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Fossil freshwater fishes and the biogeography of northern South America

Peixes fósseis de água doce e biogeografia do norte da América do Sul

Original version

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Resumo

Os vertebrados fósseis têm sido utilizados na literatura como fonte de informação sobre cenários paleogeográficos passados no neotrópico, embora os peixes em especial tenham sido menos estudados, apesar da disponibilidade em coleções e no campo. Restos fósseis apendiculares são uma das ocorrências mais comuns de bagres fósseis e tendem a ser abundantes localmente em faunas conhecidas de idade Cenozoico na América do Sul; no entanto, a anatomia comparada desses complexos anatômicos tem sido pouco estudada, com uma terminologia anatômica complexa e confusa, em que cada referência publicada ignora os termos anteriores propostos e, assim, cria vários sinônimos diferentes para a mesma característica osteológica. Foi realizada uma revisão completa da literatura, juntamente com o revisão de viventes da ordem Siluriformes, a fim de fornecer uma terminologia anatômica padronizada para os espinhos das nadadeiras dorsal e peitoral. Três faunas continentais de vertebrados foram encontradas no norte da Colômbia, numa área atualmente separada das drenagens da Amazônia-Orinoco pelos Andes da Cordillera Oriental na Colômbia e nos Andes de Merida na Venezuela. Os peixes fósseis de água doce da formação do meio do mioceno Castilletes são aqui descritos, juntamente com sua relevância em diferentes tópicos, desde taxonomia e anatomia comparada até reconstruções paleogeográficas e paleoambientais; essa assambleia fóssil está em conformidade com os modelos anteriores de conexões de paleodrenagens entre áreas cis- e trans-andinas na literatura. Duas faunas da idade do Plioceno das formações Sincelejo e Ware foram estudadas usando uma abordagem semelhante à da assembléia fóssil da formação Castilletes. As assembléias da idade do Plioceno implicam a presença de uma conexão hídrica entre as drenagens agora separadas pelos Andes, ou seja, elas estendem mais próximo do presente o mesmo padrão recuperado na assembléia de idade Mioceno médio e são contrarias aos modelos tectônicos clássicos dos Andes do norte que sugerem uma perda na conectividade de drenagem de 11 até 13 Ma. Um conjunto de métodos quantitativos para inferir o tempo de separação entre duas áreas biogeográficas usando dados da estimativa do tempo de divergência é aqui proposto e discutido como métodos promissores para estimativa estatística em biogeografia. Embora tenham sido projetados principalmente com padrões vicariantes em mente, esses métodos são extensíveis o suficiente para serem aplicáveis a qualquer tipo de evento que ocorra no tempo geológico deixando vestígios nos estudos de estimativa do tempo de divergência. Os diferentes métodos geralmente inferem um intervalo de separação de 2 a 5.8 Ma, consistente com as informações das assembléias fósseis que implicam uma conexão persistente para aproximadamente o mesmo intervalo; portanto, as faunas

fósseis das formações Sincelejo e Ware seriam a última evidência conexões de drenagem nos Andes. Dentro dessa estrutura temporal, vários padrões de biodiversidade, como composição da fauna, taxas de endemismo e padrões espaciais, e o momento da geração da biodiversidade em escala regional para continental devem ser reavaliados à luz dos resultados aqui fornecidos.

Palavras-chave: Estatistica, Andes, Siluriformes, Anatomia, Paleoictiologia.

Abstract

Fossil vertebrates have been used in the literature as a source of information on past paleogeographic settings in the Neotropics, although fishes in special have been less studied despite availability in collections and in the field. Appendicular fossil remains are one of the most common occurrences of fossil catfishes and tend to be locally abundant in well-known faunas of Cenozoic age in South America; however, the comparative anatomy of these anatomical complexes has been poorly studied, with a complex and confusing anatomical terminology where each published reference ignores previous terms provided and thus creates a number of different synonyms for the same osteological feature. It was carried out a thorough literature review along with direct examination of extant representatives of the order Siluriformes in order to provide a standardized anatomical terminology for the dorsal- and pectoral-fin spines in the order. Three continental vertebrate faunas have been found in northern Colombia, in an area that is currently separated from the Amazon-Orinoco drainages by the Andes of the Cordillera Oriental in Colombia and the Merida Andes in Venezuela. Fossil freshwater fishes from the middle Miocene Castilletes formation are herein described along with their bearing on different topics ranging from taxonomy and comparative anatomy to paleogeographic and paleoenvironmental reconstructions; this fossil assemblage conforms to previous models of paleodrainage connections between cis- and trans-Andean areas in the literature. Two faunas of Pliocene age from the Sincelejo and Ware formations were studied using a similar approach to that of the fossil assemblage of the Castilletes formation. The assemblages of Pliocene age imply the persistence of a hydric connection between drainages now separated by the Andes, that is, they extend towards the present the same pattern recovered in the assemblage of middle Miocene age and are against the classical tectonic models of the northern Andes that suggest a loss in drainage connectivity about 11–13 Ma. A set of quantitative methods for inferring the time of separation between two biogeographic areas using data from divergence time estimation are herein proposed and discussed as promising methods for statistical estimation in biogeography. Although primarily designed with vicariant patterns in mind, these methods are extensible enough as to be applicable to any kind of event occurring in geologic time that leaves traces in divergence time estimation studies. The different methods mostly suggest a separation interval of 2–5.8 Ma, consistent with the information from the fossil assemblages that imply a connection persisting to about the same interval, therefore, the fossil faunas of the Sincelejo and Ware formations would be the last evidence of drainage connections across the Andes. Within this temporal framework,

a number of biodiversity patterns such as faunal composition, endemism rates and spatial patterns, and the timing of generation of biodiversity at regional to continental scale should be reassessed in light of the results herein provided.
Keywords: Statistics, Andes, Siluriformes, Anatomy, Paleoichthyology.

Chapter 1

Praeambulus

Abstract

The main goal of the present project is to explore the biogeography of Northern South America (NSA) from a paleontological perspective and the interplay of the fossil record and the interrelationships among extant taxa as a way to infer past drainage connections and their relevance for explaining the faunal relationships among drainages in NSA. This portion of the continent present several important drainages, all of them related historically to the core Amazon/Orinoco/Guyanas, but with highly endemic and poor faunas. Such high endemism and small richness seems to be the product of tectonic events that shaped both the geography and the drainages of NSA, therefore triggering speciation and extinction events in this part of the continent. The fossil record is going to be used in the present project in order to address the question of drainage connections among cis- and trans-Andean NSA during the early Pliocene, i.e., since the last 2 Ma. This work is unique in that the fossil collections herein available are largely unstudied and are crucial for understanding the tectonic and faunal evolution of NSA during the early Pliocene. In the same way, it completes the temporal record in NSA from the middle Miocene to the Pliocene, being complementary with earlier works with important fossil faunas such as La Venta in Colombia and Urumaco in Venezuela. It is expected that this work will provide a new paleogeographic framework, as well as further information to be used in divergence time studies, that coupled with geologic information are the base for understanding the evolution of freshwater faunas in the presence of complex geological processes.

Introduction

The Neotropical freshwater fishes are by far one of the most diverse vertebrate groups in the New World (Nelson, 2006). It is not only species-rich, but also presents high endemism levels at several taxonomic and geographic scales. The Neotropics harbors ca. 320 species per km2 while Tropical Asia 165, Australasia 53, North America 42, and Europe 30 (Albert

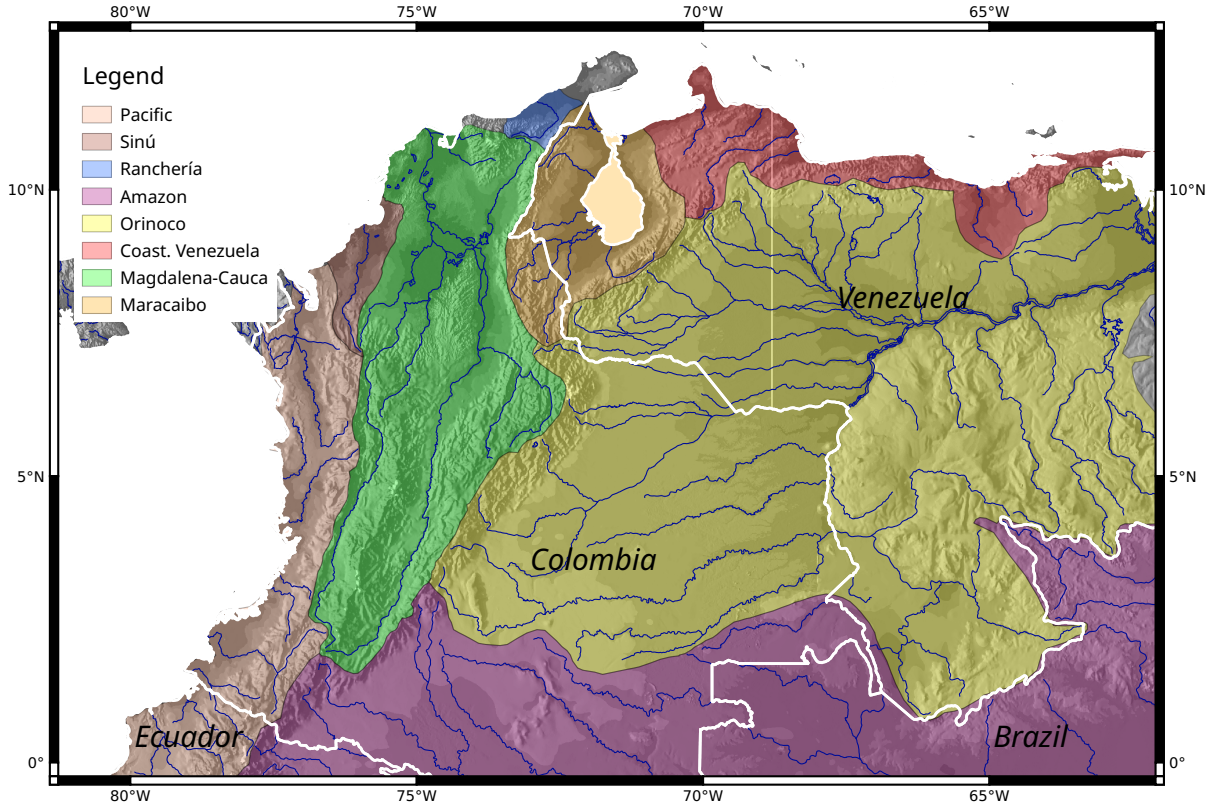

Figure 1.1: *Geographic context of major drainages in NSA. Country limits are in white and country names in italics. Drainages are colored according to the legend.*

et al., 2011). Several hypotheses have been suggested to explain the diversification and biogeographic patterns of freshwater fish biodiversity in South America, including high diversity in microhabitats, evolutionary constrains, and a complex geological and hydrological history (Albert et al., 2006, 2011; Lundberg, 1997; Lundberg et al., 1998). Such diversity arose coupled to the complex tectonic history of Northern South America (NSA hereafter) along with the consequent drainage evolution, generating several separated drainages from wider and older ones (e.g., the proto Amazonas-Orinoco; Lundberg, 1997). However, the temporal and paleogeographic context for such biotic and geological evolution remains poorly explored, with just two fossil fish faunas accounting for more than 90% of what we know about the late Cenozoic freshwater fishes of NSA (i.e., La Venta, middle Miocene of Colombia, and Urumaco, late Miocene of Venezuela). Despite such faunas have provided immense insight into the drainage evolution in NSA, much remains to be done in other lithostratigraphic units of younger age, what will provide a more precise way to look at the timing and pattern of drainage evolution and its bearing on biodiversity dynamics in geological time. Such younger units provide the unique opportunity to further constrain the orogenic history of the Northern Andes, as well as to evaluate the temporal and spatial context of the geologic history of NSA drainages.

NSA has several important river drainages (i.e., Magdalena, Maracaibo, Coastal Venezuela

and Orinoco, Figure 1.1). These drainages have changed drastically during the Neogene due to the complex tectonic and climate history of the region (Fedorov et al., 2013; Mann et al., 2006; van der Hammen et al., 1973). This area is treated as peripheral to the core Amazon region by Albert et al. (2011), and presents a poorer fish fauna when compared to the core Amazon/Orinoco/Guianas (Figure 1.2A). A large amount of its species (and even genera) is endemic to each drainage (More than half the number of species for each drainage, Figure 1.2B). The high levels of species-level and genus-level endemism of the Maracaibo and Magdalena basin suggests several speciation events during the late Neogene, and can serve as a model to study the effect of drainage history and climate change on diversification of fish lineages.

The timing of uplift of the Andes, and specially the northern Andes is still highly controversial. Some authors suggest that the Cordillera Oriental in Colombia, and the Mérida Andes and Cordillera de la Costa in Venezuela were positive by middle to late Miocene and the Perijá Range and the Mérida Andes during the late Miocene (Diaz de Gamero, 1996; Lundberg et al., 1998, and references thereir). In contrast, some authors suggest a more complex tectonic history for the Andes of NSA, arguing that the Cordillera Oriental in Colombia uplifted in pulses, with some areas being positive as early as late Paleocene (e.g., Santander Massif; Bayona et al., 2013) and with other areas uplifting from middle Eocene to middle Miocene (e.g., Perijá Range and central Cordillera Oriental; Ayala et al., 2012; Bayona et al., 2013, 2010; Caballero et al., 2010; Ochoa et al., 2012). Both scenarios would have different consequences for the freshwater fish faunas (both extant and extinct), and therefore, they could be used to better understand the evolution of the northern Andes.

A fossil vertebrate fauna was recently discovered in the Guajira Peninsula by the Smithsonian Tropical Research Institute. This fauna has been dated as spanning from 18Ma (early Miocene) to the mid Pliocene (2.7 Ma) (Moreno et al., 2015). Some of the units have yielded a continental fauna, giving a unique opportunity to study the biotic changes that took place in this area during the last 18 Ma. When analyzed along with some other fossil sites of similar age (e.g., Urumaco and San Gregorio, late Miocene to late Pliocene, both in Venezuela), one is able to explore the faunistic relationships between those areas during the Miocene to Pliocene. It is not just the geographic location of those fossil faunas but also their age what make them crucial for testing paleogeographic models, because orogenic events during late Miocene to late Pliocene are one of the conflicting aspects between the current proposals on the orogenic evolution of the Andes of NSA.

This new fossil fauna was recovered in an arid and hot region at sea level in Northern Colombia, with no present riverine connections to adjoining drainages (i.e., Magdalena and Maracaibo). The Guajira Peninsula lies to the north of the Perijá Range and presents very rich exposures of Neogene rocks, specially of late Neogene age Rollins (1965). These arid conditions along with very low precipitation (mean annual precipitation = 397 mm, mean annual temperature = 28.7 °C; Ramírez and del Valle, 2011) are strikingly contrasting with the data gathered from geology and paleontology on the environmental conditions of this

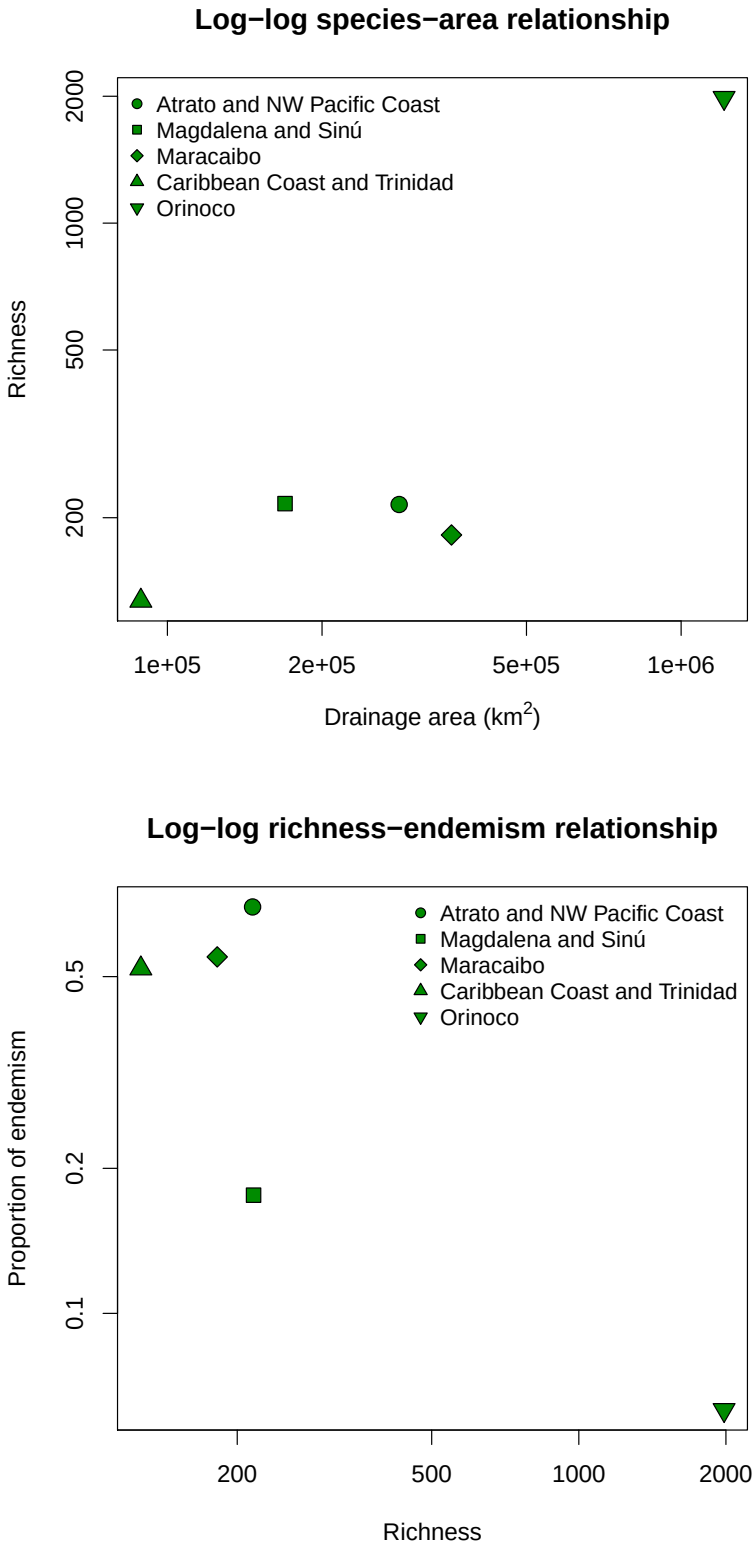

Figure 1.2: *Descriptive measures of biodiversity per drainage region. A) Log-log scatterplot of watershed area for the main drainages of NSA vs. number of species. B) Log(Number of species) vs. proportion of endemic species scatterplot for each drainage (p = endemics / total spp.). Pac = Atrato and NW Pacific; Mag = Magdalena and Sinú; Mar = Maracaibo; Car = Caribbean drainages and Trinidad; Ori = Orinoco. Note the high endemism levels for small drainages in comparison to the whole Orinoco drainage. Data taken from table 2.1 in Albert et al. (2011).*

area during the late Miocene to early Pliocene.

A preliminary paleoenvironmental reconstruction suggests that the Peninsula was a tropical forest with presence of either middle to large rivers or a deltaic area, aquatic vertebrates such as crocodylians, turtles, freshwater fishes, as well as terrestrial and amphibian mammals (Aguilera et al., 2013; Amson et al., 2016; Cadena and Jaramillo, 2015a,b; Carrillo et al., 2018; Forasiepi et al., 2014; Moreno-Bernal et al., 2016; Suarez et al., 2016). Such paleobiotic assemblage allows to explore past drainage connections with major drainages of NSA because of its intermediate location between the Magdalena and Maracaibo drainages, as well as being complementary to other fossil faunas of similar age (i.e., San Gregorio Formation in Venezuela). The main goal of this doctoral thesis is to study the freshwater fish assemblage of the Guajira Peninsula during the Miocene to Pliocene and to test different paleogeographic models by using past and present geographic distribution of the taxa recovered.

Given the state of knowledge on the tempo and pattern of drainage evolution in NSA along with the potential of the freshwater fish fossil record as a proxy for paleodrainage connections in geological time, a detailed study of the freshwater fossil fish fauna in Northern Colombia will provide a revaluation of both time and drainage separation events in NSA. The results of such study will revolutionize the tectonic models for andean orogeny in the Mérida Andes of venezuela as well as in the Cordillera Oriental of Colombia. In addition, this unique opportunity will provide a way to study the temporal component of faunal evolution, and therefore will help to explain why peripheral areas in NSA present low richness but high endemism as compared to the core Amazon/Orinoco/Guyana (Figure 2). A detailed account for the justification of this project is given below.

Justification

Recent studies on tectonic evolution of the Caribbean-South American plate dynamics have suggested a much more complex orogeny of the Andes than previously considered (Ayala et al., 2012; Bayona et al., 2010; Caballero et al., 2010; Mann et al., 2006; Ochoa et al., 2012). In spite of the large body of new geological research, geological tools are still very limited in providing information about paleotopography and landscape evolution, and consequently, there are still large controversies of when the drainages in northern South America were connected and/or separated (Bayona et al., 2013; Diaz de Gamero, 1996; Lundberg et al., 2010; Ochoa et al., 2012). Fishes on the other hand, can provide reliable information about drainage evolution, that is directly related to landscape construction and orogenic buildup. Freshwater fishes are an extremely important group when assessing paleohydrographic connections as they are directly linked to riverine environments, and both their diversification events and assemblage compositions are directly affected by drainage dynamics (Albert et al., 2006, 2011; Lundberg, 1997). Therefore, similarity in fossil fish assemblage is a powerful tool for testing drainage connections during geologic time.

Preliminary work (Aguilera et al., 2013), indicates that the early Pliocene Guajira Peninsula assemblage shows cis-Andean components (i.e., belonging to groups currently dwelling in rivers located east of the Andes as defined by the Cordillera Oriental in Colombia and the Mérida Andes and Cordillera de la Costa in venezuela). Given that all of these taxa are nowadays restricted to cis-Andean South America, their presence in the Guajira fauna suggests that by the early Pliocene a drainage connection between cis- and trans-Andean NSA was still present. On the other hand, specimens from the Sincelejo Formation in the Departamento de Sucre, northern Colombia, suggest the same kind of drainage connection between the paleo-Magdalena drainage and cis-Andean NSA. The La Venta fossil fish fauna allows the same conclusion, but the Sincelejo Formation is of early Pliocene age, extending the drainage connection between Magdalena and the proto-Amazonas-Orinoco from 12.8 Ma to around 2 Ma. This renders both the Guajira and Sincelejo faunas key to understand the final stage of drainage connection between cis- and trans-Andean NSA.

The late Miocene La Venta fauna (11–13 ma) (Lundberg, 1997) on the upper Magdalena Valley also shows a cis-Andean fauna. The San Gregorio Formation in eastern Venezuela, contains fossils of freshwater taxa nowadays extinct in Coastal Venezuela, as well as some elements currently restricted to the Maracaibo drainage (Aguilera et al., 2013) (Figure 1.1).

This geologic/paleontologic settings depicted above provide a unique opportunity to test drainage connections using the Guajira fauna in order to determine whether such paleodrainage was connected or not to the Orinoco drainage. If the fossil fauna presents components currently restricted to regions east of the Andes (cis-Andean components), then a drainage connection between the Guajira and the Orinoco for the early Pliocene needs to be advocated for explaining such faunal paleodistribution. On the other hand, if the Guajira fauna presents components currently restricted to the Magdalena drainage, it will be necessary to explore alternative models for connection with the latter drainage, but no direct connection to the paleo-Orinoco would be necessary, lending support to the idea that the Mérida Andes and Cordillera de la Costa in Venezuela were already positive areas. The hypotheses to be tested in the present project are described below.

Hypotheses and Objectives

Ho: By the late Miocene the main drainages of NSA were already formed as today, and no drainage connection was present between the Guajira Peninsula and the Orinoco drainage (Figure 1.3A). This alternative predicts a Guajira fossil fish fauna composed of taxa currently restricted to the Magdalena and/or Maracaibo drainages. As a consequence, the Mérida Andes and Cordillera de la Costa must have been uplifted by that time, restricting drainage connections between the Guajira Peninsula and the Orinoco drainage. Coupled with this consequence, the vicariant cases affected by this orogenic event are expected to correspond in timing with the late Miocene in divergence time analyses.

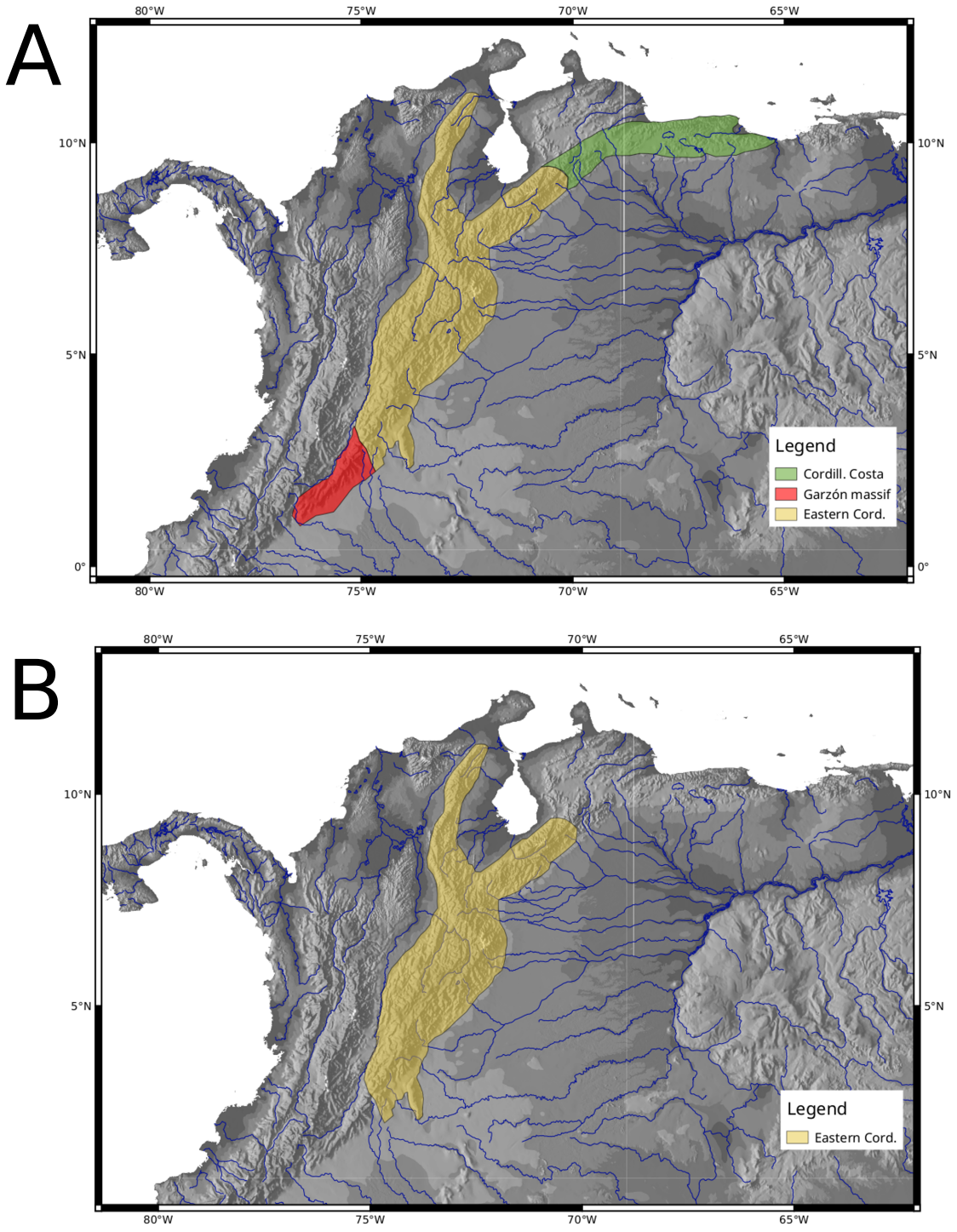

Figure 1.3: *Paleogeographic hypotheses to be tested in the present thesis. A) Null hypothesis of drainage configuration during the Pliocence. Polygons represent modern-configuration areas as water divides. B) Alternative hypothesis of drainage configuration during the Pliocene. Polygons represent the modern configuration of the Cordillera Oriental massifs while the Garzón massif and the Cordillera de la Costa in Venezuela are still not fully formed and therefore can not act as water divides. The former would allow drainage connection between the proto-Magdalena of Lundberg (1997) and the cis-Andean drainages (Amazon + Orinoco).*

Ha: The Guajira drainage was connected by the early Pliocene with the Orinoco drainage (Figure 1.3B). This alternative predicts a Guajira fossil fish fauna composed by cis-Andean taxa, suggesting drainage connections between NSA drainages and the Orinoco drainage. As a consequence, the Mérida Andes and Cordillera de la Costa were either absent or only presented partial uplift, providing space for drainage connections between the Guajira Peninsula and the Orinoco drainage. Coupled with this consequence, the vicariant cases affected by this orogenic event are expected to correspond in timing with the early Pliocene or a younger age in divergence time analyses. The objectives for the present project are as follows:

- Describe the fish assemblage present in the late Neogene sediments of the Guajira Peninsula and the Sincelejo Formation in Colombia.
- Compare the Pliocene Guajira and Sincelejo fish assemblages to with all Neogene fish faunas of NA, as well as with recent distributions.
- Test drainage connections between the Guajira Peninsula and the Orinoco based on the information provided by late Neogene fossil fish faunas as well as with time-calibrated molecular phylogenies available in the literature as well as reanalyses using the fossil information obtained in the present project.

Structure of the Thesis

The present thesis is an *opus* in five acts, as is Claudio Monteverdi's *"L'Orfeo Favola in Musica"* from 1607.

1. *Praeambulus*
2. Standardized terminology for Siluriform spines
3. A middle Miocene frehswater fish fauna from the Castilletes formation
4. Fossil fishes from the Pliocene of the Sincelejo and Ware formations
5. Statistical approaches in estimation of the time of separation between biogeographic areas

The first (and present) act settles the scene and addresses the questions to be answered and hypotheses to be tested. The second act provides the anatomical basis for the study of fossil siluriform spines (both complete and fragmentary), a prerequisite for identifying taxa from fossil spine fragments, an abundant structure often recovered from continental sediments, much neglected, and poorly understood in terms of variation and as potential sources of information for taxonomy and systematics. The third act describes the fossil assemblage in the Guajira Peninsula during the middle Miocene, a time when we expect

to evidence drainage connections across the Andes and therefore the same taxa on both sides of what we call now the Andean cordilleras. The fourth act also documents fossil assemblages but this time in more recent times, during the Pliocene in the departments of Sucre and Guajira, Colombia; this piece of information allows to mark a minimal time of persistence in drainage connection across the Andes, allowing to test initially the hypotheses of interest in the present praeambulus. Finally, the fifth act aims at testing independently the predictions of the hypothesis favored by the fossil assemblages in terms of drainage connections but this time from a statistical perspective. This last piece provides a number of analytical alternatives for using data from divergence time estimation in order to estimate a general separation time between areas as a function of individual instances recovered from these statistical estimations. Data of this nature are often found in molecular studies that frequently carry out these analysis in an almost routinely way, allowing to use reasonable samples from different biological groups for estimating general patterns in geologic time.

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