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Discovery of †Obaichthyidae gars (Holostei, Ginglymodi, Lepisosteiformes) in the Aptian Codó Formation of the Parnaíba Basin: Remarks on paleobiogeographical and temporal range

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ABSTRACT

Here we report the first †obaichthyid gar from the Lower Cretaceous (Aptian) Codó Formation of the Parnaíba Basin, Northeastern Brazil. It shows the following obaichthyid characters: numerous odontods firmly attached to the outer surface of the dermal bones, free and mobile maxilla, presence of interopercle, lack of contact between the metapterygoid and ectopterygoid, absence of lacrimomaxillary bones, and a prominent spine at the posterior margin of the scales. Due to the presence of scales bearing a prominent ventral posterior spine and a number of additional posterior marginal spines, the fish from the Codó Formation is noticeably the same species found in the Albian Santana Formation of the Araripe Basin, *Dentilepisosteus laevis*. Although probably restricted to fresh or brackish water, the new discovery adds one more taxon to the assemblages found in the Parnaíba and the Araripe basins. The new record extends the temporal range of this species down into the Aptian (about ~10 myr older than the previous occurrence).

1. Introduction

Distributed today in freshwater, and rarely coastal areas of northern parts of the Western Hemisphere, between Southern Canada and Costa Rica, lepisosteiformes, popularly known as gars, are a group of neopterygian fishes with a formerly worldwide distribution, especially during the Cretaceous and Paleogene. Lepisosteiformes *sensu* Grande 2010, had been classified into two families: Lepisosteidae, a group including modern gars, are known from the Late Cretaceous, and include the extant forms as well as various fossils from all continents, except Antarctic and Australia; and Obaichthyidae, a group until now restricted to the «mid» Cretaceous (Albian/Cenomanian) of the western part of Gondwana (Grande, 2010; Alvarado-Ortega et al., 2016).

Obaichthyid gars were first described by Wenz and Brito (1992) who proposed the new genus *Obaichthys* for two species from the Albian Santana Formation of the Araripe Basin: *O. decoratus* and *O. laevis*. Besides being the oldest lepisosteiformes known, these species also retained some characters considered primitive for neopterygians, such as the presence of a free maxilla, two post-orbital bones, and paleoniscoid-type scales (Wenz and Brito, 1992, 1996; Brito *et al.*, 2006). Grande (2010) reviewed the Lepisosteiformes and proposed a new family Obaichthyidae. He also created a second genus (*Dentilepisosteus*) for *O. laevis*. In the same paper, he described two other species of obaichthyids: *Obaichthys africanus* and ?*Dentilepisosteus kemkemensis* both from the ?Upper Cretaceous Kem Kem beds of Morocco. Recently, Brito and Yabumoto (2011) recorded another obaichthyid in the Crato Formation of the Araripe Basin, that seemed to be more related to *D. laevis* than to *O. decoratus*. Here we report the presence of the obaichthyid, *Dentilolepisosteus laevis* (Wenz and Brito, 1992) in the Aptian Codó Formation of the Parnaíba Basin, in northeastern Brazil, the first record of this species outside the Araripe Basin. This new finding extends the temporal range of *Dentilolepisosteus laevis* to the Aptian.

2. Locality, distribution, and geological age

The specimens described here were collected in the Lower Cretaceous Codó Formation, at the Parnaíba Basin, in the quarries of Perneta Ranch, near the town of Brejo, State of Maranhão,

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northeastern Brazil (Fig. 1). The Parnaíba Basin occupies an area of about 600,000 km^2, covering the states of Maranhão, Piauí, Pará, Ceará, Goiás, and parts of Tocantins. Its sedimentary succession at its depocenter reaches thicknesses of the order of 3400 m, of which about 500 m represent Mesozoic strata (Mesner and Wooldridge, 1964).

The age of the Codó Formation is widely accepted as Aptian and is mainly based on palynological data (Lima, 1982). Deposits assigned to the Codó Formation are geographically restricted and discontinuous. They are exposed in the beds of rivers that drain the center of the basin, from the western margin, at the confluence of the Tocantins and Araguaia Rivers, until near the margin of the Parnaíba River, in the town of Brejo (Santos and Carvalho, 2009). The Codó Formation is divided into three depositional cycles, following stratigraphical interpretations. The lowest cycle represents a lacustrine facies culminating with evaporite cycles, suggesting a subsequent regression or the establishment of a restricted sea; the second cycle shows a new marine transgression culminating with the third cycle with the establishment of palustrine conditions on a tidal flat (Mesner and Wooldridge, 1964; Rezende and Pamplona, 1970; Leite et al., 1975; Fernandes and Piazza, 1978; Lima and Leite, 1978). Analysis of the paleobiota of the first cycle suggests a marine – brackish lacustrine setting (Lima and Leite, 1978).

3. Palaeoenvironment

The Codo Formation has yielded numerous fossils including palynomorphs, macrophytes, foraminifera, crustaceans, bivalves, gastropods, and fishes (Santos and Carvalho, 2009; Lindoso et al., 2011; 2013; Lindoso, 2012). The fishes, which form the most abundant element of this biota, are exceptionally abundant and have affinities with the ichthyofauna of the Santana and Riachuelo formations, respectively from the Araripe and Sergipe/Alagoas basins (Santos and Carvalho, 2009). Fish taxa include *Calamopleurus cylindricus* Agassiz, 1841; *Brannerion latum* (Agassiz, 1841); *Araripelepidotes temnurus* (Agassiz, 1841); *Tharrhias araripes* Jordan and Branner, 1908; *Vinctifer comptoni* (Agassiz, 1841), *Santanichthys diasii* (Santos, 1958); *Cladocyclus gardneri* Agassiz, 1841, *Codoichthys carnavali* Santos, 1994; *Rhacolepis buccalis* Agassiz, 1841; and mawsoniid coelacanths, probably *Axelrodichthys araripensis* Maisey, 1986 (Santos, 1974, 1985, 1992, 1994; Santos and Carvalho, 2009; Carvalho et al., 2013).

4. Material and methods

The present study is based on two partial specimens from the Codó Formation, preserved in calcareous concretions and housed in the Collection of the Universidade Federal do Rio de Janeiro and Centro de Pesquisa de História Natural e Arqueologia do Maranhão, accession numbers respectively are: UFRJ-DG 828P and CPHNAMA-VT 1242. One of these specimens (UFRJ-DG 828P) was prepared using the transfer method of Toombs and Rixon (1959). The prepared fossil comprised two halves of a concretion and reveals part of the skull including dermal bones, part of the braincase, pectoral girdle, some vertebrae, and many scales (Figs. 2 and 3).

Comparative material — *Dentilepisosteus laevis*: UERJ-PMB 233 (a semi-complete specimen preserved in lateral view from the Crato Formation), UERJ-PMB 144 (a semi-complete specimen, lacking the skull, preserved in lateral view from the Crato Formation), MPSC 901 (complete specimen, preserved in lateral view from the Santana Formation); "*Belonostomus*" *carinatus*: NHMUK PV P.10062 (some isolated scales from the Marfim Formation, Recôncavo Basin); *Oniichthys (Atractosteus) falipoui*: UERJ-PMB 67 (a semi-complete, three dimensional specimen, lacking the dorsal, anal and caudal fins, from the Kem-Kem beds of Morocco).

5. Systematic palaeontology

Neopterygii Regan 1923
Holostei *sensu* Grande, 2010

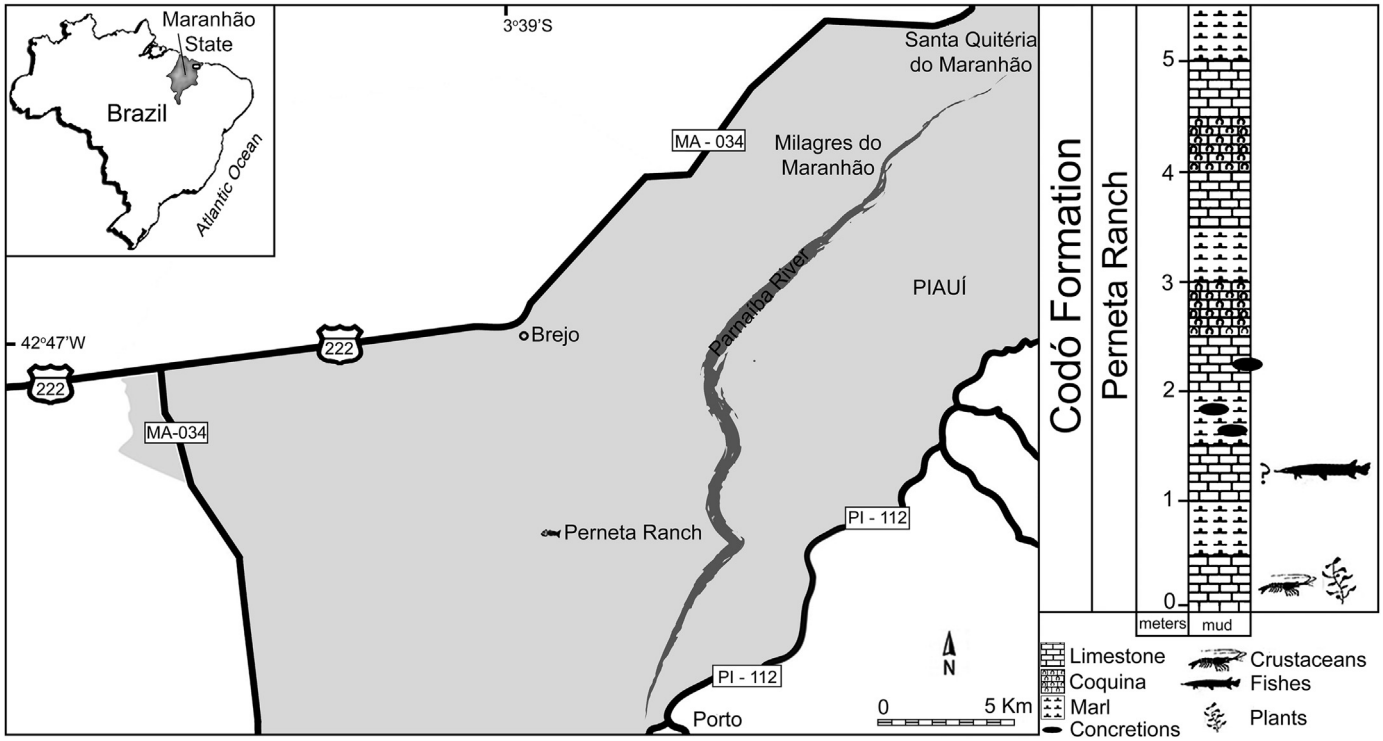

Fig. 1. Map and Stratigraphic column of the Codó Formation, Parnaíba Basin, State of Maranhão, Northeastern Brazil, indicating the location of the fossil locality.

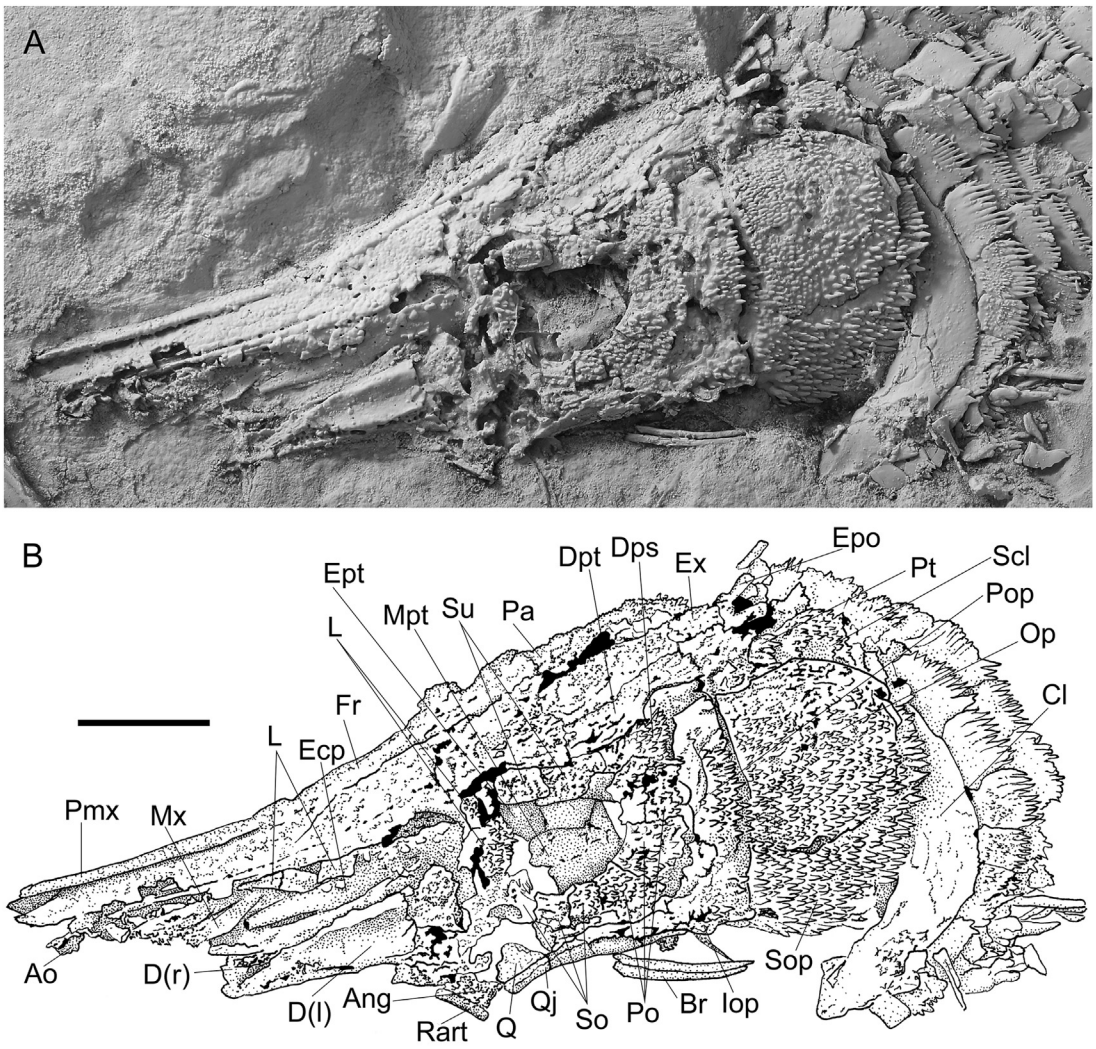

Fig. 2. *Dentilepisosteus laevis* (Wenz and Brito, 1992) from the Codó Formation, Parnaíba Basin. UFRJ-DG 828P. A) Photograph of the head region; B) anatomical interpretations. Abbreviations: Ang, angular; Ao, antorbital; Br, branchiostegals; Cl, cleithrum; D, dentary; Dps, dermosphenotic; Dpt, dermopterotic; Ecp, ectopterygoid; Epo, epiotic; Ept, endopterygoid; Ex, extrascapular; Fr, frontal; Iop, interopercle; L, lacrimal; Mpt, metapterygoid; Mx, maxilla; Op, opercle; Pa, parietal; Pmx, premaxilla; Po, postinfraorbital; Pop, preopercle; Pt, posttemporal; Q, quadrate; Qj, quadratojugal; Rart, retroarticular; Scl, supracleithrum; So, subinfraorbital; Sop, subopercle; Su, supraorbital. Scale bar equals 1 cm.

Ginglymodi sensu Grande and Bemis, 1998
Order Lepisosteiformes Hay, 1929
Family Obaichthyidae Grande, 2010
Dentilepisosteus Grande, 2010

Dentilepisosteus laevis (Wenz and Brito, 1992)
(Figs 2–4)

Description: This is a medium sized lepisosteiform. Taking into account the excellent preservation of the material and, comparing them to other specimens from the Araripe Basin, we consider that both specimens had total lengths (TL) of approximately 130 mm. The dermal bones and the scales are covered with ganoin. Dermal bones are highly ornamented by numerous odontods hindering the identification of sutures between some dermal bones.

The anterior part of the snout is not well preserved in our specimen, a state also found in the numerous specimens from the Santana Formation concretions (see Grande 2010).

The rostral (Fig. 3) is a well-developed arched tube-like element housing the ethmoidal commissure connecting the right and left antorbitals. The antorbital is partially preserved on specimen UFRJ-DG 828P. The bone seems to be somewhat triangular and is pierced by the sensory canal. The nasal is not recognizable in our specimen.

The premaxilla is a long and immovably bone located anteriorly to the frontal (Figs. 2 and 3). Although a lateral process bearing a small tooth row, considered as a familial character by Grande (2010), was present, this process was lost during the acid preparation.

The frontal is the longest element of the dermal skull being slightly longer than the premaxilla (Figs. 2 and 3). The bone is slightly wider at the rear where it contacts the parietal and dermopterotic. The suture between the frontals is almost straight, with few interdigitations. The supraorbital sensory canal extends longitudinally, close to the lateral margin of the bone. The parietal (Figs. 2 and 3) is subrectangular and well-developed being longer than wide and is approximately two thirds of the length of the frontal. The parietal is strongly sutured with the frontal but the suture is difficult to see because of the high number of odontodes. Lateral to the parietal and contacting the posterior part of the frontal is the subrectangular dermopterotic bearing the supratemporal canal. Both parietals and dermopterotics overlap posteriorly the extrascapular series.

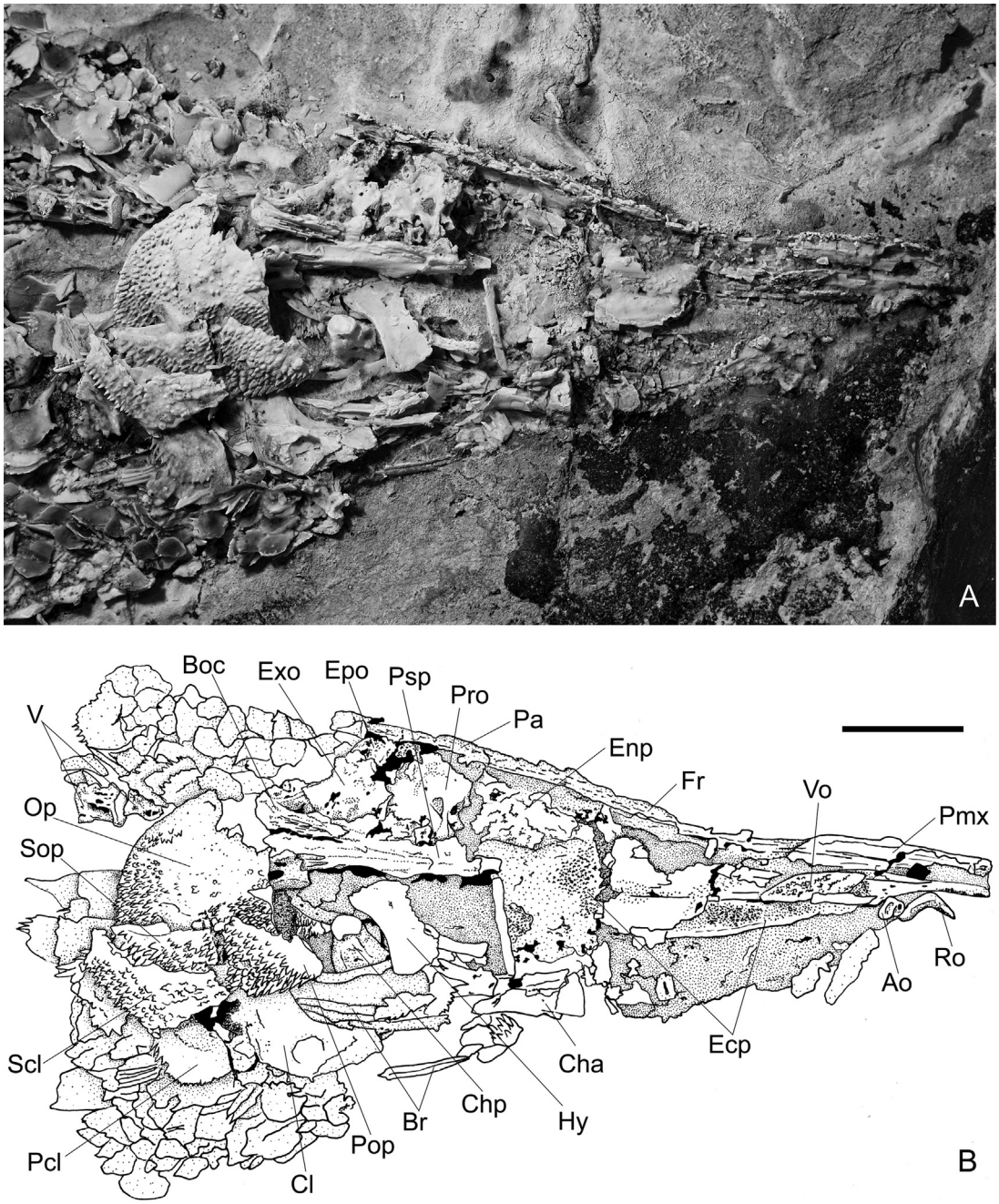

Fig. 3. *Dentilepisosteus laevis* (Wenz and Brito, 1992) from the Codó Formation, Parnaíba Basin. UFRJ-DG 828P. A) Photograph of the head region; B) anatomical interpretations. Abbreviations: Ao, antorbital; Br, branchiostegals; Boc, basioccipital; Cha, anterior ceratohyal; Chp, posterior ceratohyal; Cl, cleithrum; Ecp, ectopterygoid; Enp, entopterygoid; Epo, epiotic; Exo, exoccipital; Fr, frontal; Hy, hyomandibula; Op, opercle, Pa, parietal; Pcl, postcleithrum; Pmx, premaxilla; Pop, preopercle; Pro, prootic; Psp, parasphenoid; Ro, rostral; Scl, supracleithrum; Sop, subopercle; V, vertebrae; Vo, vomer; Scale bar equals 1 cm.

There are four extrascapulars, somewhat square in outline and much smaller than the parietals (Fig. 2). Posteriorly they overlap the anterior margin of the posttemporals while laterally they contact the dorsal part of the opercle. The supratemporal commissure runs through the anterior part of the extrascapulars.

Lateral to the premaxilla and the frontal is a series of at least three lacrimals (Fig. 2), behind which, after a gap of two bones due to preservation, the circumorbital series commences with two posterior lacrimals. The superior lacrimal contacts the first of three supraorbitals which are somewhat rectangular and form the dorsal margin of the orbit, contacting dorsally the frontal and the dermopterotic (Fig. 2). The ventral posterior lacrimal is followed by three subinfraorbitals that form the ventral margin of the orbit. These are followed by three postinfraorbitals: one ventral, forming the posteroventral corner of the orbit and two smaller elements forming the rear of the orbit. The postinfraorbital plates are on the anterior edge of the preopercle. The dorsal postinfraorbital contacts the ventral surface of the dermosphenotic. Behind the post-infraorbitals there are probably some small suborbitals. However due to the quantity of odontods the limits between these bones as well as the number of suborbitals could not be assigned. The dermosphenotic is sutured to the underside of the dermopterotic

although its limits are difficult to see due to the high number of odontods.

The posterior cheek region is closed by the L-shaped preopercle (Fig. 2). The dorsal edge of the preopercle contacts the dermopterotic, where the preopercular canal communicates with the supratemporal canal. In the preopercle, the sensory canal cannot be followed due to the highly ornamented by odontods on its outer surface.

The opercular series consists of three bones: the opercle, the subopercle, and the interopercle (Figs. 2 and 3). The opercle is almost subrounded in shape with its size as high as wide. Its anterior margin is vertical. Posteriorly, it contacts the supracleithrum and the dorsal part of the cleithrum. Its ventral border contacts the subopercle. The subopercle is a semi-triangular bone smaller than the opercle. This bone articulates anteriorly with the preopercle, anteroventrally with the interopercle and posteriorly with the cleithrum. The interopercle is an elongate triangular bone contacting dorsally the posterior margin of the preopercle. At least four thin and elongate branchiostegal rays are present in UFRJ-DG 828P and are located below the interopercle.

A few elements of the hyoid arch are partially preserved, including a long anterior ceratohyal and a strong posterior ceratohyal (Fig. 3).

Some bones of the braincase are preserved (Fig. 3) with the same configuration as those described by Wenz and Brito (1996) and Grande (2010). There are no ethmoidal ossifications.

The prootic extends on the lateral anterior wall of the braincase and is pierced by a large foramen for the hyomandibular trunk of the facial nerve (Fig. 3).

The epioccpital (pterotic of Wenz and Brito, 1996) is a small bone that, in posterior view, nearly meets its antimere on the midline. In lateral view it extends dorsally to meet the dermopterotic. It is sutured ventrally to the antero-dorsal edge of the exoccipital.

The exoccipital has a dorsal process that separates the posterior and lateral faces of the bone. The exoccipital has a large foramen for the vagus nerve situated towards the anterior margin and incompletely enclosed by this bone. The basioccipital extends below the exoccipital and is sutured with the posterior part of the parasphenoid. The basioccipital incorporates at least two vertebral centra.

Part of the right vomer is present and slightly displaced (Fig. 3). The vomer has a lateral expansion where some tiny teeth are found. Only the posterior part of the parasphenoid is present in our specimen (Fig. 3). It presents an ascending wing pierced respectively by an anterior notch for the efferent pseudobranchial artery and posteriorly by a notch for internal carotid artery. The posterior end of the parasphenoid is forked, diverging in the level of the aortic notch.

The maxilla is an elongate bone that increases in depth posteriorly. As in other species of the family, the maxilla is free and mobile (Wenz and Brito, 1992; Grande 2010). The oral border of the maxilla bears a single row of very tiny teeth.

The jaw joint lies well forward of the orbit. The dentary is long and slender, increasing in height posteriorly (Fig. 2). It presents a unique row of small marginal teeth at the anterior end of the bone. The dentary posteriorly sutures with the small retroarticular and the angular. The supraangular was not seen.

The palatal complex is well preserved in UFRJ-DG 828P. The oral face of the ectopterygoid and the endopterygoid are visible (Fig. 3). The ectopterygoid is a thin and elongated bone bearing a thin shagreen of tiny teeth on its oral surface. The endopterygoid also has tiny villiform teeth on its oral surface. The metapterygoid is a somewhat rectangular bone. It is edentulous and contacts anteriorly the posterior end of the endopterygoid.

The quadrate does not contact the metapterygoid (Fig. 2). It is fan-shaped with a well developed articular condyle for articulation with the lower jaw. Posteriorly to it there is a well ossified elongate dermal quadratojugal. The symplectic could not be observed in our material. The hyomandibula articulates dorsally into the ventral surface of the dermopterotic. The bone presents, in its middle part, a large foramen for the hyomandibular trunk of the facial (Fig. 3).

The dermal elements of the pectoral girdle include the posttemporal, supracleithrum, cleithrum, and postcleithrum (Figs. 2 and 3), but the clavicle cannot be seen.

The posttemporal bone is oblique and subtriangular. It contacts anteriorly the extrascapulars and covers the antero-dorsal edge of the supracleithrum. The lateral line canal penetrates the lateral edge of the posttemporal. The supracleithrum contacts anterodorsally the lateralmost extrascapular and the posttemporal. Ventrally it overlaps the dorsal end of the cleithrum. The supracleithrum contains the lateral line canal. The cleithrum is the largest bone of the pectoral girdle. It has an elongated lower arm which seems to be equal or longer than the upper arm. Anteriorly, it is covered by the opercle and the subopercle and posteriorly it overlaps the postcleithra. Although disarticulated in our specimen, the postcleithrum is somewhat rectangular in outline, deeper than long. Posteriorly, the postcleithra overlap the first row of scales.

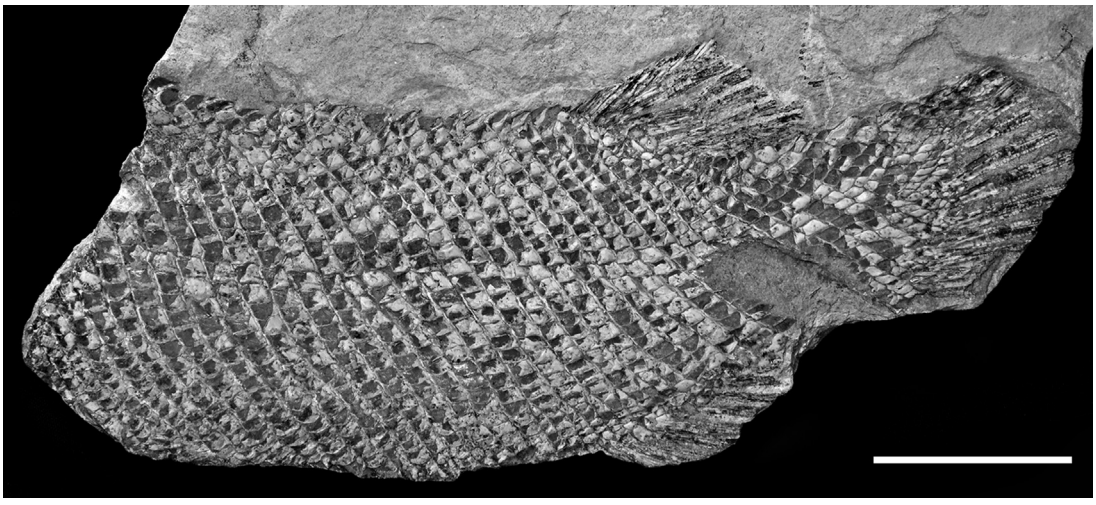

Fig. 4. *Dentilepisosteus laevis* (Wenz and Brito, 1992) from the Codó Formation, Parnaíba Basin. CPHNAMA-VT 1242. Posterior part of the body. Scale bar equals 5 cm.

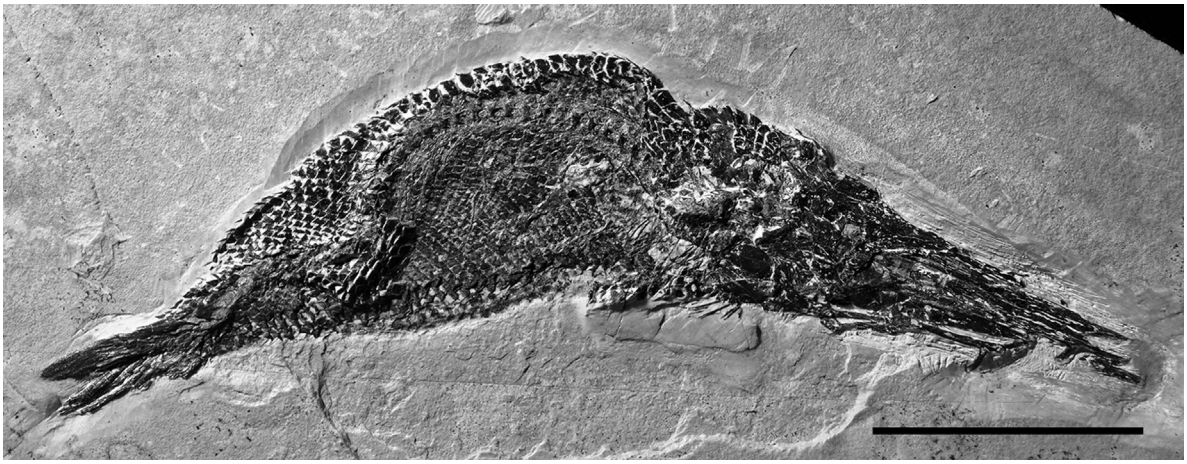

Fig. 5. *Dentilepisosteus* sp. from the Crato Formation, Aptian of Araripe Basin. UERJ-PMB 233. Scale bar equals 5 cm.

The scapulocoracoid articulates with the median surface of the cleithrum, just behind the ventral part of the dorsal arm of the cleithrum. The pectoral fin articulates with the round propterygial ossification and the distal radials. Very few pectoral fin rays are present.

A few anterior vertebral centra are visible where the scales were removed (Fig. 3). They are of opisthocoelous type, sculptured and with shallow lateral fossae.

The scales are smooth with, a prominent spine on their posteroventral corner as well as a number of additional posterior marginal spines. The flank scales, seen in internal view (Fig. 4) are arranged with about 15 rows of similar sized scales, decreasing in height posteriorly. Ventral to the flank scales are four or five rows of small, rectangular scales, only slightly higher than wide.

6. Discussion

The presence of numerous odontods firmly attached to the outer surface of the dermal bones, a free and mobile maxilla, an interopercle bone, the lack of contact between the metapterygoid and ectopterygoid, absence of lacrimomaxillary bones, as well as the presence of a prominent spine at the posterior margin of the flank scales readily confirm the Codo specimens as belonging to the Obaichthyidae.

Within Obaichthyidae the specimens from the Codó Formation have the scales bearing, in addition to the prominent spine on the ventro-posterior corner, a number of additional posterior marginal spines as well as a smooth ganoin enamel surface. These characters are sufficient to identify them as *Dentilepisosteus laevis*.

6.1. Historical distribution of the Obaichthyidae

This study demonstrates the presence of the obaichthyid *Dentilepisosteus laevis* in the Codó Formation, of the Parnaíba Basin. This species is known to date exclusively from the Albian Santana Formation, of the Araripe Basin, where it coexisted with *Obaichthys decoratus*, the type-species of the family.

Recently, Brito and Yabumoto (2011) identified the presence of an obaichthyid in the Aptian Crato Formation of the Araripe Basin. Although a more detailed study of the Crato specimens had not been performed, the anatomical characters confirm their identification as a *Dentilepisosteus* (c.f., Fig. 5). *D. laevis* from the Codó Formation together with the Crato specimen pull the temporal range of this species to the Aptian (about ~10 myr).

Faunal components of the Codó Formation (c.f. *Calamopleurus cylindricus*, *Brannerion latum*, *Araripelepidotes temnurus*, *Tharrhias araripes*, *Vinctifer comptoni*, *Santanichthys diasii*, *Cladocyclus gardneri*, and *Rhacolepis buccalis*) show similar diversity to that of the Araripe Basin. This is partially explained by the presence of an extensive system of epicontinental seaways, probably coming from the Caribbean Tethys onto the South American continent, developed during the Aptian (Berthou, 1990; Martill, 1993; Brito, 1997; Arai, 1999, 2014; Maisey, 2000, 2011). Other components of this fauna such as *Dentilepisosteus* as well as mawsoniid coelacanths such as *Axelrodichthys* were probably of freshwater origin.

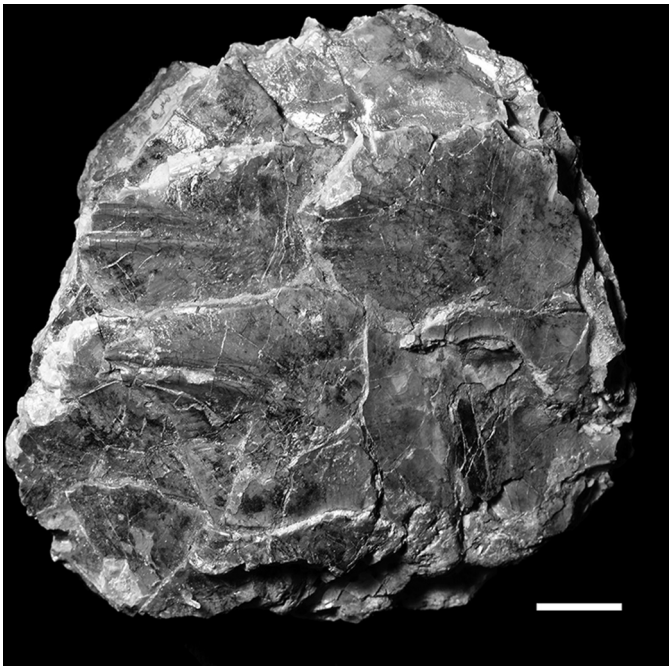

Fig. 6. Scales of the Obaichthyidae "*Belonostomus*" *carinatus* from the ?upper Hauterivian Marfim Formation, Recôncavo Basin. NHMUK PV P.10062. Isolated scales. Scale bar equals 1 cm.

Another species, ?*Dentilepisosteus kemkemensi* Grande 2010 has been described from the ?Albian/Cenomanian Kem Kem beds of Morocco, based on fragmentary material (scales and vertebrae). As in the Santana Formation, in the Kem Kem beds *Dentilepisosteus* lived in sympatry with another species of obaichthyid, *O. africanus*, and with another gar, *Oniichthys falipoui* Cavin and Brito, 2001, a

taxon considered to belong in the genus *Atractosteus* by Grande (2010) which was recently confirmed as a valid taxon (Cavin et al., 2015). This taxon may be an obaichthyid rather than a lepisosteid, although a detailed phylogenetic analysis is required.

The presence of *Dentilepisosteus* in the Brazilian northeastern basins (Parnaíba and Araripe) as well as in the Kem Kem beds of Morocco can be explained by local vicariant events as all these fossils predate or are contemporary with the complete tectonic separation between South America and Africa. During the Aptian, and most probably during part of the Albian, the epicontinental seaway system separated the South America continent from the current Northeastern Brazil although Northeastern Brazil was still connected to Africa (see Maisey 2011).

Finally another species previously described as *Belonostomus* (?) *carinatus* by Woodward (1907) from the ?upper Hauterivian, Marfim Formation of the Recôncavo Basin was recently tentatively considered as an obaichthyid (Brito and Richter, in press). This taxon had been briefly revised by Brito (1997) who considered its scales distinct from those from aspidorhynchids suggesting that these scales could belong to any holostean group. The scales of this taxon are from the caudal region, are rhombic, ganoid and have a robust peg and socket articulation. In addition they are smooth, except for the presence of bony keels (Fig. 6). The smaller scales bear a simple keel, which arises near the middle of the scale and extends downwards and backwards into a prominent spine at the postero-inferior angle. On the larger scales, the keel is less distinct and branches into a pair of parallel ridges (Woodward, 1907; Brito and Richther, n press). *«Belonostomus» carinatus* represents the oldest species of this family and is a member of the rift system paleofauna.

7. Conclusion

The material described here represents the first occurrence of Obaichthyidae in the Lower Cretaceous Codó Formation of the Parnaíba Basin.

Despite the differences in age, the Codó Formation (Aptian) specimens possess a suite of characters sufficient to identify them as *Dentilepisosteus laevis*, as species known previously only from the Santana Formation (Albian), of the Araripe Basin. This discovery therefore extends by approximately 10 myr the temporal range of this species to the Aptian.

Obaichthyid gars appear to have an exclusively western Gondwanan distribution, and a temporal distribution from the ?late Hauterivian to the Albian/Cenomanian.

The material described here represents the first occurrence of an Obaichthyidae in the Codó Formation of the Parnaíba Basin.

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