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Original article

Historical relationship of the Caribbean and Amazonian Miocene ichthyofaunas: A hypothesis reviewed under a biogeographical approach[☆]



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ARTICLE INFO

Article history:

Received 29 November 2014
 Accepted 9 June 2015
 Available online 26 June 2015

Keywords:

Miocene
 Ichthyofauna
 Palaeobiogeography
 Caribbean
 Amazonian
 South America
 Pacific

ABSTRACT

South-American foreland basins are related to the compressional tectonics that built the Andes starting in the Mesozoic; then the Neogene uplift of the Eastern Cordillera directly affected the sedimentary history of Amazonia, changing the course of the proto-Amazon/Orinoco Rivers. Marine influence in South America has a long history with episodic transgressions and regressions from the Campanian to the Late Miocene, with the Caribbean and/or the Pacific connections considered as the most likely sources. Previous studies on Neogene fish assemblages regarding historical relationships of the Caribbean and Amazonian regions based their conclusions on non-biogeographical methods. Here, we analyze the distribution of 241 Miocene fish taxa from 32 lithostratigraphic units in northern South America and the Caribbean using a biogeographical method. We identify eleven distributional patterns and nine biogeographical nodes. Our results show a close relationship between the Caribbean and Amazonian Miocene ichthyofaunas. Furthermore, they indicate that this relationship has to be separated into two distinct components: western Amazonian/Caribbean, and eastern Amazonian/Caribbean. We hypothesize that patterns and nodes that involve the Pacific margin of northern South America or southern Central America reflect pre-Andean (older) geographical configurations pointing to the eastern Pacific as a relevant component in the history of diversification of Amazonian fish biota prior to and during the Neogene.

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1. Introduction

Neotropical fish diversity has an ancient history with some higher-level endemic clades extending back into the Cretaceous. Fossils show that some modern, generic-level clades had differentiated by the Paleogene, and that the fish fauna was essentially modern by the Late Miocene (Lundberg et al., 1998). Although the majority of Neotropical fishes have a long history of evolution dating back to the final rupture of the South American and African continents (e.g., Siluriformes and Characiformes; Lundberg et al., 1998, 2010), it is thought that some lineages colonized South America much later, as a product of marine incursions in the Amazon during the Oligocene and Miocene (Hoorn, 1993; Webb, 1995; Lovejoy et al., 1998, 2006; Lundberg

et al., 1998; Monsch, 1998; Boeger and Kritsky, 2003; Wesselingh and Macsotay, 2006; Cooke et al., 2012).

Marine influence in South America has a long history with episodic transgressions and regressions from the Campanian up to the Late Miocene (Lundberg et al., 1998; Brito et al., 2007). The Western Amazon was affected by marine incursions at least twice during the Neogene (Hoorn, 1993, 1994a,b, 1996). The extent and timing of Neogene marine incursions in Amazonia is currently controversial. Some authors have suggested that marine incursions were long lasting and widespread (Räsänen et al., 1995, 1998; Webb, 1995; Gingras et al., 2002). Others have suggested that the predominant depositional context of Miocene Amazonia was freshwater, interspersed with brief and geographically limited bouts of marine influence (Hoorn, 1996; Hoorn et al., 2010; Vonhof et al., 1998, 2003; Wesselingh et al., 2002; Linhares et al., 2011). Gross et al. (2013) proposed a fluvial depositional system for Western Amazonia during the Late Miocene. Latrubesse et al. (2007) refuted the existence of an intracontinental seaway through southwestern Amazonia during the Late Miocene (11–10 Ma),

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connecting the Caribbean Sea with the Paraná Basin (Räsänen et al., 1995). Instead, they held that the depositional environment of the entire Late Miocene was continental, and that the deposits in Peruvian Amazonia attributed to a marine Miocene tidal environment are fluvial sediments (Latrubesse et al., 2010).

The Caribbean is usually considered the most likely gateway of the Miocene marine influences and incursions into the Llanos Basin (Bayona et al., 2008; Gómez et al., 2009) and upper Amazon (Hoorn et al., 1995; Wesselingh et al., 2002; Vermeij and Wesselingh, 2002), but Nuttall (1990) also considered three other possible sources: an eastern connection along the course of the current Amazon river, a southern connection via the Paraná river basin, and a western connection to the Pacific. According to the summary of Neogene palaeogeography presented by Nuttall (1990), and partially from his own palaeontological evidence, the Caribbean and/or the Pacific connections was thought the most likely, the last one thought to have lain in the Peruvian-Ecuadorian border area. Non-Caribbean marine incursions during the Miocene were considered unlikely by Hoorn et al. (1995) and Lundberg et al. (1998) for a variety of reasons, but Lovejoy et al. (2006) noted the presence of marine sister taxa in the alternative marine incursion areas.

The sedimentary basins of the Amazonia are fundamental elements that dictate the present landscape of the region. The geological evolution of the basins established the topography and the geomorphology of the rivers, lakes and marine systems that filled the depressions over the last 500 million years. The extensive continental lowlands of Amazonia interacted dramatically with the uplift of the Andes during the last 23.5 million years (Neogene times), creating a special and unique region in terms of drainage, fauna and flora (Ribeiro Wanderley-Filho et al., 2010).

The history of the sub-andean foreland basins in particular is of major relevance in understanding how past geographical configurations shaped the fish biotas in western Amazonia. Foreland basins are related to the compressional tectonics that built the Andes, which in turn were initiated by the collision of the Caribbean Oceanic Plateau with the Northern Andean margin (75–65 Ma) and break-up of the Farallon Plate during the Oligocene (27–25 Ma) (Martin-Gombojav and Winkler, 2008). Although tectonic pulses in the Andes are documented from Mesozoic time onwards, it is mainly the Late Paleogene and Neogene uplift of the Eastern Cordillera and Cordillera de Merida, the Cordillera Real, and Nazca Ridge subduction that directly affected the sedimentary history of Amazonia (Hoorn et al., 2010 and references therein). Foreland basins extend from Argentina to Venezuela along the eastern side of the Andes.

The history of the Amazonian drainage basin shows a geochronological progression that proceeds from west to east. During the Late Cretaceous, western Amazonia was a backarc basin in a predominantly marine setting, with a discontinuous proto-Andean island arc located to the west (Wesselingh et al., 2010). From the Late Cretaceous to the Late Miocene, the history of the basin was closely linked to the evolution of the Andes. Foreland basins formed east of the Andes, where the south-north trending fluvial system was located during Middle Eocene-Early Oligocene (43–34 Ma). During the Oligocene (34–24 Ma), the major drainage divided between west and east flowing Amazonian drainages system shifted from Monte Alegre in eastern Amazonia to the Purus Arch in central Amazonia. By the Early-Middle Miocene (24–11 Ma), Amazonia was mostly part of the south-north trending river system that became a complex of lakes, swamps, tidal channels and marginal marine embayments that was directed towards the Caribbean. Finally during the Late Miocene, (11–7 Ma), the transcontinental drainage of the Amazon River was established and the first Andean sediment influx was registered in the Amazon Foz basin and the Ceara Rise (Figueiredo et al., 2009).

Comparative studies on Neotropical Miocene marine ichthyofaunas remain scarce and descriptive (Longbottom, 1979; Gillette, 1984). Some studies on Neogene fish assemblages and the palaeobiogeography of the Caribbean and Amazonian regions based their conclusions regarding historical relationships on Principal Component Analyses (Aguilera et al., 2011; Aguilera and Pães, 2012). Most of the studies involving the Miocene fossil record provided taxonomic descriptions of new fossil taxa (fish or other groups), sometimes with brief discussions about taxonomic and geographical affinities (Deynat and Brito, 1994; Laurito, 1996; Távora and Garrafielo Fernandes, 1999; Aguilera and Rodrigues de Aguilera, 2001, 2004a,b; Brito and Deynat, 2004; Laurito, 2004; Fernandes dos Reis, 2005; Aguilera et al., 2008; Laurito and Valerio, 2008; Laurito et al., 2008; Ferreira Costa et al., 2009; Aguilera et al., 2013a,b; Pimiento et al., 2013). However, none of the previous studies have used a biogeographical method to analyze the distribution of the fossil taxa involved.

Historical biogeography analyzes patterns of species and supraspecific taxa at large spatial and temporal scales; it deals mainly with processes that occur over long periods of time (Morrone, 2009). These processes are responsible for the historical pathways of changes in biogeographical distributions. The main factors involve changes in the Earth's surface: creation or destruction of seas and seaways on cratonic areas, plate movements and realignments, creation of mountain ranges, and oceanographic and climatic changes (Cecca, 2002).

Biogeographical studies using only fossil taxa are rare (Fielitz, 1996; Lieberman, 2003; Cecca et al., 2005; Gallo et al., 2007). Studies adopting a biostratigraphic approach only allude to the palaeobiogeography of taxa over a short interval of time and often overlook historical relationships among taxa and areas (Silva and Gallo, 2007). On the other hand, integration of fossil and living taxa in the same analysis has been successfully undertaken (Heads, 1989, 2006, 2012; Candela and Morrone, 2003).

Interpretations of historical biogeographical patterns stress the steps of biological evolution in its spatial dimension. This allows the study of phyletic relationships relative to the evolution of their geographic distributions, as in cladistic biogeography, for example, but also means that geological work can exploit biogeographical data for palaeogeographic reconstructions (Cecca, 2002). Through a biogeographical approach, we aim to test the hypothesis of a historical relationship between the Caribbean and Amazonian Miocene ichthyofaunas.

2. Material and methods

2.1. Units of analysis

Fifty-seven sedimentary basins were used as units of analysis (Fig. 1). They contain the 32 Miocene formations from which distributional fossil records were taken. Sedimentary basins constitute historical entities that have developed under particular tectonic regimes that account for their origin, evolution and depositional history through geological time. Fluvio-lacustrine hydrographic systems have been determined by changing mountain slopes and foreland basin geometry. Table 1 lists the sedimentary basins in northern South America and the Caribbean by type, country, and Miocene formation(s) retrieved in each basin.

2.2. Taxa

The palaeo-ichthyofauna studied includes 241 taxa of fishes: 62 species of Chondrichthyes (31 genera and 16 families), and 59 species of Osteichthyes (82 genera and 48 families). In several cases, specimens were identified only to the family or subfamily level (e.g., Potamotrygonidae, Gobiidae, Loricariidae, Pseudopimelodidae,

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