorhinid taxa is not constant, as discussed by Maxwell et al. (2011b), with the absence of dentine folding reported in *Moradisaurus* (Ricqlès and Taquet, 1982) and *Labidosaurus* (Broili, 1904). Recently, Maxwell et al. (2012) suggested that *Captorhinus* would also have possessed cementum covering the tooth base.

Recent work on the histology of mosasaurian teeth by Caldwell et al. (2003) showed the great variation in modes of tooth attachment. Indeed, these authors agreed with previous assertions (e.g., Gaengler 2000) that the traditional categories of acrodonty, pleurodonty and thecodonty did not fully illustrate the diversity of tooth attachment strategies observable in nature. Caldwell et al. (2003) argued that, at least in mosasaurians (and squamates) the classification of tooth attachment is better described in terms of histological similarity than of gross morphology. In this sense, these authors described the teeth of the mosasaurid *Platecarpus* as thecodont, inserted in sockets composed of alveolar bone, and held in place by a massive bulk of cellular and acellular cementum. Periodontal ligament, a non-mineralized tissue, was also inferred by the recognition of a cribiform plate in the alveolus.

Budney et al. (2006) inferred a hinged tooth attachment in the Cretaceous snake *Dinilysia*, recognizing alveolar bone in the microstructure of the shallow alveoli. Caldwell et al. (2003) and Budney et al. (2006) argued that tissues like alveolar bone, cement or periodontal ligament, characterizing thecodont insertion, could be widespread among squamates and were not exclusive to synapsids and archosauromorphs. This hypothesis was reinforced by the recognition of cementum and alveolar bone in the extant squamate *Varanus* (Maxwell et al. 2011a).

Luan et al. (2009) described four tissue layers anchoring the teeth of the mosasaur *Clidastes* to the tooth bearing-element: acellular cementum, cellular cementum, a mineralized periodontal ligament, and interdental ridges which, were significantly different from alveolar bone. Indeed, these authors suggested that the alveolar bone described by Caldwell et al. (2003) was in fact an interdental ridge, as in *Clidastes*. Additionally, the authors described cementum participating in the tooth attachment complex of *Iguana* teeth, along with bone of attachment. Variation in the mineralization of the periodontal ligament could modulate the static or elastic state of the attachment apparatus. In this way, the tooth attachment complex was suggested to be a dynamic feature, highly influenced by function.

In a study of the Cretaceous ichthyosaur *Platypterygius*, Maxwell et al. (2011c) recognized all the main mineralized tissues in the teeth of crocodilians and mammals, namely enamel, dentine, acellular cementum, and cellular cementum, and these tissues were also probably present in other derived ichthyosaurs (Maxwell et al. 2012). Although these authors recognized that the cementum of *Platypterygius* did not resemble the mammalian or archosaurian cementum in terms of gross morphology, they recognized its similarity to the mosasaurian cementum (Caldwell et al. 2003; Luan et al. 2009). Maxwell et al. (2012) reported great variation in the quantity and arrangement of dental tissues throughout ichthyosaurian evolution. They also suggested that within-group diversity such as that observed in ichthyosaurs would not be surprising among other amniote lineages.

Mesosaurid dentition.—The analysis of specimen UFRGS-PV-0378-P stresses the adaptations adopted by the mesosaurid *Stereosternum* for an underwater feeding habit. The tooth histological framework shows great specialization. The long teeth of some mesosaurids, especially *Mesosaurus*, are agreed by many authors (MacGregor 1908; Romer 1966; Carroll 1988; Modesto 2006) to have acted as a device for underwater hunting. However, given the slenderness and the apparent fragility of these teeth, they were depicted as straining (Huene 1941; Romer 1966; Carroll 1988) or imprisoning (Modesto 2006) devices, rather than as piercing structures.

Although a little shorter, the teeth of *Stereosternum* would at first also seem fragile, if used to perforate prey. It should be noted, however, that as a long, cylindrical/conical structure, the teeth would be very resistant to compression forces applied to the tip, when piercing through flesh, for example. On the other hand, the length of the tooth would make it very fragile to lateral forces. In this way, fighting prey could cause severe damage to the teeth. Additionally, the longer the tooth was, the easier it would be to rip it out of its socket, especially with forces acting farther from the tooth base, whose action would be amplified, by the lever principle.

Nevertheless, the histological investigation of the tooth microstructure revealed a remarkable evolutionary solution for dealing with these problems. Analogous to the general bone organization, which increased mechanical resistance by adding layers of different compositions and orientations to the microstructure (Hildebrand and Goslow 1998; Junqueira and Carneiro 2008), the teeth of *Stereosternum* also show a mixed composition in the dentary wall. The different types of dentine, the layer of poorly mineralized dentine, and the varying orientations adopted by dentine tubules along the tooth presumably increased tooth resistance to tension, especially its weakness to resisting laterally oriented forces. The interglobular dentine layer could also act to dissipate tension.

The risk of tooth loss was limited by the reinforced tooth insertion, combining a tripartite periodontium and dental ankylosis. During the eruption phase, the tooth, not fused to the dentary, was instead kept in place only by the soft periodontal tissue and temporary anchorage trabeculae, until fully grown, when it became ankylosed to the jaw.

Despite these structural reinforcements, the possibility of the teeth being damaged and lost during feeding cannot be excluded. The (almost) alternate replacement mechanism in UFRGS-PV-0378-P was an adaptation to replace damaged teeth that were no longer functional. As new teeth were con-

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tinuously growing along the jaw, local tooth losses would be compensated by new sharp and usable teeth.

Some of the structural adaptations in the teeth of *Stereosternum* have been also reported in extant marine predators, mostly fishes. The association of diverse dentine types is a feature of some chondrichthyans (Carlson 1990; Botella et al. 2009). Francillion-Vieillot et al. (1990) argued that both extinct and extant fishes tend to show greater structural diversification in tooth histology compared to tetrapods. This suggests a structural effort to establish plastic, and maybe elastic, resistance both to the strain imposed by the water and by predatory habits.

The tooth insertion in *Stereosternum* is in part similar to that observed by Moy-Thomas (1934) in some Osteichthyes, where the tooth lies inside a tooth socket formed by a circular upgrowth of the alveolar wall. From the internal surface of the socket, bone trabeculae fuse with the teeth, also held by periodontal ligaments (Moy-Thomas 1934). The fully grown teeth of *Stereosternum*, however, differ from the supporting mechanisms in these fishes by complete ankylosis of the fully grown tooth base.

The presence of alveolar bone and cementum, and the inferred presence of periodontal tissue, in *Stereosternum*, a basal amniote, contribute to the idea that these attachment tissues did not evolve independently in mammals and archosaurs (classically regarded as thecodonts). In fact, these tissues could be a conservative characteristic among amniote lineages, subject to within-group variation, driven by the diversity of feeding habits or other selective pressures. The inferred presence of a tripartite periodontium in an early reptilian like *Stereosternum* supports this idea.

The main mesosaurid diet seems to have been crustaceans. Recently, Piñeiro et al. (2012) presented evidence of a great amount of crustacean carapaces in coprolites and putative gastric content of mesosaurids from Uruguay. Additionally, some of the samples also contained small bones among the gastric contents, claimed by the authors to be referable to a small mesosaurid. Similar evidence was also given by Raimundo-Silva (1999) for coprolites assigned to *Brazilosaurus*.

It is possible that mesosaurids, and probably *Stereosternum*, preferred small or soft prey like juvenile mesosaurids or fish, which would be easier to capture and swallow, in addition of crustaceans. Additionally, selective predation could certainly reduce damage to the dentition. Some extant predators are indeed reported to prefer postmolt crustaceans (Gordon 1974), given the increased vulnerability and declined evasiveness of prey (Lankford and Targett 1997). Postmolt soft-bodied crustaceans could also have been a selected prey of mesosaurids, although evidence is lacking.

The microstructure of the teeth in *Brazilosaurus* and *Mesosaurus* remains poorly known. The comparative study of the feeding apparatus using histological techniques, and the addition of more *Stereosternum* specimens, and of different imaging techniques, could greatly increase understanding of mesosaurid paleobiology.

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