Anais da Academia Brasileira de Ciências (2019) 91(Suppl. 2): e20160456
(Annals of the Brazilian Academy of Sciences)
Printed version ISSN 0001-3765 / Online version ISSN 1678-2690
http://dx.doi.org/10.1590/0001-3765201720160456
www.scielo.br/aabc | www.fb.com/aabcjournal

Distributional patterns of Aptian-Albian paleoichthyofauna of Brazil and Africa based on Track Analysis*

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Manuscript received on July 25, 2016; accepted for publication on September 7, 2016

How to cite: PARMÉRA TCC, GALLO V, SILVA HM AND FIGUEIREDO FJ. 2019. Distributional patterns of Aptian-Albian paleoichthyofauna of Brazil and Africa based on Track Analysis. An Acad Bras Cienc 91: e20160456. DOI 10.1590/0001-3765201720160456.

Abstract: The Aptian-Albian paleoichthyofauna in Brazil and Africa is quite diverse, yet their geographic patterns still require accounts. This work consists of a panbiogeographical analysis of paleoichthyofauna from Aptian-Albian through track analysis. Geographic coordinates were obtained and converted into paleocoordinates. Individual Tracks (ITs) and Generalized Tracks (GTs) were built wi*th the aid of Arc*View GIS v3.2 program using Trazos2004 extension. As a result, four GTs and tree Biogeographic Nodes (A, B and C) had been identified. GTs 1 and 2 shows two different faunas. GT3 indicates similarity between Brazil and Africa paleoichthyofauna suggesting the break-up of Gondwana as the event that separated it. GT4 represents a probable local seaway produced by transgressions. In the Node A a unique fauna was found indicating the presence of a third biota with its own characteristics. Node B is associated with the break-up of the supercontinent Gondwana. Node C was related to fauna exchange promoted by marine ingression and epicontinental seas that occurred during Aptian-Albian. We concluded that there is a relationship between the distributional patterns of biota and events such as the break-up of Gondwana, the formation of Atlantic Ocean and eustatic movements that affected South America and Africa.

Key words: Aptian-Albian, Gondwana Break-up, historical biogeography, track analysis.

INTRODUCTION

The paleoichthyofauna of the Cretaceous, mainly restricted to the Aptian-Albian, is diversified and known since 19th century (e.g., Agassiz 1841, Jordan and Branner 1908, Woodward 1908, Jordan 1910, 1919, Schaeffer 1947, Silva Santos 1985a, b, c, Maisey 1991, Figueiredo and Gallo 2004, Santos and Carvalho 2009, Brito et al. 2013).

The Aptian-Albian assemblages possess many fossil representatives in Brazilian marginal and interior basins and these have been used to illustrate the relationships between South America and Africa (Maisey 1993, 2000). Furthermore, divergence of several taxa may have occurred before continental drift (Lundberg 1993). Brazilian fossil records of this age range come from several basins, such as

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* Contribution to the centenary of the Brazilian Academy of Sciences.

Araripe, Parnaíba, Pernambuco-Paraíba, Potiguar, Sanfranciscana, São Luís, Sergipe-Alagoas and Tucano, and include many taxa (e.g., †*Lepidotes*, †*Vinctifer comptoni*, †*Dastilbe crandalli*, †*Rhacolepis buccalis*).

The Araripe Basin is an interior basin located in Northeast Brazil. Its Aptian-Albian sequence is represented by the Crato and Santana formations, respectively, and they indicate the post-rift stage. The paleoenvironments found in these lithostratigraphic units are lacustrine, coastal and platform, being composed of shales, limestones and sandstones (Assine 2007).

The Codó Formation represents the Aptian-Albian section of the Parnaíba Basin. Shales, limestones, siltstones, sandstones, gypsite and anhydrite are the main lithotypes found in this unit, suggesting lacustrine, shallow marine, and fluvio-deltaic paleoenvironments (Vaz et al. 2007).

The Cabo Formation encompasses the Aptian-Albian interval of the Pernambuco-Paraíba Basin. This lithostratigraphic unit comprises shales, sandstones and conglomerates and the paleoenvironment proposed is lacustrine with alluvial fans (Córdoba et al. 2007).

The Aptian-Albian interval in the Potiguar Basin is represented by the Açu Formation, whose paleoenvironment was identified as transgressive marine with sandstones and shales (Neto et al. 2007a).

The Areado Formation represents the Aptian-Albian sequence from the Sanfranciscana Basin. This unit is constituted by shales, sandstones and conglomerates, which correspond to the rift stage. The paleoenvironments are interpreted as lacustrine, fluvial and desert (Zalán and Silva 2007).

The interval in the São Luís Basin is represented by the Itapecuru Formation, which consists of shales, siltstones and sandstones from fluvial, alluvial and coastal paleoenvironments during the rift stage of break-up (Zalán 2007).

In the Sergipe-Alagoas Basin, the Aptian-Albian interval is composed of the Maceió, Muribeca and Riachuelo formations. Sandstones, shales and calcisiltites are found in these units, and correspond to rift, post-rift and drift stages. Paleoenvironments are interpreted as alluvial-fluvial, deltaic-lacustrine and marine (Neto et al. 2007b).

The Tucano Basin includes the Marizal Formation with sandstones and conglomerates from an alluvial paleoenvironment produced during the post-rift stage (Costa et al. 2007a, b).

The Cocobeach Group belongs to the Gabon Basin and consists of interbedded and laterally gradational fluvial sandstones and lacustrine shales. Turbidites are interbedded with the latter. The unit was deposited in a series of nonmarine rift basins formed due to the onset of rifting between Africa and South America (Ala and Selley 1997).

The strata of Iullemmeden Basin are known as Continental Intercalaire (Greigert 1966, Moody and Sutcliffe 1991). The Continental Intercalaire is divided into three groups: Agadez, Irhazer and Tegama (Moody and Sutcliffe 1991). The paleovertebrate fauna of the Aptian-Albian portion belongs to Irhazer Group, whose strata are predominantly composed by shales with localized bars of fine-grained calcareous sandstones. The fine-grained nature and extensive lateral distribution of the siltstones indicate a low energy fluvio-lacustrine depositional paleoenvironment (Moody and Sutcliffe 1991).

The Tataouine Basin is divided in three formations: Douiret, Aïn el Guettar and Zebbag (Bouaziz et al. 1988, Zarbout et al. 1994). Vertebrate fossils are found in the conglomeratic beds from the Douiret and Aïn el Guettar formations, which are dated as Aptian and Albian, respectively. The paleoenvironment of Douiret Formation is interpreted as fluvial, whereas in the Aïn el Guettar Formation it is considered shallow marine (Anderson et al. 2007).

The Galula Formation is included in Rukwa Rift Basin and is composed of red sandstones, conglomerates and mudstones. This formation comprises a large grain size range of sediments besides having an alluvial architecture and lithofacies (Roberts et al. 2010).

Historical biogeography allows recognize the distribution of taxa and their areas of endemism. This approach is essential when fossil groups are considered (Morrone and Crisci 1995, Gallo and Figueiredo 2010).

The Panbiogeographic methods (Croizat 1958, 1964) allow to recovery the distributional patterns of taxa considering their geographical occurrence as well as the geological history of areas. Its basic track analysis method specifies the evolution of different groups and areas if they share a common history among their distributions over time. Such patterns can be recognized by events of wide scale, which mainly comprise vicariant and extinction hypotheses (Crisci 2001). Furthermore, Panbiogeography can be applied to paleontological data (Gallo et al. 2007), and according to Croizat (1958, 1964) distributions of fossil and living taxa should be integrated in the same analysis. In addition, data related to paleogeographic distributions allow to recreate ancient explanatory scenarios (Upchurch 2008).

Carvalho (2009) stated that Panbiogeography is a useful tool to analyze distributional patterns of biota and he wrote that it represents a "robust, objective, empirically testable, fast, low-cost method, based on available taxonomic information".

Some studies have been developed using geographic distributions of fossil fish applying methods of historical biogeography (e.g., Gallo et al. 2007, Silva and Gallo 2007, Miguel et al. 2014). Gallo et al. (2007) analyzed the distributional patterns of Turonian marine biotas, including several fish taxa (e.g., lamniforms, pycnodontiforms, ichthyodectiforms, crossognathiforms, salmoniforms and aulopiforms). The authors concluded that final break-up of Gondwana and Laurasia was determinant vicariant event for biogeography of Atlantic Ocean and shaped the distributions of the Turonian biota. Silva and Gallo (2007) employed Parsimony Analysis of Endemicity to analyze the distribution of enchodontoid fishes occurring only in the Cenomanian. The authors delimited two areas of endemism in Tethys Ocean. The first was composed of Morocco and southern Italy whereas the latter comprises Lebanon and Israel.

Miguel et al. (2014) identified distributional patterns of mawsoniid fishes, applying the panbiogeographical method of track analysis. The authors concluded that tectonic events related to the break-up of Pangaea and Gondwana and the evolution of Atlantic Ocean were vicariant events that shaped the distribution of this taxon throughout the Mesozoic.

The goal of this study was to identify the distributional patterns of the ichthyofauna within the Aptian-Albian interval (~125 to 100 Mya). Furthermore, we tested Souza-Lima's (2006, 2007) hypothesis regarding the formation of the Proto-South Atlantic due to the crustal distension of Gondwana from Jurassic, where currently Sergipe-Alagoas, Camamu, Almada and Cumuruxatiba basins are found, and then simultaneously opening towards the north and south, in Pernambuco-Paraíba, Espírito Santo, Campos, Santos and Pelotas basins.

MATERIALS AND METHODS

We listed geographical occurrences of the ichthyofauna within the Aptian-Albian interval obtained from the Paleontological Collection of Instituto de Biologia Roberto Alcantara Gomes, Universidade do Estado do Rio de Janeiro, as well as from the analysis of literature, supplemented by records of the website Paleobiology Database (http://www.paleodb.org).

Georeferencing from free websites, such as the Global Gazetteer, version 2.2 (http://www.falingrain.com), was employed in the case of missing geographic coordinates. The modern geographic coordinates were converted in paleocoordinates using the software Point Tracker for Windows (Scotese 2008).

The panbiogeographical method of track analysis was applied using ArcView v3.2 (ESRI 1999) with the extension Trazos2004 (Rojas 2007). It consisted of plotting the 223 occurrences on a map of 120 millions of years, provided by the Shapefile Library (Scotese 2008).

Overall, the method consists of connecting the occurrence points with lines, named individual tracks, using the criterion of minimum spanning trees. Individual tracks correspond to the geographical coordinates of taxon or the place where the evolution of this taxon occurred. After, these individual tracks are superimposed and when congruence is detected, generalized tracks are indicated. These latter indicate the existence of an ancestral biota that was fragmented by events such as climate change or tectonic processes. At the intersection or convergence of the generalized tracks biogeographic nodes are verified. The nodes represent the intersection of different ancestral biotas and they are interpreted as hybrid areas (Craw et al. 1999, Grehan 2001, Heads 2004, Morrone 2004, 2009).

RESULTS

The overlapping of the 38 individual tracks (ITs) resulted in four generalized tracks (GTs) (Figure 1, Table I): GT1 (Northern Araripe), GT2 (Southern Araripe), GT3 (Trans-Gondwana) and GT4 (Seaway). From the intersection of the generalized tracks, three biogeographic nodes were found: Node A (Araripe) was formed by GT1 and GT2; Node B (Gondwanic) by GT1 and GT3; and Node C (Nigerian Seaway) by GT3 and GT4.

Fifty-eight taxa showed a single occurrence preventing their use in the track analysis (Table II). However, these records are important for

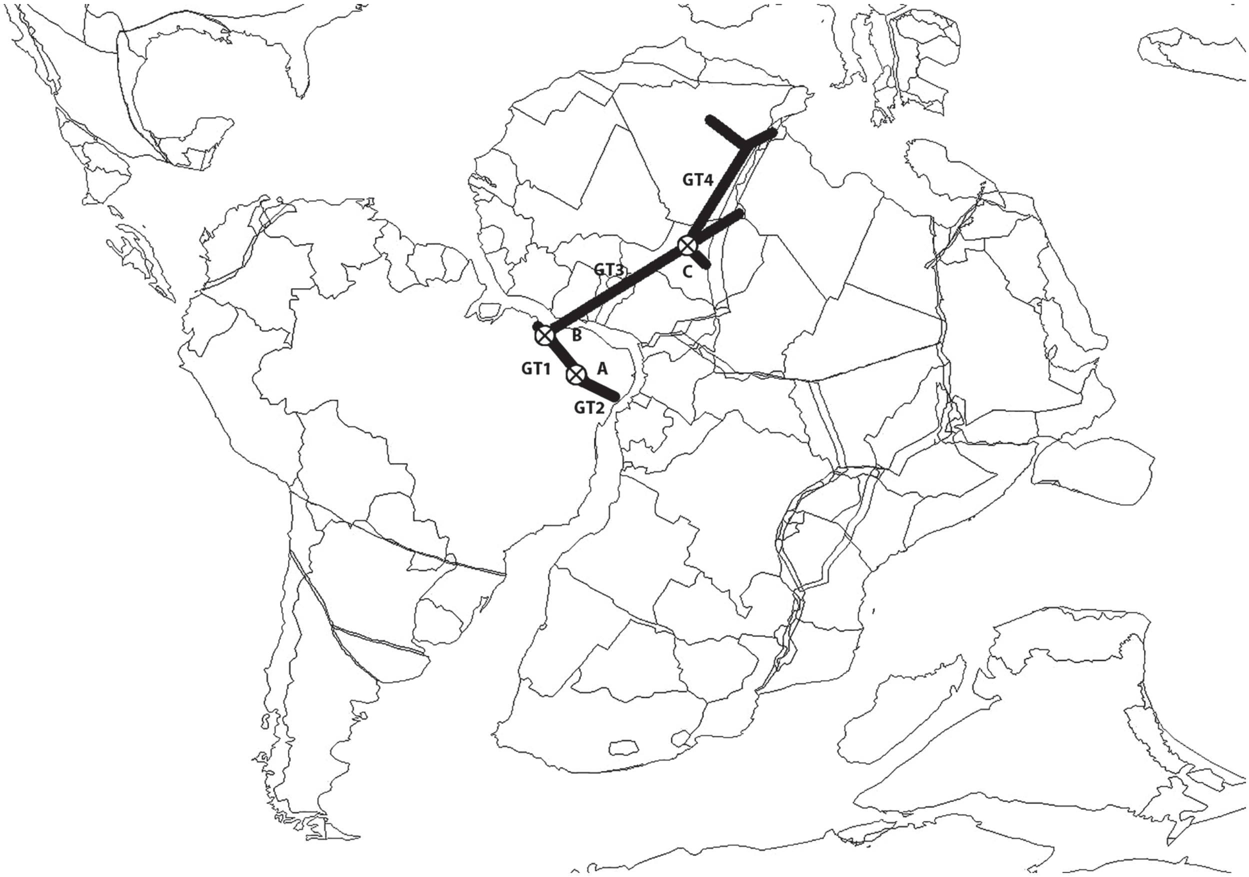

Figure 1 - Map showing the four generalized tracks and three biogeographic nodes. GT1 (Northern Araripe), GT2 (Southern Araripe), GT3 (Trans-Gondwana), GT4 (Marine Connection). Node A (Araripe), Node B (Gondwanic), Node C (Nigerian Seaway).

TABLE I
Generalized Tracks (GTs), their respective locations (names) and Individual Tracks.

Generalized Tracks	Individual Tracks
GT1 (Northern Araripe)	*Araripelepidotes temnurus*, *Brannerion latum, Calamopleurus cylindricus, Tharrhias rochae*
GT2 (Southern Araripe)	*Beurlenichthys ouricuriensis*, *Cladocyclus alagoensis*, *C. gardneri, Neoproscinetes penalvai*, *Rhacolepis buccalis*, *Tharrhias araripis*, *Vinctifer longirostris*
GT3 (Trans-Gondwana)	*Asiatoceratodus tiguidensis*, *Eotrigonodon* sp., *Neoceratodus africanus*
GT4 (Nigerian Seaway)	*Caturus* sp., *Cretodus* sp., *Hybodus* sp., *Lissodus* sp., *Mawsonia tegamensis, Mawsonia* sp., *Onchopristis dunklei*, *O. numidus*, *Priohybodus arambourgi*

TABLE II
Occurrences excluded from the Individual Tracks.

Taxon	Brazil	Africa	References
Asiatoceratodus sp.	X		Castro et al. (2004), Toledo and Bertini (2005), Ramos et al. (2009)
Asteracanthus sp.		X	Murray (2000)
Atractosteus africanus		X	Murray (2000)
Axelrodichthys maiseyi	X		Carvalho et al. (2013)
Axelrodichthys sp.		X	Gee (1988)
Bartschichthys sp.	X		Ramos et al. (2009), Candeiro et al. (2011)
Brannerion sp.	X		Forey and Maisey (2010)
Britoichthys marizalensis	X		Figueiredo (2004)
Bullichthys santanensis	X		Mayrinck et al. (2010)
Casieroides yamangaensis		X	Taverne (1975)
Ceratodus humei		X	Lefranc (1976)
Ceratodus pectinatus		X	Lefranc (1976)
Ceratodus sp.		X	Murray (2000)
Chanopsis lombardi		X	Casier (1961)
Chardonius longicaudatus		X	Murray (2000)
Chirocentrites guinensis		X	Cavin et al. (2013)
Chiromystus mawsoni	X		Silva Santos (1949)
Clupavichthys dufouri		X	Gayet (1989)
Clupavus brasiliensis	X		Silva Santos (1985b)
Codoichthys carnavalii	X		Silva Santos (1994), Figueiredo and Ribeiro (2016)
Cratoamia gondwanica	X		Brito et al. (2008)
Cretodus semiplicatus		X	Cuny et al. (2004)
Dentilepisosteus laevis	X		Grande (2010)
Diabodus tataouinensis		X	Cuny et al. (2004)
Egertonodus sp.		X	Cuny et al. (2010)
Ellimma branneri	X		Figueiredo (2006)
Ellimma cruzae	X		Silva Santos (1990), Figueiredo and Ribeiro (2016)
Ellimmichthys goodi		X	Eastman (1912)
Ellimmicththys maceioensis	X		Malabarba et al. (2004)
Gyrodus sp.		X	Cuny et al. (2010)
Iansan beurleni	X		Brito and Seret (1996)
Iemanja palma	X		Wenz (1989)
Laeliichthys ancestralis	X		Silva Santos (1985c)
Lepidotes wenzae	X		Brito and Gallo (2003)
Leptostyrax macrorhiza		X	Murray (2000)

TABLE II (continuation)

Taxon	Brazil	Africa	References
Lupaceratodus useviaensis		X	Gottfried et al. (2009)
Mercediella riachuelensis	X		Koerber (2012)
Nanaichthys longipinnus	X		Amaral and Brito (2012)
Nolfia riachuelensis	X		Figueiredo (2009)
Notelops sp.	X		Ramos et al. (2009)
Obaichthys decoratus	X		Wenz and Brito (1992), Grande (2010)
Ogunichthys triangularis	X		Alvarado-Ortega and Brito (2010)
Oshunia brevis	X		Wenz and Kellner (1986)
Palaeonotopterus greenwoodi		X	Taverne and Maisey (1999)
Parachanos aethiopicus		X	Arambourg and Schennegans (1935)
Placidichthys tucanensis	X		Brito and Alvarado-Ortega (2008)
Pliodetes nigeriensis		X	Wenz (1999)
Proportheus kameruni		X	Cavin et al. (2013)
Pseudoleptolepis minor		X	Taverne (1975)
Ptychodus sp.		X	Lefranc (1976)
Rhacolepis latus	X		Silva Santos (1985a)
Santanasalmo elegans	X		Gallo et al. (2009)
Scapanorhynchus sp.		X	Murray (2000)
Stahlraja sertanensis	X		Brito et al. (2013)
Synechodus sp.		X	Murray (2000)
Tharrhias castellanoi	X		Silva Santos (1963)
Tribodus limae	X		Brito and Ferreira (1989), Brito (1992)
Tribodus tunisiensis		X	Cuny et al. (2004)

understanding the Aptian-Albian fish faunas of those continents.

The individual tracks of *Mawsonia lavocati*, *Calamopleurus africanus* and *Enchodus* sp. did not form any generalized track. The same also applies to *Dastilbe crandalli*, *Lepidotes* sp., *Mawsonia gigas*, *Santanichthys diasii* and *Vinctifer comptoni*, because of their wide distribution in Western Gondwana.

The individual tracks of *Araripichthys castilhoi*, *Axelrodichthys araripensis*, *Notelops brama*, *Paraelops cearensis*, *Placidichthys bidorsalis*, *Santanaclupea silvasantosi* and *Vinctifer araripensis* are present in Node A.

DISCUSSION AND CONCLUSIONS

The large number of taxa (112) represented by 219 occurrences permits an overview of the paleoichthyofauna from Brazil and Africa during the Aptian-Albian. The 38 individual tracks obtained confirmed the great biodiversity in the range studied, as well as allowing the identification of distributional patterns.

In Brazil, most of the paleoichthyofauna was found in the Araripe Basin, which is considered an important Konservat Lagerstätte due to its diversity and the exceptional preservation of fossils.

In Africa, the majority of species occurs in the northwest region. This distribution can be explained by the intense tectonic processes during the Aptian-Albian, such as the break-up of Gondwana and the opening of South Atlantic Ocean, as well as eustatic sea-level changes that resulted in the development of epicontinental seas.

Overall, the generalized tracks are associated with the break-up of Gondwana and with regional events such as the East Brazilian Rift System

(EBRIS; Chang et al. 1992), that are related to this fragmentation.

Generalized tracks 1 and 2 (Figure 1) are located in the Araripe Basin and show the existence of two distinct faunas: one of which extended its distribution to the north (GT1 - Northern Araripe) and the other, to the south (GT2 - Southern Araripe).

The Node A (Figure 1), named here Araripe Node, is complex, because it possesses a mix of biota from GT1 and GT2, and also a local assemblage of fishes.

Maisey (2000) argued that the separation of South America and Africa occurred through many successive geologic events, rather than a single rifting event followed by simple rotational drifting (e.g., Szatmari et al. 1987, Popoff 1988). Popoff (1988) assumed a model for the South American Plate composed of at least three subplates exhibiting sequential and overlapping rift-drifting histories. This indicated rotational movement about an axis in the Ceará region suggested by Szatmari et al. (1987). This event would produce northerly compression between South America and Africa so that connections persisted through a long period of the Late Cretaceous. Szatmari et al. (1987) argued that compressional events on the equatorial Atlantic floor from the Late Cretaceous to Paleogene favored connections via oceanic islands formed from midocean ridges. As a result, many possibilities for vicariance and geodispersal arise.

Maisey (1993) stated that an event spanning about 100 million years, such as the tectonic separation between South America and Africa can be viewed as a causal factor in biogeographical analyses. Thus he claimed that other events of shorter temporal duration had more effective impact upon the biota. According to Maisey (1991), the region of Araripe Basin has sufficient data to indicate the existence of marine transgressions, extending from the Neocomian to the Aptian. This probably connected the northeast Brazilian rift basins to the interior basins, as well as the South and North Atlantic oceans (Martill et al. 2007), considering that marine ingressions continued through the Turonian (Maisey 1991) (Figure 2).

In addition, possible events of mass mortality of fishes that occurred during these transgressions may have been a result of abrupt changes in salinity associated with deoxygenation caused by the increase of microbial organisms (Martill et al. 2008, Saraiva 2008).

The generalized track 3 (Figure 1), named Trans-Gondwana, is located in the north center of Western Gondwana. This is consistent with widespread vicariant effects from Aptian-Albian, as the final break-up of Gondwana, which separated Africa from South America, with special emphasis on Brazil. Gondwana fragmentation was not produced by a single episode, but from a complex process involving a series of geological events such as several sequences of rifts (Maisey 2000). This event led not only to the separation of continents, but also the formation of South Atlantic Ocean. This process was identified by Souza-Lima et al. (2002) through an asynchronous sequence of geological events that affected the Brazilian eastern and equatorial margins.

The rifting occurred in two directions, from south to north on the Brazilian side and from west to east in the equatorial margin. The presence of a marine connection in the equatorial margin represents the extension of North Atlantic Ocean towards the south. This seaway clearly separated the paleoichthyofauna of Gondwana and Laurasia and replaced the Tethys Sea (Souza-Lima et al. 2002).

Maisey (2000) supported this approach and suggested that this new marine connection allowed marine organisms to extend their distributions to new areas. Arai (2009) pointed out that during the Aptian-Albian interval, Gondwana remained most of time flooded by marine transgressions, which would have allowed an exchange of marine fauna between Africa and Brazil.

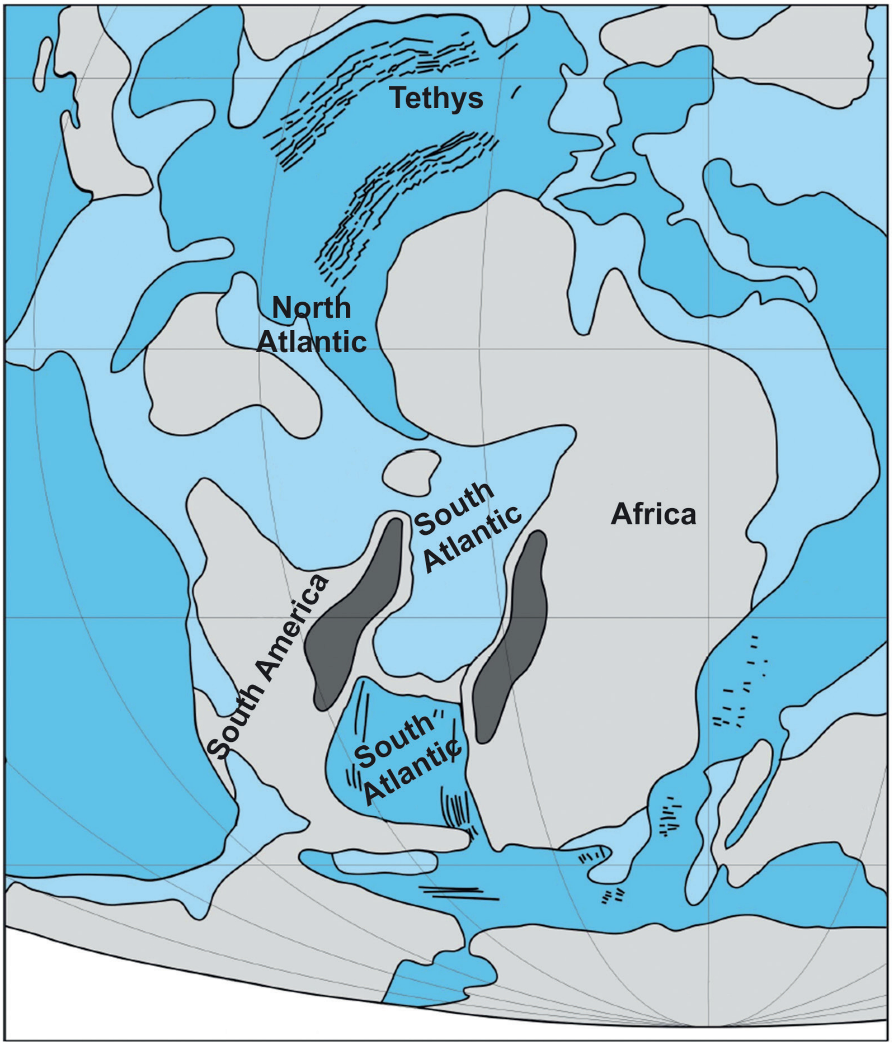

Figure 2 - Paleogeographic reconstruction of Atlantic Ocean in the Albian (modified from Azevedo 2004).

This could explain the similarity of the paleoichthyofauna of the two continents and the vicariant event that separated them.

The Gondwanic Node (Node B) obtained from the connection between generalized tracks 1 and 3 (Figure 1) is associated with the same vicariant event resulting from rifting, with GT1 representing the Brazilian biota and GT3 the African biota.

The GT4 (Figure 1) is located in the north of Western Gondwana and represents a probable local seaway produced by marine transgressions. Azevedo (2004) proposed a paleogeographical reconstruction for the Albian, adopting the base map of Hay et al. (1999). This reconstruction emphasized the existence of a shallow, intra or epicontinental sea on that region, corroborating the data herein obtained which support the existence of a marine connection, indicated by GT4 (Figure 3). Due to the break-up of South America and Africa, the waters of South Atlantic invaded the North and Central Atlantic, increasing resurgence and dispersion of hot and salty water, and stimulating biological productivity in other parts of oceans (Pletsch et al. 2001). Moreover, during the Albian, the South Atlantic was occupied by species from the Tethys Sea (Pletsch et al. 2001).

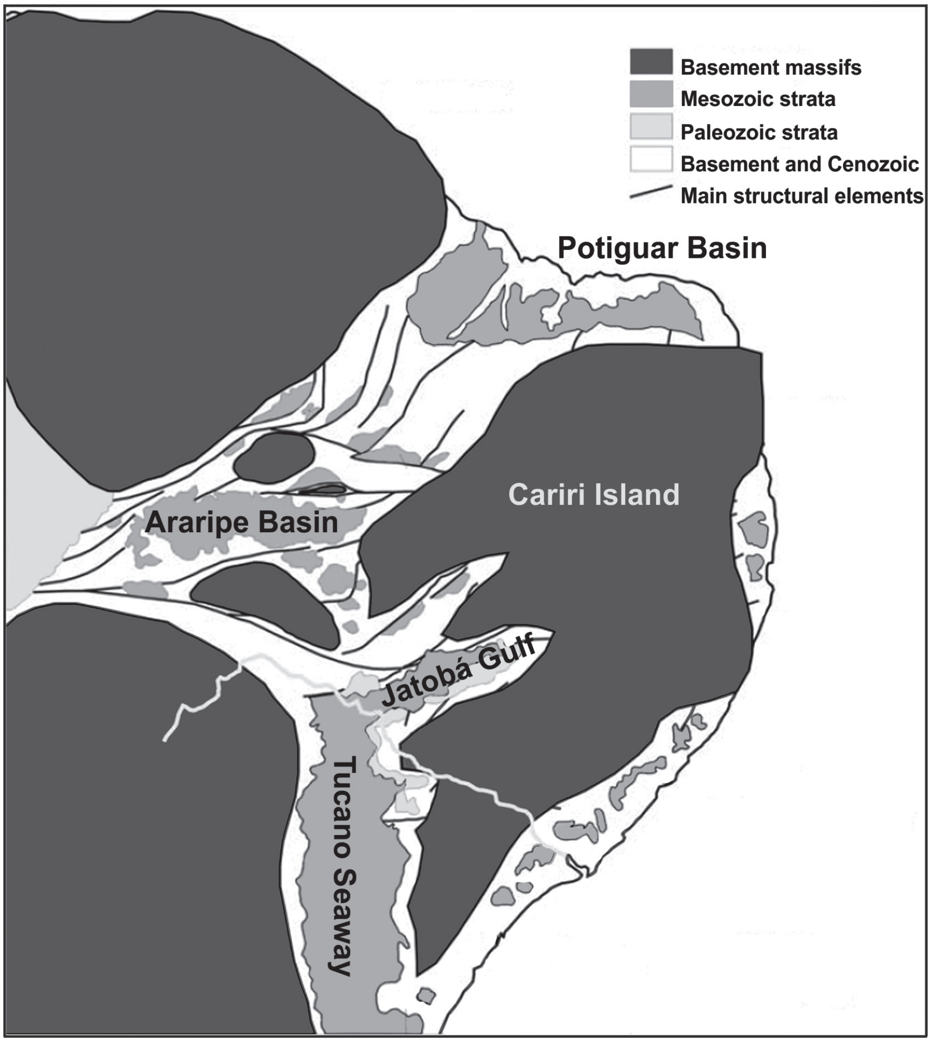

Figure 3 - Map showing possible intermittent marine connections between South and North Atlantic during Cretaceous (modified from Martill et al. 2007).

Several studies show the existence of a Trans-Saharan marine connection during Cenomanian and Turonian that connects the Tethys Sea and South Atlantic across the Sahara to West Africa. Simultaneously, the rising sea level caused the appearance of several other marine connections, including the Proto-North Atlantic (Gallo et al. 2007).

Pletsch et al. (2001) also supported this idea suggesting that there was a rising sea level in the South Atlantic during Cenomanian-Turonian. This transgression also produced an increase of nutrients and temperature and, consequently, improved the primary production (Herbert and Sarmiento 1991). However, the appearance of a Turonian marine connection could have started earlier than the Aptian-Albian, which could explain the existence of a huge fish fauna at this locality.

This can be explained if rising sea level and formation of epicontinental seas occurred as an intermittent process and not as a single event. Moreover, at the end of the Aptian, there was an equatorial marine connection between the North and South Atlantic and this epicontinental transgression continued until reaching its maximum extent in the Cenomanian and Turonian (Maisey 1991).

The Node C (Nigerian Seaway), obtained by the intersection of generalized tracks 3 and 4 (Figure 1), can be related to the exchange of fauna due to the existence of epicontinental seas, in several parts of Gondwana, caused by marine transgressions occurred during the Aptian-Albian.

All data indicate that the generalized tracks and biogeographical nodes are associated with the great vicariant effect caused by the fragmentation of Gondwana.

ACKNOWLEDGMENTS

We are much indebted to Marise Sardenberg Salgado de Carvalho for valuable comments on earlier draft of the manuscript. We are also grateful to Michael Heads for his insightful review of the manuscript. This research is part of a project supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ).

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