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ARTICLE



Shark (Chondrichthyes) microremains from the Lower Cretaceous Quiricó Formation, Sanfranciscana Basin, Southeast Brazil

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ABSTRACT

The first chondrichthyan teeth, dermal and oropharyngeal denticles from the Lower Cretaceous lacustrine Quiricó Formation (Sanfranciscana Basin), in southeastern Brazil are described. Eight microremains morphologies have been recovered from lower levels of this formation, dated as possibly Valanginian with basis on ostracods. The dermal denticles belongs to indeterminate Hybodontiformes; some teeth are ascribed to? Lonchidiidae. The presence of *Tribodus* is suggested by some dermal denticles, but this assignment requires confirmation with more complete material. The new specimens indicate a much greater diversity of chondrichthyans in the Quiricó Formation than previously thought. The associated occurrence of hybodontiforms, the coelacanthiform *Mawsonia* and early neopterygians observed in the Sanfranciscana Basin is not uncommon for the Cretaceous sedimentary strata of Brazil and Africa. However, the use of the Quiricó Formation shark remains as biostratigraphic tool is limited, due to their current poor taxonomic and relatively broad temporal distribution.

ARTICLE HISTORY

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KEYWORDS

Hybodontiformes teeth; dermal denticles; oropharyngeal teeth; *Tribodus*; Valanginian

Introduction

The lacustrine deposits of the Quiricó Formation (Areado Group, Sanfranciscana Basin) are an important window to Early Cretaceous environments of the central-western Gondwana (Sgarbi et al. 2001; Bittencourt et al. 2015). Its diverse biota, which includes charophytes, terrestrial palynomorphs, macroremains of angiosperms and gymnosperms, insects, crustaceans, fishes and dinosaurs, is far from being fully understood, partly due to insufficient fieldwork (Bittencourt et al. 2015, 2017, 2018).

The fish fauna of the Quiricó Formation is diverse. Its lower levels (probably pre-Aptian) yielded cephalic and fin spines of hybodontiforms, scales of ginglymodians, amiiformes, and the coelacanth Mawsonia gigas Woodward, 1907 (Carvalho and Maisey 2008). The occurrence of Sclerorhynchidae chondrichthyans has been mentioned (Machado et al. 2017), but not formally described so far. The association of Hybodontiformes and Coelacanthiformes has been registered in other Lower Cretaceous sedimentary basins in Brazil (Carvalho and Maisey 2008; Cupello et al. 2012b, 2016; Pinheiro et al. 2013), suggesting a possible biostratigraphic correlation with the Sanfranciscana Basin. The upper levels of the Quiricó Formation, dated at minimum Barremian, have yielded the gonorhynchiform Dastilbe moraesi Silva Santos (in Scorza and Silva Santos 1955), possibly synonymous with D. crandalli Jordan, 1910 from Araripe and Sergipe-Alagoas basins (Brito and Amaral 2008), and the rare osteoglossomorph fish Laeliichthys ancestralis Silva Santos, 1985. Scales of neopterygians, possibly lepisosteids, were described from one northern outcrop of the Areado Group (Bittencourt et al. 2017).

In this paper, we report new chondrichthyan microremains from the same levels of the previous recorded hybodontiformes (lower Quiricó Formation). The new material consists of distinct morphologies of dermal and oropharyngeal denticles and teeth, which significantly contributes to the understanding of the Early Cretaceous fish fauna diversity of Brazil.

Geological setting

The material described herein was collected at the classical locality known as 'Fazenda Tereza' in João Pinheiro (Figure 1(a)), NW Minas Gerais (Carvalho and Maisey 2008; Leite et al. 2018). The sedimentary strata in this locality are composed of laminated siltstones, mudstones, with centimetric lenses of fine-to-medium grained sandstones. These rocks pertain to the Quiricó Formation (Figure 1(b)) of the Sanfranciscana Basin, which has been interpreted as lacustrine and playa-lake environment (Campos and Dardenne 1997a; Sgarbi et al. 2001; Mescolotti et al. 2015). The material was collected from the mudstone level, within the range of the podocopidan ostracod *Cypridea hystrix* Krömmelbein, 1962 (probably Valanginian, Leite et al. 2018). Except possibly for this lower level, the age of the Quiricó Formation is poorly constrained, being considered as Barremian-Aptian by most authors (Bittencourt et al. 2015; Leite et al. 2018).

The pelitic levels where the chondrichthyan microremains come from are lower in the regional stratigraphy than the organic and carbonatic shales with abundant remains of *Dastilbe moraesi*, also attributed to the Quiricó Formation. Those shales crop out further west in Presidente Olegário town, and are probably older than laminated limestones of the Crato Formation, Araripe Basin in northeastern Brazil (Lima 1979; Arai et al. 1995), which have been dated as minimally Aptian (see Sayão et al. 2011).

The Sanfranciscana Basin corresponds to a significant proportion of the Phanerozoic sedimentary-infill of the São Francisco Craton (Campos and Dardenne 1997b; Alkmin and Martins-Neto 2001). Its lower section (Figure 1(b)) comprises the Carboniferous–Permian

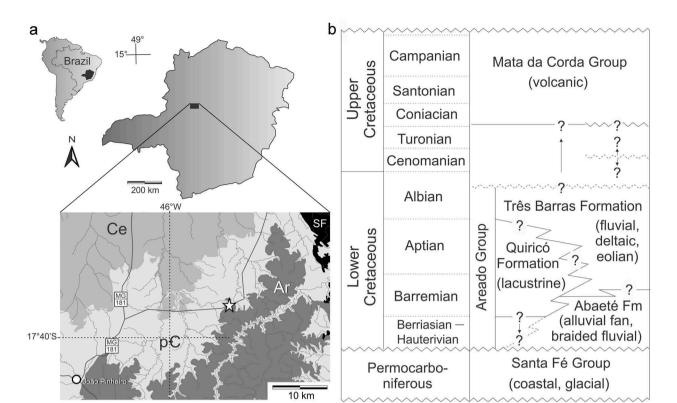


Figure 1. (a) Geologic map of the region, showing the location of the outcrop (modified from CPRM-CODEMIG 2014). Ar: Areado Group; Ce: Cenozoic cover; pE: Precambrian basement; SF: Santa Fé Group; (b) Lithostratigraphic units of the Sanfranciscana Basin cropping out in its southern region. After Campos and Dardenne (1997a), Sgarbi et al. (2001), Maraschin et al. (2016), Bittencourt et al. (2018), Leite et al. (2018).

glacial-lacustrine deposits of the Santa Fé Group (Campos and Dardenne 1994). The Mesozoic horizons (Areado Group) encompass the conglomeratic, so far afossiliferous Abaeté Formation; the Quiricó Formation; and the psamitic Três Barras Formation (Sgarbi et al. 2001), which yielded dinosaur footprints and enigmatic chert levels with marine microfossils (Kattah and Koutsoukos 1992; Pessagno and Dias-Brito 1996; Carvalho and Kattah 1998; Dias-Brito et al. 1999). In the southern portion of the Sanfranciscana Basin (Figure 1(a)), the Areado Group is capped by the volcanic rocks of the Mata da Corda Group or undifferentiated Cenozoic cover (Campos and Dardenne 1997a).

Methods

The mudstone samples were disaggregated with oxygen peroxide 30% and screen-washed utilising 1 mm, 250 μm and 90 μm mesh sieves. The microremains were picked from the sediment under stereomicroscope. Additional cleansing was performed by immersing the specimens in diluted (3%) acetic acid for a minute and then washing them in distilled water. Some microremains were coated with carbon for visualisation under the scanning electron microscope JEOL JSM-6510. All specimens are housed at the Instituto de Geociências of UFMG (IGC-P) in Belo Horizonte.

For the description of the specimens, the material was separated according to differences in their morphology. The descriptive terms were based on the works of Reif (1978), Brito (1992), Thies (1995), and Maisey and Denton (2016). The high-rank systematics follow Maisey (2012) in considering Elasmobranchii and Neoselachii synonymous. Hybodontiformes are regarded as stem-group Elasmobranchii.

Results

Systematic palaeontology

Chondrichthyes Huxley, 1880 Hybodontiformes Patterson, 1966 Hybodontiformes indet. Morphology I

?Tribodus sp.

Material

Fourteen isolated dermal denticles (IGC-P 0090/1 to 0090/14) (Figure 2(a-d)).

Description

These dermal denticles are thorn-like shaped and possess a rugose, ventrally pitted, oval base and a laterally flat, posteriorly recurved sail-like crown that emerges from the base through a short neck. They measure 150–400 μm long, and 100–300 μm high. In the smaller denticles (Figure 2(d)), the posterior tip of the crown is more projected dorsally. The anterior edge of the crown is convex and the posterior one concave. Roughly parallel, evenly spaced-out crests of different length ornament the crown on both sides. They curve posteriorly at the top, where they meet forming amedian serrated keel. Thinner, shorter and straight crests are interposed between the larger crests. The base of the crown contains several lateral foramina for the vascular canals ('neck canals' of Maisey and Denton 2016). The oval base bears mediolateral crests, which are thicker than those of the crown and are aligned with them on the neck. The basal perimeter of the denticle is irregularly indented between the crests.

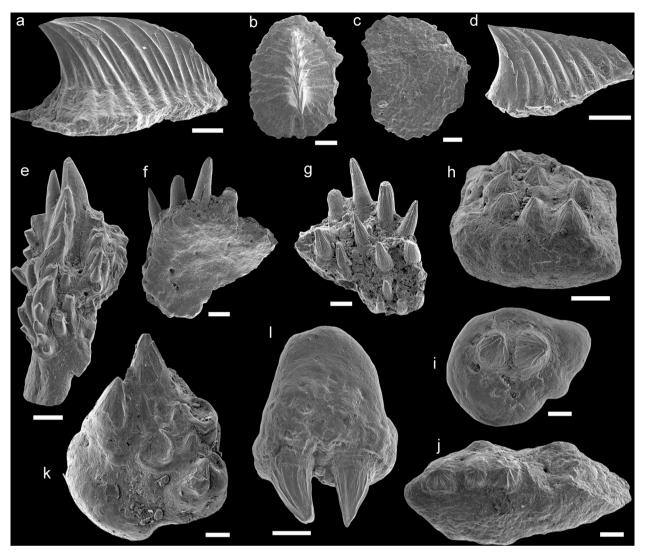


Figure 2. Elasmobranch microremains from the Quiricó Formation assigned to Hybodontiformes. A–D, Morphology I (?Tribodus): (a) dermal denticles in lateral (IGC-P 0090/4); (b) apical (IGC-P 0090/1); (c) basal (IGC-P 0090/3); and (d) lateral (IGC-P 0090/7) views. E–J, Hybodontiformes indet. possibly oropharyngeal denticles: (e) multicuspided denticle (IGC-P 0353, morphology II); striated multicuspided dermal denticle in ventral (f) and dorsal (g) views (IGC-P 00091, morphology III); (h–j) dental plates in apical views (morphology IV; respectively IGC-P 0092/2, 0092/16, 0092/1); (k) dermal denticle in frontal view (morphology V, IGC-P 0351/1); (l) dermal denticle in frontal view (morphology VI, IGC-P 0351/2). Scale bars A–D: 500 μm; E: 100 μm; F–L: 200 μm.

Remarks

The above-mentioned dermal denticle morphology fits well into the 'hybodontid scale type' described by Reif (1978) as thorn or coneshaped crown with numerous ridges running down from the apex, neck not well-developed and numerous canals occurring around it; their base can be flat, concave or slightly convex, also containing many randomly distributed canals. The shape and orientation of the crown associated to the presence of ridges in the denticles is a general trait of chondrichthyans, acting as a drag reduction mechanism (Raschi and Tabit 1992). However, many hybodontiforms do not possess dermal denticles with a laterally flat, sail-like crown as described here. The hybodontid Hybodus delabechei Charlesworth, 1839 is an example (Reif 1978), where the curvature on the apical portion of the dorsal edge of the crown is not pronounced, rendering its posterior end significantly higher than the anterior one. Thies (1995, Figure 1(d)) also described unidentified Hybodontoidea dermal denticles from the Kimmeridgian of Germany (his morphology 4) with a laterally flat crown. In this case, the crown is significantly higher in comparison to the scales described here. The blade-like morphology I (Figure 2(a-d))

denticles are more similar to those of Tribodus limae Brito and Ferreira, 1989, originally described from the Aptian-Albian of the Romualdo Formation, Araripe Basin (see also Maisey 1991; Maisey and Denton 2016), and 'Hybodus' fraasi Brown, 1900, from the Upper Jurassic of the Solnhofen Formation (Maisey 1986). In both T. limae and 'H'. fraasi, those denticles are formed by a rounded base and a median, relatively short sail-like crown, with the whole structure bearing basal-apical crests (Maisey 1986; Brito 1992; Leidner and Thies 1999; Maisey and Denton 2016). Unfortunately, the dermal denticles of 'H'. fraasi are not described in as much detail as those of *T. limai*, thus several characters such as size and crown shape variation, presence and distribution of neck canals and indentation between ridges cannot be properly compared. Maisey and Denton (2016) did not find any diagnostic character in the dermal denticles of T. limai, except when considering the whole morphological range of the shagreen, i.e. including both the thorn-like denticles and the cock's comb-like denticles. which are apparently absent in other Hybodontiformes. On the other hand, the thorn-like dermal denticles of 'Hybodus' basanus, for instance, are shorter and bear a lower number of crown crests,

with even thicker basal crests (Maisey 1983). Thus, the available data support a larger number of similarities between the thorn-like dermal denticles of the Sanfranciscana Basin and those of Tribodus limai, although a definitive assignment to this species is hampered by the lack of unambiguous diagnostic characters (Maisey and Denton 2016). The closer affinity with Tribodus is chronostratigraphically and biogeographically better supported than any potential affinity with known Hybodus species. We therefore tentatively ascribe the denticles described here to ?Tribodus sp.

> Hybodontiformes Patterson, 1966 Hybodontiformes indet. Morphology II

Material

One dermal denticle (IGC-P 0353) (Figure 2(e)).

Description

Denticle with complex system of cusps, distributed in a sinuous central row and accessory rows of cusplets flanking it on both right and left sides. The total length (considering the base and cusps is ca. 870 µm). The cusps are smooth, without the conspicuous crests. Some cusps have sharp margins, suggesting a rudimentary keel. The cusps are usually recurved, whereas the cusplets are in general straight. In the central row, the posterior cusps are broad-based and deeper than the anterior ones, often coalescing apically.

Remarks

Dermal denticles with complex system of cusps/cusplets, either coalescing or not, are known to occur for instance, in the Carboniferous listracanthid Acanthorhachis spinatus Martill et al. 2013, and the Permocarboniferous hybodontoid Lissodus sardiniensis Fischer et al. 2010, demonstrating the plasticity of dermal denticle architectures across chondrichthyan species broadly separated in deep time. The morphology II differs in being significantly smaller and with compact, not hollow cusps, compared to A. spinatus, and in possessing less recurved, and lower cusps, arranged in multiple parallel row compared to L. sardiniensis.

The hybodontiform *Tribodus limai* has a distinct type of dermal denticle morphology referred to as cock's comb-like (Maisey and Denton 2016), which are superficially similar to that of IGC-P 0353. Its size varies from 250 to 600 µm, which is somewhat shorter than the morphology described here. They both have a central row of tall, recurved, smooth cusps and a number of cusplets on both sides. However, these dermal denticles of T. limai lack apical fusion of cusps and the cusplets are more regularly distributed. Based on the resemblances shared with T. limai, IGC-P 0353 is provisionally ascribed to an indeterminate Hybodontiformes, but the scarce sampling hinders its identification at less inclusive taxonomic levels.

Hybodontiformes indet. Morphology III

One dermal denticle (IGC-P 0091) (Figure 2(f-g)).

Description

This multicuspid dermal denticle has three series of longitudinally aligned cusps (the largest one is ca. 600 µm high), each containing three to four elements, all attached to a slightly curved, broad base possessing small foramina on the ventral side. The cusps bear irregular and sub-parallel crests. The cusps are larger on one side of the basal plate than those on the opposite side.

Remarks

As previously discussed for the morphology II, dermal denticles with parallel rows of cusps are observed in Tribodus limai and other chondricthyans from Palaeozoic and Mesozoic rocks (Reif 1978; Thies 1995; Liao et al. 2007; Fischer et al. 2010; Martill et al. 2013; Maisey and Denton 2016; Bhat et al. 2018). In the case of morphology III, it differs from the cock's comb-like denticles of T. limai on the marginal (not central) location of the highest cusps row; the cusps are not fused to each other and, the abundance of the irregular striae. It also differs from superficially similar Acanthorachis Martill et al. 2013 dermal denticles, due to the occurrence of striae and the more regular distribution of cusps. The morphology III is assigned to an indeterminate Hybodontiformes until more complete material allows for more precise taxonomic identification. It probably represents an oropharyngeal denticle.

Hybodontiformes indet. Morphology IV

Material

Twenty-two dental plates (IGC-P 0092/1 to 0092/22) (Figure 2 (h-j)).

Description

This morphology is composed of multiple small pyramidal-shaped denticles, individually attached to a common thick and rounded base, forming thick plates. The largest plate is 2 mm long, but none of the specimens is complete. The cusps may abut, but never overlap or merge with one another and present pronounced vertical crests and are often slightly curved.

Remarks

This morphology is typical of denticles on the lower jaw and roof of the mouth (Reif 1978; Thies 1995; Manzanares et al. 2014). Such oropharyngeal multicuspid denticles are found in several species of hybodontiform sharks, but they are not diagnostic of any particular genera or species. Maisey and Denton (2016) described a similar morphology in the oropharyngeal region of T. limae. However, the morphology IV denticles are distinctive in their globose shape, their more delicate striae and more sharply pointed, rather than truncated tips.

Hybodontiformes indet. Morphology V

Material

One dermal denticle (IGC-P 0351/1) (Figure 2(k)).

Description

This morphology of dermal denticle presents a wide and deep base with distinctive upright, high, recurved, pointed, robust cusps. The cusps are attached to a shallow socket and bear a basal constriction around its axis. Above the constriction, the cusps have the longitudinal striation, and are fuse to each other in some specimens.

Remarks

The striation of the cusps is common to Cretaceous hybodontiforms, to which this specimen is tentatively referred. Yet, its exact identification is hampered by lack of more diagnostic material. This morphology resembles some indeterminate chondrichthyan dermal denticles described from the Triassic Tiki Formation, in India (Bhat et al. 2018). Yet, they differ by the irregular distribution of the cusps in IGC-P 0351/1, whereas in the afore-mentioned chondrichthyan, these occur side by side in a single row.

Hybodontiformes indet. Morphology VI

Material

One dermal denticle (IGC-P 0351/2) (Figure 2(l)).

Description

Similar to the morphology V, but this specimen is characterised by a deep base with irregular and shallow foramina. It bears two spaced-out, robust cusps inserted in a rounded concavity, gently recurved towards one another. The cusps present a slight basal constriction and irregular, fine striations.

Remarks

The main difference compared to morphology V is the absence of cusp fusion or coalescence. Both morphologies, V and VI may represent the same taxon, pending more complete material to confirm it

Hybodontiformes indet. Morphology VII

Material

One tooth, possibly oropharyngeal (IGC-P 0084) (Figure 3(a-b)).

Description

The tooth has three main conical cusps with longitudinal striations, which are separated from one another by large gaps. The two lateral cusps diverge from the central one by angles of 30° and 40°. On the buttress of the main cusps there are faint concentric markings. Two accessory cusplets can be seen on the base of the root. The root is

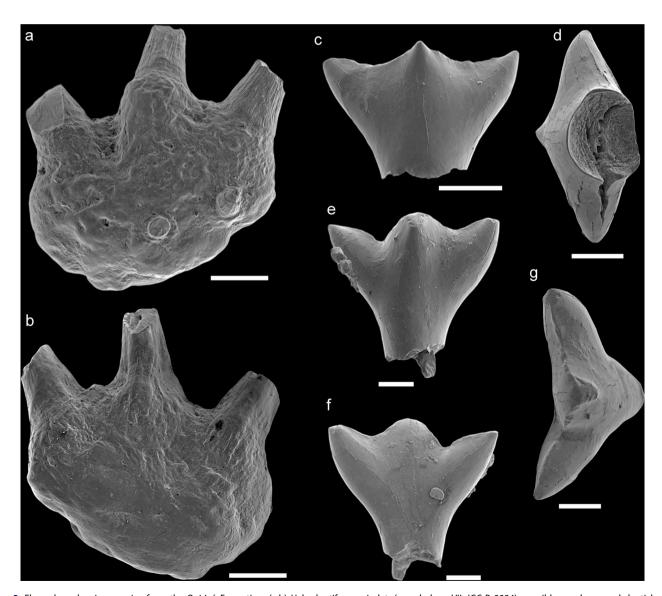


Figure 3. Elasmobranch microremains from the Quiricó Formation. (a,b) Hybodontiformes indet. (morphology VII, IGC-P 0084), possible oropharyngeal denticle. C–G, Morphology VIII (?Lonchidiidae). Probable oral teeth in (c) labial and (d) basal views (IGC-P 0093/1); (e) labial, (f) lingual, and (g) occlusal views (IGC-P 0093/2). Scale bars A–B: 1 mm; C–G: 200 μm.

labio-lingually flattened. A region of anaulacorhize (sponge-like) vascularisation is observed on its purported labial surface, between the base and the lower half of the root and the base of the crown.

Remarks

The functional oral position of this specimen is difficult to ascertain given its poor state of preservation. One hypothesis is that it could be a cephalic spine, a structure commonly associated with male Hybodontiformes. Cephalic spines are well known in the genus Tribodus, where they have been found attached to relatively complete specimens (Lane 2010; Cupello et al. 2012a). Yet, differently from the morphology VII, they have a single large posteriorly recurved cusp; and a triradiate constricted base. Recurved harpoonlike cephalic spines are known from other hybodont species, for instance, Asteracanthus aegyptiacus Agassiz, 1837 from the Cretaceous of Niger (Michaut 2017). In addition, in our specimen two additional cusplets can be seen accreted to the labial surface of the base. Therefore, we interpret this specimen as an oropharyngeal denticle.

Many species of hybodontiformes have been solely classified based on their teeth (Duffin 2001; Rees and Underwood 2008; Hodnett et al. 2013; Pinheiro et al. 2013) but the anaulacorhize nature of the root is a synapomorphy of Hybodontiformes (Maisey 1987; Hodnett et al. 2013).

There are similarities between this morphology VII and the dermal denticles of the morphologies V and VI. These include striated cusps and a bulging base with a basal constriction. Nevertheless, morphology VII cannot be ascribed to any species commonly found in the Cretaceous of the interior basins of Brazil and elsewhere, such as Hybodus Agassiz, 1837, Acrodus Woodward, 1888, Polyacrodus Jaeckel, 1889, Parvodus Rees and Underwood, 2002, Planohybodus, 2008 and Tribodus. Furthermore, this morphology VI is not compatible with a durophagous diet (as seen in Tribodus), nor does it have a cutting edge, as observed in Priohybodus D'Erasmo, 1960.

> Hybodontiformes indet. Morphology VIII ?Lonchidiidae

Material

Eight teeth (IGC-P 0093/1 to 0093/8) (Figure 3(c-f)).

Description

This tooth morphology is characterised by a rod-like peduncle uniting one central cusp and two lateral cusplets, roughly of the same height, which are separated by concave spaces. Together they form a broad trident that is labiolingually recurved, its lingual surface being slightly concave, whereas the labial surface is convex. There is no evidence of a labial peg. The teeth measure $400-900 \ \mu m$ mesiodistally (across the cusps and cusplets). The occlusal ridges are well-developed and connect the apical area of the central cusp to the cusplets. The shape of the central cusp is variable: it appears either as a low-pointed keel, separated from the lateral cusps by broad, rounded notches (Figure 3(c)), or as a more prominent structure, apically rounded and laterally bound to angular notches (Figure 3(e)). There is no evidence of longitudinal striations marking the outer surface of the keels. The teeth roots have not been preserved in any of the recovered specimens.

Remarks

This gracile and 'tridentate' morphology with occlusal crest resembles the teeth of some species of Lonchidiidae sensu Rees and Underwood (2002), a group of hybodontiform sharks with controversial systematics (see Manzanares et al. 2017). The lonchiidid teeth have a wide morphological range, and some characters variably observed in the family, including the typical Y-shape aspect in occlusal view and the low crowns and cusps (Duffin 1985; Duffin and Sigogneau-Russell 1993; Heckert et al. 2007; Prasad et al. 2008; Rees and Underwood 2008; Fischer et al. 2010; Kirkland et al. 2013; Johns et al. 2014; Manzanares et al. 2017), are also seen in the specimens described here. Other characters common to the family, such as the developed labial peg and minor accessory cusplets in the occlusal area, were not observed, but these are not universally present in lonchidiids (Manzanares et al. 2017).

Due to the scarcity and fragility of the material, it was not possible to observe the ultrastructure of the enameloid, which has been described by other authors (Johns et al. 2014; Manzanares et al. 2017). In this case, we provisionally assign these teeth to an indeterminate lonchiidid.

Discussion

Research on elasmobranch dermal denticles as well as oral and oropharyngeal teeth is hampered by the fact that these skeletal elements show a wide range of usually poorly described morphologies along the body of the same individual. Little is known of these variation in fossil chondrichthyans, even in well-preserved specimens (Reif 1978; Maisey 1989; Thies 1995; Maisey and Denton 2016). Also, chondrichthyan dermal denticles are less studied than their teeth, which limits the availability of data for comparative studies.

The thorn-like dermal denticles described here are morphologically comparable with those described for Tribodus limae. The diagnosis of the species includes large, thorn-like dermal denticles measuring 2.5 to 3.0 mm (Brito and Ferreira 1989; Maisey 1991). Similar dermal denticles found in the Quiricó Formation have a wider range of sizes and shapes. Their thorny morphology results from the sharply pointed posterior end of the blade-like crown. Specimens IGC-P 0090/1 to 0090/9 share this morphology. Other hybodontiforms have a similar type of dermal denticles (e.g. 'Hybodus' fraasi Brown, 1900 in Maisey 1986), but the variation within the same species and across different species within that clade is poorly known. The hybodontid T. limae is also diagnosed by a slender fin spine reaching 12.5 cm long, with lateral faces bearing 8-10 sharp continuous ridges, and the anterior one forming a keel (Brito and Ferreira 1989). Most fin spines previously collected from the same beds (Carvalho 2002) are compatible in size, but the number of ridges can be larger. On the other hand, the number of ridges can vary with size and ontogeny in chondrichthyans.

Due to the lack of unambiguous diagnostic features of the thornlike dermal denticles, we tentatively refer these microremains to Tribodus. This taxon is also known in Brazil from the Albian of the Romualdo Formation of the Araripe Basin (Brito and Ferreira 1989; Brito 1992) and the Itapecuru Group of the São Luís-Grajaú Basin (Dutra and Malabarba 2001). Additional Tribodus specimens or species have been recovered from several localities from Valanginian to Cenomanian in Africa and Europe (Maisey 2000; Vullo et al. 2005, 2007; Lane and Maisey 2012). However, those records are mostly based on teeth and are not comparable to the material described in this paper. The possible occurrence of Tribodus in the Valanginian of Sanfranciscana Basin would expand the temporal range of this taxon into the Early Cretaceous of Brazil, but it is in accordance with previous records of the genus.

Six distinct dermal denticle and teeth morphologies are attributed to Hybodontiformes indet. Albeit the elucidation of their affinities relies on more complete or abundant specimens, they are distinct from dermal denticles and teeth of *Tribodus*, indicating that

at least two species of hybodontiforms are present in the lower lacustrine strata of the Quiricó Formation. The assignment of some specimens to Lonchidiidae, if proven correct, would represent the first record of this family in the Sanfranciscana Basin.

Several authors have noticed that the sedimentary basins along the Atlantic continental margin of Brazil and their African lithostratigraphic counterparts, together with some interior basins in the northnortheast region of the Brazil, variably display faunal similarities including sarcopterygian fishes (i.e. the coelacanthiform Mawsonia and dipnoans), the actinopterygian Lepidotes and hybodontiform sharks (Woodward 1888, 1907; de Saint-seine 1955; Casier 1961; Gee 1988; Brito et al. 1994; Maisey 2000; Cupello et al. 2012b). These similarities are of limited biostratigraphic value due to lack of strict temporal and taxonomic constraints. In addition to the wide temporal range of Tribodus, records of Mawsonia span from the Berriasian (Woodward 1907), or perhaps even earlier into the Late Jurassic (Soto et al. 2012), to the Aptian-Albian (Wenz 1981; Yabumoto 2002; Fragoso 2014; Cupello et al. 2016). The 'basket'-genus Lepidotes is also long-lived, possibly spanning from Late Jurassic to Late Cretaceous (Gallo 2005). Nevertheless, the occurrence of Lepidotes in the Sanfranciscana Basin awaits confirmation (Carvalho and Maisey 2008; Bittencourt et al. 2017).

The low taxonomic 'resolution' of several specimens recovered from northern Brazil and Africa also imposes limitations to the degree of temporal accuracy of geological correlations. Due to lack of more diagnostic material, Hybodontiformes are frequently identified above the genus level and the genus Lepidotes is problematic (López-Arbarello 2012).

Conclusions

We report for the first time elasmobranch dermal denticles, oropharyngeal denticles, dental plates and oral teeth for the Lower Cretaceous Sanfranciscana Basin (lower portion of the Quiricó Formation, possibly Valanginian). This is a relevant fossil site on the central-western Gondwana due to its temporal and geographic proximity to the proto Atlantic Ocean. The material is assigned to indeterminate Hybodontiformes. Further taxonomic refinement depends on more complete or abundant materials. Thorn-like dermal denticles may belong to Tribodus, an hybodontid shark previously registered in northern Brazil, Africa and Europe, ranging from Valanginian to Cenomanian. The faunal association of hybodontiforms with the coelacanthiform Mawsonia and ginglymodian fishes is not uncommon in Lower Cretaceous fossil sites in Brazil and Africa. However, the relatively long temporal range of these taxa and the lack of precise taxonomic resolution of many of these occurrences limit the use of this shark microremains association as accurate biostratigraphic tool. We also conclude that fish-based, long-range correlations between the Quiricó Formation and other Lower Cretaceous sedimentary strata of South America and Africa remains poorly constrained.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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