

Lepisosteoid-type fish scales in the Barremian-Aptian (Lower Cretaceous) of the Sanfranciscana Basin, Southeastern Brazil

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ABSTRACT

Lepisosteoid-type scales are described in detail for the first time from the Barremian-Aptian (Lower Cretaceous) Quiricó Formation of the Sanfranciscana Basin, Southeastern Brazil. The specimens studied herein have been recovered from a new outcrop in northern Minas Gerais state and comprise a few nearly complete posterior scales and hundreds of scale fragments extracted from the sedimentary matrix. The scales are rhombic and preserve both the ganoine and the basal plate. The ganoine layer is thin, pierced by foramina and ornamented by microtubercles, showing the typical arrangement of superimposed sheets. The basal plate is composed by lamellar and woven bone, with flattened and isodiametric osteocytes, canaliculi of Williamson, and Sharpey's fibers. An EDS analysis suggests diagenetic alteration of the basal plate but not the ganoine layer. The morphology of the specimens is similar to that of early neopterygian fishes, including ginglymodians and aspidorhynchids. A less inclusive identification is hampered by the fragmentary condition of the material and the lack of specific diagnostic features in this type of scale. This can be also extended to some isolated scales commonly referred to *Lepidotes* recovered from several sedimentary basins in the Jurassic-Cretaceous of Brazil. The results add a new record of ganoid scales in the Sanfranciscana Basin, and highlight the importance of more complete specimens rather than isolated scales for a genus-level identification of early neopterygian fishes.

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1. Introduction

Actinopterygian fishes in the Barremian-Aptian (Lower Cretaceous) of the Sanfranciscana Basin, Southeastern Brazil, have been recovered from the lacustrine strata of the Quiricó Formation and include the ostariophysian *Dastilbe crandalli* (Scorza and Silva Santos, 1955) and the rare osteoglossomorph *Laeliichthys ancestralis* Silva Santos, 1985. Other fish records are undescribed fin spines and cephalic spines of hybodont sharks; bones and teeth of amiiform; semionotid scales and vertebrae; all associated with bones of the coelacanthiform *Mawsonia gigas* (Carvalho, 2002; Carvalho and Maisey, 2008).

The previously recorded scales have been referred to semionotid due to the presence of ganoine (Carvalho, 2002; Carvalho and Maisey, 2008), an outer layer of shiny acellular enamel tissue

(Schultze, 1966, 1977, 2016; Sire, 1994; Richter and Smith, 1995; Sire et al., 2009; Sasagawa et al., 2013). Disarticulated ganoid scales commonly recorded in Upper Jurassic and Lower Cretaceous sections of several sedimentary basins in Brazil, including Iguatu, Sousa, Recôncavo, Tucano, Jatobá, Lima Campos and Sergipe-Alagoas (Gallo and Brito, 2004; Gallo, 2005; Pinheiro et al., 2011; Silva et al., 2011) are referred to *Lepidotes* (Silva Santos, 1963, 1969; Pinheiro et al., 2011; de Paiva et al., 2013). However, as pointed out by several authors (see review of Sire et al., 2009), scales with multiple layers of ganoine, i.e. true ganoid scale, are apomorphic for actinopterygians.

Different types of ganoid scales (Goodrich, 1907; Kerr, 1952; Schultze, 1966, 1977, 2016; Sire, 1995; Sire et al., 2009) are distinguished by: 1) the presence of tubular dentine capped by the ganoine (palaeoniscoid type); 2) the occurrence of elasmodine, a plywood-like tissue overlain by the dentine layer (polypteroid type); 3) the presence of a basal plate of cellular bone directly covered by the ganoine layer (lepisosteoid type). The latter is typical to ginglymodians (Sire et al., 2009), but it has also been

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reported in some early teleosts (Brito and Meunier, 2000; Meunier and Brito, 2004).

In order to assess the morphology of isolated lepisosteoid scales and their taxonomic utility, we describe scales of this type collected from a new outcrop further northern in Minas Gerais state, also referred to the Quiricó Formation. This new record will also contribute to a better understanding of the Early Cretaceous paleobiota of the Sanfranciscana Basin.

2. Geological setting

The material studied herein has been collected from a side road outcrop near the locality of São Geraldo, district of Coração de Jesus, northern Minas Gerais (Fig. 1A). Recent works (Zaher et al., 2011; Chaves and Andrade, 2013; Knauer et al., 2013) have referred the Mesozoic sections from this region to the Areado Group (Sanfranciscana Basin), which is traditionally divided into the Abaeté (fluvial and wadi deposits), Quiricó (lacustrine paleoenvironment) and Três Barras (fluvio-deltaic and aeolian paleoenvironments) formations (Barbosa, 1965; Grossi Sad et al., 1971; Campos and Dardenne, 1997; Sgarbi et al., 2001). Such a division is based on the well-studied extensive outcrops of the Areado Group in the Planalto Mata da Corda, northwestern Minas Gerais (Sgarbi et al., 2001). This area encompasses the outcrops of Presidente Olegário and João Pinheiro, from where previous records of actinopterygians and coelacanthiforms have been described (Scorza and Silva Santos, 1955; Carvalho and Maisey, 2008).

The fossiliferous sections in the Coração de Jesus region, which recently yielded the skeletons of the titanosaur sauropod *Tapuia-saurus macedoi* and an undescribed abelisauroid theropod (Zaher et al., 2011), are mainly composed of mudstone strata of lacustrine origin frequently interbedded with centimetric levels of calcrites, claystone and sandstones, overlain by metric levels of fine to medium grained sandstones with cross stratification (Fig. 1B).

The association of facies described above is referred to the Quiricó Formation (Sgarbi, 1991; Campos and Dardenne, 1997), which has been dated as Barremian-Aptian based on the presence of palynomorphs, ostracods and conchostracans (Cardoso, 1971; Lima, 1979; Rohn and Cavalheiro, 1996; Sgarbi et al., 2001; do Carmo et al., 2004; Bittencourt et al., 2015). The abundant fish scales occur in a single 2–5 cm clay-rich horizon within a 7 m thick basal level of massive mudstone, with significant contribution of fine to very fine sand grains (Figs. 1–2). Ostracod shells and fragmentary isolated archosaur bones have also been found in the outcrop.

3. Material and methods

The scales occur mostly as hundreds of disarticulated and incomplete fragments, ranging from 4 mm to less than 1 mm. Those fragments above 1 mm more frequently preserve both the ganoine and the cellular bone, in varied degrees of preservation. More complete scales are rare and include six semi-articulated elements and some isolated specimens (Figs. 2–3). Less common rod-like

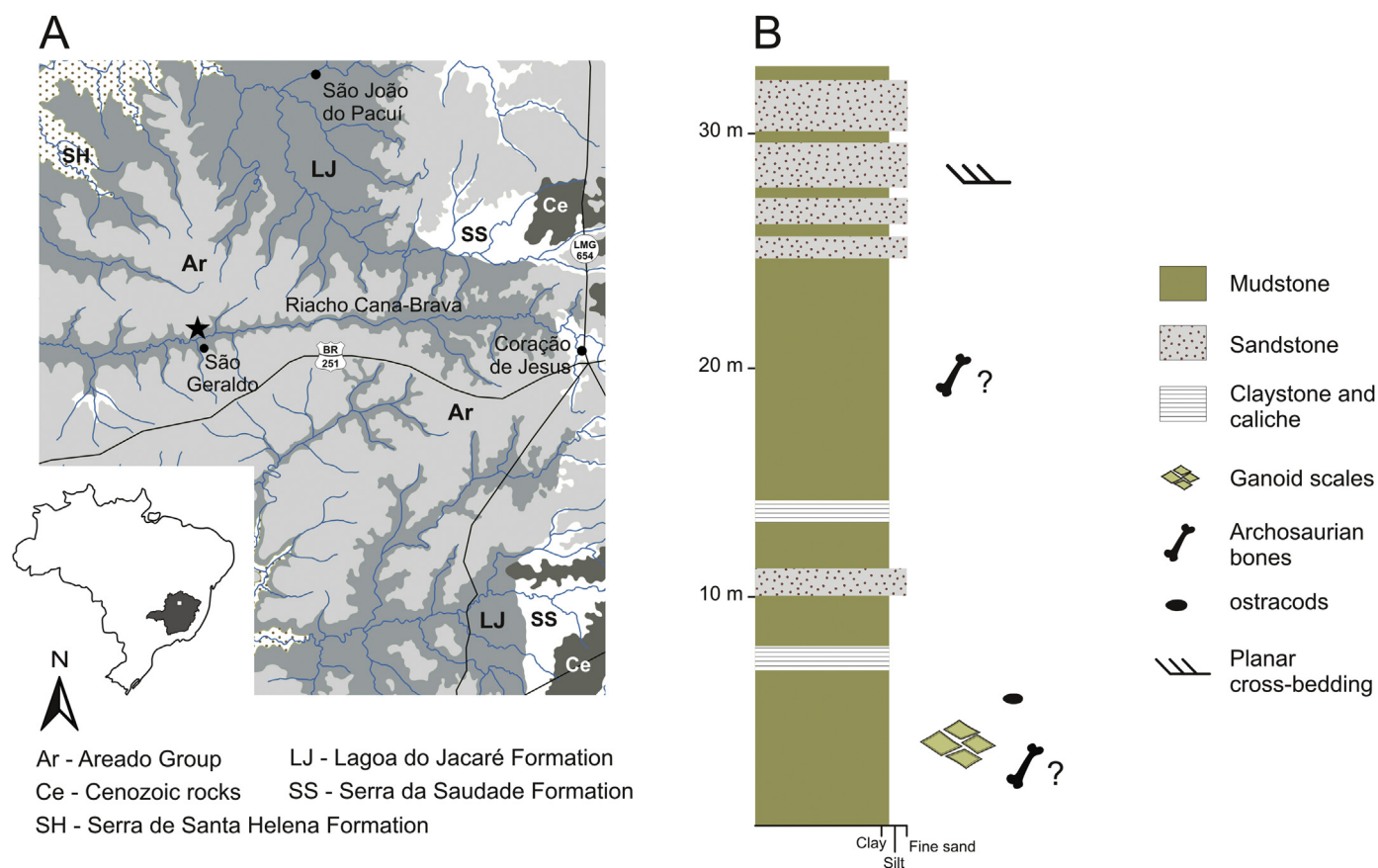


Fig. 1. Location and stratigraphy of the outcrop from where the IGC-P scales have been recovered. A, Geological map (1:100,000) of the region of São Geraldo (modified from Chaves and Andrade, 2013; Knauer et al., 2013), showing the distribution of the lithologies of the main stratigraphic units outcropping in the region, including the Neoproterozoic sections of the Bambuí Basin (Lagoa do Jacaré, Serra de Santa Helena and Serra da Saudade formations); the Cenozoic covers and the Areado Group, which basically corresponds here to the Quiricó Formation. The black star indicates the fossiliferous outcrop. B, Stratigraphic section of the outcrop. Note that the position of the archosaurian bones within the column is tentative.

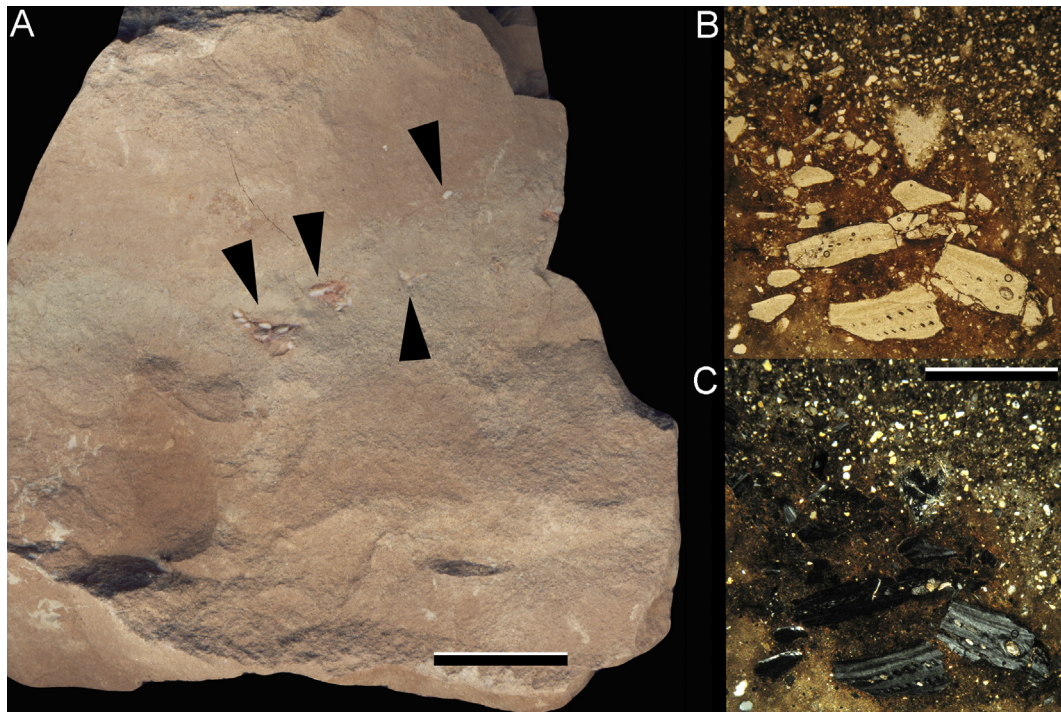


Fig. 2. Lepisosteoid scales from the Barremian-Aptian of the Sanfranciscana Basin. A, Sample of the mudstone with the clay-rich level containing several isolated and scattered scale fragments (black arrows) (IGC-P 0016). B, Thin section (normal light) of the mudstone (IGC-P 0021) showing the scale and bone fragments within the clay-rich layer. Note the conspicuous silty level at the upper portion of the section, and the sand contribution across the sample. C, The same as B, under polarized light. Scale bar for A = 10 mm; B and C (left bar) = 2 mm.

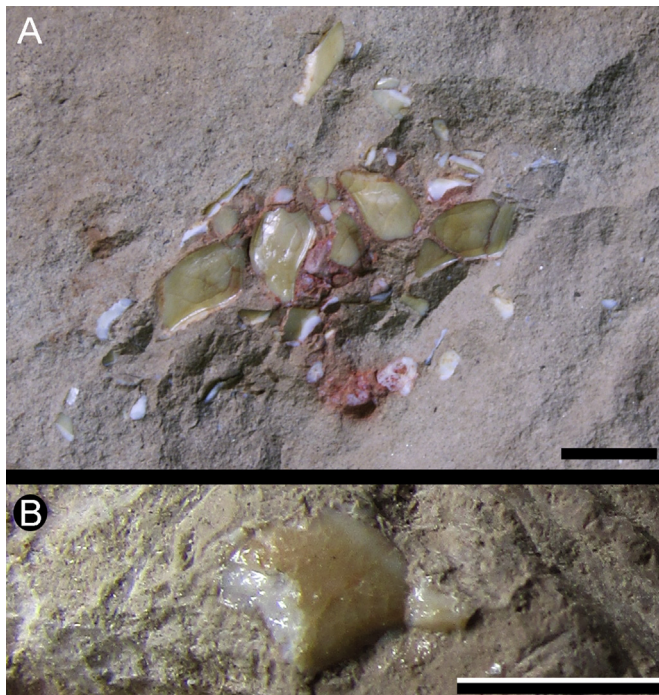


Fig. 3. Lepisosteoid scales from Barremian-Aptian of the Sanfranciscana Basin. A, Sample of the mudstone with the clay-rich level containing six semi-articulated scales (IGC-P 0014). B, Isolated ganoid scale (IGC-P 0015). Scale bar = 5 mm.

bony fragments occur associated with the scales and may represent remnants of fin-rays or vertebral elements.

Due to the scattered distribution of the scales within the sedimentary matrix and their small size, the mechanical preparation

has been performed only on the larger and more complete scales (6–7 mm). The rock samples in which nearly complete scales were inconspicuous have been disaggregated with hydrogen peroxide 30% and sieved in 18, 35 and 230 mesh sieves. Then, the material was screened under stereomicroscope for fossil microremains.

Assorted fragments with both ganoine and cellular bone received a carbon coating for scanning electron microscope (SEM) in a JEOL JSM-6510 microscope and energy-dispersive spectroscopy (EDS) analyses in a JEOL JSM-6360LV equipment. Thin sections (~30 µm) of the mudstone containing scales and bone fragments were analyzed under petrographic microscope.

All the specimens studied herein are housed in the Instituto de Geociências of the Universidade Federal de Minas Gerais (IGC-P).

4. Systematic paleontology

Actinopterygii (Cope, 1887)

Neopterygii (Regan, 1923)

Gen. et sp. indet.

Material. Six semi-articulated ganoid scales and associated remains (IGC-P 0014); incomplete isolated ganoid scale (IGC-P 0015); two fragments of mudstone with isolated scales (IGC-P 0016, 0017); scale fragments mounted for SEM analysis (IGC-P 0018); hundreds of small isolated scale fragments registered as IGC-P 0019; two thin sections of mudstone with scale fragments (IGC-P 0020, 0021).

Horizon. Quiricó Formation, Areado Group, Barremian-Aptian of the Sanfranciscana Basin, Southeastern Brazil.

Description. The scales have rhombic shape, as is common for ganoid scale (Figs. 3, 4A), especially those from the posterior half of the trunk, which has more prominent and sharply pointed anterior and posterior extremities (Gallo, 2005). Both the dorsal and ventral borders are low-angled or rounded. The largest scales are c. 2 mm thick and 7 mm long. The ganoine cap is shiny, beige

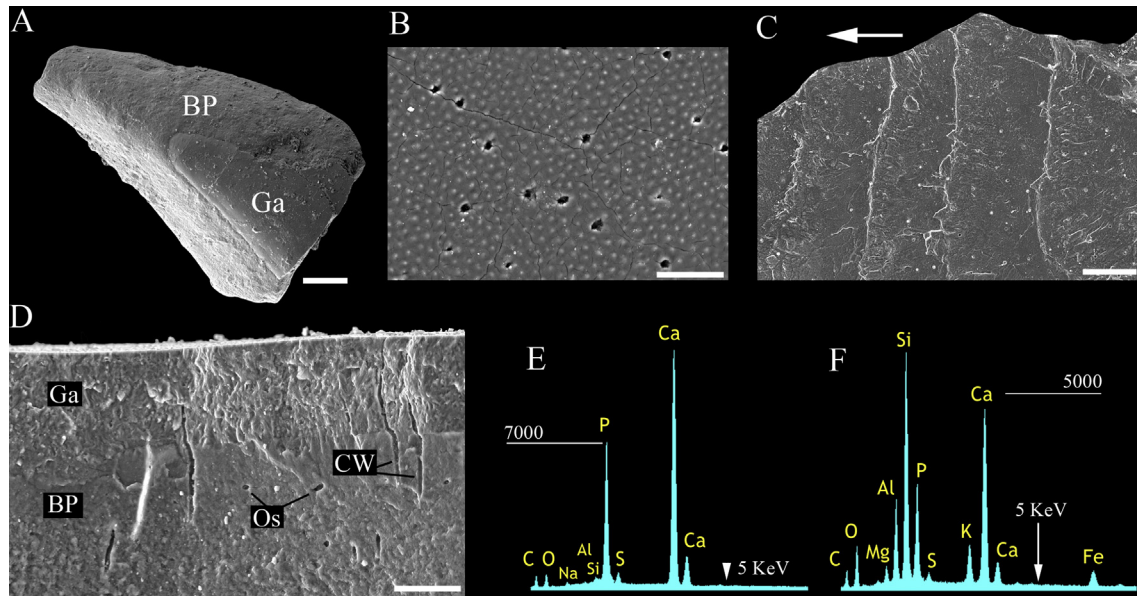


Fig. 4. Lepisosteoid scales from the Barremian-Aptian of the Sanfranciscana Basin under SEM (IGC-P 0018). A, Fragment of one scale showing the ganoine layer partially covering the basal plate. B, Detail of the surface of the ganoine layer with numerous microtubercles and foramina. C, Internal surface of the ganoine layer evidencing the superimposed sheets of ganoine. Note that the arrow indicates the outward direction of the sheet accretion, and that each vertical irregular line marks the boundary of older sheets. D, Scale fragment in cross section showing the ganoine layer and the basal plate. E, EDS results for the ganoine layer and F, the basal plate. BP: basal plate; CW: canaliculus of Williamson; Ga: ganoine layer; Os: osteocyte lacuna. Scale bars for A = 200 μm ; B and C = 50 μm ; D = 100 μm .

and covers most of the white cellular bone (Fig. 3). Its outer surface is ornamented by microscopic tubercles (c. 14,000 per mm^2) of varied diameters ($5.5 \pm 1.3 \mu\text{m}$), spaced by $4.1 \pm 1.0 \mu\text{m}$ to one another (Fig. 4B). The size of the microtubercles varies across the surface of the scale: in some portions, tubercles with c. 4 μm or less are more common, whereas in others, those above 5 μm predominate.

The ganoine layer is also pierced by frequent (c. 335 per mm^2) foramen-sized apertures ($6.3 \pm 1.9 \mu\text{m}$), which are not uniformly distributed across the surface (Fig. 4B). The shape of the foramina is variable. Those more regularly circular are 4–6 μm in diameter, but the apertures larger than that are more irregular, perhaps due to damage. No evidence of inset odontodes (Brito and Meunier, 2000) has been noticed. Marginally, the outer ganoine surface bears concentric growth lines, and this portion projects slightly ventrally over the cellular bone.

In thin sections (Figs. 4–5), the scales present the typical lepisosteoid morphology (Sire and Meunier, 1994; Sire et al., 2009; Schultze, 2016), comprising a thin (c. 20–60 μm thick) acellular enamel layer (ganoine cap) and a deeper (up to 1 mm in the material analyzed here) basal plate composed by cellular bone. The ganoine layer is arranged as superimposed sheets (3–5 in the material recovered here), vertically striated in cross section and thicker at the borders (Fig. 5A–B). The outer sheets are progressively longer than their inner precedents (Figs. 4C, 5B), and the spacing between successive layers is variable in one analyzed sample ($0.14 \pm 0.02 \text{ mm}$) (Fig. 4C).

The basal plate contains numerous canaliculi of Williamson (Figs. 4–5) in some portions of the scales (c. 380 per mm^2), with varied diameters ($3.75 \pm 0.8 \mu\text{m}$). Some canaliculi cross through the ganoine-basal plate boundary and reach the surface of the scale (Figs. 4D, 5C). The best preserved scale analyzed in thin section, and several scattered fragments of basal plates within the matrix, show the predominance of lamellar bone and the presence of Sharpey's fibers.

The osteocyte lacunae are mostly flattened within lamellae, bearing extensive canaliculi network (Fig. 5C). They are not exceptionally numerous, with less than 30 per mm^2 in the 30 μm -thin section. Isodiametric osteocytes, which are common within

the woven bone (Meunier and Brito, 2004), are occasionally observed in the deeper portions of some scales scattered within the matrix (Fig. 5E). Yet, even these fragments are predominantly composed by lamellar bone.

The EDS analysis showed the predominance of calcium and phosphorus within the ganoine layer (Fig. 4E), suggesting that no significant chemical alteration of this portion of the scale took place during fossilization. This is not unexpected, because hypermineralized tissues of enamel are widely considered as resistant to diagenesis (Domingo et al., 2009). On the other hand, the basal plate is mainly composed of silicon, aluminum and iron, besides calcium, phosphorus and oxygen (Fig. 4F), suggesting some diagenetic alteration of the bone via permineralization.

5. Discussion

The scales from the Sanfranciscana Basin described herein (IGC-P specimens) are similar to the rhombic ganoid scales commonly described for several actinopterygians (Sire et al., 2009). They are also similar to the ganoid scales previously mentioned for the Sanfranciscana Basin (Carvalho and Maisey, 2008).

Considering specifically the fish fauna from the Mesozoic sedimentary basins in Brazil, the IGC-P scales are macroscopically similar to those of some ginglymodians, including *Lepidotes* and *Araripelepidotes*, the aspidorhynchid *Vinctifer*, and the Ophiodontidae. In the former genera, the relatively large rhombic scales are abundant in the posterior half of the body (Maisey, 1991; Brito et al., 1998; Gallo, 2005). Within putative *Lepidotes* species, the scales of *L. mawsoni* are distinct from those described in this paper by bearing a ventral excrescence, resulting in a quite deeper scale, and the presence of crenulated posterior ganoine (Gallo, 2005). In *Vinctifer*, the rhombic scales are small and restricted to the region close to the caudal portion of the body (Silva Santos, 1985; Maisey, 1991; Brito and Meunier, 2000). In the Brazilian Cretaceous ophiodontids, *Placidichthys bidorsalis* (Santana Formation) and *P. tucanensis* (Marizal Formation), the anterior scales are also deeper than wide and the caudal ones have diamond shape (Brito, 2000; Brito and Alvarado-Ortega, 2008).

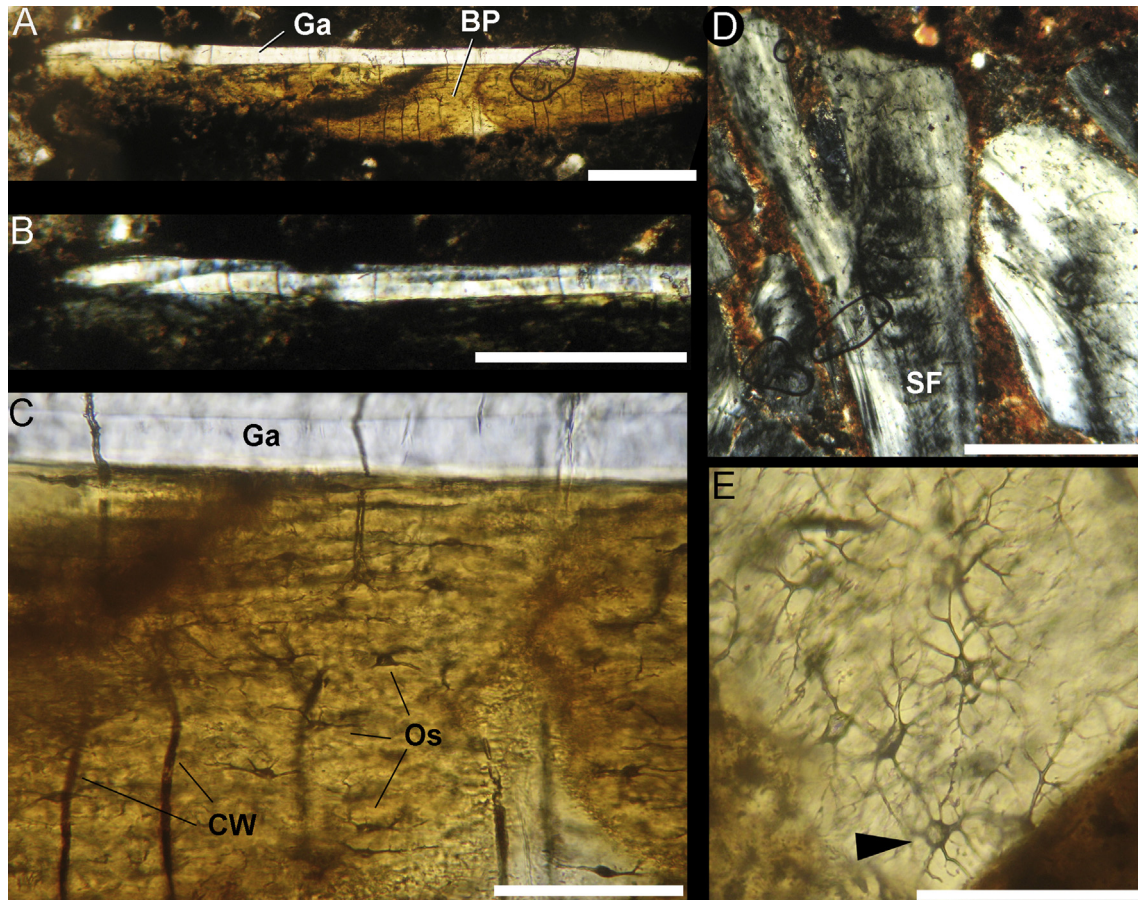


Fig. 5. Thin section of the lepisosteoid scales from the Barremian-Aptian of the Sanfranciscana Basin. A, Thin section of the mudstone (IGC-P 0020) showing one isolated and incomplete lepisosteoid scale. B, Detail of the left border of the scale showed in A, evidencing the superimposed sheets of the ganoine layer and the terminal thickening of each sheet. C, Detail of the cross section showed in A depicting the lamellar bone immediately below the ganoine layer, with frequent osteocyte lacunae and canaliculi of Williamson. D, Thin section of the mudstones (IGC-P 0021) with fragments of scales bearing Sharpey's fibers. E, Scale fragment with isodiametric osteocyte lacunae. A, C, E: normal light; B, D: polarized light. BP: basal plate; CW: canaliculus of Williamson; Ga: ganoine layer; Os: osteocyte lacuna; SF: Sharpey's fibers. Scale bar for A, B, D = 200 µm; C = 100 µm; E = 40 µm.

The SEM images revealed the absence of odontodes on the outer surface of the scales of the Sanfranciscana Basin. Differently, small hook-like odontodes pointing to the anterior portion of the body, and attached into the scale through a circular cavity in the ganoine, have been described in posterior scales of *Vinctifer comptoni*, living gars and polypterids (Brito and Meunier, 2000).

The foramina on the surface of the IGC-P scales are distinct from the odontode cavities mentioned above. Transverse sections of the scales suggest that at least some foramina on the IGC-P specimens correspond to the canaliculi of Williamson that extends from the basal plate up to the surface of the ganoine layer (Figs. 4D, 5C). Canaliculi of the basal plate crossing through the ganoine layer up to the scale surface is not uncommon in ganoid scales (Kerr, 1952; Meunier and Brito, 2004; Gallo, 2005), but the abundance of foramina in the specimens described here may be a peculiar feature to these samples.

The ganoine microtubercles are invariably seen in ganoid scales of actinopterygians, but in the case of the Sanfranciscana specimens, the microtubercles are more frequent and less spaced among each other than in *Vinctifer comptoni* (Brito and Meunier, 2000) and some *Lepidotes* species from Brazil (Gallo-da-Silva, 1998; Gallo, 2005).

Several authors advocate using the diameter of the microtubercles and the distance between them (intertubercular distance) as key to identify actinopterygian taxa with ganoid scale (Gayet and Meunier, 1986, 1993; Brito et al., 2000; Daget et al., 2001; Gayet and

Meunier, 2001; Gayet et al., 2002). Semionotids and lepisosteids have been distinguished by the intertubercular distance (Gayet and Meunier, 1986), whereas *Lepisosteus*, *Paralepidosteus*, *Atractosteus* and the Polypteriformes have been set apart with basis on both the diameter of the microtubercles and the intertubercular distance (Gayet and Meunier, 2001; Gayet et al., 2002).

Yet, these variables in the scales of *Lepidotes mantelli* and *Lepidotes elvensis* fall well within the range of *Lepisosteus* and/or *Obaichthys* (Meunier and Gayet, 1992; Gayet and Meunier, 1993; Gayet et al., 2002). In addition, the microtubercle diameter and intertubercular distance in the scales of the Sanfranciscana Basin are more similar to those of some *Lepisosteus* (e.g. the Tertiary *Lepisosteus fimbriatus*) than to those of the *Lepidotes* species mentioned above (Gayet et al., 2002). Several *Lepidotes* from Brazil, including *L. dixsepiensis*, *L. mawsoni*, *L. souzai*, *L. oliveirai*, *L. piauihyensis* and *L. roxoi* have microtubercles of similar size but in general more distant to one another in comparison to *Lepisosteiformes* (Gallo-da-Silva, 1998). This may be due to the lack of standard measurements among distinct workers or it represents a true taxonomic pattern. In any case, the scales described herein cannot be referred to any of the previously described taxa from Brazil based on those variables.

The histological data suggest that the scales described herein are of lepisosteoid-type (Sire et al., 2009), which is distinct from the palaeoniscoid-type noticed in *Obaichthys* (Brito et al., 2000). Besides living gars, lepisosteoid scales were also recorded in Mesozoic

ginglymodians and aspidorhynchids (Brito and Meunier, 2000; Meunier and Brito, 2004; Gallo, 2005). The IGC-P, aspidorhynchid and early ginglymodian scales are similar to one another in the prevalence of lamellar bone with flattened osteocytes, with minor portions of woven bone with isodiametric lacunae. The number of osteocytes in the scales of the Sanfranciscana Basin is similar to that of *Lepidotes dixseptiensis*, but it is significantly lower than in *L. oliverai* and *L. piauihyensis* (Gallo, 2005). The size of the canaliculi of Williamson within the basal plate is similar to those of aspidorhynchids (Brito and Meunier, 2000) and their frequency is lower than in *Lepidotes piauihyensis* (Gallo, 2005).

The distinction between different taxa based on quantitative data of scale structures has limited usefulness when dealing with isolated scales. The number of osteocytes and canaliculi of Williamson, for instance, which may be useful for distinguishing species within early neopterygians (Gallo-da-Silva, 1998), are quite variable and not readily applicable to isolated scales.

As demonstrated above, the scales of the Sanfranciscana Basin are comparable to those of ginglymodians and aspidorhynchids from the Jurassic-Cretaceous of Brazil. The systematics of both taxa is under dispute. Although not universally accepted (Arratia, 2001), aspidorhynchids are probably teleosts (see review of Brito, 1999; Meunier and Brito, 2004). Some authors argue that ginglymodians splits as Lepisosteiformes and Semionotiformes (Grande, 2010; López-Arbarello, 2012). The position of the problematic *Lepidotes* within Lepisosteiformes has been recently advocated (López-Arbarello, 2012), but this is controversial (e.g. Olsen and McCune, 1991; Cavin and Suteethorn, 2006). Some *Lepidotes* species from Brazil, including *L. piauihyensis* and *L. souzai*, have been considered of uncertain genera (López-Arbarello, 2012), but at least *L. piauihyensis* has been recovered as closely related to other *Lepidotes* from Europe (Cavin, 2010).

Besides a controversial systematics, which renders doubtful taxonomy to several early neopterygian taxa, no unambiguous autapomorphic feature of these clades is strictly based on scales. Therefore, we refrain from referring the isolated specimens from the Sanfranciscana Basin to any specific or generic taxa previously described. They are at best assigned to an indeterminate early Neopterygii, until more complete evidence is available. This is also valid for the ganoid scales previously mentioned for the Sanfranciscana Basin (Carvalho, 2002). We also reinforces that the identification of Jurassic-Cretaceous neopterygian species and genera based only on a superficial analysis of isolated scales (see review of Gallo and Brito, 2004) may be elusive because of the lack of autapomorphic features in these structures or the alpha taxonomy of problematic taxa as *Lepidotes*.

6. Concluding remarks

We described for the first time lepisosteoid scales from the Barremian-Aptian deposits of the Sanfranciscana Basin (Quiricó Formation), Southeastern Brazil. The specimens are quite fragmentary, but the microstructural assessment disclosed many similarities with the ganoid scales of early neopterygians, including ginglymodians and aspidorhynchids. These taxa bear lepisosteoid type scales and are common in Mesozoic strata of several sedimentary basins in Brazil. However, data at hand did not allow referring the isolated specimens described herein to any of these clades.

Some isolated scales frequently uncovered from the Jurassic-Cretaceous sections in Brazil are readily assigned to *Lepidotes*, which is mostly based on general resemblance shared by distinct types of “ganoid scales”. Our study reinforced that, in such cases, taxonomic referral based on isolated scales may be equivocal because of the lack of diagnostic traits at less inclusive clades of early neopterygians.

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References

- Arratia, G., 2001. The sister-group of Teleostei: consensus and disagreements. *Journal of Vertebrate Paleontology* 21, 767–773.
- Barbosa, O., 1965. Geologia econômica e aplicada a uma parte do Planalto Central brasileiro, XIX Congresso Brasileiro de Geologia. SBG, Rio de Janeiro, pp. 1–11.
- Bittencourt, J.S., Kuchenbecker, M., Vasconcelos, A.G., Meyer, K.E.B., 2015. O registro fóssil das coberturas sedimentares do Cráton do São Francisco em Minas Gerais. *Geonomos* 23, 39–62.
- Brito, P.M., 1999. The caudal skeleton of aspidorhynchids (Actinopterygii, Halecostomi): phylogenetic implications. In: Arratia, G., Schultze, H.-P. (Eds.), *Mesozoic Fishes 2-Systematics and the Fossil Record*. Verlag Dr. Friedrich Pfeil, München, pp. 249–264.
- Brito, P.M., 2000. A new halecomorph with two dorsal fins, *Placidichthys bidorsalis* n. g., n. sp. (Actinopterygii: Halecomorphi) from the Lower Cretaceous of the Araripe Basin, northeast Brazil. *Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science* 331, 749–754.
- Brito, P.M., Alvarado-Ortega, J., 2008. A new species of *Placidichthys* (Halecomorphi: Ionoscopiformes) from the Lower Cretaceous Marizal Formation, northeastern Brazil, with a review of the biogeographical distribution of the Ophiopsidae. *Geological Society, London*, pp. 145–154. Special Publications 295.
- Brito, P.M., Martill, D.M., Wenz, S., 1998. A semionotid fish from the Crato Formation (Aptian, Lower Cretaceous) of Brazil: palaeoecological implication. *Oryctos* 1, 37–42.
- Brito, P.M., Meunier, F.J., 2000. The morphology and histology of the scales of Aspidorhynchidae (Actinopterygii, Halecostomi). *Geobios* 33, 105–111.
- Brito, P.M., Meunier, F.J., Gayet, M., 2000. The morphology and histology of the scales of the Cretaceous gar *Obaichthys* (Actinopterygii, Lepisosteidae): phylogenetic implications. *Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science* 331, 823–829.
- Campos, J.E.G., Dardenne, M.A., 1997. Estratigrafia e Sedimentação da Bacia Sanfranciscana: uma revisão. *Revista Brasileira de Geociências* 27, 227–240.
- Cardoso, R.N., 1971. Contribuição ao estudo da Formação Areado: estratigrafia e descrição dos filópodos fósseis. Arquivos do Museu de História Natural 1, 9–47.
- Carvalho, M.S.S., 2002. O gênero *Mawsonia* (Sarcopterygii, Actinistia) no Cretáceo das Bacias Sanfranciscana, Tucano, Araripe, Parnaíba e São Luís. Unpublished PhD thesis. Universidade Federal do Rio de Janeiro, 176 pp.
- Carvalho, M.S.S., Maisey, J.G., 2008. New occurrence of *Mawsonia* (Sarcopterygii: Actinistia) from the Early Cretaceous of the Sanfranciscana Basin, Minas Gerais, southeastern Brazil. *Geological Society*, pp. 109–144. Special Publication 295.
- Cavin, L., 2010. Diversity of Mesozoic semionotiform fishes and the origin of gars (Lepisosteidae). *Naturwissenschaften* 97, 1035–1040.
- Cavin, L., Suteethorn, V., 2006. A new semionotiform (Actinopterygii, Neopterygii) from Upper Jurassic – Lower Cretaceous deposits of North-East Thailand, with comments on the relationships of semionotiforms. *Palaeontology* 49, 339–353.
- Chaves, M.L.S.C., Andrade, K.W., 2013. FOLHA CORAÇÃO DE JESUS – SE-23-X-A-V. CODEMIG, Belo Horizonte.
- Cope, E.D., 1887. Zittel's manual of palaeontology. *The American Naturalist* 21, 1014–1019.
- Daget, J., Gayet, M., Meunier, F.J., Sire, J.Y., 2001. Major discoveries on the dermal skeleton of fossil and Recent polypteriforms: a review. *Fish and Fisheries* 2001, 113–124.
- de Paiva, H.C.L., da Silva, R.C., Santos, C.C., Reis, C., 2013. First occurrence of *Lepidotes* (Osteichthyes, Actinopterygii, Lepisosteiformes) in the São Sebastião Formation, Berriasian-Aptian of the Tucano Basin, Bahia, Brazil. *Brazilian Journal of Geology* 43, 653–660.

- do Carmo, D.A., Tomassi, H.Z., Oliveira, S.B.S.G., 2004. Taxonomia e distribuição dos ostracóides da Formação Quiricó, Grupo Areado (Cretáceo Inferior), Bacia Sanfranciscana, Brasil. *Revista Brasileira de Paleontologia* 7, 139–149.
- Domingo, L., Grimes, S.T., Soler-Gijón, R., López-Martínez, N., 2009. Analysis of the geochemical variability in lepisosteid scales from the Fontllonga-3 site (early Danian, Tremp Formation, South Central Pyrenees, Spain): implications for palaeoenvironmental studies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 274, 204–214.
- Gallo-da-Silva, V., 1998. Revisão das espécies do gênero *Lepiotes* Agassiz, 1832 (Actinopterygii, Semionotiformes) do Mesozóico do Brasil, com comentários sobre as relações filogenéticas da família Semionotidae. Unpublished PhD thesis. Universidade de São Paulo, 367 pp.
- Gallo, V., 2005. Redescription of *Lepidotes piauhyensis* Roxo and Lofgren, 1936 (Neopterygii, Semionotiformes, Semionotidae) from the ?Late Jurassic-Early Cretaceous of Brazil. *Journal of Vertebrate Paleontology* 25, 757–769.
- Gallo, V., Brito, P.M., 2004. An overview of Brazilian semionotids. In: Arratia, G., Tintori, A. (Eds.), *Mesozoic Fishes 3-Systematics, Paleoenvironments and Biodiversity*. Verlag Dr. F. Pfeil, München, pp. 253–264.
- Gayet, M., Meunier, F.J., 1986. Apport de l'étude de l'ornementation microscopique de la ganoïne dans la détermination de l'apparence générique et/ou spécifique des écaillés isolées. *Comptes Rendus de l'Académie des Sciences de Paris, Série II* 3, 1259–1262.
- Gayet, M., Meunier, F.J., 1993. Conséquences paléobiogéographiques et biostratigraphiques de l'identification d'écaillés ganoïdes du Crétacé supérieur et du tertiaire inférieur d'Amérique du Sud. *Documents des Laboratoires de Géologie de Lyon* 125, 169–185.
- Gayet, M., Meunier, F.J., 2001. À propos du genre *Paralepidosteus* (Ginglymodi, Lepisosteidae) du Crétacé Gondwanien. *Cybio* 25, 153–159.
- Gayet, M., Meunier, F.J., Werner, C., 2002. Diversification in Polypteriformes and special comparison with the Lepisosteiformes. *Palaeontology* 45, 361–376.
- Goodrich, E.S., 1907. On the scales of fish, living and extinct, and their importance in classification. *Proceedings of the Zoological Society of London* 77, 751–773.
- Grande, L., 2010. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy: the resurrection of Holostei. *American Society of Ichthyologists and Herpetologists*, pp. 1–871. Special Publication 6.
- Grossi Sad, J.H., Cardoso, R.N., da Costa, M.T., 1971. Formações cretácicas em Minas Gerais: uma revisão. *Revista Brasileira de Geociências* 1, 2–13.
- Kerr, T., 1952. The scales of primitive living actinopterygians. *Proceedings of the Zoological Society of London* 122, 55–78.
- Knauer, L.G., Fantinel, L.M., Costa, R.D., Romano, A.W., Santos Júnior, A.G., Horta, R.M., 2013. FOLHA IBIÁ – SE.23-X-A-IV. CODEMIG, Belo Horizonte.
- Lima, M.R., 1979. Palinologia dos calcários laminados da Formação Areado, Cretáceo de Minas Gerais. 2º Simpósio Regional de Geologia, Rio Claro 203–216.
- López-Arbarelo, A., 2012. Phylogenetic interrelationships of ginglymodian fishes (Actinopterygii: Neopterygii). *PLoS One* 7, e39370.
- Maisey, J.G., 1991. *Santana Fossils: An Illustrated Atlas*. Neptune, New York.
- Meunier, F.J., Brito, P.M., 2004. Histology and morphology of the scales in some extinct and extant teleosts. *Cybio* 28, 225–235.
- Meunier, F.J., Gayet, M., 1992. Nouveau remaniement de laganoïne chez un semionotidae du crétacé supérieur de Bolivie: Intérêt paléobiologique. *Geobios* 25, 767–774.
- Olsen, P.E., McCune, A.R., 1991. Morphology of the *Semionotus elegans* species group from the Early Jurassic part of the Newark Supergroup of eastern North America with comments on the Family Semionotidae (Neopterygii). *Journal of Vertebrate Paleontology* 11, 269–292.
- Pinheiro, F.L., Figueiredo, A.E.Q., Fortier, D.C., Viana, M.S.S., Schultz, C.L., 2011. Fauna de vertebrados eocretácicos de um afloramento da Bacia de Lima Campos, Ceará, Brasil. *Revista Brasileira de Paleontologia* 14, 189–198.
- Regan, C.T., 1923. The Skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower Neopterygian Fishes. *Proceedings of the Zoological Society of London* 1923, 445–461.
- Richter, M., Smith, M., 1995. A microstructural study of the ganoine tissue of selected lower vertebrates. *Zoological Journal of the Linnean Society* 114, 173–212.
- Rohn, R., Cavalheiro, M.C.T., 1996. Conchostráceos cretácicos da Bacia de Tucano (Bahia) e avaliações do potencial cronoestratigráfico destes crustáceos no Mesozóico do Brasil. 4º Simpósio sobre o Cretáceo do Brasil. UNESP, Águas de São Pedro 157–167.
- Sasagawa, I., Ishiyama, M., Yokosuka, H., Mikami, M., 2013. Teeth and ganoid scales in *Polypterus* and *Lepisosteus*, the basic actinopterygian fish: an approach to understand the origin of the tooth enamel. *Journal of Oral Biosciences* 55, 76–84.
- Schultze, H.-P., 1966. Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von Ganoid-zu rundschuppen). *Neues Jahrbuch für Geologie und Paläontologie* 126, 232–314.
- Schultze, H.-P., 1977. Ausgangsform und Entwicklung der rhombischen Schuppen der Osteichthyes (Pisces). *Paläontologische Zeitschrift* 51, 152–168.
- Schultze, H.-P., 2016. Scales, enamel, cosmine, ganoine, and early osteichthyans. *Comptes Rendus Palevol* 15, 83–102.
- Scorza, F.P., Silva Santos, R., 1955. Ocorrência de folhelho fossilífero no município de Presidente Olegário, Minas Gerais. *Boletim do Departamento Nacional de Produção Mineral – Divisão de Geologia e Mineralogia* 155, 1–27.
- Sgarbi, G.N.C., 1991. Geologia dos sedimentos lacustres da Formação Areado, Bacia cretácica do São Francisco. 2º Simpósio de Geologia do Sudeste. SBG, São Paulo 67–75.
- Sgarbi, G.N.C., Sgarbi, P.B.A., Campos, J.E.G., Dardenne, M.A., Penha, U.C., 2001. Bacia Sanfranciscana: o registro Fanerozoico da Bacia do São Francisco. In: Pinto, C.P., Martins-Neto, M.A. (Eds.), *Bacia do São Francisco: Geologia e Recursos Naturais*. SBG, Belo Horizonte, pp. 93–138.
- Silva, M.C., Carvalho, M.S.S., Barreto, A.M.F., Carvalho, I.S., 2011. Paleoictiofauna da Formação Aliança (Jurássico Superior), Bacia de Jatobá, Nordeste do Brasil. In: Carvalho, I.S., Srivastava, N.K., Strochschoen Jr., O., Lana, C.C. (Eds.), *Paleontologia: Cenários de Vida*. Interciência, Rio de Janeiro, pp. 595–608.
- Silva Santos, R., 1963. Peixes do Cretácico do Rio Grande do Norte. *Anais da Academia Brasileira de Ciências* 35, 67–74.
- Silva Santos, R., 1969. Sobre um *Lepidotes* da Formação Itaparica, estado da Bahia. *Boletim de Geologia do Instituto de Geociências da Universidade Federal do Rio de Janeiro* 4, 43–46.
- Silva Santos, R., 1985. Sobre a presença do *Vinctifer* Jordan (Pisces, Aspidorhynchiformes) na Formação Muribeca, Estado de Alagoas. In: Campos, D.A., Ferreira, C.S., Brito, I.M., Viana, C.F. (Eds.), *Coletânea de Trabalhos Paleontológicos*. DNPM, Brasília, pp. 147–150.
- Sire, J.-Y., 1994. Light and TEM study of nonregenerated and experimentally regenerated scales of *Lepisosteus oculatus* (Holostei) with particular attention to ganoine formation. *The Anatomical Record* 240, 189–207.
- Sire, J.-Y., 1995. Ganoine formation in the scales of primitive actinopterygian fishes, lepisosteids and polypterids. *Connective Tissue Research* 33, 213–222.
- Sire, J.Y., Meunier, F.J., 1994. The canaliculi of Williamson in holostean bone (Osteichthyes, Actinopterygii): a structural and ultrastructural study. *Acta Zoologica* 75, 235–247.
- Sire, J.Y., Donoghue, P.C.J., Vickaryous, M.K., 2009. Origin and evolution of the integumentary skeleton in non-tetrapod vertebrates. *Journal of Anatomy* 214, 409–440.
- Zaher, H., Pol, D., Carvalho, A.B., Nascimento, P.M., Riccomini, C., Larson, P., Juarez-Valieri, R., Pires-Domingues, R., Silva Jr., N.J.d., Campos, D.A., 2011. A complete skull of an Early Cretaceous sauropod and the evolution of advanced titanosaurs. *PLoS One* 6, 1–10.