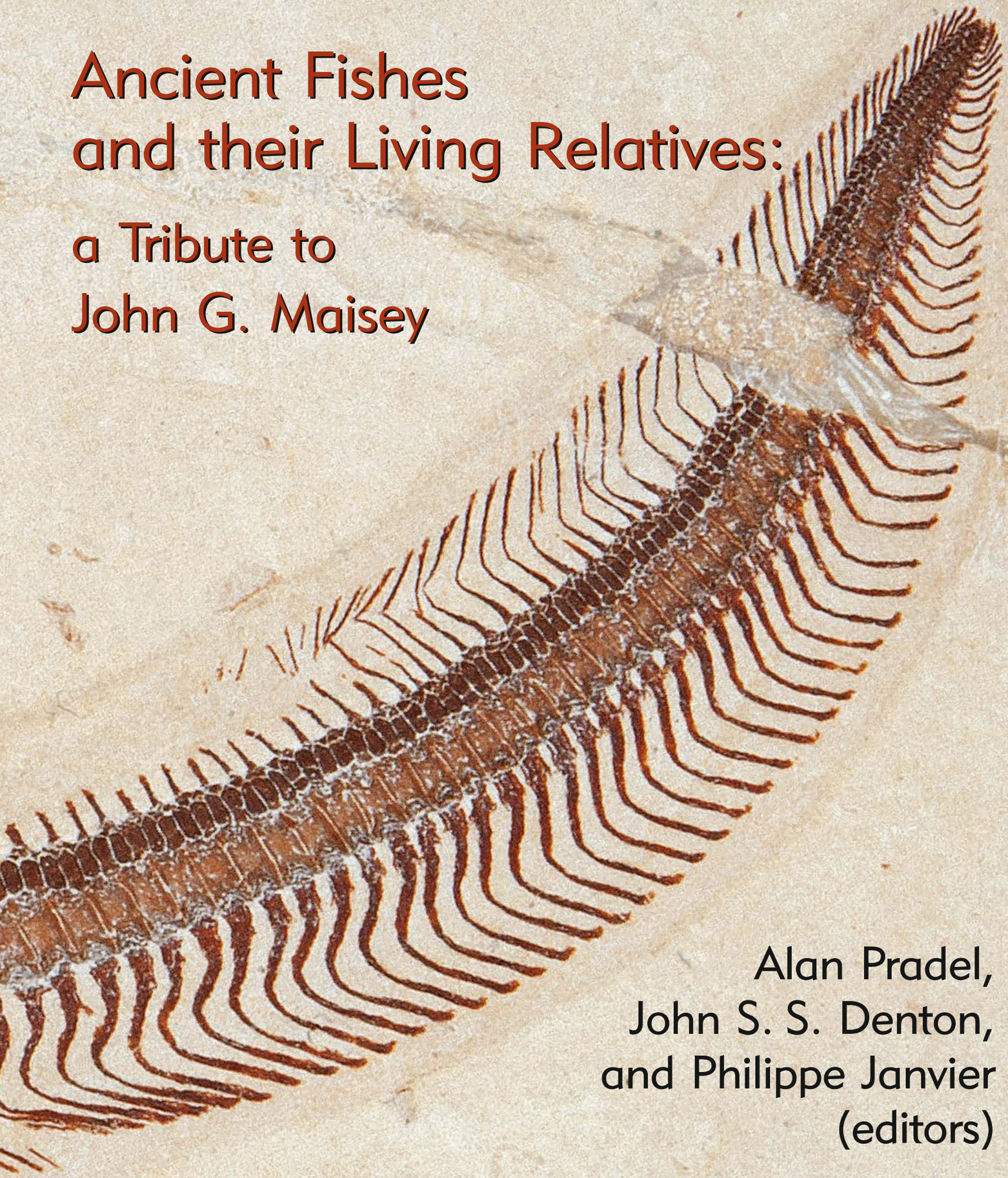
Ancient Fishes and their Living Relatives:

a Tribute to John G. Maisey



Alan Pradel,
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The Cretaceous fishes of Brazil: a paleobiogeographic perspective

Rafael M. Lindoso* and Ismar de S. Carvalho**

Abstract

Brazilian paleoichthyology has been predominantly characterized by studies in the Lagerstätte Santana Formation of the Araripe Basin. It is dominated by actinopterygian fishes, but rare coelacanths and elasmobranchs occur. In rift basins of the East Brazilian Rift System (EBRIS), fossil fishes are also abundant and diversified, including approximately 27 genera of chondrichthyans and about 34 genera of bony fishes. These records reveal a complex paleobiogeographic scenario assigned to a variety of tectonic settings, which had a Tethyan influence. Nevertheless, recent discoveries in Aptian strata of the Parnaíba Basin have increased our understanding regarding Early Cretaceous ecosystems prevailing Northeastern Brazil.

Introduction

In Brazil, the Cretaceous fossil fish record has been assigned to complex tectonic settings related to the development of the Equatorial and South Atlantic oceans during the Jurassic-Cretaceous interval. The evolution of an East Brazilian Rift System (EBRIS) occurred between South America and Africa as a result of an extensive seafloor spreading (Chang et al. 1992). In non-rift basins within the EBRIS region, as well as within interior continental ones, the diastrophism also played an important role in the fossil fish distribution (Maisey 2000). Most of these geological settings with fossil fishes are associated with carbonate deposits of lacustrine or marine origin. Furthermore, such records have been considered in the light of hypotheses of an epicontinental seaway through north-eastern Brazil in the late Aptian, which have been increasingly supported by geochemical and paleontological data (Assine 1992, Arai 1995, 1999, 2009, 2014, Maisey 2000, 2011, Assine et al. 2016, Lindoso et al. 2016, Arai & Assine, 2020, Araripe et al. 2021).

A better understanding of the paleoichthyofauna of Brazil comes from the Araripe Basin (Fig. 1). In this Mesozoic intracratonic sedimentary system, the Santana Formation comprises a famous fossil concentration and conservation Lagerstätten, with a vertebrate fauna dominated by actinopterygian fishes, but also including rare coelacanths and elasmobranchs (Martill & Brito 2017). The Araripe Basin is also the most extensive among the continental interior basins and exhibits the most complex geological history. This Lower Cretaceous succession, approximately 110 million years old, has been described by John Maisey as one of the world's most important Gondwanan fossil assemblages (Maisey 1991).

In the Brazilian coastal basins (EBRIS), the paleoichthyofauna is abundant and diversified, including approximately 27 genera of chondrichthyans and about 34 genera of bony fishes. It includes mainly Cretaceous records from Pelotas, Santos, Sergipe-Alagoas, Pernambuco, Paraíba, Potiguar, and São Luís basins (Gallo et al. 2012) (Fig. 2). During the Late Cretaceous, biotic distributions within the EBRIS region were assigned to rifting of Gondwana, leading to important vicariant processes (Maisey 2000, Santos & Carvalho 2009, Parméra

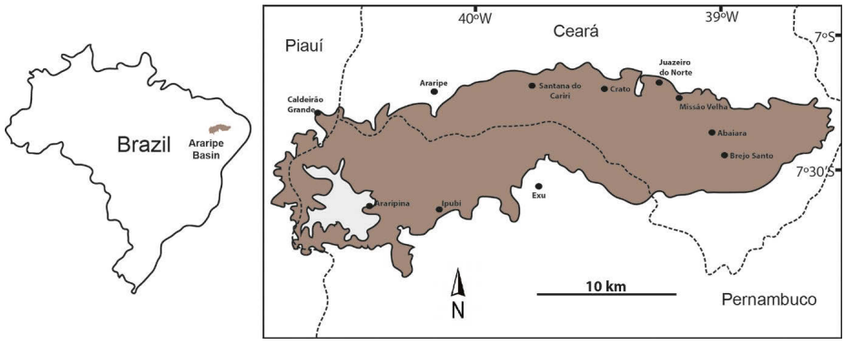

Fig. 1. Simplified map of the Araripe Basin localized between the Ceará, Pernambuco and Piauí States, north-eastern Brazil.

Fig. 2. Main north-eastern Brazilian sedimentary basins where Cretaceous fossil fishes are found.

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2016). These tectonically-driven events have affected both pelagic and benthic marine organisms as well as continental freshwater ones (Maisey 2000).

In this study we present a synthesis concerning the Cretaceous fishes of Brazil and their paleobiogeographic significance. Some of the ideas presented herein remain unsolved, and this work aims to expand the debate.

Paleoichthyofauna synthesis

The history of Brazilian paleoichthyology begins with João da Sylva Feijó in his reports of December 11th 1800 to the Portuguese authorities (Nobre 1978), followed by the German expeditions of Johann Baptist von Spix and Carl Friedrich Philipp von Martius between 1817 and 1820 (Spix & Martius 1823). The numerous fossil fishes coming from the Santana Formation were subsequently analyzed by George Gardner and Louis Agassiz in 1841. Throughout the 20th century, important studies were conducted in this lithostratigraphic unit: Woodward (1901, 1908), Jordan & Branner (1908), Jordan (1919, 1921), D'Erasmo (1938), Dunkle (1940), Silva-Santos (1945, 1947, 1950, 1958, 1960), Silva-Santos & Valença (1968), Campos & Wenz (1982), Silva-Santos (1985a,b), Maisey (1986), Wenz & Kellner (1986), Wenz (1989), Brito (1988), Brito & Ferreira (1989), and Brito & Martill (1999). John Maisey and contributors (1991) produced the most comprehensive treatment on the sedimentology and paleontology of the Santana Formation at the time in his book Santana Fossils: An Illustrated Atlas. The book is one of the most complete and richly illustrated works regarding a sedimentary basin in Brazil, comprising a systematic description of vertebrate and invertebrate taxa, as well as plants.

In the Santana Formation, Chondrichthyes are represented solely by Hybodontidae and Rajiforms (family incertae sedis). By contrast, Actinopterygii are diversified and represented by Holostei, Teleosteomorpha, Teleostei, Elopomorpha Ostarioclupeomorpha, and some incertae sedis families related to Clupeocephala, Clupeomorpha, and Otophysi; Sarcopterygii are represented by Coelacanthiformes (Brito & Yabumoto 2011). Although less abundant, this ichthyofauna has been correlated with that of the Codó Formation of the Parnaíba Basin, considered late Aptian in age (Lima 1982, Silva-Santos 1994, Santos & Carvalho 2009, Lindoso et al. 2011, 2016). Recently, the first record of an obaichthyid gar (*Dentilepisosteus laevis*) was reported for the Codó Formation, as well as the first record of genus *Santanichthys*, enhancing the faunal similarities between Codó and Santana formations (Brito et al. 2016, Lindoso et al. 2016). Nevertheless, in his first visit to outcrops of the Codó Formation, John Maisey observed that part of this lithostratigraphic unit represents a condensed section, which preserves Crato, Ipubi, and Romualdo ichthyofaunas (Maisey pers. comm. 2015). In fact, most of the fishes of the Codó Formation occur as fully articulated skeletons without scales, which indicates low sedimentation rate. This scenario fits with John's suggestion that the entire Crato, Ipubi, and Romualdo ichthyofaunas occur in a unique section of the Codó Formation (see Maisey 2000: 295). In this lithostratigraphic unit, endemic forms are represented by the species *Codoichthys carnavalii* and *Axelrodichthys maiseyi* (Silva-Santos 1994, Carvalho et al. 2013).

In the Brazilian Equatorial and East continental margins, fossil fish records are represented in the Pelotas, Santos, Sergipe-Alagoas, Pernambuco, Paraíba, Potiguar, and São Luís basins, spanning the entire Cretaceous (Gallo et al. 2012). In the Atlântida Formation, Pelotas Basin, Chondrichthyes are scarce, with representatives tentatively attributed to Lamniformes (e.g. isolated odontaspidoid tooth). Representatives of Osteichthyes include Pycnodontidae, Clupeomorpha, Euteleostei, Dercetidae, Enchodontidae, and Holocentridae (Gallo & Figueiredo 1999, Figueiredo et al. 2001, Gallo et al. 2006, Figueiredo & Gallo 2006). In the Santos Basin, offshore southern Brazil, fossil fishes have been described from wells in an interval ranging from the Albian to Recent (Miller et al. 2002). Here, chondrichthyans are represented by Triakidae, Carcharhinidae, Ginglymostomatidae, Lamnidae indet., and Scyliorhinidae. Teleostei are represented by Myctophidae, Sternoptychidae, and undetermined teeth (Miller et al. 2002).

The diversity of fossil fishes from the Riachuelo Formation, Sergipe-Alagoas Basin, is similar to that of the Codó and Santana formations (Santos & Carvalho 2009, Gallo 2015, Lindoso et al. 2016). The Riachuelo Formation is divided into the Taquari, Maruim, and Angico members, with the latter two having only isolated fossil remains. The ichthyofauna of the Taquari Member is represented by diversified Osteichthyes, all them also present in the Santana Formation (Gallo et al. 2012). Some endemic species seem to occur in the lower Aptian of the Coqueiro Seco Formation (e.g. *Gibsonichthys miguelcampensis*, *Falconichthys santerezae* and *Mafficioliichthys atolensis*), and the Morro do Chaves Formation (e.g. *Lepidotes alagoensis*, *Pseudoellimma gallae*, *Atolvorator longipectorales*) (Maffizzoni 2000, Gallo & Brito 2004, Gallo & Coelho 2008, Figueiredo 2009). The Morro do Chaves Formation has the most abundant and diversified ichthyofauna from the Sergipe-Alagoas Basin (Gallo et al. 2012).

Marine forms of Chondrichthyes (Rhombodontidae and Ptychodontidae) and Osteichthyes (Pycnodontidae, Amiidae, Teleostei incertae sedis, Albulidae, Dercetidae and Enchodontidae) occur in the Cotinguiba Formation from Sergipe-Alagoas Basin (Woodward 1907, Löfgren & Oliveira 1943, Silva-Santos & Salgado 1969, Carvalho & Gallo 2002, Coelho 2004; Gallo et al. 2007). In the Calumbi Formation, Chondrichthyes are more diversified, and are represented by Hexanchidae, Cretoxyrhinidae, Odontaspididae, Anacoracidae, Sclerorhynchidae and Rhinobatidae. Osteichthyes, besides those taxa already known for the Cretaceous from the Sergipe-Alagoas Basin, include Xiphiidae and Latimeriidae (Souza-Lima 2001).

There are scarce fossil fishes in the Cretaceous strata from the Pernambuco Basin. In the Aptian-Albian of Cabo Formation, Osteichthyes are represented by *Ellimma cruzae* and *Dastilbe crandalli* (Silva-Santos 1990). In the Estiva Formation, rare pycnodontid teeth occur (Barbosa et al. 2008). The coastal Paraíba Basin, sometimes considered as an extension of the Pernambuco Basin (e.g. Pernambuco-Paraíba Basin), exhibits an abundant paleoichthyofauna; its records comprise only the Itamaracá, Gramame, and Maria Farinha formations. In the mid-Campanian to lower Maastrichtian Itamaracá Formation, Chondrichthyes are recorded by Ptychodontidae, Hexanchidae, Cretoxyrhinidae, Ginglymostomatidae, Odontaspididae, Anacoracidae, Mitsukurinidae, and Rhombodontidae; Osteichthyes are represented by the taxa Pycnodontidae, Saurodontidae, and Enchondontidae. Most of this assemblage is also in the Maastrichtian Gramame and Paleocene Maria Farinha formations, but with some distinct taxa (e.g. *Cretalamna appendiculatta*, *Squalicorax kaupi*, *Paleoballistum dossantosi*, Diodon sp.) (Rebouças & Silva-Santos 1956, Silva-Santos & Figueiredo 1987, Silva 2007, Gallo et al. 2009).

The Osteichthyes Chanidae, Pycnodontidae, and Semionotidae are also found in the Açu and Jandaíra Formations from the Potiguar Basin. These litostratigraphic units represent a continental drift phase in EBRIS (Duarte & Santos 1962, Silva-Santos 1963, Soares et al. 2003, Gallo & Brito 2004, Machado & Brito 2006). In the São Luís Basin, the northernmost Cretaceous sedimentary area in South America, vertebrate fossils occur mainly in the bone bed Laje do Coringa, a stratigraphic horizon of the Alcântara Formation (Cenomanian) that is characterized by fluvial and marine taxa such as Hybodontidae, Myliobatidae, and Sclerorhynchidae (Chondrichthyes); and Semionotidae, Lepisosteidae, Amiiformes, Pycnodontidae, Mawsoniidae, and Ceratodontidae (Osteichthyes) (for an overview, see Medeiros et al. 2014).

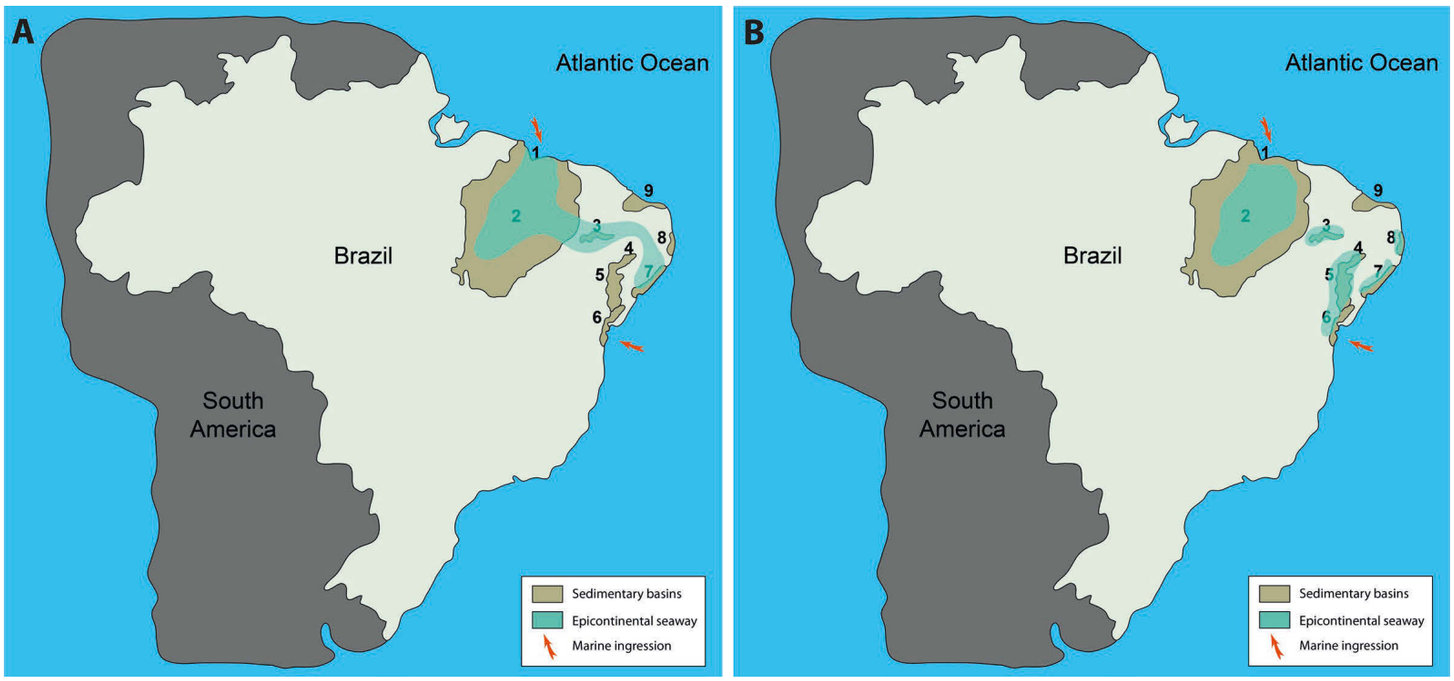

Fig. 3. a. Distribution of fossil fishes in the Brazilian Northeastern Marginal and Interior basins (BNMIBs) during the Early Cretaceous, based on paleontological data. The fossil fishes record in these basins indicates a greater similarity among Codó (Parnaíba Basin), Santana (Araripe Basin) and Riachuelo (Sergipe-Alagoas Basin) formations; **b.** evidence for dispersal and vicariance episodes is indicated by speciation in some genera of fish related to intermittent connection of some BNMIBs. Sedimentary basins in map: 1, São Luís; 2, Parnaíba; 3, Araripe; 4, Jatobá; 5, Tucano; 6, Recôncavo; 7, Sergipe-Alagoas; 8, Pernambuco-Paraíba; 9, Potiguar. Modified from Lindoso et al. (2016).

Discussion

Support for hypotheses of an equatorial seaway over territories of Western Gondwana during the Early Cretaceous has been strengthened in recent years (see Arai 2014). The reasons for this interesting debate involve geochemical and paleontological (e.g. foraminifera, echinoids, mollusks, dinoflagellates, isopods, and fishes) data of Tethyan affinity present within EBRIS and interior continental basins (Beurlen 1964, 1966, Koutsoukos 1992, Arai & Coimbra 1990, Arai 1999, 2009, 2014, Brito & Yabumoto 2011, Maisey 2000, 2011, Lindoso et al. 2013, 2016), as well as extensive gypsum beds (Assine 1992). This biotic record is well represented in the Aptian-Albian intervals of the São Luís, Parnaíba, Araripe, Tucano and Sergipe-Alagoas basins, which suggests that this seaway was established in the present-day region of northeastern Brazil (Arai 2009, 2014). According to Maisey (2000), the Aptian transgression created opportunities for the dispersal of marine biota into new areas.

A better characterization of the paleoichthyofauna of interior continental basins has been crucial for the understanding of Tethyan influence in the Aptian marine sedimentation within EBRIS. In the Araripe Basin, marine taxa are represented by the genus *Rhacolepis*, *Vinctifer*, *Araripichthys*, and *Notelops*, which occur in slightly older deposits from Venezuela, Colombia and Mexico (Silva-Santos & Oliveira 1994, Moody & Maisey 1994, Schultze & Stöhr 1996, Maisey 2000, Maisey & Moody 2001). This Tethyan heritage is also expanded to Africa (e.g. *Araripichthys*, *Cladocyclus*, *Goulmimichthys*) (Cavin 1995, Brito & Yabumoto 2011).

In the Codó Formation, upper Aptian of the Parnaíba Basin, fish assemblages are more similar to those in the Santana and Riachuelo formations than to others Brazilian Northeastern Marginal and Interior basins (BNMIBs) (Silva-Santos 1991, Lindoso et al. 2016). Recent discovery of the obaichthyid *Dentilepisosteus laevis* in the Codó Formation reinforces a faunal identity with the Aptian Santana Formation and extends the temporal range of this taxon downward into the Aptian (Brito et al. 2016). These findings suggest greater connectivity between the aquatic environments of Parnaíba, Araripe and Sergipe-Alagoas basins, but with intermittent periods in these connections revealed by independent dispersals (e.g. among clupeomorphs and coelacanths) and perhaps vicariant speciation (Fig. 3) (Lindoso et al. 2016). Similar assemblages have also indicated paleogeographic relationship between the Araripe and Recôncavo-Tucano basins (Silva-Santos 1991).

Paleogeographic reconstructions depicting the probable route of Aptian marine ingressions are dubious. Marine entrance would have occurred independently or combined, via Parnaíba, Sergipe-Alagoas and Potiguar basins (for an overview, see Arai 2014). According to this latter author, "the probable route for the water entering the Northeastern Brazil seaway is through the São Luís, Parnaíba, Araripe and Sergipe basins." However, this model has been challenged by paleocurrent analyses of fluvial deposits, as well as by faciological data (Assine et al. 2016). According to this author, three distinct drainage basins were settled in the north-eastern Brazil as a result of drainage division between the Parnaíba, Potiguar, and Araripe basins. This scenario would imply independent marine ingressions of N–NE–SE directions.

Additionally, rift valleys along the Recôncavo-Tucano-Jatobá and Cariri-Potiguar trends were occupied by epicontinental seaways (Maisey 2000). Thus, different seaways separated Northeastern Brazil from the rest of South America but left it contiguous with Africa and, in another way, the northern Brazil from both South America and Africa (Fig. 4) (Maisey 2011). Evidence from fossil fish include a relatively cosmopolitan Gondwanan taxa during the pre-rift phase followed by greater diversity and perhaps a high degree of local endemism during sin-rift times (Maisey 2000, 2011). Alternatively, the absence of common taxa between the Marizal and Santana formations has been attributed to differences in time of deposition (Brito & Alvarado-Ortega 2008).

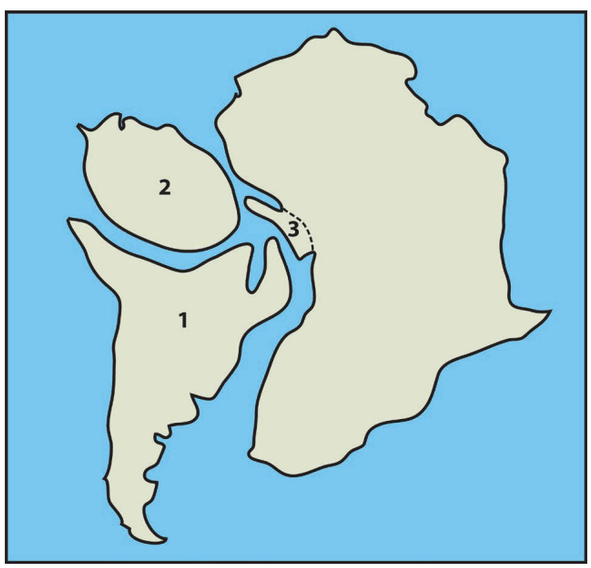

Fig. 4. Paleogeographical model proposed by John Maisey for the Western Gondwana in the Aptian, which postulate a division by epicontinental seaways into three land-masses, "mainland" South America (1), northern Brazil (2) and Africa + northeastern Brazil (3). Modified from Maisey (2011).

Conclusions

In north-eastern Brazil, fossil fish assemblages were characteristic of transgressive events during the Early Cretaceous. Speciation patterns in endemic faunas are well represented in the EBRIS and the interior continental basins. However, absence of controlled excavations has precluded a better understanding of the temporal evolution of these ecosystems and consequent paleobiogeographic scenarios. The intracratonic position of the Araripe Basin, in conjunction with its excellent fossil preservation, is obviously critical in clarifying the possible routes of marine ingressions. Nevertheless, findings of new upper Aptian fossiliferous localities in the Parnaíba Basin have been crucial in corroborating the biogeographical history of Western Gondwana. As John Maisey might say: "we now are able to at least formulate appropriate questions to ask concerning this major event in Earth history.".

Acknowledgements

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John G. Maisey (right) and the publisher visiting Neuschwanstein castle in Bavaria on Nov. 11, 2014

Knowledge of fossil sharks (chondrichthyans) has advanced tremendously over the past decade, giving scientists a window into a historically understudied branch of the evolutionary tree of fishes, and revealing anatomies and ecologies just as diverse and fascinating as those of bony fishes (osteichthyans). This volume assembles cutting-edge research on the biology, anatomy, and evolution of sharks and bony fishes, featuring works by paleobiologists and associated researchers from 11 countries, spanning topics from taxonomy to statistical methodology, in honor of Professor John G. Maisey, for his pioneering work on Paleozoic chondrichthyan anatomy, taxonomy, and paleobiogeography over his half-century career at the American Museum of Natural History. With an introduction and 16 chapters, this volume erects two new families and two new genera, and provides 160 figures and illustrations, and 29 plates, including the most comprehensive collection of high-resolution images of a rare fossil shark held predominantly in private collections.

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