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Ichthyofauna from the Codó Formation, Lower Cretaceous (Aptian, Parnaíba Basin), Northeastern Brazil and their paleobiogeographical and paleoecological significance

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ABSTRACT

Although fossils from the Codó Formation have been known for over seventy years, their abundance and biotic diversity have only recently become better understood. Numerous specimens of fossil fishes have been collected at new localities in Brejo municipality, Northeastern Brazil, and are interpreted here in the light of evidence for an epicontinental seaway extending from the Equatorial Atlantic (Tethys Ocean). Similarities are noted among fossil fish assemblages from the Codó, Santana and Riachuelo formations, which suggests connections (perhaps intermittent) between the Parnaíba, Araripe and Sergipe-Alagoas basins during the Early Cretaceous (Aptian–Albian). Paleoecological observations suggest that the Codó Formation formed under a restricted lacustrine environment with little marine influence.

1. Introduction

The breakup of South America and Africa during the Early Cretaceous was an important event, leading to the progressive development of the Equatorial and South Atlantic oceans, along with the establishment of lacustrine environments in the continental interior of South America. This in turn permitted the evolution of a diversified and somewhat endemic ichthyofauna. Although fishes were widely distributed across Northeastern Brazil during the Aptian–Albian, until now the ichthyofaunas of the Santana Formation of the Araripe Basin have received most attention, due to their *Fossil-Lagerstätten* status. Distribution patterns of the fishes from western Gondwana during the Early Cretaceous are still poorly known, although they were apparently affected by the emplacement of an epicontinental seaway coming from the Tethys Ocean and extending across the interior of NE Brazil (Maisey, 2000, 2011; Arai, 2009, 2014).

Previously, the distribution of Cretaceous fossil fishes from Northeastern Brazil has been interpreted paleobiogeographically, especially between the Araripe (Santana Formation), Parnaíba (Codó Formation), Recôncavo and Tucano (Marfim and Marizal formations, respectively) basins and the Atlantic coastal basins of Sergipe-Alagoas (Riachuelo and Muribeca formations) and Paraíba-Pernambuco (Cabo Formation) (Silva Santos, 1990a, 1990b, 1990c, 1991a, 1991b; Maisey, 2000; Santos and Carvalho, 2009). Additionally, stratigraphic correlations between Aptian–Albian nearshore and epicontinental marine and transitional deposits have been extended to include parts of Venezuela, Colombia, Mexico, Australia, West Africa and even Antarctica (Moody and Maisey, 1994; Schultze and Stöhr, 1996; Maisey, 2000; Maisey and Moody, 2001).

There have been few previous studies of fossil fishes from the Codó Formation of Northeastern Brazil, although many taxa have been recorded. Silva Santos (1994a) recognized eleven species of fishes from the Codó Formation: *Araripelepidotes temnurus*, *Vinctifer comptoni*, *Calamopleurus cylindricus*, *Cladocyclus gardneri*, *Brannerion latum*, *Rhacolepis buccalis*, *Tharrhias araripis*, *Dastilbe elongatus* (= *Dastilbe crandalli*), *Santanichthys diasii*, *Codoichthys carnavalii*, and *Axelrodichthys araripensis*. Several of these taxa occur also in the Santana and Riachuelo formations, although the clupeid *C. carnavalii* is still known only from the Codó Formation (Silva Santos, 1994a; Santos and Carvalho, 2009). Additionally, a new species of mawsoniid, *Axelrodichthys maiseyi*, was recently described from concretions in shales and limestones on the margin of the Itapecuru River, between Codó and Timbiras cities (Carvalho et al., 2013). In Brejo municipality of Northeastern Maranhão,

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Abbreviations: Ar2, posterior articular element; Bop, branchiopercle; Br, branchiostegals; Cl, cleithrum; D, dentary; Dpt, dermopterotic; Dsp, dermosphenotic; Ep, epurals; Es, extrascapular; Fr, frontal; G, gular; H, hyomandibular; Hpx, hypaxial fin rays of caudal fin; Hsap, anterior process of haemal arch or spine; Hyp, hypural; Io, infraorbital; Ioc, infraorbital channel; Iop, interopercular; Mpt, metapterygoid; Mx, maxilla; Na, nasal; Npu, preural neural arch; Op, opercular; Pa, parietal; Phy, parhypural; Pmx, premaxilla; Pop, preopercle; Ptt, posttemporal; Pu, preural centrum; Q, quadrate; Rar, retroarticular bone; Smx, supramaxilla; So, suborbital; Sop, subopercle; Sts, scutes; Stt, supratemporal; Su, supraorbital bones; T, jaw teeth; U, ural centrum; Un, uroneural.

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the Faveirinha and Perneta outcrops (Fig. 1) have provided numerous specimens of fishes in massive, laminated and concretionary limestones (Lindoso et al., 2011, 2013a).

In this paper, we describe fossil fishes of the Codó Formation from new fossiliferous localities in Maranhão State and evaluate their paleobiogeographical and paleoecological significance. Although the route of the hypothesized marine ingression is still somewhat conjectural, the Codó Formation may be one of the earliest lithostratigraphic units in NE Brazil affected by the Tethyan seaway during the Early Cretaceous (Arai, 2014).

2. Geological setting

The Parnaíba basin is located in Northeastern Brazil, occupying a large area extending across the states of Maranhão, Piauí and part of Tocantins, Pará and Ceará, with a total preserved area of 600,000 km^2 (its original margins probably extended even farther). In geological terms, it is a reactivated Paleozoic basin (Campbell, 1949; Mesner and Wooldridge, 1964) containing a Mesozoic sedimentary sequence that includes the Codó Formation. This unit was first recognized by Lisboa (1914), who described bituminous shales associated with carbonates in the Codó region of Maranhão. The maximum thickness of the unit is approximately 180 m.

According to Carneiro (1974) and Rezende (2002), the Corda, Grajaú and Codó formations are interfingered and chronostratigraphically equivalent. The Corda Formation consists of reddish-brown, very fine, semi-friable and semi-cohesive sandstones. The Grajaú Formation consists of whitish-pale-beige medium/coarse sandstones and conglomerates. The Codó Formation is overlain by the Itapecuru Formation (middle Albian to Late Cretaceous), which is composed of fine, friable sandstones and pelites (Vaz et al., 2007).

Outcrops of the Codó Formation are limited and discontinuous, appearing in river channels that drain the central basin at the confluence of the Tocantins and Araguaia rivers, in Brejo city and Codó (Santos and Carvalho, 2009). The Formation is thought to be of Aptian/Albian age (Lima, 1982), and supposedly formed in an arid to semiarid climate regime (Rossetti et al., 2001).

According to Lima and Leite (1978), deposition of the Codó Formation occurred under marine and brackish lacustrine conditions. Stratigraphic and facies analyses in the vicinity of Codó by Rossetti et al. (2001) indicated three successive lacustrine depositional environments: (1) central lake; (2) transitional lake; and (3) marginal lake. In a palynostratigraphic study, Antonioli (2001) and Antonioli and Arai (2002) also recognized a three-fold lithostratigraphic division of this sequence, but suggested that it was not entirely lacustrine in origin. Instead, they identified a lower sequence, with an incipient marine character, a middle part (essentially evaporitic), and an upper sequence, again with a marine character. The presence of isopods in limestones of the Codó Formation also suggests a lacustrine/marine paleoenvironment (Lindoso et al., 2013b).

3. Material and methods

The specimens described here were collected between 2008 and 2014 during fieldwork at outcrops near Brejo city, in Northeastern Maranhão. Besides fishes, numerous other fossils were collected, including plants, gastropods and crustaceans.

The fossil fishes are housed at the Universidade Federal do Rio de Janeiro (UFRJ, Department of Geology) and Centro de Pesquisa de História Natural e Arqueologia do Maranhão (CPHNAMA, Division of Paleontology) as UFRJ-DG 845P, UFRJ-DG 827P, UFRJ-DG 825P, UFRJ-DG 840P, UFRJ-DG 828P, UFRJ-DG 812P, UFRJ-DG 870P, UFRJ-DG 834P and CPHNAMA-VT 1241, CPHNAMA-VT 1242.

The material was compared with specimens from the Santana Formation, housed at the American Museum of Natural History (AMNH) in New York, USA, as well as with other specimens from the Codó Formation housed at the Departamento Nacional de Produção Mineral (DNPM) in Rio de Janeiro, Brazil.

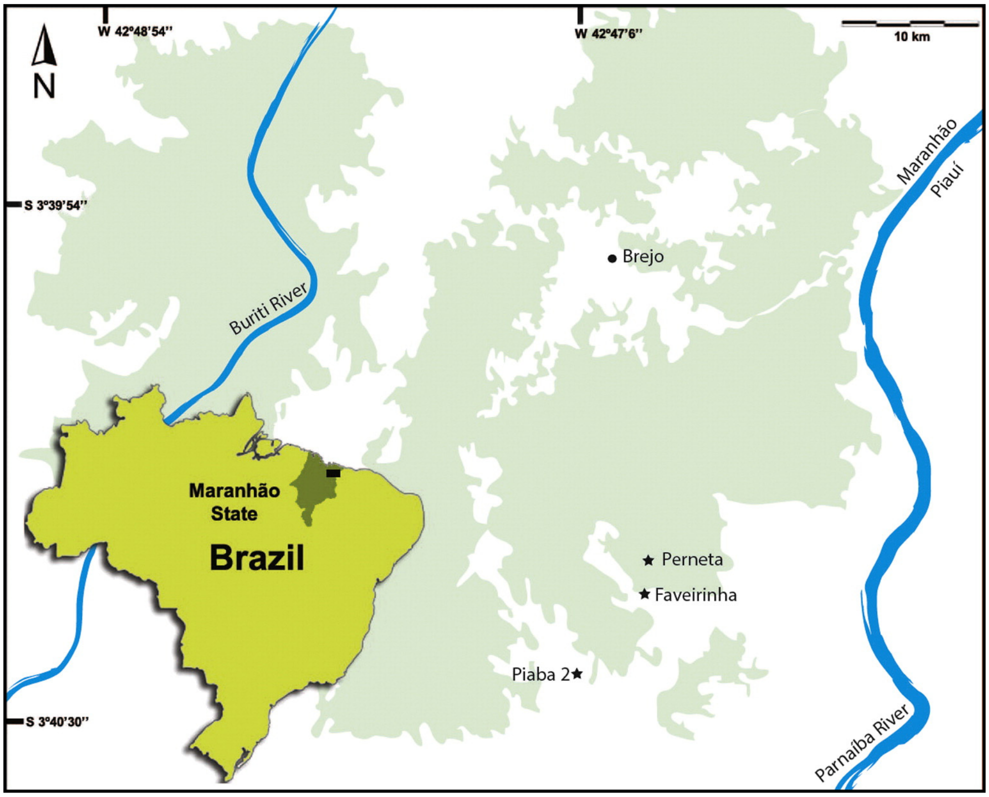

Fig. 1. Location of the main fossiliferous outcrops in Brejo municipality (black stars), Northeastern Maranhão State, Brazil.

4. Systematic palaeontology

Neopterygii Regan, 1923
Holostei Müller, 1844 (sensu Grande, 2010)
Semionotiformes Arambourg and Bertin, 1958
Semionotidae Woodward, 1890 (sensu Olsen and McCune, 1991)
Genus *Araripelepidotes* Silva Santos, 1990a
Type species *Araripelepidotes temnurus* Agassiz, 1841

Material—UFRJ-DG 845P is an almost complete specimen in a carbonate concretion, seen in right lateral view. Most of the skull, trunk and tail are preserved. UFRJ-DG 827P is an incomplete specimen in a carbonate concretion, preserved in left lateral view; most of the skull and trunk (including tail) is missing. UFRJ-DG 838P is an incomplete specimen in carbonate concretion in right lateral view; only the posterior part of the skull and the anterior half of the trunk are preserved.

Locality—Faveirinha Quarry and Perneta Ranch, Brejo City, Maranhão State.

Description—UFRJ-DG 845P (Fig. 2) is 215 mm standard length (SL) missing the nasal and jaws. The circum-orbital series is complete, with seven infraorbitals and two supraorbitals. The fifth infraorbital is well developed and extends from the orbit to the ventral lobe of the preoperculum (a characteristic feature of this genus; Maisey, 1991). Three suborbitals are aligned vertically and limited dorsally by the dermopterotic–dermosphenotic and ventrally by the fifth infraorbital. The antorbital is partially preserved. The ventral lobe of the preoperculum extends obliquely forward below the level of the orbit; the preoperculum is slightly inclined anteriorly. The opercular series is incomplete, and the cleithrum and supracleithrum are not distinguishable. The interopercular is poorly preserved, but is apparently elongated anteriorly. The preserved parts of the skull roof include the frontal, parietal and supratemporal-postemporal; the dermopterotic is separated from the frontal by the dermosphenotic (another characteristic feature of the genus). Fringing fulcral scales are present in all the preserved fins (the pelvic fin is missing) and are especially well developed in the dorsal fins. Dorsal and anal fins are situated on the posterior half of the body; the beginning of the anal is located immediately behind the end of the dorsal. The pectoral fin includes at least nine rays, the anal has ten rays, the dorsal has nine, and the caudal fin has thirteen; this latter homocerca. Absence of hunchback elevation and presence of isometric ganoid scales.

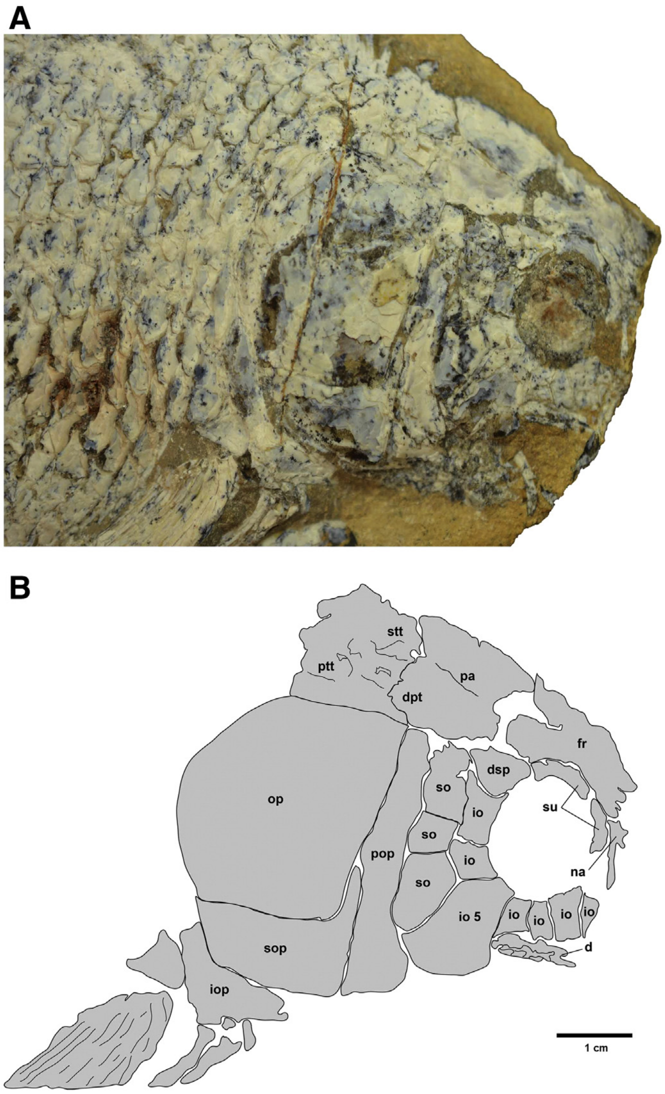

Fig. 2. *Araripelepidotes temnurus*, UFRJ-DG 845P. A) photograph of the skull in right lateral view; B) anatomical interpretations.

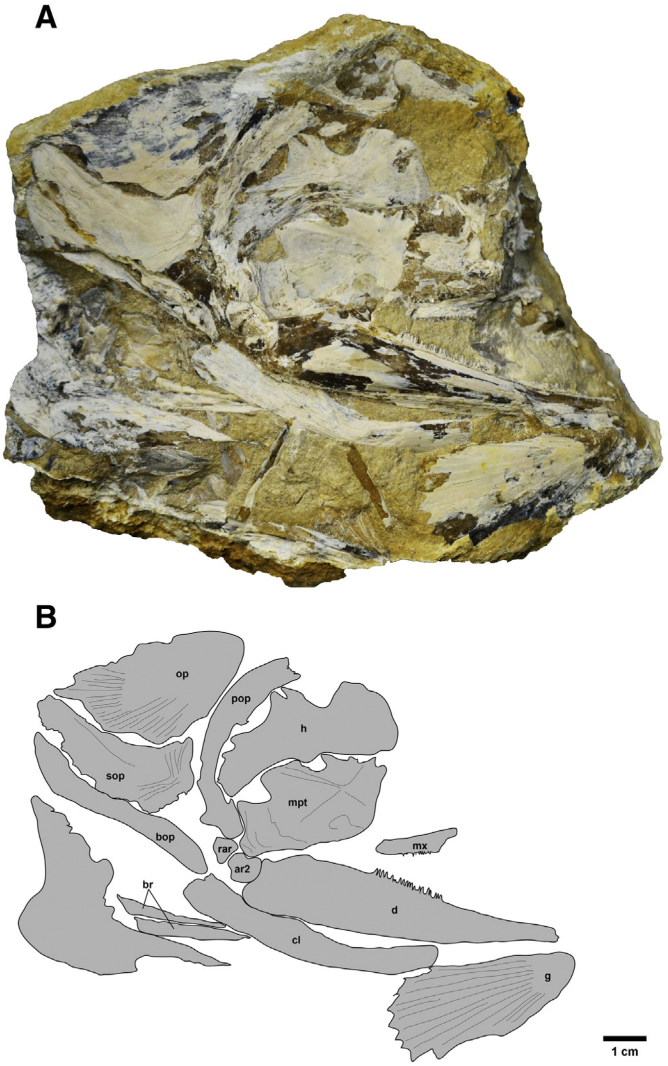

Fig. 3. *Calamopleurus cylindricus*, UFRJ DG-832P. A) photograph of the skull in right lateral view; B) anatomical interpretations.

This taxon was first described from the Santana Formation as *Lepidotes temnurus* (Agassiz, 1841), but was later placed in a new genus *Araripelepidotes* by Silva Santos (1990a). It is a relatively abundant taxon in carbonate concretions from the Romualdo Member, but is rare in laminated limestones of the Crato Member (Maisey, 1991; Brito et al., 1998; Gallo and Brito, 2004). *Araripelepidotes* differs from *Lepidotes* and other semionotiforms in having a well developed fifth

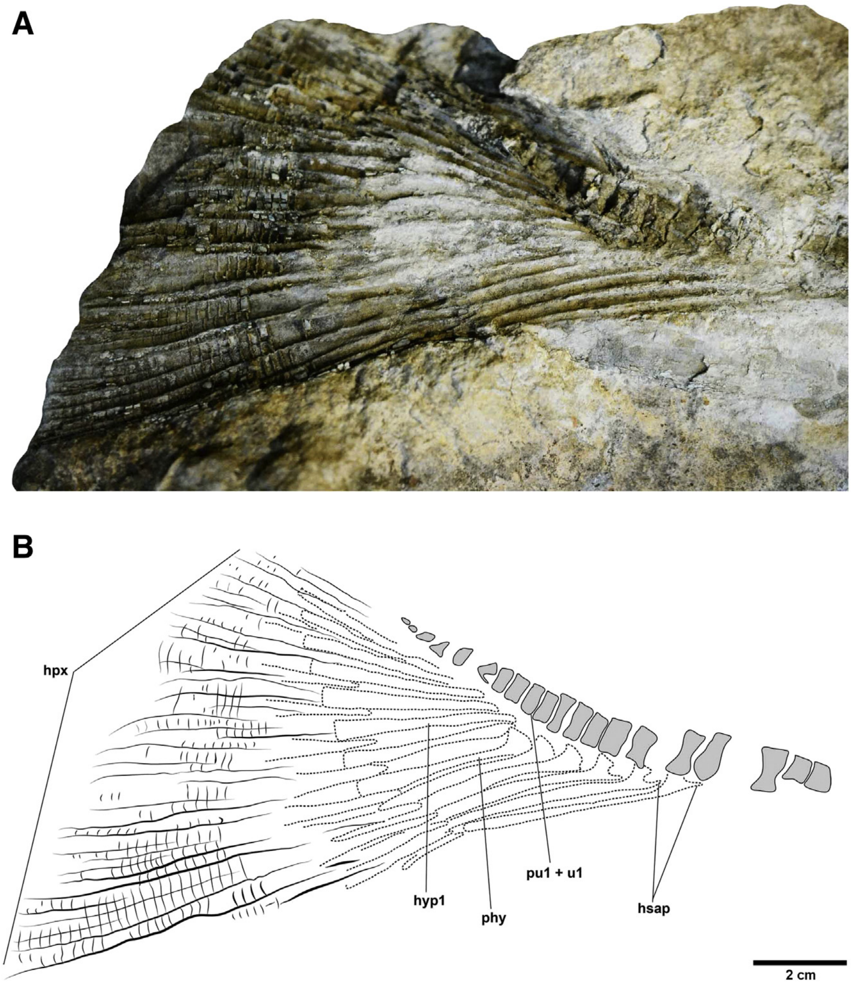

Fig. 4. *Calamopleurus cylindricus*, UFRJ DG-1504P. A) photograph of the tail; B) anatomical interpretations.

infraorbital which contacts the preopercle, a comparatively short skull, unornamented dermal bones, separation of the dermopterotic and frontal by the dermosphenotic, and absence of a predorsal elevation (Maisey, 1991; Brito et al., 1998; Gallo and Brito, 2004; Brito, 2007). Another diagnostic feature of *A. temnurus* is the weak and edentulous lower jaw (Thies, 1996), although this feature could not be observed in the Codó specimens. We attribute the lack of the lower jaw in UFRJ DG-845P to taphonomic factors such as disarticulation prior to burial. The state of preservation of the specimens UFRJ DG-827P and UFRJ DG-838P shows that they were buried in an almost complete condition, with only the anterior portion of the skull missing in UFRJ DG-838P.

Halecomorphi Cope, 1872 (sensu Grande and Bemis, 1998)
Amiidae Bonaparte, 1837
Vidalamiinae Grande and Bemis, 1998
Genus *Calamopleurus* Agassiz, 1841
Type species *Calamopleurus cylindricus* Agassiz, 1841
Figs. 3, 4 and 5

Material—UFRJ DG-832P, incomplete skull preserved approx. 155 mm long, seen from the right side, in a limestone concretion. UFRJ DG-1504P, impression of the distal portion of the trunk approx. 320 mm long, including the caudal fin in massive limestone. UFRJ DG-1524-P, incomplete skull dorsoventrally preserved in limestone concretion.

Locality—Perneta Ranch and Piaba 2, Brejo City, Maranhão State.

Description—In UFRJ DG-832P (Fig. 3), the dentary is large and supports a robust row of caniniform teeth that have an acrodine cap with sharpened margins. The most anterior teeth in the jaw are taller than those farther posteriorly. The gular plate is fan-shaped, with its posterior margin terminating in several pointed serrations. The opercle is incomplete and its surface has been largely obliterated. The anterior portion of the subopercle is ornamented with striated and irregular grooves. The preopercle is also mostly obliterated, and partly covers the hyomandibula.

In UFRJ DG-1504P (Fig. 4), some vertebrae and part of the caudal fin skeleton are preserved. Traces of the anal fin are also visible, and the caudal fin is homocercal, with a slightly convex margin. Impressions of the caudal fin rays suggest that 8 hypurals, 2 or 3 epurals and 12–13 hypaxial rays were originally present. There are 33 preural caudal centra. UFRJ DG-1524-P (Fig. 5) exhibits part of the skull roof including frontals, parietals, dermosphenotic, dermopterotic, supraorbitals and left extrascapular. The extrascapular is incomplete and shows a subtriangular shape. Left parietal longer than right parietal. Frontal long and sutured to each other through a midline, pattern of striation and roughness suggests the frontal and other bones of the skull roof were quite ornate. Supraorbitals longer than dermosphenotic, dermopterotic length reaching all length of the parietal and posterior part of the frontal. Premaxilla with strong dorsal process and large olfactory foramina. 5 to 6 robust premaxillars teeth. Presence of a low and subtriangular supramaxilla. Opercular series incomplete. Teeth strong with acrodine cap on apex.

UFRJ DG-1504P (Fig. 4) differs from *Calamopleurus mawsoni* in having 33 instead of 39 preural caudal centra. It also agrees with

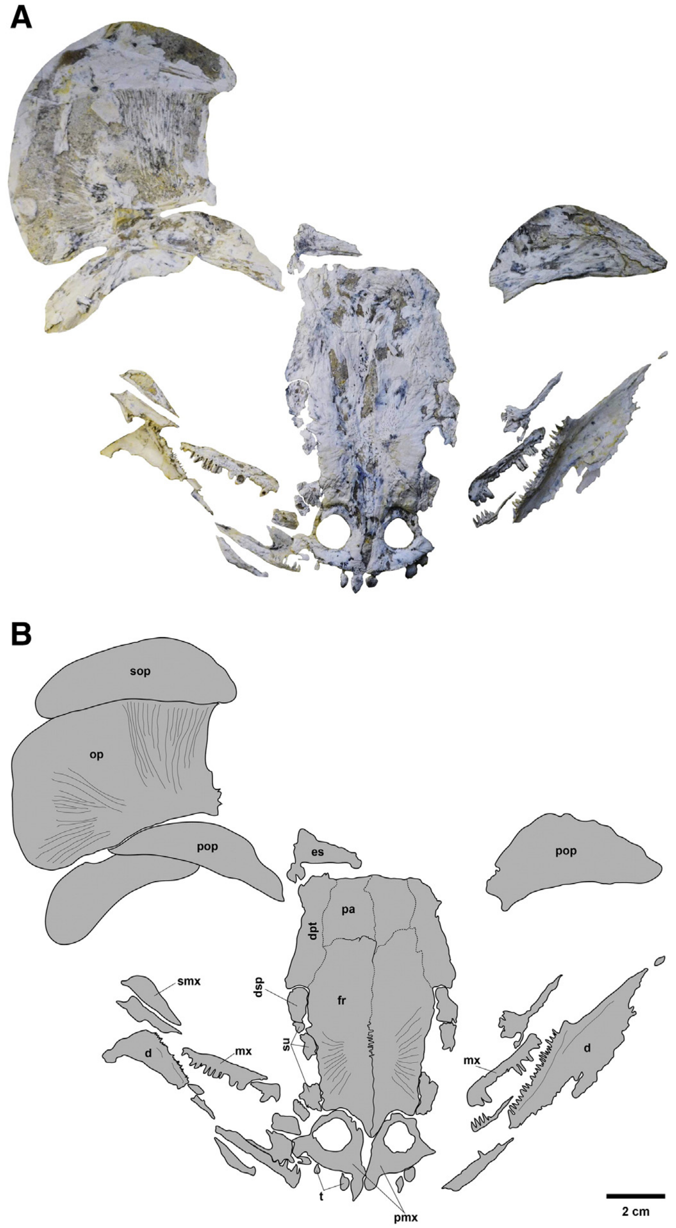

Fig. 5. *Calamopleurus cylindricus*, UFRJ DG-1524-P. A) photograph of the skull in dorsal view; B) anatomical interpretations.

C. cylindricus and differs from *C. africanus* in the proportions of the frontals, supramaxilla and gular (Forey and Grande, 1998).

Teleostei *sensu* Patterson and Rosen, 1977
Ostariophysi *sensu* Rosen and Greenwood, 1970
Otophysi *sensu* Rosen and Greenwood, 1970
Characiphysi Fink and Fink, 1981
Characiformes *sensu* Fink and Fink, 1981
Genus *Santanichthys* Silva Santos, 1995
Type species *Leptolepis diasii* Silva Santos, 1958
Santanichthys diasii Silva Santos, 1995
Fig. 6

Material—UFRJ-DG 1482-P, specimen measuring 29 mm standard length (SL), partially preserved in laminated limestone (skull, most of the trunk and part of the caudal fin).

Locality—Perneta Ranch, Brejo City, Maranhão State.

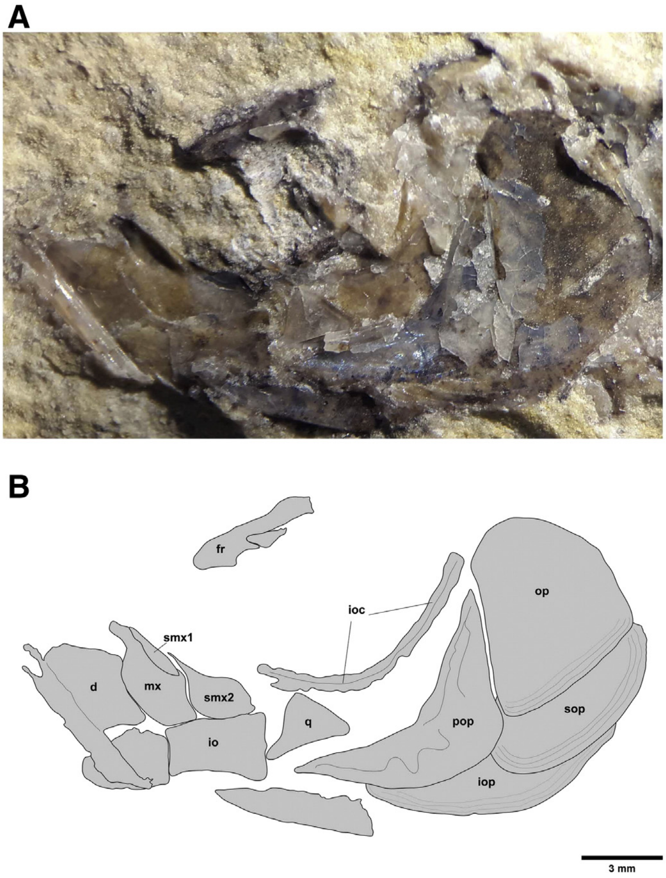

Fig. 6. *Santanichthys diasii*, UFRJ-DG 1482-P. A) photograph of the skull in left lateral view; B) anatomical interpretations.

Description—In this specimen (Fig. 6), the head is 10 mm long (one third of the total body length). Two supramaxillae are present; the first is elongated and narrow, the second is large and elliptical. The dentary is edentulous. Four infraorbitals are preserved; infraorbital 2 has a diamond shape and infraorbital 3 is subtriangular. The operculum is trapezoidal with its lower half ornamented by striae rising toward the border; the same ornament pattern is present on the suboperculum. The preoperculum is semilunar, with a long sensory canal which branches postero-inferiorly. The interoperculum is strongly ornamented with thin grooves extending up beyond the inferior border of the suboperculum. Cycloid scales are also present, ornamented with concentric striae.

S. diasii was originally described as *Leptolepis diasii* (Silva Santos, 1958). Later, Silva Santos (1991b) erected the genus *Santanichthys* for *L. diasii* based on the presence of a fronto-occipital fontanelle and epipleurals in the middle region of the thorax. *Santanichthys* was redescribed by Filleul and Maisey (2004), who concluded that it represents the earliest known otophysan and perhaps the earliest characiform. UFRJ DG-1482-P (Fig. 6) is referred to *S. diasii* here, based on the following similarities: gape of mouth very inclined; presence of two supramaxilla (the first one long and narrow; the second one large and elliptical); dentary apparently toothless; opercle trapezoidal; presence of some striae on inferior border of the opercle and subopercle; preopercle semilunar with preopercular canal posteriorly sends off striated postero-inferior border; absence of abdominal scutes. Most of the caudal elements of specimen UFRJ DG-1482-P are not preserved, which preclude effective comparisons with others otophysans (e.g. *Leptoleis bahiaensis*, Grupo Ilha, Reconcavo Basin).

Clupeomorpha (Division 2)
Order Incertae Sedis.
Family Incertae Sedis.
Genus *Codoichthys* Silva Santos, 1994a
Type species *Codoichthys carnavalii* Silva Santos, 1994a
Figs. 7 and 8

Material—UFRJ DG-1166P, incomplete specimen measuring 50 mm standard length (SL) preserved in massive limestone.

Location—Quarry Faveirinha, Brejo City, Maranhão State.

Description—The body is fusiform, with dorsal and ventral scutes. Dorsal scutes are smooth, located between the posterior margin of the skull and the anterior border of the dorsal fin, becoming progressively larger toward the latter. The dorsal scutes are supported by pre-dorsal bones. Ventral scutes are broad and extend from the posterior margin of the skull to the origin of the anal fin. These scutes increase progressively in size toward the pelvic fin and decrease toward the anterior border of the anal fin. The pelvic fin is opposite the dorsal and the pectoral fin is located lateroventrally. The dorsal fin contains 16 rays and the anal 12 rays, but the pectoral and pelvic fins are incomplete. The ventral outline of the body is moderately convex. Much of the cranial skeleton has been obliterated. Only the posterior margin of the opercle and part of the dentary are preserved, the latter exhibiting a slight convexity. There are between 34 and 36 vertebrae. The caudal skeleton is incomplete, with only ural centra 1 and 2 no hypurals preserved. The proximal region of the parhypural is well developed and fused to the centrum of the first pre-ural. The first uroneural is fused to neural of the first pre-ural.

UFRJ DG-1166P (Figs. 7 and 8) differs from *Santanaclupea silvasantosi* in having both dorsal and ventral scutes. The pelvic fin is located opposite the dorsal; the dorsal fin has 16 rays and the anal fin has 12 rays; the anal fin has a convex, rounded outline ventrally. In the caudal skeleton, the neural spine of the first pre-ural is well developed. Additionally, *S. silvasantosi* shows two supramaxilla (unlike the single supramaxilla present in *C. carnavalii* [Silva Santos, 1994a]).

UFRJ DG-1166P resembles *Ellimma branneri* (a basal clupeomorph from the Aptian Muribeca Formation, Sergipe-Alagoas Basin, in having a rounded ventral outline of the body and both dorsal and abdominal scutes (Chang and Maisey, 2003) (Fig. 8). However, the abdominal scutes in *E. branneri* are attached to a series of plates arranged laterally (Chang and Maisey, 2003: Fig. 2). Although the dorsal scutes in UFRJ DG-1166P are not well preserved, they seem to lack a median keel and ornament, which are present in *E. branneri* (Chang and Maisey, 2003: Fig. 7A, B).

Ellimma cruzi occurs in micaceous shales of the Cabo Formation (Aptian), Pernambuco, where it is associated with the gonorhynchiform *D. crandalli* (Silva Santos, 1990c). *E. cruzi* differs of UFRJ DG-1166P in having a more convex ventral margin; the pelvic fin is smaller than the pectoral; the maximum convexity is located in the ventral border of the body; the distance between the pelvic and the base of the ventral lobe of the caudal fin is shorter than in *C. carnavalii*; the dorsal outline is also more rounded in *E. cruzi*, although not as much as the ventral margin; the dorsal fin located exactly in the middle of the distance between the tip of the snout and the base of the caudal fin; and the dorsal surface of its scutes are heavily ornamented (Silva Santos, 1990c). In UFRJ DG-1166P, the dorsal fin is located along the posterior half of the body between the tip of the snout and the base of the caudal lobe, the dorsal outline of the body is straight, and its dorsal scutes are unornamented.

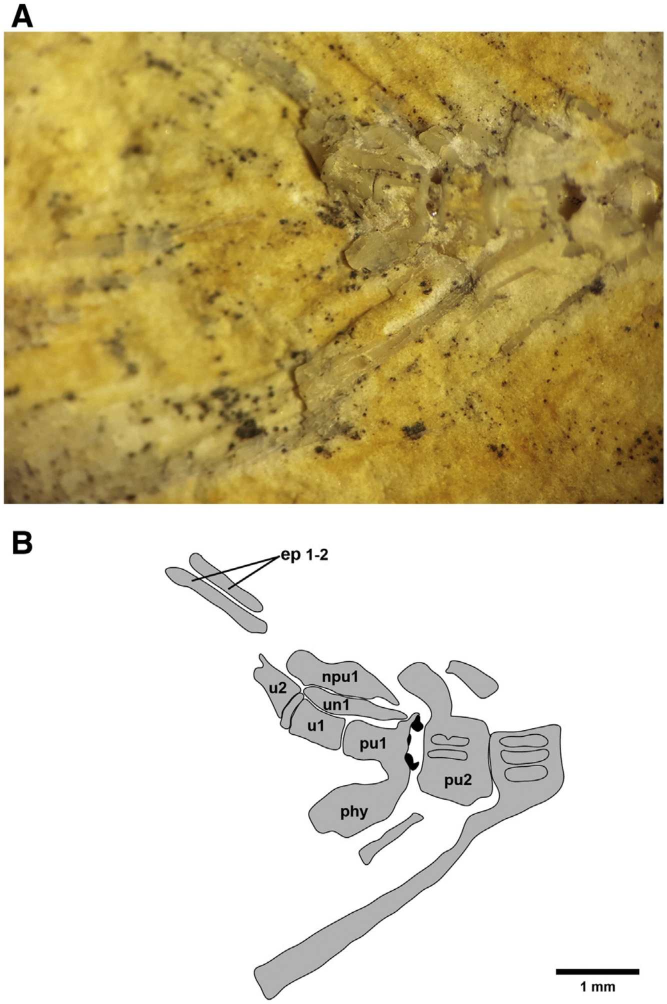

Fig. 7. *Codoichthys carnavalii*, UFRJ DG-1166P. A) photograph of the tail region; B) anatomical interpretations.

5. Discussion

There are numerous Early Cretaceous fossil fish occurrences across north-eastern Brazil (Maisey, 2000), but only some have received much attention (e.g., in the Araripe, Recôncavo, Sergipe and Alagoas basins). Previously, fossil fishes from the Codó Formation were known from only a few localities in eastern and northern Maranhão State (Table 1). Silva Santos (1994a) listed eleven species, ten of which were described already from elsewhere (mainly from the Santana Formation of the Araripe Basin), plus a clupeomorph, *C. carnavalii*. Carvalho et al. (2013) described a new species of mawsonid (*A. maiseyi*) from an outcrop in the margin of the Itapecuru River, between the cities of Timbiras and Codó, east Maranhão. Duarte and Silva Santos (1993) described specimens of *D. elongatus* (= *D. crandalli*) associated with dicotyledonous plant remains from Umburanas. *A. temnurus* (a distinctive semionotid in the Santana Formation) was reported from the Codó Formation (Silva Santos, 1994a), although no specimens were described or illustrated until now.

The Cretaceous fossil fishes of the Parnaíba Basin thus include a large number of taxa that also occur in the Araripe Basin to the south-east. Several of these shared taxa are extremely abundant in Araripe, so it is perhaps not surprising that some should also occur in the Codó Formation. However, despite the relatively low number of specimens so far collected (no more than a few hundred, compared with tens of thousands from Araripe), these Codó samples include taxa that are rare in Araripe (e.g., gars, coelacanths). Moreover, some of the most abundant taxa from Araripe (e.g., *Vinctifer*, *Rhacolepis*) are represented by relatively few specimens from the Codó Formation. The abundance of *S. diasii* in the Codó Formation may be underestimated due to its superficial resemblance to juvenile specimens of *D. crandalli*, which is also very abundant in limestone exposures at Faveirinha and Perneta. The co-occurrence of *Dastilbe* with many other fishes in the Codó Formation contrasts with the situation in the Araripe Basin, where this taxon is abundant only in the Crato Member, where it dominates the fish assemblage. As at Araripe, clupeomorphs are rare in the Codó Formation; so far, *C. carnavalii* is the only one documented (Silva Santos, 1994a). However, recent collecting at the Perneta Ranch locality produced what may be a second species of clupeomorph. The only clupeomorph thus far

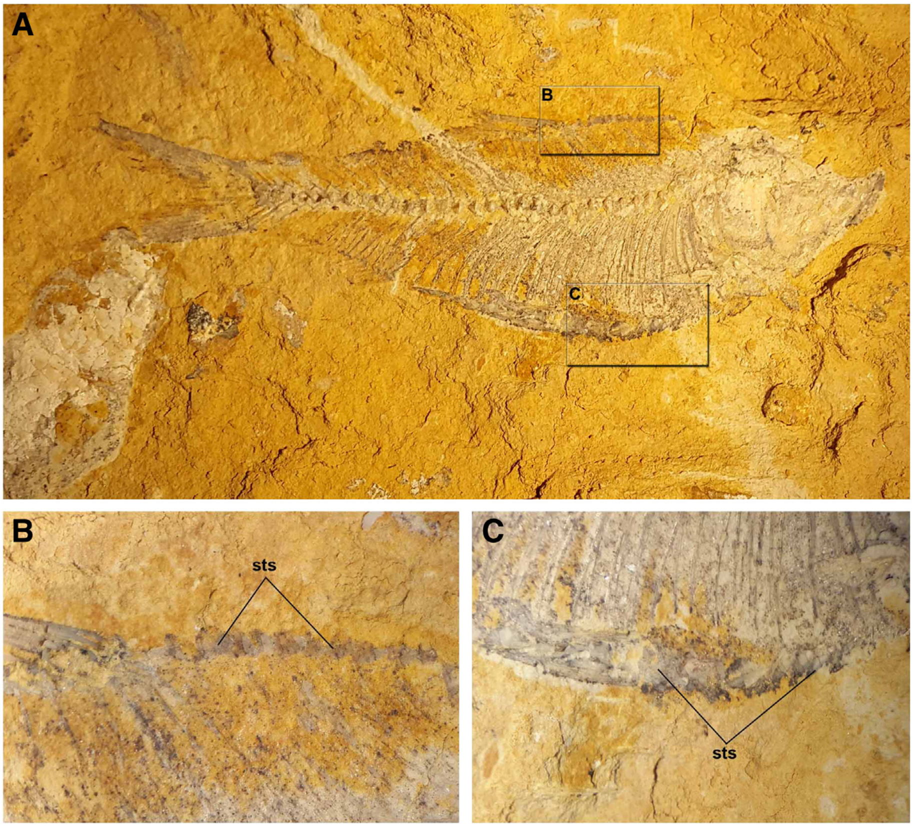

Fig. 8. *Codoichthys carnavalii*, UFRJ DG-1166P. A) photograph of the entire specimen; B) detail of the dorsal scutes; C) detail of the ventral scutes.

described from the Santana Formation is *S. silvasantosi* which is apparently restricted to concretions, shales and marls of the Romualdo Member.

Some of the taxa listed by Silva Santos (1994a), from Umburanas Quarry in Brejo, have not yet been recognized at Faveirinha or Perneta (e.g. *C. gardneri*, *R. buccalis*, *B. latum*, *T. araripis*, *T. rochae*). It is unclear whether this represents a 'real' absence or is simply due to insufficient sampling. The generally poor preservation of many fossil fishes from the Codó localities makes them less than ideal for systematic study and identification; for example, numerous specimens of small fishes have been referred to *D. crandalli* from limestones of open pit mines in Brejo municipality, largely on the basis of meristic features (e.g. fin ray counts) rather than definitive morphological features.

5.1. Paleobiogeography

The distribution of Early Cretaceous fossil fishes is particularly difficult to interpret in the Brazilian Northeastern Marginal and Interior Basins (BNMIBs) of western Gondwana, because they were affected by a history of complex, syn- and post-depositional tectonic events, related to continental separation that began in the Late Jurassic (Kimmeridgian–Tithonian). These unfolding tectonic events may have presented numerous opportunities for local speciation (Arai, 1995, 1999, 2009, 2014; Maisey, 2000, 2011).

Numerous authors have attempted to recognize biogeographic patterns among fossil fishes within the syn- and post-rift deposits of this region (Silva Santos, 1963, 1994a, 1994b; Maisey, 1991, 2000, 2011;

Table 1
Fossil fishes from the Codó Formation.

Araripelepidotes temnurus	Umburanas, Brejo City, Maranhão State	Silva Santos (1994a)
Calamopleurus cylindricus	Umburanas, Brejo City, Maranhão State	Silva Santos (1994a)
Santanichthys diasii	Umburanas, Brejo City/Pedrinha, Barra do Corda City, Maranhão State	Silva Santos (1994a)
Codoichthys carnavalii	Umburanas, Brejo City, Maranhão State	Silva Santos (1994a)
Brannerion latum	Umburanas, Brejo City, Maranhão State	Silva Santos (1994a)
Tharrhias araripis	Umburanas, Brejo City/Curador Village, Codó City/Barra do Corda City, Maranhão State	Silva Santos (1994a)
Tharrhias rochae	Umburanas, Brejo City/Curador Village, Codó City/Barra do Corda City, Maranhão State	Silva Santos (1994a)
Vinctifer comptoni	Curador Village, Codó City/Barra do Corda City, Maranhão State	Campbell (1949); Silva Santos (1994a)
Cladocyclus gardneri	Umburanas, Brejo City, Maranhão State	Silva Santos (1994a)
Dastilbe crandalli	Umburanas, Brejo City/Uchoa and bank of the Mearim River, Barra do Corda City/Curador Village, Codó City, Maranhão State	Duarte and Silva Santos (1993); Silva Santos (1994a)
Rhacolepis buccalis	Livramento, Codó City, Maranhão State	Silva Santos (1994a)
Axelrodichthys maiseyi	right bank of the Itapecuru River, near the cities of Codó and Timbiras, Maranhão State	Carvalho et al. (2013)
Dentilepisosteus laevis	Perneta Ranch, Brejo City, Maranhão State	Brito et al. (2016)

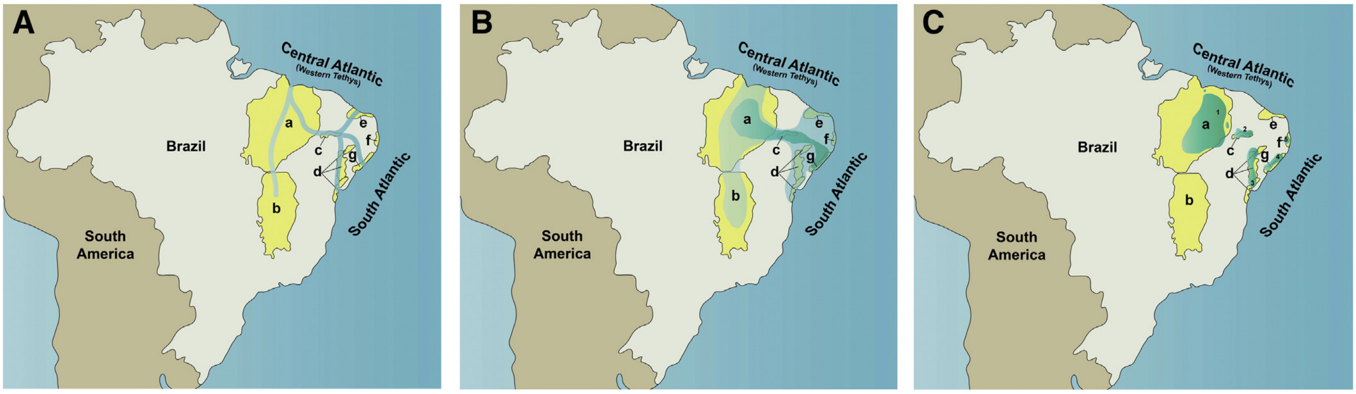

Fig. 9. Main paleogeographic and paleobiogeographic scenarios discussed on text. A) Possible routes of entrance of the epicontinental seaway (Tethys Sea) in the BNMIBs according Silva Santos (1991a); Martill (1993) and Arai (2014); B) distribution of fossil fishes in the BNMIBs showing a greater similarity among Codó, Santana and Riachuelo formations (a, c, g; dark green region) than others BNMIBs (b, e, f, d; light green region); C) posterior moment of supposed vicariance, speciation and dispersal of fossil fishes related to the precarious connection of some BNMIBs (e.g. clupeomorfs in 1–5). Sedimentary basins shown on map: a—Parnaíba, b—Sanfranciscana, c—Araripe, d—Recôncavo-Tucano-Jatobá, e—Potiguar, f—Paraíba-Pernambuco, g—Sergipe-Alagoas. Lithostratigraphic units shown on map: 1—Codó Formation, 2—Santana Formation, 3—Marfim Formation, 4—Muribeca Formation, 5—Cabo Formation.

Duarte and Silva Santos, 1993; Martill, 1993; Forey and Grande, 1998; Grande and Bemis, 1998; Malabarba et al., 2002; Gallo and Brito, 2004; Brito, 2006; Brito and Amaral, 2008; Santos and Carvalho, 2009; Gallo and Figueiredo, 2012; Carvalho et al., 2013; Lindoso et al., 2013a). Brito (1984) attempted to correlate various interior and marginal basins using the aspidorhynchiform *Vinctifer* (which he considered a biozone marker). However, the genus is not well constrained stratigraphically (Martill, 1988; Maisey, 1991). *Vinctifer*, along with several other fishes in the Santana Formation of the Araripe Basin, is closely related to taxa from western Tethyan marine deposits elsewhere; for example in Venezuela (e.g. *Vinctifer* cf. *comptoni*, *Rhacolepis*, *Araripichthys axelrodi*), Colombia (e.g. *Rhacolepis*, *Vinctifer*, *Notelops*), and Mexico (*Rhacolepis*, *Vinctifer*, *Notelops*, *Paraelops*, *Cladocyclus*, *Ellimichthys*, *Axelrodichthys*) (Maisey, 2000).

It has long been suspected that an ephemeral equatorial seaway extended across north-eastern Brazil during part of the Early Cretaceous, but opinions have differed over its extent and direction of propagation. Silva Santos (1991a) suggested that a marine ingression began on the eastern coast of the South Atlantic (Sergipe-Alagoas Basin; Muribeca and Riachuelo formations, respectively) and then spread northward, passing through the Reconcavo-Tucano basins (Marfim and Marizal formations, respectively), the Araripe Basin (Santana Formation) and then Parnaíba (Codó Formation). Martill (1993) advocated a short marine episode in the Araripe Basin, with possible ingressions extending from the Potiguar (Alagamar Formation), Parnaíba (Codó Formation) and the Reconcavo, Tucano and Jatobá complex. Newer paleontological evidence suggests a different hypothesis, with the seaway extending first from Caribbean Tethys into several Brazilian sedimentary basins (with the notable exception of the Pelotas Basin; Arai, 2014). According to this hypothesis, an Aptian marine ingression may have started in the São Luís Basin (Codó Formation) and subsequently extended into the Parnaíba, Araripe, Tucano and Sergipe basins (Arai, 2014; see Fig. 9A). The similarities between marine fossil assemblages recovered from these basins and those of the Tethyan Caribbean (e.g. dinoflagellates, equinoids, foraminifera, molluscs, crustaceans and fishes), along with the absence of marine sediments coeval with the Santana Formation in basins located between the Araripe and Potiguar basins, adds credence to this hypothesis (Arai, 2006, 2009, 2014; Maisey, 2000, 2011).

The fossil fishes of the Codó Formation are generally similar to those from the Araripe (Santana Formation), Tucano (Marizal Formation), Reconcavo (Marfim Formation), and Sergipe-Alagoas (Riachuelo and Muribeca formations) basins (Silva Santos, 1991b; Santos and Carvalho, 2009). There is nevertheless some evidence to suggest that resident fish populations may have been temporarily isolated from those of adjacent basins, providing opportunities for speciation (Tables 2 and 3). It is also possible that different lineages invaded various basins at various times, For example, different clupeomorph genera are present in the Codó (*C. carnavalii*); Santana (*S. silvasantosi*); Marfim (*Ellimmichthys longicostatus*), Muribeca (*E. branneri*) and Cabo formations (*E. cruzi*) (Fig. 9C). These forms are not closely related to each other (i.e., as sister taxa), suggesting that their distribution is most likely the result of independent and unrelated dispersals rather than vicariant isolation. However, other taxa (e.g., the amiiform *Calamopleurus*) is represented by different species in different basins, which may conceivably have arisen by vicariant isolation; *C. cylindricus* (the largest vertebrate found so far in the Codó Formation) is also well known from the Santana Formation in the Araripe Basin. Another species, *C. mawsoni*, occurs in the Ilhas Formation (Neocomian, Recôncavo Basin (Grande and Bemis, 1998; Maisey, 1991). In addition, *C. africanus* was described from the Cretaceous Kem Kem beds of southern Morocco (Forey and Grande, 1998).

Similarities noted here between the fossil fish assemblages of the Codó, Santana and Riachuelo formations may thus be related to a relatively prolonged period of continuous or intermittent connection between the Parnaíba, Araripe and Sergipe-Alagoas basins by a seaway (Fig. 9B), although the factors responsible for their distribution are far from clear.

5.2. Paleoecology

Sedimentological, geochemical and stratigraphic studies of the Codó Formation suggest a lacustrine environment with marine influence under arid to semi-arid conditions (Campbell, 1949; Mesner and Wooldridge, 1964; Lima, 1982; Aranha et al., 1990; Antonioli, 2001; Paz and Rossetti, 2001; Rossetti et al., 2001; Paz, 2005). The region now located in Codó municipality of eastern Maranhão was probably occupied by stable, well-stratified, saline lakes characterized by periodic closure and anoxia (Paz, 2005). In Brejo municipality, articulated specimens of fishes and crustaceans occur together on single bedding planes (Fig. 10), suggesting mass mortality events (Lindoso and Carvalho, 2014). These may have been triggered by episodic changes in salinity, temperature, or oxygen levels, and perhaps poisoning by algal blooms (Martill et al., 2008). Additionally, Paz and Rossetti (2001) suggested that such mass mortality events in the Codó lake may have resulted from sudden lowering of the lake level and subaerial exposure of its margins. Karstification structures (e.g. dolines) in the Brejo municipality point to a climate regime with alternating hot/arid and rainy conditions for the Codó Formation (Gonçalves et al., 2006; Lindoso and Carvalho, 2014).

Table 2
Distribution of fossil fishes in Brazilian Northeastern Marginal and Interior Basins (BNMIBs) during the Early Cretaceous (Aptian–Albian).

Species	Codó Fm. (Aptian)	Santana Fm. (Aptian/Albian)	Riachuelo Fm. (Albian)	Muribeca Fm. (Aptian)	Marizal Fm. (Aptian)	Marfim Fm. (Ilhas Group)	Areado Fm. (Aptian)	Cabo Fm. (Aptiano)
Acrodus nitidus						+		
Amiidarum mawsoni					genus	+		
Araripelepidotes temnurus	+	+						
Araripichthys castilhoi		+						
Axelrodichthys araripensis		+						
Axelrodichthys maisey	+							
Belonostomus carinatus						+		
Brannerion latum	+	+						
Brannerion vestitum		+						
Calamopleurus cylindricus	+	+						
Calamopleurus mawsoni						+		
Cladocyclus alagoensis		?		+				
Cladocyclus gardneri	+	+	+		genus	genus		
Cladocyclus mawsoni						+		
Chiromystus mawsoni				+		+		
Clupavus braziliensis					+			
Codoichthys carnavali	+							
Dastilbe crandalli	+	+	+	+	?		+	+
Dentilepisosteus laevis	+	+						
Diplomystus longicaustatus						+		
Ellimma branneri				+				
Ellimma cruzi								+
Ellimmichthys longicostatus						+		+
Iemanja palma		+						
Itaparica woodwardi						+		
Lepidotes bahiaensis		genus				+		
Lepidotes mawsoni						+		
Lepidotes roxoi						+		
Lepidotes wenzae		+						
Mawsonia gigas		cf. *gigas*				+		
Neoproscinetes penalvai		+	+					
Nightia sp.			+					
Notelops brama		+	+					
Ophiopsis longipectoralis					+			
Ophiopsis cretaceus		+						
Oshunia brevis		+						
Obaichthys decoratus		+						
Paraelops cearenses		+						
Placidichthys bidorsalis		+			genus			
Rhacolepis buccalis	+	+	+					
Rhacolepis defiorei		+						
Rhinobatos beurleni		+						
Santanichthys diasii	+	+	+					
Santanaclupea silvasantosi		+						
Scombroclupeoides scutata						+		
Scutatuspinosus itapagipensis						+		
Tharrhias araripis	+	+	+					
Tribodus limae		+						
Vinctifer araripinensis		+						
Vinctifer comptoni	+	+	+					
Vinctifer longirostris					+			
Vinctifer punctatus				+				

Although the development of an equatorial seaway in the late Aptian is considered a crucial event in the biogeographic history of western Gondwana (Maisey, 2000, 2011), there is little evidence of maritime influence within the Codó Formation. For example, isotopic analyzes of evaporites from the Codó and Grajaú regions yielded ^{87}Sr/^{86}Sr ratios higher than those of late Aptian seawater (Paz, 2005). In the Codó region, there is no paleontological, sedimentological or geochemical evidence for a possible marine invasion (Paz and Rossetti, 2001). The abundance of articulated ostracods (including young and adult stages) as well as frequent occurrences of complete fossil fishes in the uppermost levels of the sequence are consistent with progressive dissection of the lake system as proposed by Paz and Rossetti (2001).

Some maritime influence is nevertheless suggested by field observations in Brejo municipality, where limestone coquinas include supposedly marine gastropods (e.g. *Paraglauconia*) showing little evidence of abrasion, suggesting low-energy conditions. Many of the fishes from these levels are widely distributed in Northeastern Brazil (e.g. *Calamopleurus*, *Vinctifer*) and at least some of them are known from marine deposits elsewhere. *Santanichthys* is also considered a marine form (Figueiredo and Gallo, 2004), in which case its presence in the Codó lake may be related to initial ingression of salt waters emanating from the equatorial Atlantic. However, fossils indicative of open marine conditions (e.g., ammonites, brachiopods, echinoderms, corals) are absent. Instead, high levels of terrestrial plant debris in these deposits suggest an endorheic drainage system with freshwater influx into the Codó lake. Although isopods have broad ecological distribution, occurring in benthic freshwater, terrestrial and marine habitats (Ruppert et al., 2005), *Codoisopus brejensis* is assigned to a lagunar/marine environment for the Codó Formation (Lindoso et al., 2013b).

Table 3
The relation of distribution of shared taxa (in gray) and speciation or dispersal events (in black) in BNMIBs during the Early Cretaceous (Aptian–Albian). The Parnaíba, Araripe and Sergipe-Alagoas basins were supposedly connected for a long time more than others basins in BNMIBs. The black rectangles suggest an intermittent precariousness in the connections among basins in BNMIBs.

Species	Codó Fm. (Aptian)	Santana Fm. (Aptian/Albian)	Riachuelo Fm. (Albian)	Muribeca Fm. (Aptian)	Marizal Fm. (Aptian)	Marfim Fm. (Ilhas Group)	Areado Fm. (Aptian)	Cabo Fm. (Aptian)
Acrodus nitidus						■		
Amiidarum mawsoni					░	░		
Araripelepidotes temnurus	░	░						
Araripichthys castilhoi		■						
Axelrodichthys araripensis		■						
Axelrodichthys maisey	■							
Belonostomus carinatus						■		
Brannerion latum	░	░						
Brannerion vestitum								
Calamopleurus cylindricus	░	░						
Calamopleurus mawsoni						■		
Cladocyclus alagoensis				■				
Cladocyclus gardneri	░	░	░		░	░		
Cladocyclus mawsoni						■		
Chiromystus mawsoni				░		░		
Clupavus braziliensis					■			
Codoichthys carnavali	■							
Dastilbe crandalli	░	░	░	░			░	░
Dentilepisosteus laevis	░	░						
Diplomystus longicaustatus						■		
Ellimma branneri				■				
Ellimma cruzi								■
Ellimmichthys longicostatus						░		░
Iemanja palma		■						
Itaparica woodwardi						■		
Lepidotes bahiaensis		░				░		
Lepidotes mawsoni						■		
Lepidotes roxoi						■		
Lepidotes wenzae		■						
Mawsonia gigas		░				░		
Neoproscinetes penalvai		░	░					
Nightia sp.			■					
Notelops brama		░	░					
Obaichthys decoratus		░						
Ophiopsis longipectoralis					■			
Ophiopsis cretaceus		■						
Oshunia brevis		■						
Paraelops cearenses		■						
Placidichthys bidorsalis		░			░			
Rhacolepis buccalis	░	░	░					
Rhacolepis defiorei		■						
Rhinobatos beurleni		■						
Santanichthys diasii	░	░	░					
Santanaclupea silvasantosi		■						
Scombroclupeoides scutata						■		
Scutatuspinosus itapagipensis						■		
Tharrhias araripis	░	░	░					
Tribodus limae		■						
Vinctifer araripinensis		■						
Vinctifer comptoni	░	░	░					
Vinctifer longirostris					■			
Vinctifer punctatus				■				

6. Conclusions

The fossil fishes reported here from new outcrops in Brejo, Maranhão State, add to previously observed similarities between fossil fish assemblages of the Codó, Santana and Riachuelo formations. These findings suggest that greater connectivity existed between the aquatic environments of these basins than between other BNMIBs. However, these connections may have been intermittent, with independent dispersals (e.g., among clupeomorphs) and perhaps occasional vicariant speciation. Paleontological data are still somewhat equivocal about the depositional environments of the Codó Formation, especially the extent of any marine influence. Many of the fishes found in Brejo have relatively widespread distributions in Northeastern Brazil, and some are known from marine deposits elsewhere. Others nevertheless seem more restricted geographically (e.g., *Santanichthys*, as well as the isopod *Codoisopus*). There is still much paleoecological

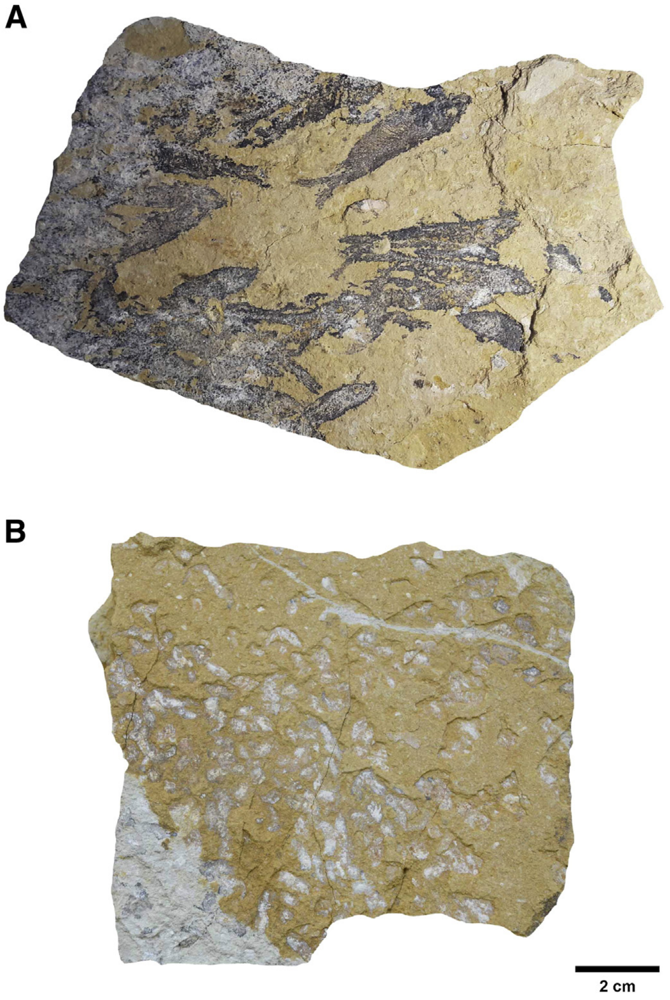

Fig. 10. Mass mortality of fishes (A) and crustaceous (B) from the Codó Formation in the Brejo municipality. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and paleoenvironmental ambiguity and uncertainty regarding the depositional environment of the Codó Formation, but this situation will hopefully be better understood with further investigation.

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