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Author contributions

EGC and OA conceived and designed the project. EGC, MR, FR, and OA designed and performed the experiments. FR and OA performed the field trip and sample collection. EGC, FR, MR, and OA analyzed the context of the information. EGC and OA wrote the paper. EGC, MR, FR, and OA revised and edited the manuscript.

AMPHI-AMERICAN NEOGENE TELEOSTEAN TROPICAL FISHES

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Abstract

During the last 20 years of paleontological expeditions in different sedimentary basins of Brazil, Colombia, Costa Rica, Ecuador, Jamaica, Trinidad, Panama, the Dominican Republic and Venezuela, teleost otoliths have been found along the Tropical Western Central Atlantic (TWCA) and the Tropical Eastern Central Pacific (TECP); these otoliths relate to the amphi-American distribution of fishes and the paleoceanographic and paleoenvironmental changes in the region during the Cenozoic. This study analyzes of the marine fish fossil based on comprehensive species records belonging to the Neogene period and listed at the generic level. Joint classification and ordination techniques were used to identify and analyze data comprising 169 genera belonging to 56 families and 20 orders, which were mostly represented by the demersal species that inhabit shallow waters. Analyses of principal components were used to calculate the covariance and the variance between formations, countries, basins, and age. The results showed that the main faunistic changes along the geochronological sequence in the Neogene basins of tropical America were a consequence of

paleoenvironmental changes.

Key words: paleobiogeography, marine paleoenvironment, tropical America, otolith, fossil fish.

1. Introduction

During the last 20 years, paleontological expeditions conducted in the Neogene sedimentary basins in almost 45 formations from ten countries/basins of Tropical America have revealed that the presence of fossil bony fishes with extraordinary body sizes is a myth. The early natural history from the New World in Columbian times excessively promotes the discoveries of giant fishes and minimizes the importance of small to medium sizes demersal fishes (Keegan, 1989; Asuá and French, 2016). However, with few exceptions, most of the Teleostean fossil species records are even smaller than the living counterparts.

Contextual interpretation of stratigraphical information and microfacies reveals that these fossil fishes inhabited sandy and mudstone bottoms in shallow water, some of which are associated with ancient estuarine systems in the Proto-Caribbean, pre-Amazon delta, and exceptionally, in coastal marine areas influenced by upwelling.

Teleostean otolith and diagnostic bones of Neogene fishes are thoroughly preserved in several Miocene to Pleistocene basins in countries along the tropical western central Atlantic (TWCA) and the tropical eastern central Pacific (TECP). However, the preservation of articulate fossil skeletons is rare; therefore, diagnostic structures of isolated bones have been used for taxonomical identification.

Most of the studies of Neogene teleostean fish associations published in the last decade from tropical America were focused on the taxonomic scope of families (e.g., Myctophidae: Schwarzhans and Aguilera, 2013; Sciaenidae: Aguilera et al., 2016; Carapidae, Ophidiidae and Bythitidae: Schwarzhans and Aguilera, 2016; Ariidae: Aguilera and Marceniuk, 2018; Diodontidae: Aguilera et al., 2017; Tetraodontidae: Aguilera et al., 2018), whereas other contributions discussed the context of fish assemblages by countries/formations (e.g., Trinidad: Nolf, 1976; Dominican Republic: Nolf and Stringer, 1992; Costa Rica: Laurito, 1996; Jamaica: Stringer, 1998; Ecuador: Landini et al., 2002; Brazil: Aguilera et al., 2014; Venezuela: Nolf and Aguilera, 1998; Aguilera and Rodrigues de Aguilera, 2001; Núñez-Flores, 2017).

The exceptional teleostean fish paleodiversity in the TWCA and TECP provides a valuable opportunity to understand the origin of modern fauna and to elucidate the macroevolutionary responses in coastal fauna affected by: (1) the paleoceanographic and paleoenvironmental changes in the region as a consequence of tectonic dynamics between the Caribbean, the North and South American plates, the Nazca and Cocos plates, with all interacting during the geographic configuration of the Proto-Caribbean and the orogenesis of the greater and lesser Antilles islands (Bachmann, 2001; Coates et al., 2005; Pindell et al., 2005; Pindell and Kennan, 2009; Montes et al., 2019); (2) the rise of the Andes cordillera, which isolated the inflow of the northern drainage system of the Amazonian effluents to the Proto-Caribbean (Rod, 1981; Díaz de Gamero, 1996; Shephard et al., 2010; Aguilera et al., 2013); (3) the onset of the transcontinental Amazon River (Damuth and Kumarm, 1976; Wolff and Carozzi, 1984; Brandão and Feijó, 1994; Silva et al., 1998; Figueiredo et al., 2009; Watts et al., 2009; Rossetti et al., 2015); (4) the Miocene marine incursion in northwestern South America (Hoorn et al., 2017; Jaramillo et al., 2017); (5) the sea level and climate changes during the Oligocene-Miocene global cooling Mi-1 and Miocene Climatic Optimum (Haq et al.,1987; Zanchos et al., 2001; Kominz et al., 2008; Stewart et al., 2017); and (6) the severance of the

Central American Seaway (CAS) by the uplift of the Talamanca cordillera and the complete isolation of the Atlantic/Pacific oceans by the Panamanian isthmus, and the final configuration of the Caribbean Sea (Montes et al., 2012, 2015; Coates and Stallard, 2013; O'Dea et al., 2016; Jaramillo et al., 2017; Molnar, 2017; Jaramillo, 2018).

A paleobiogeographical review of biotic responses as a consequence of CAS isolation was made at length by Leigh et al. (2013) and corroborated the chronological dynamics of paleoceanography and paleoenvironmental influences of the Caribbean and Amazon River within the context of fish fauna distribution (Echeverry and Gallo, 2015).

Phylogenies, the divergence time of origin, and the diversification of modern species use fossil species records as references for calibrating the molecular clock (retrospective molecular age) (e.g., Anguillormes: Santini et al., 2013; Apogonidae: Mabuchi et al., 2014; Ariidae: Marceniuk et al., 2012; Batrachoididae: Greenfield et al., 2008; Centropomidae: Tringali et al., 1999; Diodontidae: Yamanoue et al., 2011; Haemulidae: Tavera et al., 2012; Lutjanidae: Gold et al., 2011; Sciaenidae: Lo et al., 2015; Tetraodontidae: Arcila and Tyler, 2017); however, future research in evolutionary trends could support an accurate interpretation about the diversification of tropical species.

The similarity of the marine fauna preserved in Miocene sediments from Ecuador, Colombia, Costa Rica, Panama, and Venezuela promoted the designation of the Gatunian Faunal Province (between TCWA and TECP), named after the late Miocene Gatun Formation in Panama (Woodring, 1974; Petuch, 1982, 1988, 2004; Landau et al., 2008). In contrast, the fauna after the closure of the Isthmus of Panama was sufficiently distinct to warrant the use of the term Pliocene Caribbean Province (Landau et al., 2008). Both provinces reflect the lithostratigraphic sequences across the Caribbean and the shift from one to the other broadly records a widespread biological extinction and turnover in the TCWA and TECP marine fauna.

Based on the compositional structure of fish assemblages preserved in fossil bones, teeth, and otoliths, the Gatunian Faunal Province can be divided into five sub-provinces: Antillean, Costa Rican, Panamanian, Venezuelan, and Western Central Atlantic (Aguilera et al., 2011; Aguilera and Páes, 2012). The relationship of the Brazilian equatorial fish faunas amongst these sub-provinces has yet to be explored.

In this study, we used detailed basinal information from teleostean fossil fishes to more comprehensively expose the biogeographical and geochronological dynamics of the tropical fishes of the Americas, following the country, basin, and age trends. We also connected the observed macroevolutionary differences with the tectonic and paleoenvironmental context, showing that extinction and the biotic turnover were related to paleoenvironmental changes and habit loss. This is because habitat loss plays a major role in extinction and geographic isolation as a consequence of paleoceanographic and geographic changes (e.g., onset of the Amazon and Orinoco delta; complete uplift of Isthmus of Panama), thus triggering vicariance.

2. Materials And Methods

2.1. Study Area

The Neogene tropical America teleostean otolith fish assemblages were obtained from nine countries/basins (Fig.1) during paleontological expeditions in Brazil, Colombia, Costa Rica, Ecuador, Panama, and Venezuela, and they were reviewed and organized under the scope of: (1) The Federal University of Pará, the Museu Paraense Emilio Goeldi and the Federal Fluminense University, Brazil (Pirabas Paleontology Project), (2) the Universidad del Norte, Colombia (La Guajira Paleontology Project), (3) the Smithsonian Tropical Research Institute, Panama (Panama Paleontology Project), and (4) the Francisco de Miranda University, Venezuela (Venezuelan Paleontology Project). Specimens from Trinidad and the Dominican Republic were studied based on additional samples and collections at the Basel Museum of Natural History and the Smithsonian National Museum of Natural History in Washington D.C. Data from Jamaica as well as complementary information were retrieved from published literature (Supplementary table 1).

All formations and locations were described by stratigraphic age, countries, and basins following the stratigraphic information detailed in relevant literature (e.g., Schwarzhans and Aguilera, 2013; Aguilera et al., 2016). The stratigraphic data follow the International Chronostratigraphic Chart (ICS: Cohen et al., 2013), edition 2019/05, modified in the context of the Neogene fish records of tropical America (Fig. 2) by Schwarzhans and Aguilera (2013) and Aguilera et al. (2016).

2.2. Sampling design

For the taxonomic list of species, we adopted the most recent published fossil species descriptions per country, basin, and stratigraphic age. In addition, we used novel unpublished data. For this study, the taxonomy was normalized according to the standard ecological and paleontological methods (Foote and Miller, 2007; Greffard et al., 2011; Carrillo-Briceño et al., 2018). A comparative analysis of fine versus coarse taxonomic resolution may be adequate for trends of paleobiogeographic and paleoenvironmental analyses. However, despite the highest possible level of taxonomic resolution to diminish distortions caused by preservation and sampling biases, endemic groups, and nomenclatural issues, we chose the generic level, such as the most accurate taxonomy, to be analyzed. However, fossil records of few relevant families without generic and specific identifications are included as well (e.g., Gobiidae, gen. sp. ind.). Biases in the analyses can be attributed to rare taxa that occur as singletons in a country/basin or the absence of (unpreserved or not yet studied) taxa in a specific country/basin (e.g., Cuba and Puerto Rico).

Most of the fossil fish were recovered from different expeditions (except for a few units), and most of them corresponded to independent field trips using different collecting methods (e.g., bulk samples *vs.* individual outcrop picking). Additionally, fossil preservation, taxonomic research, and the available published data are different in terms of identification level. Finally, the stratigraphic sequences along tropical America show a preservation gap. The stratigraphical position, facies analyses, paleodepth interpretations, and analysis of associated fauna are the main data for paleoenvironmental interpretations.

2.3. Data analysis

The data of fish genera occurrences were arranged in a matrix formed by 30 columns and 171 rows, and each genus was assigned an Identification Code (ID) consisting of the first four letters. Each country and basin were represented in columns (nine countries) in five stratigraphic ages (EM: early Miocene, MM: middle Miocene, LM: late Miocene, PI: Pliocene, and PE: Pleistocene). A row represents the genera occurrence for each country/basin (Supplementary table 2).

To verify whether a fossil fish assemblage structure changed according to the geochronological periods, a Permutational Analysis of Variance (PERMANOVA) was conducted on both the quantitative and qualitative data. The similarity matrix was built using Euclidean distance, and permutation of residuals was performed under reduced model to compare all periods (Anderson et al., 2008).

An ordination technical principal component analysis (PCA) was applied to the sedimentary basins to detect spatial or temporal patterns of the smallest available taxonomic records (genera) along with the stratigraphic age. The analysis was performed with CANOCO version 4.5 software (TerBraak and Smilauer, 2002).

Differences in the taxonomic structure between basins of specific countries sampled in the tropical Americas were tested by calculating the average taxonomic distinctness (Δ+) and the variation in the taxonomic distinctness (Λ+) following the procedure of Clarke and Warwick (1999). To determine the Δ+ and Λ+, which measure the degree to which genera are taxonomically related to each other and the degree to which taxa are highly or poorly represented, respectively a presence/absence matrix of all the basins was used as well as an aggregation matrix with five taxonomic levels (genera, family, order, class, and phylum). The average taxonomic distinctiveness is not dependent on the sampling effort (Clarke and Warwick, 2001). Furthermore, a test can be constructed for the null hypothesis that a species list (species richness S) from one locality (or time) has the same taxonomic distinctness structure as the 'master' list (e.g., of all species in that biogeographic region) from which it is drawn. This is ensured by simple randomization: If “s” species are observed in a particular sample, repeated drawings are made at random of “s” species from the master list and Δ+ is computed for each drawing, thus creating a funnel and a 95% probability range of values of Δ+ expected under the null hypothesis, in which the true Δ+ can be compared. Values below the lower probability limit suggest biodiversity that is 'below expectations'. This process can be performed for a range of sub-list sizes and the limits plotted against S to obtain a 95% 'funnel' of expected values (the funnel arises from the uncertainty being greater for smaller sub-list). This can be repeated for Λ +, thus providing a second 95% funnel set. Δ+ and Λ+ were calculated from the master list of all genera using the Taxdtest subroutine of the PRIMER v6 Program (Clarke and Gorley, 2006). To calculate the average indices’ taxonomic distinctness and their variation, the basins of VMM (Venezuela middle Miocene), VPE (Venezuela Pleistocene), CRMM (Costa Rica middle Miocene), TPI (Trinidad Pliocene), JPI

(Jamaica Pliocene) were excluded because only one or two genera are present, which is insufficient for calculating these indices (Clarke and Warwick, 1999).

Abbreviations used in the text and figures are as follows: BR: Brazil; CO: Colombia; CR: Costa Rica; DR: Dominican Republic; E: Ecuador; J: Jamaica; P: Panama; T: Trinidad; V; Venezuela; EM: early Miocene (23.03–20.43 Ma); MM: middle Miocene (15.97–13.65 Ma); LM: late Miocene (11.61–7.25 Ma); PI: Pliocene (5.33–2.59 Ma); PE: Pleistocene (1.81–0.13 Ma); FM: Formation.

3. Results

3.1 Fish assemblage

A total of 169 genera of fossil teleostean fishes were identified by their otoliths (except *Chilomycterus* and *Lagocephalus*) for the Miocene-Pleistocene fossiliferous formations from tropical America (Figs. 3-7, Tables 1-5), distributed in 20 orders and 56 families. The most representative families and the numbers of genera of the ichthyofauna were: Sciaenidae (29), Myctophidae (16), Ophidiidae (11), Ariidae (9), Bythitidae (6), Congridae (6), Haemulidae (6) and Sparidae (5). These genera accounted for 52% of the total frequency of the fish assemblage and were mainly associated with deposits in shallow water, near-shore environments, or coastal marine areas with upwelling influences.

3.2. Stratigraphic distribution and frequency of teleostean fish genera by age

The permutational variance analysis (PERMANOVA) showed no significant difference between the Miocene, Pleistocene and Pliocene (Pseudo-F= 0.81249, P= 0.468).

Our PCA indicated that the early Miocene was characterized by two distinctive fish assemblages of the tropical equatorial Atlantic coast, where PC1 was represented by fishes from the Venezuela basin that explained 63.7% of the variance. This assemblage was characterized by the dominance of Sciaenidae that inhabited shallow waters. PC2 indicated that the fishes recorded in the Colombia basin explained 22.5% of the variance. This assemblage was characterized by the diversity of Sciaenidae and Myctophidae. The first two PCA axes explained 86.5% (0.637+ 0.225) of the variability of this data (Fig. 3, Table 1).

During the middle Miocene, the fish assemblages showed affinities with the Atlantic corridor and amphi-American fossil fish distribution among the basin. PC1 was represented by the Trinidad basin, which explained 40.2% of the variance. The assemblage was dominated by genera of Sciaenidae, Myctophidae, Congridae, and Ophidiidae. PC2 was represented by the Brazilian basin, which explained 31.5% of the variance, as represented by the records of Sciaenidae and Ariidae. The first two PCA axes explained 71.7% (0.402 + 0.315) of the variability (Fig. 4, Table 2).

In the late Miocene, fossil fish assemblages were associated with the Panama basins, explaining 40.8% of the variance in the PC1. This assemblage was represented by genera of Sciaenidae and Haemulidae. PC2 came from the Dominican Republic basins, explaining 25.3 % of the variance, and the assemblage was represented by the genera of Sciaenidae, Myctophidae, and Bythitidae. The first two PCA axes explained 74.1% of the data variability (Fig. 5, Table 3).

PC1 from the Pliocene was represented by the Ecuador basin, explaining 31.9% of the variances and was characterized by the Haemulidae, Paralichthyidae, Clupeidae, Congridae, and Sciaenidae genera. PC2 in this age was from Panama and Costa Rica, which explained 20.7% of the variance, and the fish assemblage was represented by the Myctophidae genera. The first two PCA axes explained 52.6% of the variability (Fig. 6, Table 4).

During the Pleistocene, PC1 from the Panama and Costa Rica basins explained 62.2% of the variance, as characterized by the dominance of Myctophidae and Ophidiidae genera, whereas PC2 from the Panama basin explained 23.9 % of the variance, being dominated by the Bythitidae and Ophidiidae genera. The first two PCA axes explained 86.1% of the variability (Fig. 7, Table 5).

3.3. Context of taxa by paleoenvironment

Most of the genera evaluated in this study inhabited shallow tropical waters of a less than 100 m depth (e.g., Ariidae and Sciaenidae). However, exceptional fish faunas represented by open marine mesopelagic Myctophidae have been recorded from coastal marine paleoenvironments with upwelling influences. Other genera are typical pelagic fish during the adult stage, but during their juvenile stage, these genera were found near the coast (e.g., Carangidae and Clupeidae). There was a high diversity of fish associated with soft bottoms (e.g., Paralychthidae and Cynoglossidae), rocky bottoms, and/or coral reefs (e.g., Sparidae and Haemulidae), and brackish and/or estuarine areas (e.g., Mugilidae and Centropomidae) (Tables 2–6).

3.4. Potential use of a fish assemblage in the geochronological approach

In this study, we registered exceptional records of extinct species from a specific stratigraphic age. Examples include †*Frizzellithus* Schwarzhans, 1993 and †*Protonebris* Aguilera, Schwarzhans and Béarez, 2016, occurring exclusively in the early Miocene; †*Amazonsciaena* Aguilera, Schwarzhans and Béarez, 2016 occurring only in the middle Miocene; and †*Cantarius* Aguilera, Moraes-Santos, Costa, Ohe, Jaramillo and Nogueira, 2013, †*Equetulus* Aguilera and Schwarzhans, 2014, †*Protolarimus* Aguilera and Schwarzhans, 2014 and †*Xenotolithus* Schwarzhans, 1993, from the early Miocene to late

Miocene. Representative images of these fossil genera are included in Figure 8. All records are consistent in the tropical American Neogene basins (Supplementary figure 1, 2).

3.5 Average taxonomic distinctness and variation of the taxonomic distinctness

The Δ+ represented in these areas of tropical America was 55. The Δ+ model built at the sedimentary basin level showed that most of the values within the 95% confidence intervals were statistically different, except for the late Miocene of Costa Rica, Pliocene of Venezuela, and Pleistocene of the Ecuador and Trinidad basins (Fig. 9.1). The index of Λ+ followed the same behavior, where the sedimentary basins were within the 95% confidence interval. The early and late Miocene of Trinidad (greater variation of the taxonomic distinctness Λ+), early Miocene of Colombia, late Miocene and Pleistocene of Ecuador, and Pliocene of Venezuela, which are located outside of the trusted channel (Fig. 9.2).

4. Discussion

4.1 Paleoecology

The fossil teleostean fish assemblage from tropical America during the early Miocene to the Pleistocene is characterized by a high diversity of genera that inhabit coastal marine environments. The 169 genera recorded from nine sedimentary basins include 158 extant and 11 extinct genera reflecting a wide geographical distribution, heterogeneous environments, and different stratigraphic arrangements.

The number of recognized teleostean genera increased from the early Miocene to the late Miocene (125 genera) and then decreased toward the Pliocene (115 genera) (Fig. 10). This was consistent with observations made from fossil sharks and ray diversity from the Neogene of the tropical Americas (Carrillo-Briceño et al., 2018) and mollusks (Jackson et al., 1993), the latter of which reached its highest abundance and diversity during the late Miocene in Panama.

The families that presented the greatest number of genera throughout all ages were as follows: Sciaenidae [inner shelf, estuarine freshwater, common in Angostura, Cantaure, Canoa, Cercado, Gatun and Manzanilla formations, and dominant in Pirabas Urumaco and Rio Banano formations (Aguilera et al., 2016)], Myctophidae [mesopelagic, common in Brasso, Cantaure, Gurabo, Mao and Onzole formations, and dominant in Armuelles, Bowden, Burica, Cayo Agua, Cercado, Chagres, Cubagua, Escudo de Veraguas, Gurabo, Nancy Point, Swan Cay, Shark Hole Point, and Tobade formations (Schwarzhans and Aguilera, 2013)], Ophidiidae [benthic on shelf to bathybenthic, common in Angostura, Canoa, Cercado and Onzole formations (Schwarzhans and Aguilera, 2016)], Congridae [shelf, littoral, common in Baitoa, Bowden, Brasso, Cantaure, Gurabo, Manzanilla, Mao, Nariva, Pirabas, and Tamana formations (Nolf, 1976; Nolf and Stringer, 1992; Nolf and Aguilera, 1998; Stringer, 1998; Aguilera et al., 2014)], and Ariidae [inner shelf, estuarine, freshwater, and common in Cantaure, Manzanilla, Pirabas, and Urumaco formations (Aguilera et al., 2013, 2020)].

The Sciaenidae dominate the generic diversity in the early Miocene, late Miocene, and Pleistocene. The genera diversity of Myctophidae was dominant during the Pliocene, and Ophidiidade was dominat in the middle Miocene (Fig. 11). This result shows that most locations sampled for the Gatunian Province reflected a wide range of shallow marine environments with an exceptional upwelling influence in coastal marine areas.

The dominance of Sciaenidae fossil genera in this "trans-American" marine region during the Miocene to the Pleistocene could be attributed to the area being considered a diversification center of Sciaenidae since at least the early Miocene (Sasaki, 1989; Xu et al., 2014; Lo et al., 2015; Aguilera et al., 2016). This diversification is due to their resilience under high salinities associated with their life history (Costa et al., 2014). This family inhabits mostly marine shallow waters (except *Protosciaena*, which can live at depths as low as 600 m) as well as brackish and estuarine environments, but some are exclusively freshwater taxa (Chao, 1976; Cook et al., 2012; Aguilera et al., 2016).

The environmental preferences of ancient to modern Sciaenidae were transitional from euryhaline to marine and freshwater (Lo et al., 2015; Cooke et al., 2011). Additionally, the hydrological systems located in the northern part of South America, which are associated with the western Amazon mega-wetlands of Pebas and the shifts of the paleo-Amazon and paleo-Orinoco, offered a favorable setting for the evolution of the Sciaenidae (Torres, 2006; Beheregaray et al., 2015; Aguilera and Rodriguez de Aguilera, 2003; Aguilera et al., 2016).

The exceptional fish fauna diversity, as represented by open marine mesopelagic Myctophidae in the Neogene Marine biota of tropical America (Schwarzhans and Aguilera, 2013), has been recorded from coastal marine paleoenvironments with upwelling influences [e.g., the Cantaure and Cubagua formations in Venezuela (Nolf and Aguilera, 1988; Aguilera and Rodrigues de Aguilera, 2001), the Cercado, Gurabo, and Mao formations in the Dominican Republic (Nolf and Stringer, 1992), and the Bowden Formation in Jamaica (Stringer, 1998)]. Multiple studies exist for both Holocene dredged sediments (Schwarzhans, 2013) and Mio-Pliocene sediments (e.g., Schwarzhans and Aguilera, 2013) where the abundance of Myctophidae can directly be related to a pelagic environment. However, Myctophidae are so common that one can also find specimens in shallow water environments, albeit subordinately (Schwarzhans, personal communication). This result does not contradict the occurrences of fossil Myctophidae in shallow water sedimentary deposits at the coastal margin of Proto-Caribbean islands at the oceanfront, which is bounded by a submarine trench and is influenced by oceanographic events such as the force of coastal upwelling. Opposing that is the fish assemblage from the coastal plain and shallow water of the Pirabas Formation in Brazil (Aguilera et al., 2014) or the fish assemblage of the Urumaco Formation in Venezuela (Sánchez-Villagra and Aguilera, 2006); both do not contain a single otolith of Myctophidae.

4.2. Geochronological correlation of fauna

The faunal changes along the geochronological sequence in Neogene tropical America basins following unequivocal paleoenvironmental associations were in accordance with the following points: (1) The early Miocene evolutionary response (turnover) to the global cooling episode and the Mi-1 glaciation (Stewart et al., 2017; Egger et al., 2018) during the Oligocene-Miocene, as characterized by the South Caribbean (Venezuela and Colombia Basin) show a Western central Atlantic corridor faunal assemblage. (2) The middle Miocene assemblage relationship of the tropical Atlantic corridor was characterized by the Trinidad and Brazil basins and their associated fauna, with connectivity to the sedimentary basin of Ecuador (Fig.12). (3) The Trinidad assemblages from the middle Miocene, with the influence of the Atlantic/Pacific seaway, were replaced by the Caribbean group (Panama, Dominican Republic and Venezuela) in the Late Miocene as consequence of the Andes uplift, the origin of the transcontinental Amazon River, and the onset of the Amazon delta. (4) The Panama and Costa Rica Pliocene assemblages form a strongly linked Central America group separated from an Ecuadorian group, and the Caribbean islands (Trinidad, the Dominican Republic, and Venezuela) show an additional group. These new arrangements appear to be closely related to the uplift of the Isthmus of Panama and the generic diversification (turnover). (5) The Pleistocene assemblages are the new faunal arrangement for the Caribbean (Costa Rica and Panama) with fauna from Ecuador (Fig.13). The paleoceanographic, geographic, hydrographic, and climate changes are unique natural conditions showing that the marine fauna can be the best macroevolutionary response to the environmental changes.

4.3. Chrono-bioindicators

Until now, otoliths of fossil fishes have been used for biostratigraphic purposes, but admittedly with mixed results. Unpreserved or eroded otolith and disarticulate fish skeletons (mostly not diagnostic) as well as gaps without a uniform distribution into the rock matrix are the main obstacles to an accurate validation. However, the use of fossil otoliths as a geochronological approach from the Neogene tropical America (Fig. 3) suggest that six genera of Sciaenidae and one of Ariidae are useful for stratigraphic purposes at the genus level. The Sciaenidae genera are represented by †*Frizzellithus* (Cantaure FM, Venezuela; Castillete and Jimol FMs, Colombia) and †*Protonebris* (Castillo FM, Venezuela) recorded exclusively from the early Miocene, †*Amazonasciaena* (Pirabas FM, Brasil), exclusively from the middle Miocene, and †*Equetulus* (Pirabas FM, Brasil; Castillete FM, Colombia; Cantaure and Urumaco FMs, Venezuela; Tuira and Gatún FMs; Panama and Angostura FM, Ecuador), †*Protolarimus* (Cantaure and Urumaco FM Venezuela, Castillete FM Colombia) and †*Xenotolithus* (Pirabas FM, Brasil; Manzanilla and Brasso FM, Trinidad), which ranged from the early Miocene to the late Miocene. The Ariidae are represented by †*Cantarius* (Cantaure FM, Venezuela; Castillete FM, Colombia), which ranged from the early Miocene to the late Miocene. Aguilera et al. (2016) noted that because of their high speciation, the diversification and extinction of individual lineages in the evolution of Sciaenidae presented a rich and dense otolith record, whose distribution may be related to paleoenvironmental changes in time and space.

4.4. Taxonomic relationship

During the late Miocene, the fish of Panama had the highest taxonomic distinctness (Fig.10) compared to the other basins, and had relatively high richness, which implied that this type of marine system had paleoenvironmental characteristics that allowed a more diverse ichthyofauna. Unlike sedimentary basins that had values below the confidence limit, these samples may be associated with possible habitat disturbances because some habitat types may have naturally lower taxonomic distinction values than others. According to Clarke and Warwick (1998), taxonomic distinction values do not fall below the lower limit of the 'funnel' unless the habitats degrade in some way. For example, the fish assemblages from the central Atlantic-South Caribbean corridor supported by Colombia early Miocene (COEM) and Trinidad early Miocene (TEM) diversity were affected by the marine assemblage of a fluvial-deltaic system of the mega-Amazon (Wesselingh et al., 2001; Hoorn, 2010). In the Pliocene Ecuador (EPE), a cyclic sedimentation pattern that may be interpreted as repeated sea-level oscillations (Cantalamessa et al., 2005) that probably affected the taxonomic structures of the fishes.

5. Conclusion

A complete statistical approach of otolith records from the Neogene of the tropical Americas reveals abundant and diverse demersal fish from all included basins. Sciaenidae and Ariidae were important elements in all Miocene and Pliocene samples and showed a consistently high diversity, including regionalization, over space and time. The paleoceanographic, geographic, hydrographic, and climate changes triggered the turnover and the diversity of present day tropical amphiamerican fish fauna.

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Author contributions

EGC and OA conceived and designed the project. EGC, MR, FR, and OA designed and performed the experiments. FR and OA performed the field trip and sample collection. EGC, FR, MR, and OA analyzed the context of the information. EGC and OA wrote the paper. EGC, MR, FR, and OA revised and edited the manuscript.

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Figures, tables and legends

Fig. 1. Maps of the sampled regions. 1. Ecuador (1.1) and Brazil (1.2); 2. Costa Rica (2.1) and Panama (2.2–2.5); 3. Colombia (3.1), Venezuela (3.2-3.3), Trinidad (3.4) and the Dominican Republic (3.5); and 4. Jamaica. (Modified from Aguilera et al., 2016).

Fig. 2. Stratigraphic correlation chart depicting stratigraphic positions of otoliths obtained from the countries and basins of the tropical Americas. (Modified from Schwarzhans and Aguilera, 2013; Aguilera et al., 2016).

Fig. 3. Principal component analysis (PCA) arranged by genera (blue) and country-basin (red) from the early Miocene of tropical America. Abbreviations, COEM: Colombia early Miocene; DEM: the Dominican Republic early Miocene; TEM: Trinidad early Miocene; and VEM: Venezuela early Miocene (for genera abbreviation see Table 1).

Fig. 4. Principal components analysis (PCA) arranged by genera (blue) and country-basin (red) from the middle Miocene of tropical America. Abbreviation, BMM: Brazil middle

Miocene; CRMM: Costa Rica middle Miocene; EMM: Ecuador middle Miocene; and TMM: Trinidad middle Miocene (for genera abbreviation see Table 2).

Fig. 5. Principal components analysis (PCA) arranged by genera (blue) and country-basin (red) from the late Miocene of tropical America. Abbreviation, CRLM: Costa Rica late Miocene; DLM: Dominican Republic late Miocene; ELM: Ecuador late Miocene; PLM: Panama late Miocene; TLM: Trinidad late Miocene; and VLM: Venezuela late Miocene; (for genera abbreviation see Table 3).

Fig. 6. Principal components analysis (PCA) arranged by genera (blue) and country-basin (red) from the Pliocene of tropical America. Abbreviation, CRPI: Costa Rica Pliocene; DPI: The Dominican Republic Pliocene; EPI: Ecuador Pliocene; JPI: Jamaica Pliocene; PPI: Panama Pliocene; TPI: Trinidad Pliocene; and VPI: Venezuela Pliocene (for genera abbreviation see Table 4).

Fig. 7. Principal components analysis (PCA) arranged by genera (blue) and country-basin (red) from the Pleistocene of tropical America. Abbreviation, CRPE: Costa Rica Pleistocene; EPE: Ecuador Pleistocene; PPE: Panama Pleistocene; TPE: Trinidad Pleistocene; and VPE: Venezuela Pleistocene (for genera abbreviation see Table 5).

Fig. 8. Selected Ariidae and Sciaenidae otoliths from the Neogene of tropical America as a potential geochronological fossil guide. 1–3, Cantarius nolfi Aguilera, Moraes-Santos, Costa, Ohe, Jaramillo and Nogueira, 2013, Castilletes FM, early Miocene, Colombia; 4–5. Amazonasciaena rossettiae (Aguilera and Schwarzhans, 2014), Pirabas FM, middle Miocene, Brazil; 6–7, Frizzellithus longecaudatus (Nolf and Aguilera, 1998), Castilletes FM, early Miocene, Colombia; 8–9, Equetulus amazonensis Aguilera and Schwarzhans, 2014, Pirabas FM, middle Miocene, Brazil; 10–12, Equetulus davidandrewi (Nolf and

Aguilera, 1998), Cantaure FM, early Miocene, Venezuela; 13, Equetulus fitchi (Schwarzhans, 1993), Manzanilla FM, late Miocene, Trinidad; 14–16, Protolarimus henrici (Nolf and Aguilera, 1998), Cantaure FM, early Miocene, Venezuela; 17–18, Protolarimus? mauryae Aguilera and Schwarzhans, 2014; Pirabas FM, middle Miocene, Brazil; 19–21, Xenotolithus retrolobatus Aguilera and Schwarzhans, 2014, Pirabas FM, middle Miocene, Brazil; 22¬–24, Xenotolithus sasakii Schwarzhans, 1993, Manzanilla FM, late Miocene, Trinidad; 25–27, Xenotolithus sineostialis Aguilera, Schwarzhans and Bearez, 2016, Manzanilla FM, late Miocene, Trinidad. Scale bar = 2 mm. (Original Sciaenidae photos courtesy of W. Schwarzhans and modified from Aguilera et al. 2014).

Fig. 9. Averange taxonomic distinctness (Δ+) and variation of the taxonomic distinctness (Λ+) (1 and 2, respectively) for the fish groups of the sites sampled from the Miocene to the Pleistocene of tropical America. A 95% confidence funnel obtained from the global species list is shown in continuous lines and the theoretical average of Δ+ and Λ+ is shown in a segmented line.

Fig. 10. Stratigraphical frequency of fossil fish genera in the Neogene Tropical Western Central Atlantic and Tropical Eastern Pacific. Green: observed, blue: projected, and yellow: extinct. EM: early Miocene; MM: middle Miocene; LM: late Miocene; PI: Pliocene; and PE: Pleistocene.

Fig. 11. Geochronologic sequence of sedimentary basins by country-age of tropical America. Early Miocene (Colombia, the Dominican Republic, Trinidad and Venezuela) to middle Miocene (Brasil, Costa Rica, Ecuador, Trinidad and Venezuela).

Fig. 12. Geochronologic sequence of sedimentary basins by country-age of tropical America. Late Miocene (Costa Rica, the Dominican Republic, Ecuador, Panama, Trinidad and

Venezuela), Pliocene (Costa Rica, Dominican Republic, Ecuador, Jamaica, Panama, Trinidad and Venezuela) and Pleistocene (Costa Rica, Ecuador, Jamaica Panama and Venezuela).

Fig. 13. Most frequent families with the highest number of genera of tropical American fish. EM: early Miocene; MM: middle Miocene; LM: late Miocene; PI: Pliocene; PE: Pleistocene. green: Sciaenidae, orange: Myctophidae, gray: Ophidiidae, yellow: Congridae, blue: Ariidae

Table 1. Early Miocene abbreviations and remarks used in Figure 3.

Table 2. Middle Miocene abbreviations and remarks used in Figure 4.

Table 3. Late Miocene abbreviations and remarks used in Figure 5.

Table 4. Pliocene abbreviations and remarks used in Figure 6.

Table 5. Pleistocene abbreviations and remarks used in Figure 7.

Supplementary material

Supplementary table 1. References of fossil fish records by authors, formations, ages, countries, and basins. (Modified of Aguilera et al., 2011)

Supplementary table 2. Fossil otoliths of fish organized by country, family, genera, ID and age.

Supplementary figure 1. Fossil otoliths fish of tropical Americas and geochronological distribution of families and genera.

Supplementary figure 2. Fossil otoliths fish of tropical Americas and geochronological distribution of families and genera.

Early Miocene

Axis 1 **Venezuela Basin (VEM)**

ID	Family	Genera	Score	Habitat
ALBU	Albulidae	*Albula*	0.1298	Demersal
APOG	Apogonidae	*Apogon*	0.1298	Reef-associated
ARIOP	Ariidae	*Ariopsis*	0.1298	Demersal
BAGR	Ariidae	*Bagre*	0.1298	Demersal
CANT	Ariidae	*†Cantarius*	0.1298	†
CATH	Ariidae	*Cathorops*	0.1298	Demersal
NOTA	Ariidae	*Notarius*	0.1298	Demersal
PORI	Batrachoididae	*Porichthys*	0.1298	Demersal
BREG	Bregmacerotidae	*Bregmaceros*	0.1298	Demersal
TRAC	Carangidae	*Trachurus*	0.1298	Demersal
HARE	Clupeidae	*Harengula*	0.1298	Pelagic
OPIS	Clupeidae	*Opisthonema*	0.1298	Pelagic
PELL	Clupeidae	*Pellona*	0.1298	Pelagic
CONG	Congridae	*Conger*	0.1298	Demersal
HILD	Congridae	*Hildebrandia*	0.1298	Demersal
PCON	Congridae	*Paraconger*	0.1298	Demersal
CHIL	Diodontidae	*Chilomycterus*	0.1298	Demersal
ORTH	Haemulidae	*Orthopristis*	0.1298	Demersal
HYPO	Hemirhamphidae	*Hyporhamphus*	0.1298	Pelagic
PYTH	Heterenchelyidae	*Pythonichthys*	0.1298	Demersal
MYRI	Holocentridae	*Myripristis*	0.1298	Demersal
LACT	Lactariidae	*Lactarius*	0.1298	Mesopelagic
LOBO	Lobotidae	*Lobotes*	0.1298	Demersal
OCYU	Lutjanidae	*Ocyurus*	0.1298	Reef-associated
STEI	Merlucciidae	*Steindachneria*	0.1298	Demersal
MUGI	Mugilidae	*Mugil*	0.1298	Demersal
UPEN	Mullidae	*Upeneus*	0.1298	Demersal
CERA	Myctophidae	*Ceratoscopelus*	0.1298	Mesopelagic
MYCT	Myctophidae	*Myctophum*	0.1298	Mesopelagic
OPIG	Opistognathidae	*Opistognathus*	0.1298	Demersal
CITH	Paralichthyidae	*Citharichthys*	0.1298	Demersal
BEMB	Percophidae	*Bembrops*	0.1298	Demersal

Continue…

ID	Family	Genera	Score	Habitat
PLOT	Plotosidae	*Plotosus*	0.1298	Demersal
POLX	Polymixiidae	*Polymixia*	0.1298	Demersal
ILIS	Pristigasteridae	*Ilisha*	0.1298	Pelagic
NEOP	Pristigasteridae	*Neoopisthopterus*	0.1298	Pelagic
APLO	Sciaenidae	*Aplodinotus*	0.1298	Demersal
ATRA	Sciaenidae	*Atractoscion*	0.1298	Demersal
EQUE	Sciaenidae	*†Equetulus*	0.1298	†
FRIZ	Sciaenidae	*†Frizzellithus*	0.1298	†
LARI	Sciaenidae	*Larimus*	0.1298	Demersal
PANE	Sciaenidae	*Paranebris*	0.1298	Demersal
PARL	Sciaenidae	*Paralonchurus*	0.1298	Demersal
PARQ	Sciaenidae	*Pareques*	0.1298	Demersal
PLAG	Sciaenidae	*Plagioscion*	0.1298	Demersal
PLAR	Sciaenidae	*†Protolarimus*	0.1298	†
PLYC	Sciaenidae	*Polycirrhus*	0.1298	Demersal
PRNE	Sciaenidae	*Protonebris*	0.1298	Demersal
PROT	Sciaenidae	*Protosciaena*	0.1298	Demersal
STEL	Sciaenidae	*Stellifer*	0.1298	Demersal
ANCH	Sparidae	*Archosargus*	0.1298	Demersal
SPAD	Sparidae	*Sparidarum*	0.1298	Demersal
SPHYA	Sphyraenidae	*Sphyraena*	0.1298	Demersal
PEPR	Stromatidae	*Peprilus*	0.1298	Demersal

Axis 2 **Colombian Basin (COEM)**

ID	Family	*Genera*	Score	Habitat
ARIO	Ariidae	*Ariopsis*	0.1503	Demersal
DIAP	Myctophidae	*Diaphus*	0.1503	Mesopelagic
HYGO	Myctophidae	*Hygophum*	0.1503	Mesopelagic
OPHS	Sciaenidae	*Ophioscion*	0.1503	Demersal
CENT	Engraulidae	*Cetengraulis*	-0.2254	Pelagic
LUTJ	Lutjanidae	*Lutjanus*	-0.2254	Demersal
SNYD	Carapidae	*Snyderidia*	-0.2254	Demersal
UMBR	Sciaenidae	*Umbrina*	-0.2254	Demersal

Middle Miocene

Axis 1		**Trinidad Basin (TMM)**		
ID	Family	Genera	Score	Habitat
ANTE	Antennariidae	*Antennarius*	0.1336	Reef-associated
BATH	Bathyclupeidae	*Bathyclupea*	0.1336	Mespelagic
BREG	Bregmacerotidae	*Bregmaceros*	0.1336	Demersal
CALA	Bythitidae	*Calamopteryx*	0.1336	Reef-associated
CARG	Carangidae	*Gen., sp. Ind.*	0.1336	Demersal
CETN	Centropomidae	*Centropomus*	0.1336	Demersal
OPIS	Clupeidae	*Opisthonema*	0.1336	Pelagic
ARIO	Congridae	*Ariosoma*	0.1481	Demersal
HILD	Congridae	*Hildebrandia*	0.1336	Demersal
RHEC	Congridae	*Rhechias*	0.1336	Demersal
SYMP	Cynoglossidae	*Symphurus*	0.1336	Demersal
ANCH	Engraulidae	*Anchoa*	0.1336	Pelagic
EPIG	Epigonidae	*Epigonus*	0.1481	Mesopelagic
HAEM	Haemulidae	*Haemulon*	0.1481	Demersal
POMA	Haemulidae	*Pomadasys*	0.1336	Demersal
MYRI	Holocentridae	*Myripristis*	0.1336	Demersal
GADL	Moridae	*Gadella*	0.1336	Mesopelagic
DIAP	Myctophidae	*Diaphus*	0.1336	Mesopelagic
LEPI	Myctophidae	*Lepidophanes*	0.1336	Mesopelagic
MYCT	Myctophidae	*Myctophum*	0.1336	Mesopelagic
LEPO	Ophidiidae	*Lepophidium*	0.1481	Demersal
BROT	Ophidiidae	*Brotula*	0.1336	Mesoopelagic
NEOB	Ophidiidae	*Neobythites*	0.1245	Demersal
LONC	Opistognathidae	*Lonchopisthus*	0.1481	Demersal
CITH	Paralichthyidae	*Citharichthys*	0.1336	Demersal
ILIS	Pristigasteridae	*Ilisha*	0.1336	Pelagic
CTEN	Sciaenidae	*Ctenosciaena*	0.1481	Demersal
SCIA	Sciaenidae	*Sciaena*	0.1336	Demersal
STEL	Sciaenidae	*Stellifer*	0.1336	Demersal
CYNO	Sciaenidae	*Cynoscion*	0.1245	Demersal
POLY	Sternoptychidae	*Polyipnus*	0.1481	Mesopelagic
SAUR	Synodontidae	*Saurida*	0.1481	Demersal

Axis 2		**Brasil Basin (BMM)**		
ID	Family	Genera	Score	Habitat
ALBU	Albulidae	*Albula*	0.1198	Demersal
APOG	Apogonidae	*Apogon*	0.1987	Reef-associated
ARIU	Ariidae	*Gen., sp. Ind.*	0.1987	Demersal
CATH	Ariidae	*Cathorops*	0.1987	Demersal
ASPI	Ariidae	*Aspistor*	0.1198	Demersal
BAGR	Ariidae	*Bagre*	0.1198	Demersal
NOTA	Ariidae	*Notarius*	0.1198	Demersal
PORI	Batrachoididae	*Porichthys*	0.2093	Demersal
THAL	Batrachoididae	*Thalassophryne*	0.2093	Demersal
BATR	Batrachoididae	*Batrachoides*	0.1198	Demersal
SANO	Batrachoididae	*Sanopus*	0.1198	Reef-associated
OGIB	Bythitidae	*Ogilbichthys*	0.1198	Reef-associated
OGIL	Bythitidae	*Ogilbia*	0.1198	Demersal
DECA	Carangidae	*Decapterus*	0.1198	Demersal
CARA	Carapidae	*Carapus*	0.1198	Demersal
PCON	Congridae	*Paraconger*	0.1092	Demersal
CHIL	Diodontidae	*Chilomycterus*	0.2093	Demersal
DIAT	Gerreidae	*Diapterus*	0.1198	Demersal
GOBI	Gobiidae	*Gen. sp. Ind.*	0.1987	Demersal
HYPO	Hemirhamphidae	*Hyporhamphus*	0.1198	Pelagic
PYTH	Heterenchelyidae	*Pythonichthys*	0.1987	Demersal
OSTI	Holocentridae	*Ostichthys*	0.1198	Demersal
OCYU	Lutjanidae	*Ocyurus*	0.1198	Reef-associated
OTOP	Ophidiidae	*Otophidium*	0.1092	Demersal
CYCL	Paralichthyidae	*Cyclopsetta*	0.1198	Demersal
SYAC	Paralichthyidae	*Syacium*	0.1092	Demersal
AMAZ	Sciaenidae	*†Amazonasciaena*	0.1198	†
APLO	Sciaenidae	*Aplodinotus*	0.1198	Demersal
EQUE	Sciaenidae	*†Equetulus*	0.1198	†
PARQ	Sciaenidae	*Pareques*	0.1198	Demersal
PLAG	Sciaenidae	*Plagioscion*	0.1198	Demersal
PLAR	Sciaenidae	*†Protolarimus*	0.1198	†
XENO	Sciaenidae	*†Xenotolithus*	0.1198	†
PRTO	Sciaenidae	*Protosciaena*	0.1092	Demersal
SCOR	Scorpaenidae	*Gen. sp. Ind.*	0.1092	Demersal
SPHA	Sparidae	*†Sphaerodus*	0.2093	†
ARCH	Sparidae	*Archosargus*	0.1198	Demersal

Late Miocene

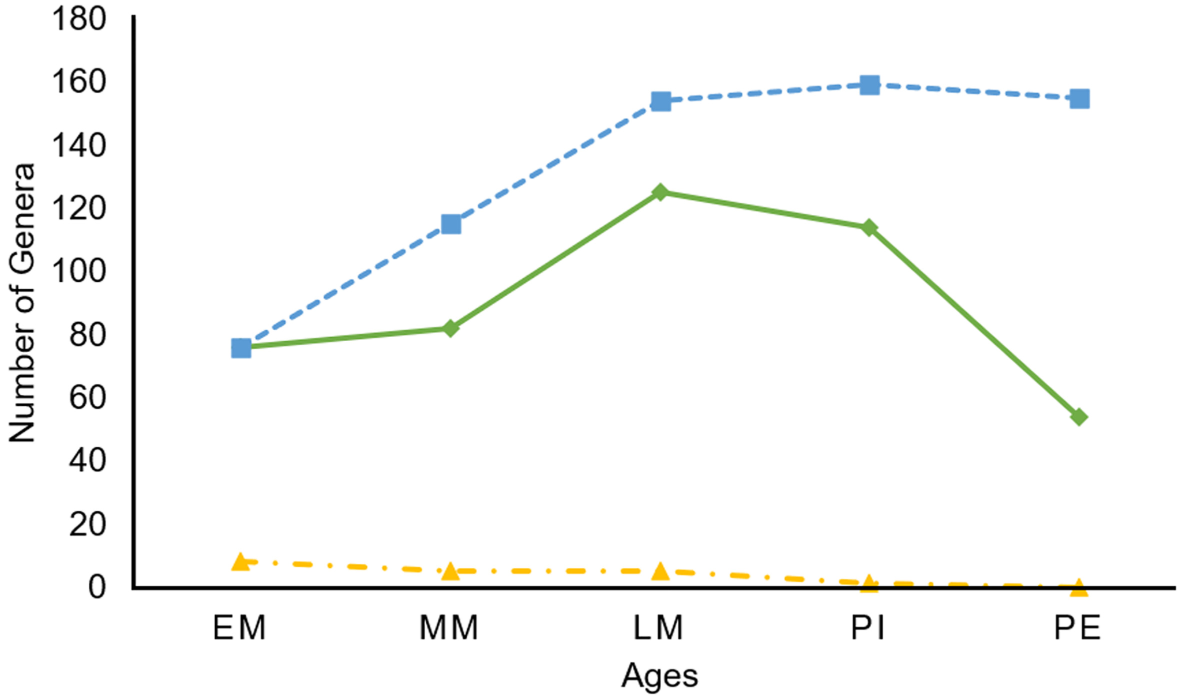
Axis 1		**Panamá and Venezuela basins (PLM and VLM)**			**Continue…**				
ID	Family	Genera	Score	Habitat	ID	Family	Genera	Score	Habitat
PRAS	Acropomatidae	*Parascombrops*	0.1312	Demersal	CITH	Paralichthyidae	*Citharichthys*	0.1312	Demersal
APOG	Apogonidae	*Apogon*	0.1104	Reef-associated	SYAC	Paralichthyidae	*Syacium*	0.1312	Demersal
BAGR	Ariidae	*Bagre*	0.1312	Demersal	PRTO	Sciaenidae	*Protosciaena*	0.1492	Demersal
MEMB	Atherinidae	*Membras*	0.1312	Pelagic	SCIA	Sciaenidae	*Sciaena*	0.1312	Demersal
BREG	Bregmacerotidae	*Bregmaceros*	0.1492	Demersal	CTEN	Sciaenidae	*Ctenosciaena*	0.1104	Demersal
TRAC	Carangidae	*Trachurus*	0.1312	Demersal	POLY	Sternoptychidae	*Polyipnus*	0.1492	Mesopelagic
OPIS	Clupeidae	*Opisthonema*	0.1492	Pelagic	MAUR	Sternoptychidae	*Maurolicus*	0.1312	Mesopelagic
HARE	Clupeidae	*Harengula*	0.1312	Pelagic	SAUR	Synodontidae	*Saurida*	0.1492	Demersal
HILD	Congridae	*Hildebrandia*	0.1492	Demersal	PRIO	Triglidae	*Prionotus*	0.1492	Demersal
ARIO	Congridae	*Ariosoma*	0.1104	Demersal	**Axis 2**		**Dominican Republic Basin (DLM)**		
SYMP	Cynoglossidae	*Symphurus*	0.1312	Demersal	ID	Family	Genera	Score	Habitat
ANCH	Engraulidae	*Anchoa*	0.1312	Pelagic	ALBU	Albulidae	*Albula*	0.1578	Demersal
ENGR	Engraulidae	*Engraulis*	0.1104	Pelagic	ARIU	Ariidae	*Gen., sp. Ind.*	0.1373	Demersal
GERR	Gerreidae	*Gerres*	0.1312	Demersal	DINE	Bythitidae	*Gen. sp. Ind.*	0.1578	Demersal
EUCI	Gerreidae	*Eucinostomus*	0.1104	Demersal	CALA	Bythitidae	*Calamopteryx*	0.1373	Reef-associated
POMA	Haemulidae	*Pomadasys*	0.1492	Demersal	CARA	Carapidae	*Carapus*	0.1373	Demersal
ORTH	Haemulidae	*Orthopristis*	0.1312	Demersal	CYNG	Cynoglossidae	*Cynoglossus*	0.1373	Reef-associated
HAEM	Haemulidae	*Haemulon*	0.1104	Demersal	MOHA	Gerreidae	*Moharra*	0.1373	Demersal
LACT	Lactariidae	*Lactarius*	0.1104	Bathydemersal	HYPO	Hemirhamphidae	*Hyporhamphus*	0.1373	Pelagic
LUTJ	Lutjanidae	*Lutjanus*	0.1492	Demersal	PYTH	Heterenchelyidae	*Pythonichthys*	0.1373	Demersal
STEI	Merlucciidae	*Steindachneria*	0.1312	Demersal	HYGO	Myctophidae	*Hygophum*	0.1373	Mesopelagic
GADL	Moridae	*Gadella*	0.1312	Demersal	MYCT	Myctophidae	*Myctophum*	0.1373	Mesopelagic
MUGI	Mugilidae	*Mugil*	0.1492	Demersal	BROT	Ophididae	*Brotula*	0.1578	Demersal
LAMP	Myctophidae	*Lampadena*	0.1312	Mesopelagic	PLOT	Plotosidae	*Plotosus*	0.1373	Demersal
NEOB	Ophidiidae	*Neobythites*	0.1312	Demersal	BAIR	Sciaenidae	*Bairdiella*	0.1443	Demersal
LONC	Opistognathidae	*Lonchopisthus*	0.1492	Demersal	MENT	Sciaenidae	*Menticirrhus*	0.1373	Demersal
OPIG	Opistognathidae	*Opistognathus*	0.1312	Demersal	DIPL	Sparidae	*Diplodus*	0.1578	Demersal

Pliocene

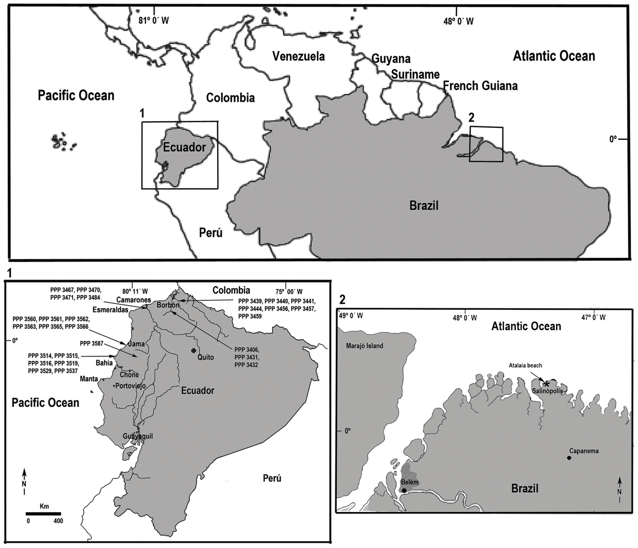
Axis 1		**Ecuador Basin (EPI)**			**Axis 2**		**Panama and Costa Rica basins (PPI and CRPI)**		
ID	Family	Genera	Score	Habitat	ID	Family	*Genera*	Score	Habitat
ARIU	Ariidae	*Gen., sp. Ind.*	0.1509	Demersal	PRAS	Acropomatidae	*Parascombrops*	0.2061	Demersal
PORI	Batrachoididae	*Porichthys*	0.1505	Demersal	CALA	Bythitidae	*Calamopteryx*	0.2061	Reef-associated
BREG	Bregmacerotidae	*Bregmaceros*	0.1505	Demersal	LOBI	Myctophidae	*Lobianchia*	0.2061	Demersal
TRAC	Carangidae	*Trachurus*	0.1765	Demersal	HAEM	Haemulidae	*Haemulon*	0.1869	Demersal
CETN	Centropomidae	*Centropomus*	0.1509	Demersal	ALBU	Albulidae	*Albula*	0.1775	Demersal
CLUP	Clupeidae	*Clupea*	0.1509	Pelagic	BENT	Myctophidae	*Benthosema*	0.1775	Epipelagic
OPIS	Clupeidae	*Opisthonema*	0.1264	Pelagic	DIPL	Sparidae	*Diplodus*	0.1775	Demersal
RHEC	Congridae	*Rhechias*	0.1264	Demersal	POLY	Sternoptychidae	*Polyipnus*	0.1775	Mesopelagic
RHYG	Congridae	*Rhynchoconger*	0.1264	Demersal	SPAR	Sparidae	*Sparus*	0.1775	Demersal
SYMP	Cynoglossidae	*Symphurus*	0.1509	Demersal	NEOB	*Ophidiidae*	*Neobythites*	0.1583	Demersal
ANCH	Engraulidae	*Anchoa*	0.1509	Pelagic	UMBR	Sciaenidae	*Umbrina*	0.1474	Demersal
ORTH	Haemulidae	*Orthopristis*	0.1509	Demersal	SAUR	Synodontidae	*Saurida*	0.1412	Demersal
POMA	Haemulidae	*Pomadasys*	0.1509	Demersal	PLOT	Plotosidae	*Plotosus*	0.1209	Demersal
ANIS	Haemulidae	*Anisostrema*	0.1264	Reef-associated	BATH	Bathyclupeidae	*Bathyclupea*	0.1136	Demersal
LACT	Lactariidae	*Lactarius*	0.1509	Demersal	CARG	Carangidae	*Gen., sp. Ind.*	0.1136	Demersal
LUTJ	Lutjanidae	*Lutjanus*	0.1765	Demersal	GERR	Gerreidae	*Gerres*	0.1136	Demersal
STEI	Merlucciidae	*Steindachneria*	0.1765	Demersal	OCYU	Lutjanidae	*Ocyurus*	0.1136	Reef-associated
LAEM	Moridae	*Laemonema*	0.1264	Demersal	GADL	Moridae	*Gadella*	0.1136	Demersal
OPIG	Opistognathidae	*Opistognathus*	0.1509	Demersal	DION	Myctophidae	*Diogenichthys*	0.1136	Pelagic
SYAC	Paralichthyidae	*Syacium*	0.1765	Demersal	LAMP	Myctophidae	*Lampadena*	0.1136	Pelagic
CITH	Paralichthyidae	*Citharichthys*	0.1509	Demersal	TRIP	Myctophidae	*Triphoturus*	0.1136	Pelagic
ISOP	Sciaenidae	*Isopisthus*	0.1264	Demersal	MYCT	Myctophidae	*Myctophum*	0.1136	Mesopelagic
STEL	Sciaenidae	*Stellifer*	0.1264	Demersal					
MAUR	Sternoptychidae	*Maurolicus*	0.1509	Demersal					

Pleistocene

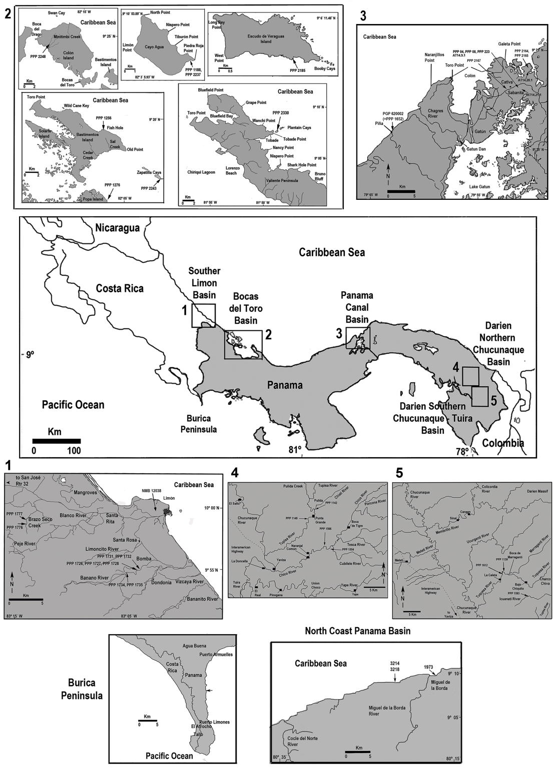
Axis 1		**Costa Rica and Panama basins (CRPE and PPE)**			**Continue…**				
ID	Family	*Genera*	Score	Habitat	ID	Family	*Genera*	Score	Habitat
PRAS	Acropomatidae	*Parascombrops*	0.1917	Demersal	BROT	Ophidiidae	*Brotula*	0.1917	Demersal
ALBU	Albulidae	*Albula*	0.1049	Demersal	OTOP	Ophidiidae	*Otophidium*	0.1917	Demersal
APOG	Apogonidae	*Apogon*	0.1917	Reef-associated	LEPO	Ophidiidae	*Lepophidium*	0.1194	Demersal
ARIO	Ariidae	*Ariopsis*	0.1917	Demersal	NEOB	Ophidiidae	*Neobythites*	0.1049	Demersal
PORI	Batrachoididae	*Porichthys*	0.1917	Demersal	LONC	Opistognathidae	*Lonchopisthus*	0.1917	Demersal
BREG	Bregmacerotidae	*Bregmaceros*	0.1917	Demersal	OPIG	Opistognathidae	*Opistognathus*	0.1049	Demersal
CALA	Bythitidae	*Calamopteryx*	0.1049	Reef-associated	CITH	Paralichthyidae	*Citharichthys*	0.1917	Demersal
OGIB	Bythitidae	*Ogilbichthys*	0.1049	Reef-associated	SYAC	Paralichthyidae	*Syacium*	0.1917	Demersal
CETN	Centropomidae	*Centropomus*	0.1049	Demersal	PRTO	Sciaenidae	*Protosciaena*	0.1049	Demersal
PCON	Congridae	*Paraconger*	0.1049	Demersal	POLY	Sternoptychidae	*Polyipnus*	0.1917	Demersal
RHYG	Congridae	*Rhynchoconger*	0.1049	Demersal	**Axis 2**		**Panama Basin (PPE)**		
SYMP	Cynoglossidae	*Symphurus*	0.1917	Demersal	ID	Family	*Genera*	Score	Habitat
ANCH	Engraulidae	*Anchoa*	0.1049	Pelagic	BOTH	Bothidae	*Gen. et sp. Ind.*	0.2114	Demersal
EUCI	Gerreidae	*Eucinostomus*	0.1049	Demersal	DINE	Bythitidae	Gen. sp. Ind.	0.2114	Demersal
GOBI	Gobiidae	*Gen. sp. Ind.*	0.1917	Demersal	ECHI	Bythitidae	*Echiodon*	0.2114	Demersal
HAEM	Haemulidae	*Haemulon*	0.1917	Demersal	CLUP	Clupeidae	*Clupea*	0.2114	Pelagic
PRTO	Lutjanidae	*Pristipomoides*	0.1917	Demersal	CONG	Congridae	*Conger*	0.2114	Demersal
LUTJ	Lutjanidae	*Lutjanus*	0.1049	Demersal	PYTH	Heterenchelyidae	*Pythonichthys*	0.2114	Demersal
COEL	Macrouridae	*Coelorhinchus*	0.1917	Reef-associated	OCYU	Lutjanidae	*Ocyurus*	0.2114	Reef-associated
STEI	Merlucciidae	*Steindachneria*	0.1049	Demersal	OPHD	Ophidiidae	*Ophidion*	0.2208	Demersal
GADL	Moridae	*Gadella*	0.1917	Mesopelagic	CHER	Ophidiidae	*Cherublemma*	0.2114	Demersal
DIAP	Myctophidae	*Diaphus*	0.1917	Mesopelagic	PLOT	*Plotosidae*	*Plotosus*	0.2114	Demersal
MYCT	Myctophidae	*Myctophum*	0.1917	Mesopelagic	SAUR	Synodontidae	*Saurida*	0.2114	Demersal
BENT	Myctophidae	*Benthosema*	0.1049	Mesopelagic					


180
160
140
120
100
80
60
40
20
0
Number of Genera
EM
MM
LM
PI
PE
Ages

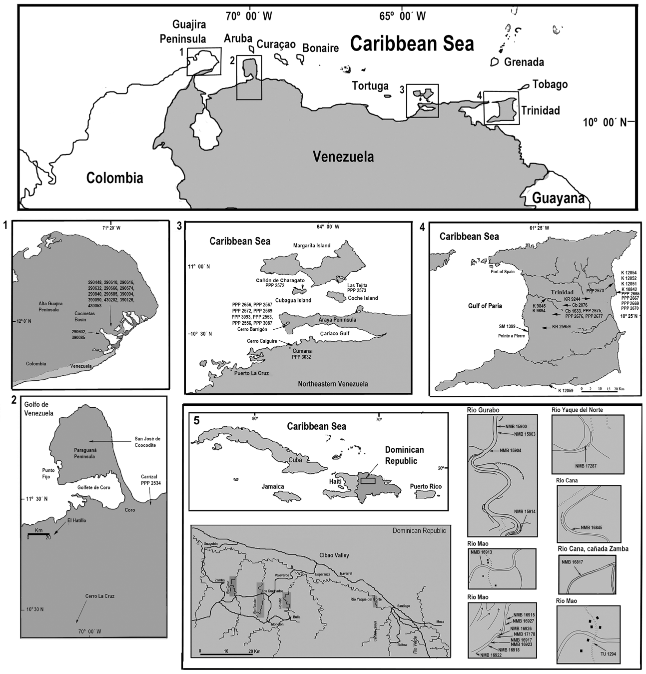
1.


81° 0´ W
48° 0´ W
Venezuela
Guyana
Suriname
French Guiana
Atlantic Ocean
Pacific Ocean
Colombia
1
Ecuador
2
0°
Brazil
Perú
1
PPP 3467, PPP 3470, PPP 3471, PPP 3484
80° 11´ W
Camarones
Esmeraldas
Colombia
75° 00´ W
Borbón
PPP 3439, PPP 3440, PPP 3441, PPP 3444, PPP 3456, PPP 3457, PPP 3459
PPP 3560, PPP 3561, PPP 3562, PPP 3563, PPP 3565, PPP 3566
0°
PPP 3587
Jama
PPP 3514, PPP 3515, PPP 3516, PPP 3519, PPP 3529, PPP 3537
Bahía
Chone
Quito
PPP 3406, PPP 3431, PPP 3432
Manta
Portoviejo
Ecuador
Pacific Ocean
Guayaquil
Perú
N
Km
0
400
2
49° 0´ W
48° 0´ W
Atlantic Ocean
47° 0´ W
Marajó Island
Atalaia beach
Salinópolis
0°
Capanema
Belém
Brazil
N

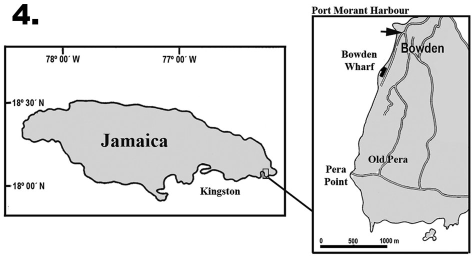
2.

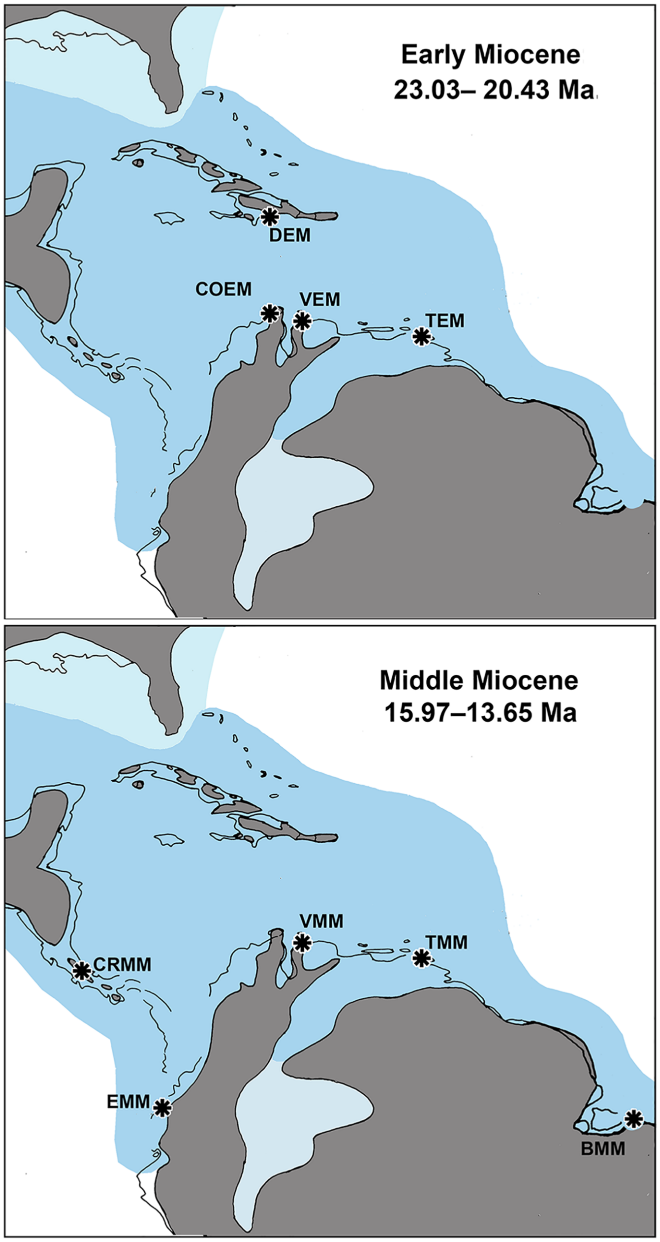

2
Caribbean Sea
Bocas del Toro
Colon Island
Bastimentos Island
PPP 2246
North Point
Cayo Agua
Escudo de Veraguas Island
Booky Cays
Caribbean Sea
Toro Point
Fish Hole
Old Point
Zapatilla Cays
Bluefield Point
Caribbean Sea
Chiriqui Lagoon
Valiente Peninsula
3
Caribbean Sea
Galeta Point
Naranjitos Point
Toro Point
Colon
Chagres River
Pina
Gatun
Lake Gatun
Gatun Dam
Nicaragua
Caribbean Sea
Costa Rica
Souther Limon Basin
1
Bocas del Toro Basin
2
Panama Canal Basin
3
Darien Northern Chucunaque Basin
9°
4
5
Panama
Pacific Ocean
Burica Peninsula
Darien Southern Chucunaque Tuira Basin
Km
0
100
81°
78°
Colombia
1
Caribbean Sea
Mangroves
Limon
Blanco River
Santa Rita
Brazo Seco Creek
Peje River
Santa Rosa
Limoncito River
Bomba
Banano River
Dondonia
Vizcaya River
Bananito River
4
5
North Coast Panama Basin
Burica Peninsula
Costa Rica
Panama
Puerto Armuelles
Pacific Ocean
Km
0
5
Caribbean Sea
Miguel de la Borda River
Km

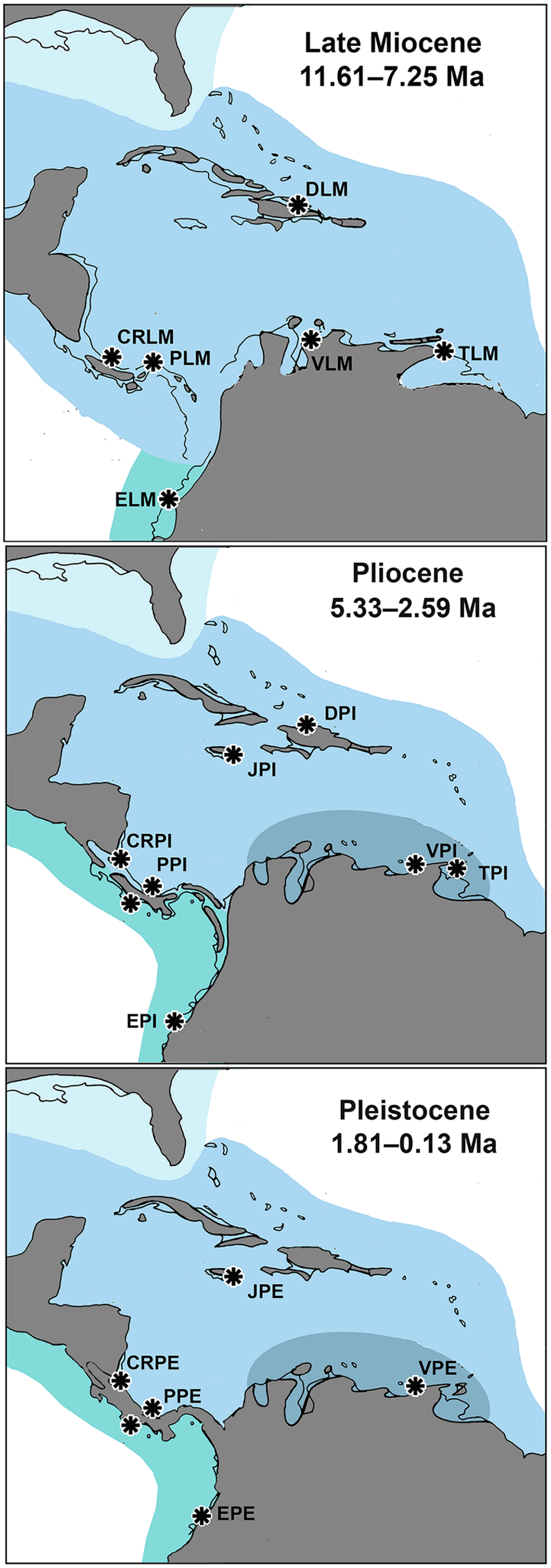
3.

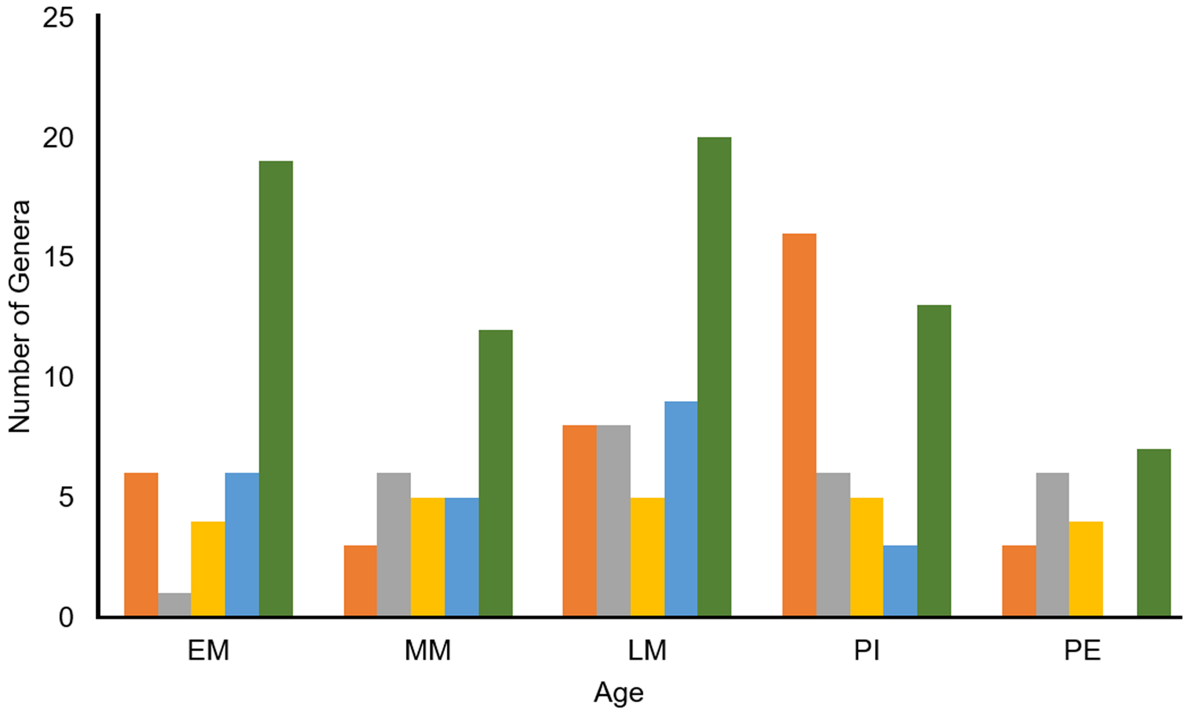

Guajira Peninsula
70° 00´ W
65° 00´ W
1
Aruba
2
Curaçao
Bonaire
Caribbean Sea
Grenada
Tortuga
3
4
Tobago
Trinidad
10° 00´ N
Colombia
Venezuela
Guayana
1
Alta Guajira Peninsula
Cocinetas Basin
Colombia
Venezuela
3
64° 00´ W
Caribbean Sea
Margarita Island
11° 00´ N
Cañon de Charagato PPP 2572
Cubagua Island
Las Tetas PPP 2573
Coche Island
Cerro Barrigon
Araya Peninsula
Cariaco Gulf
Cerro Caiguire
Cumana PPP 3032
Puerto La Cruz
Northeastern Venezuela
4
Caribbean Sea
Port of Spain
Gulf of Paria
Trinidad
Pointe a Pierre
2
Golfo de Venezuela
Paraguana Peninsula
San José de Cocodite
Punto Fijo
Golfete de Coro
Carrizal PPP 2534
11° 30´ N
Coro
El Hatillo
Cerro La Cruz
70° 00´ W
5
Caribbean Sea
Cuba
Dominican Republic
Jamaica
Haiti
Puerto Rico
Dominican Republic
Cibao Valley
Rio Gurabo
Rio Yaque del Norte
Rio Cana
Rio Mao
Rio Cana, cañada Zamba
Rio Mao
Rio Mao

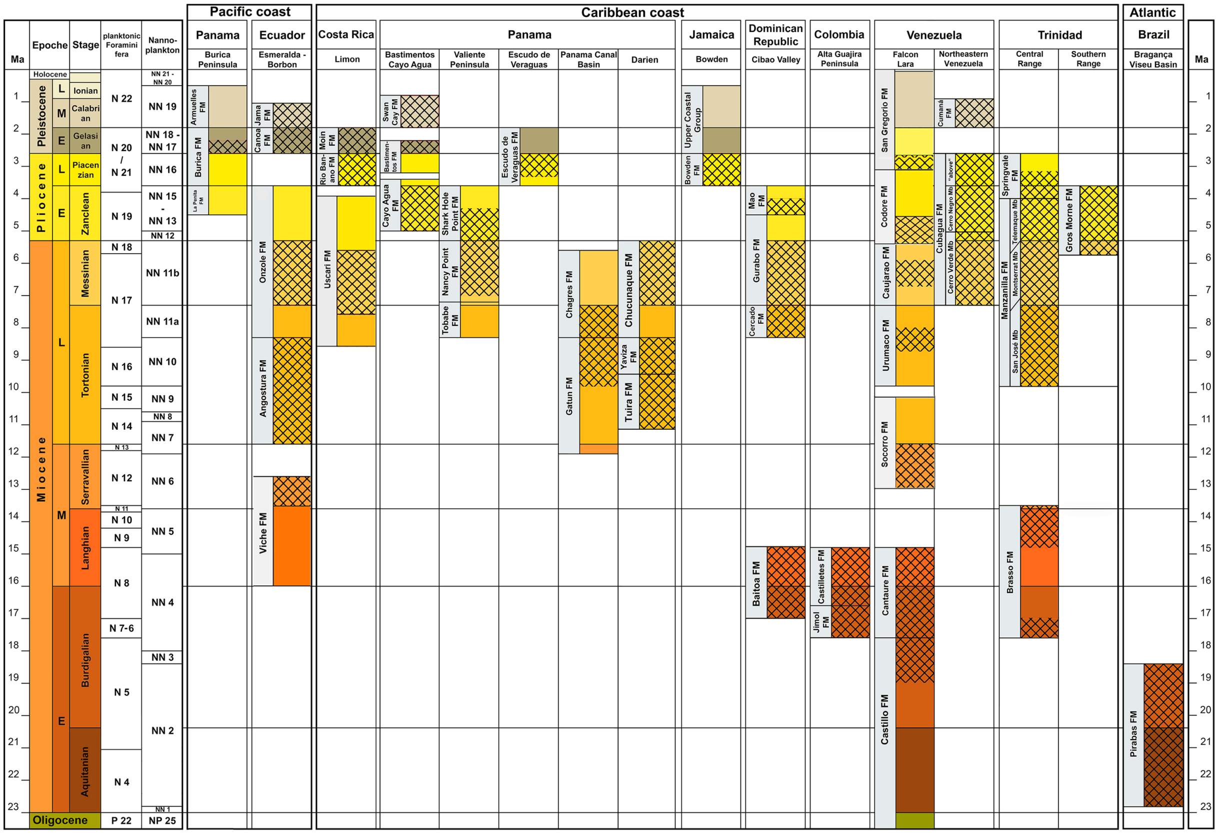
4.


78° 00´ W
77° 00´ W
18° 30´ N
Jamaica
18° 00´ N
Kingston
Port Morant Harbour
Bowden
Bowden Wharf
Old Pera
Pera Point
0
500
1000 m


Early Miocene
23.03– 20.43 Ma
DEM
COEM
VEM
TEM
Middle Miocene
15.97–13.65 Ma
VMM
TMM
CRMM
EMM
BMM


Late Miocene
11.61–7.25 Ma
DLM
CRLM
PLM
VLM
TLM
ELM
Pliocene
5.33–2.59 Ma
DPI
JPI
CRPI
PPI
VPI
TPI
EPI
Pleistocene
1.81–0.13 Ma
JPE
CRPE
PPE
VPE
EPE


25
20
15
10
5
0
Number of Genera
EM
MM
LM
PI
PE
Age


Pacific coast
Caribbean coast
Atlantic
Ma
Epoche
Stage
planktonic Foraminifera
Nanno-plankton
Panama
Burica Peninsula
Ecuador
Esmeralda - Borbon
Costa Rica
Limon
Panama
Bastimentos Cayo Agua
Valiente Peninsula
Escudo de Veraguas
Panama Canal Basin
Darien
Jamaica
Bowden
Dominican Republic
Cibao Valley
Colombia
Alta Guajira Peninsula
Venezuela
Falcon Lara
Northeastern Venezuela
Trinidad
Central Range
Southern Range
Brazil
Bragança Viseu Basin
Holocene
Pleistocene
Pliocene
Miocene
Oligocene
L
M
E
Ionian
Calabrian
Gelasian
Piacenzian
Zanclean
Messinian
Tortonian
Serravallian
Langhian
Burdigalian
Aquitanian
N 22
N 20 / N 21
N 19
N 18
N 17
N 16
N 15
N 14
N 13
N 12
N 11
N 10
N 9
N 8
N 7-6
N 5
N 4
P 22
NN 21 - NN 20
NN 19
NN 18 - NN 17
NN 16
NN 15 - NN 13
NN 12
NN 11b
NN 11a
NN 10
NN 9
NN 8
NN 7
NN 6
NN 5
NN 4
NN 3
NN 2
NN 1
NP 25
Armuelles FM
Burica FM
La Peñita FM
Canoa FM
Jama FM
Onzole FM
Angostura FM
Viche FM
Moin FM
Rio Banano FM
Uscari FM
Swan Cay FM
Bastimentos FM
Cayo Agua FM
Shark Hole Point FM
Nancy Point FM
Tobabe FM
Escudo de Veraguas FM
Chagres FM
Gatun FM
Chucunaque FM
Yaviza FM
Tuira FM
Upper Coastal Group
Bowden FM
Mao FM
Gurabo FM
Cercado FM
Baitoa FM
Castilletes FM
Jimol FM
San Gregorio FM
Codore FM
Caujarao FM
Urumaco FM
Socorro FM
Cantaure FM
Castillo FM
Cumaná FM
Cubagua FM
"above"
Cerro Negro Mb
Cerro Verde Mb
Springvale FM
Manzanilla FM
Telemaque Mb
Montserrat Mb
San José Mb
Brasso FM
Gros Morne FM
Pirabas FM
1
2
3
4
5
6
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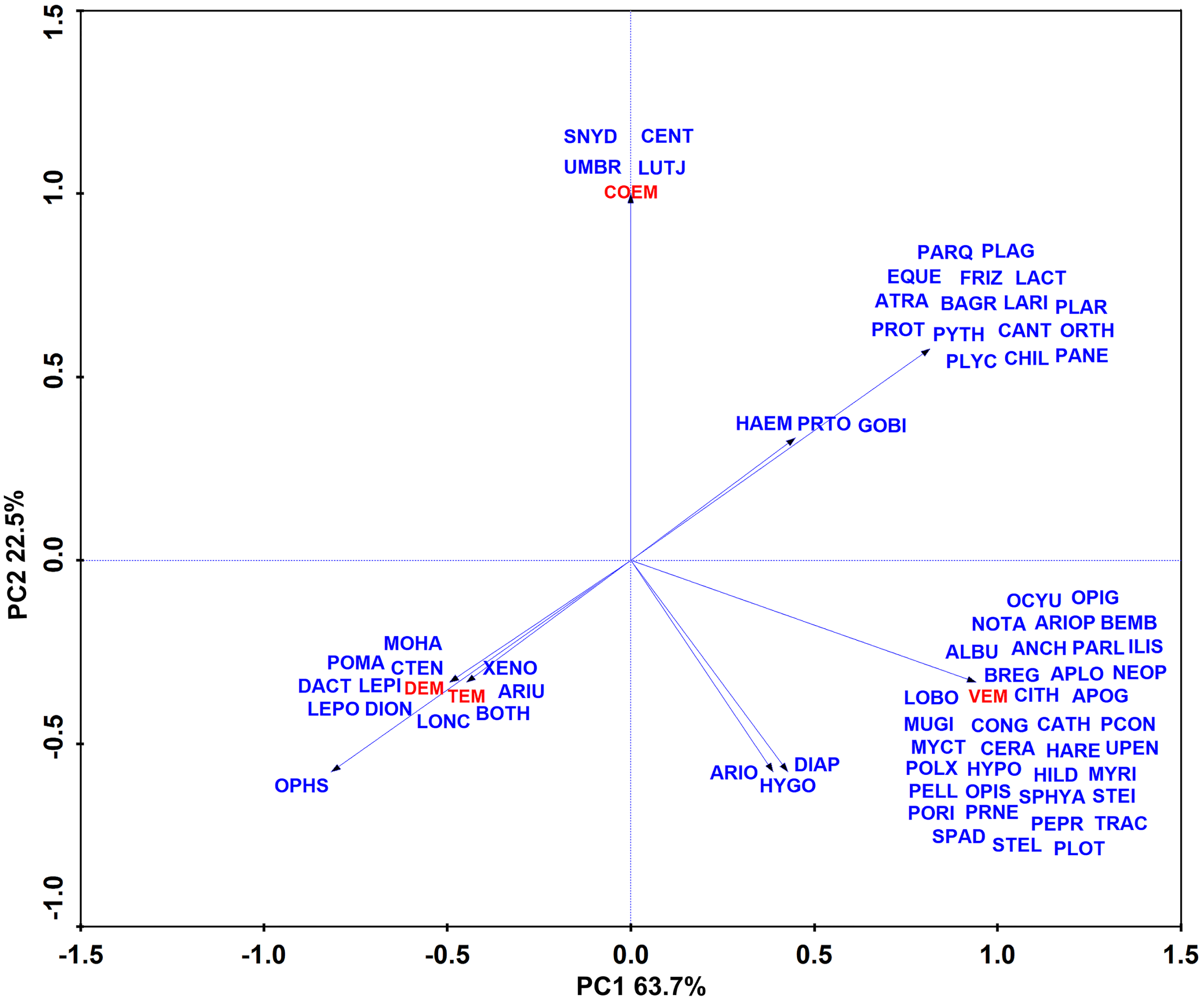
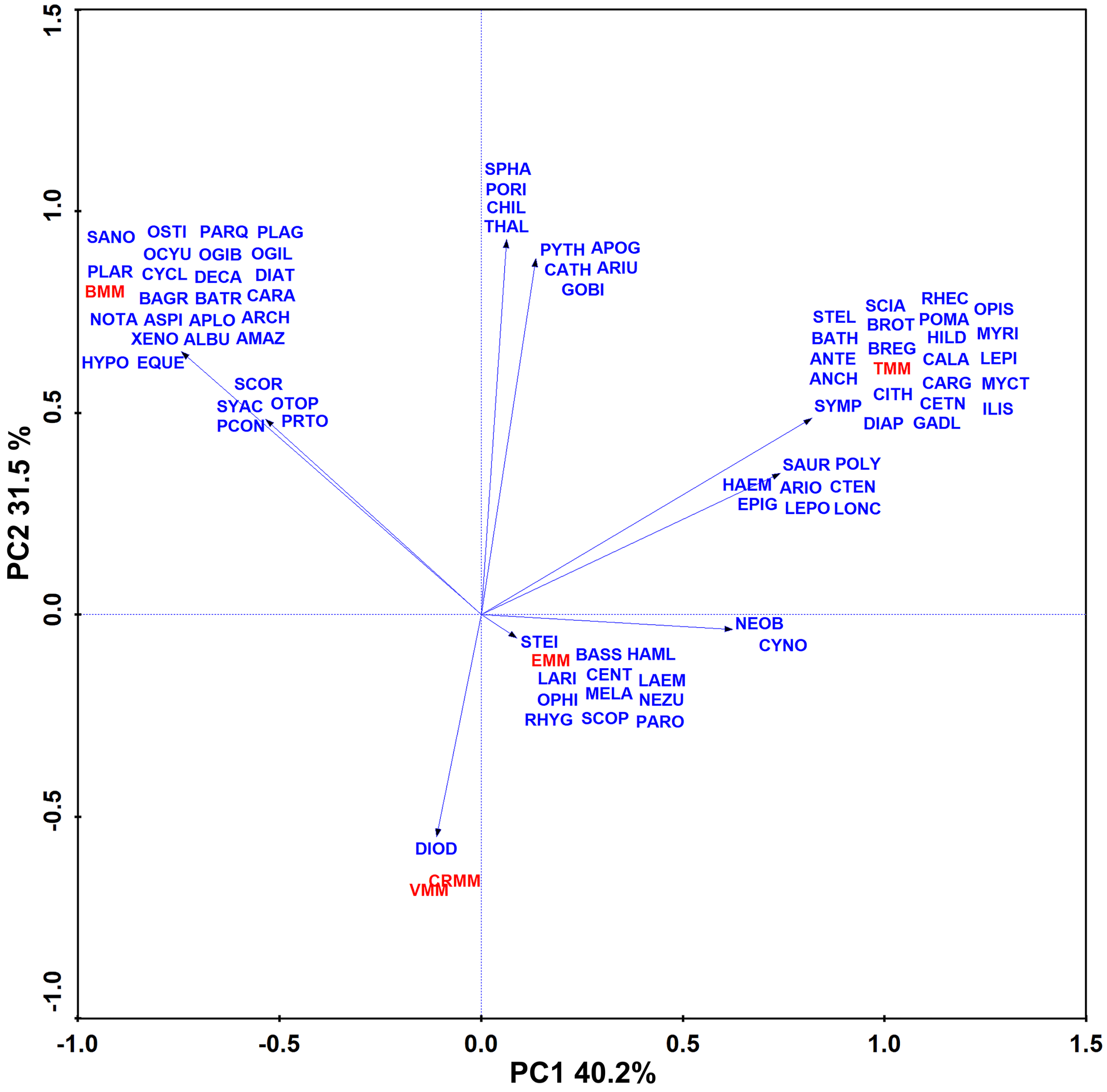
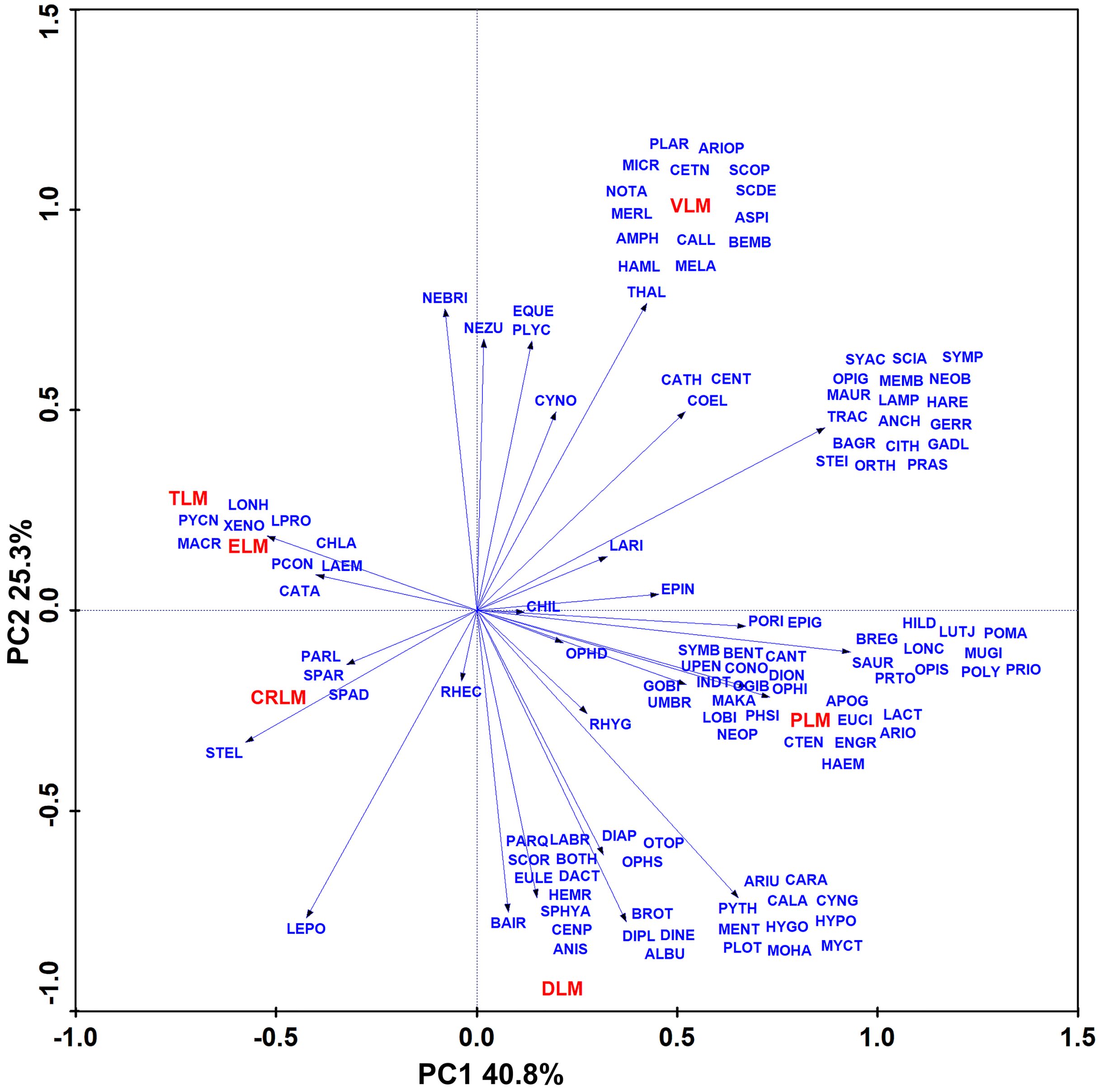
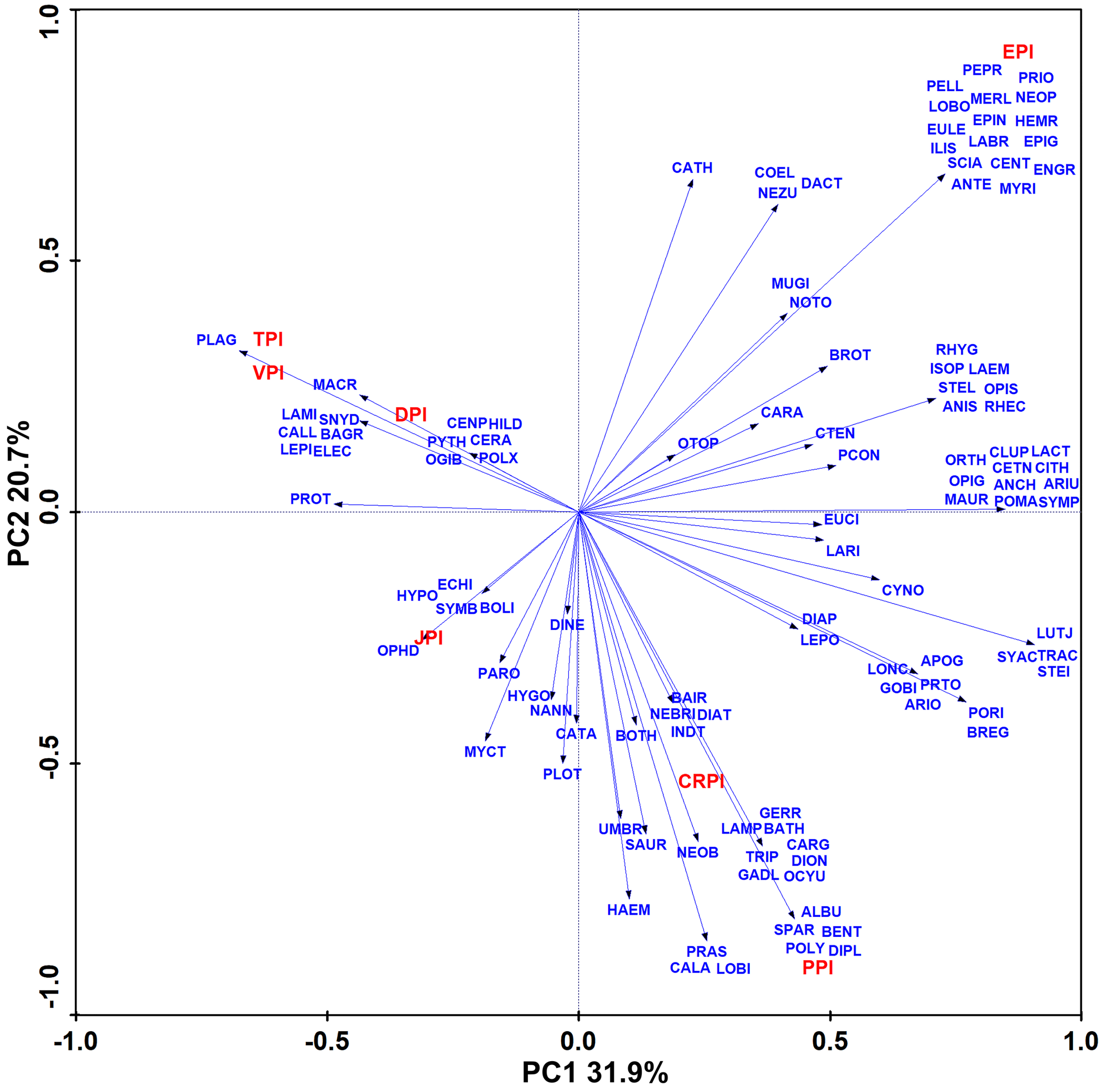
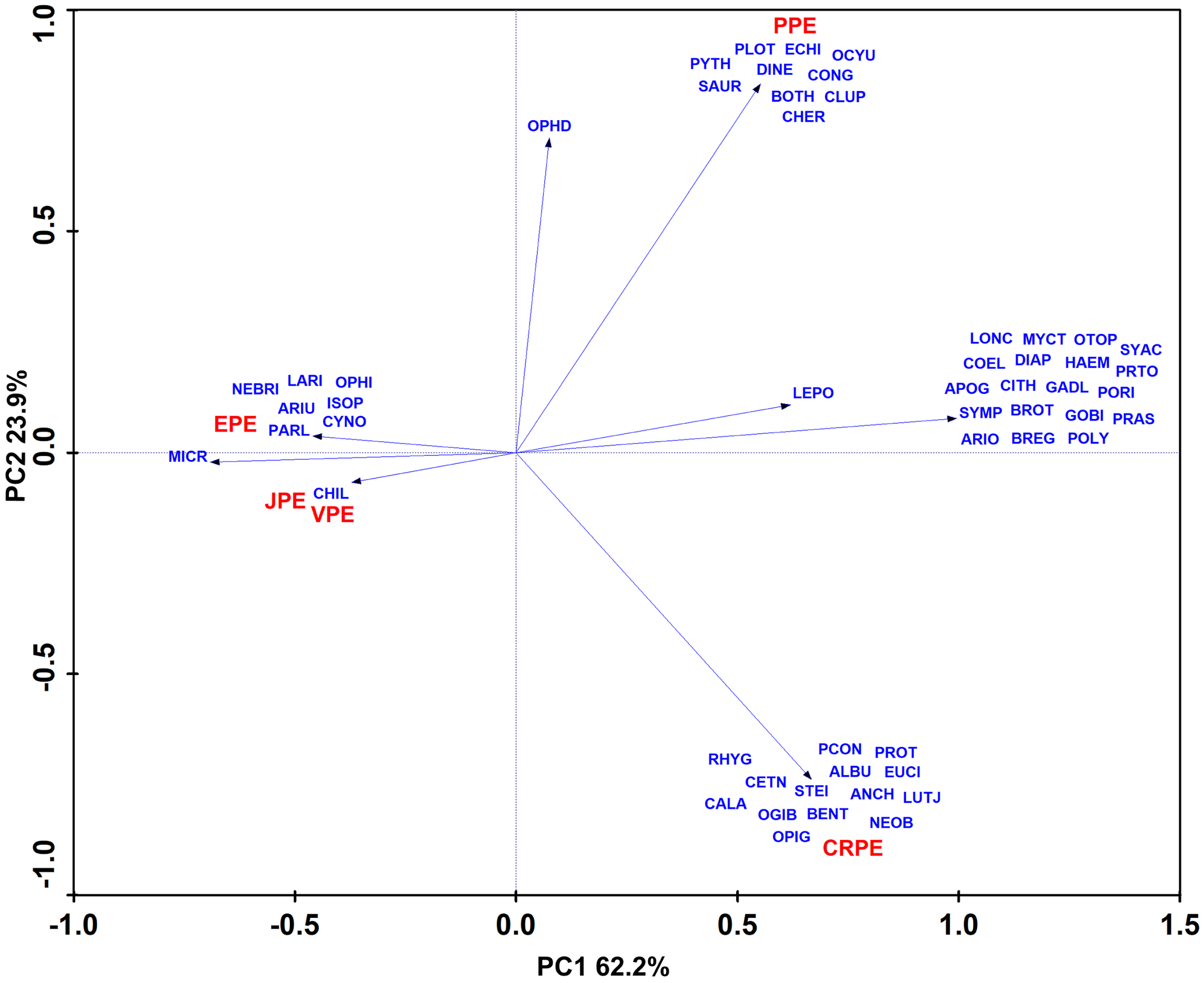
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

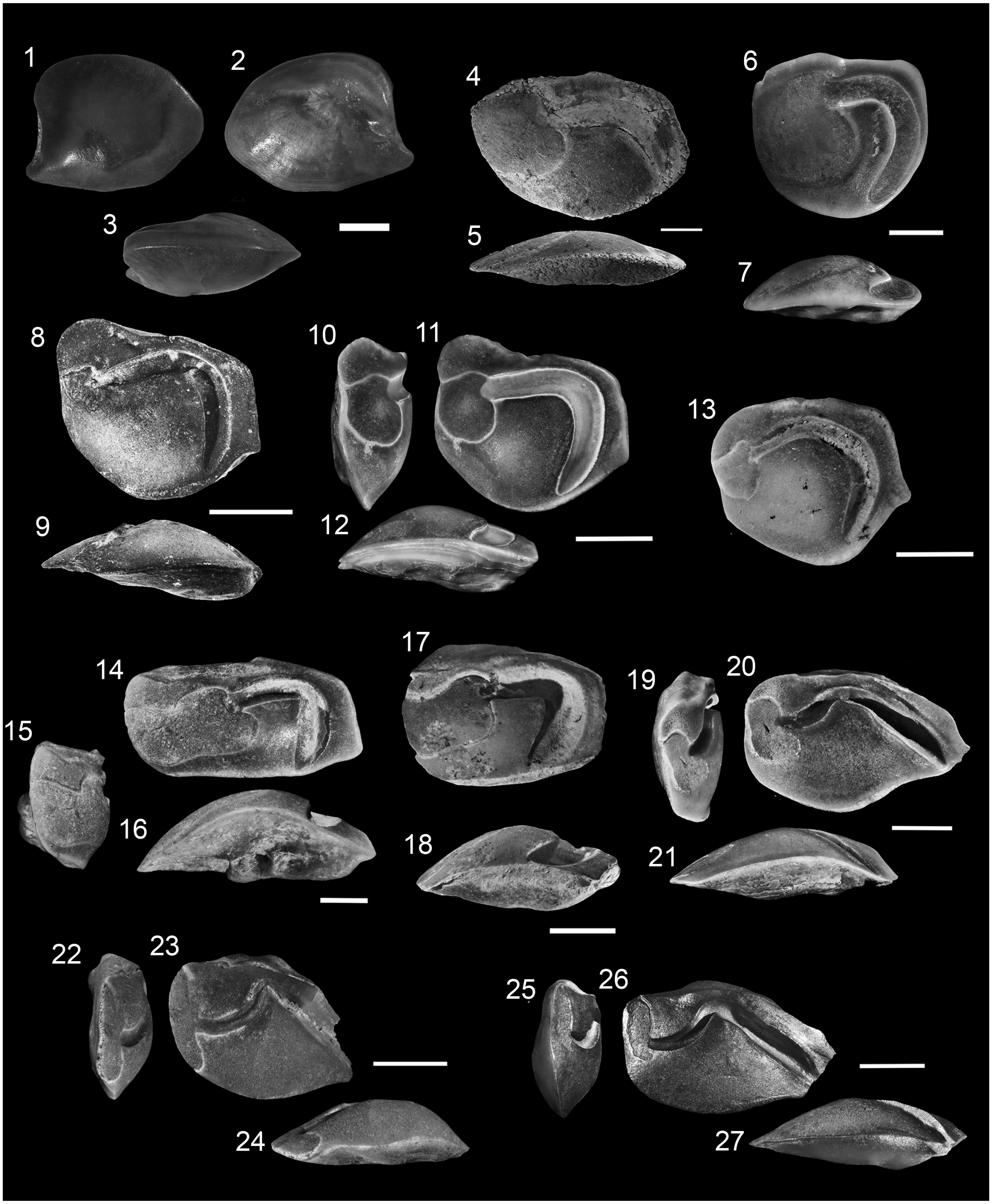

SNYD
CENT
UMBR
LUTJ
COEM
PARQ
PLAG
EQUE
FRIZ
LACT
ATRA
BAGR
LARI
PLAR
PROT
PYTH
CANT
ORTH
PLYC
CHIL
PANE
HAEM
PRTO
GOBI
OCYU
OPIG
NOTA
ARIOP
BEMB
ALBU
ANCH
PARL
ILIS
BREG
APLO
NEOP
LOBO
VEM
CITH
APOG
MUGI
CONG
CATH
PCON
MYCT
CERA
HARE
UPEN
POLX
HYPO
HILD
MYRI
PELL
OPIS
SPHYA
STEI
PORI
PRNE
PEPR
TRAC
SPAD
STEL
PLOT
DIAP
ARIO
HYGO
MOHA
POMA
CTEN
XENO
DACT
LEPI
DEM
TEM
ARIU
LEPO
DION
LONC
BOTH
OPHS
PC2 22.5%
PC1 63.7%
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5


1.5
1.0
0.5
0.0
-0.5
-1.0
PC2 31.5 %
-1.0
-0.5
0.0
0.5
1.0
1.5
PC1 40.2%
SPHA
PORI
CHIL
THAL
PYTH APOG
CATH ARIU
GOBI
SANO OSTI PARQ PLAG
OCYU OGIB OGIL
PLAR CYCL DECA DIAT
BMM
BAGR BATR CARA
NOTA ASPI APLO ARCH
XENO ALBU AMAZ
HYPO EQUE
SCOR
SYAC OTOP
PCON PRTO
SCIA RHEC
STEL BROT POMA OPIS
BATH HILD MYRI
BREG
ANTE CALA LEPI
TMM
ANCH
CITH CARG MYCT
SYMP CETN ILIS
DIAP GADL
SAUR POLY
HAEM ARIO CTEN
EPIG LEPO LONC
NEOB
CYNO
STEI
EMM BASS HAML
LARI CENT LAEM
OPHI MELA NEZU
RHYG SCOP PARO
DIOD
CRMM
VMM


PC2 25.3%
PC1 40.8%
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
1.5
PLAR
ARIOP
MICR
CETN
SCOP
NOTA
SCDE
VLM
MERL
ASPI
AMPH
CALL
BEMB
HAML
MELA
THAL
NEBRI
EQUE
NEZU
PLYC
CYNO
CATH
CENT
COEL
SYAC
SCIA
SYMP
OPIG
MEMB
NEOB
MAUR
LAMP
HARE
TRAC
ANCH
GERR
BAGR
CITH
GADL
STEI
ORTH
PRAS
TLM
LONH
PYCN
XENO
LPRO
CHLA
MACR
ELM
PCON
LAEM
CATA
LARI
EPIN
CHIL
PORI
EPIG
HILD
BREG
LUTJ
POMA
LONC
MUGI
SAUR
OPIS
POLY
PRIO
PRTO
SYMB
BENT
CANT
UPEN
CONO
DION
OPHD
GOBI
INDT
OGIB
OPHI
UMBR
MAKA
APOG
LOBI
PHSI
PLM
EUCI
LACT
ARIO
NEOP
CTEN
ENGR
HAEM
PARL
SPAR
SPAD
CRLM
RHEC
RHYG
STEL
PARQ
LABR
DIAP
OTOP
SCOR
BOTH
OPHS
EULE
DACT
HEMR
SPHYA
BAIR
CENP
ANIS
BROT
DIPL
DINE
ALBU
ARIU
CARA
PYTH
CALA
CYNG
MENT
HYGO
HYPO
PLOT
MOHA
MYCT
LEPO
DLM


EPI
PEPR
PRIO
PELL
MERL
NEOP
LOBO
EPIN
HEMR
EULE
LABR
EPIG
ILIS
SCIA
CENT
ENGR
ANTE
MYRI
CATH
COEL
DACT
NEZU
MUGI
NOTO
PLAG
TPI
VPI
MACR
DPI
LAMI
SNYD
CENP
HILD
CALL
BAGR
PYTH
CERA
LEPI
ELEC
OGIB
POLX
BROT
RHYG
ISOP
LAEM
STEL
OPIS
ANIS
RHEC
CARA
OTOP
CTEN
PCON
ORTH
CLUP
LACT
CETN
CITH
OPIG
ANCH
ARIU
MAUR
POMA
SYMP
PROT
EUCI
LARI
CYNO
ECHI
HYPO
SYMB
BOLI
DINE
JPI
OPHD
DIAP
LEPO
LUTJ
SYAC
TRAC
STEI
APOG
LONC
GOBI
PRTO
ARIO
PORI
BREG
PARO
HYGO
NANN
CATA
BAIR
NEBR
DIAT
INDT
BOTH
MYCT
PLOT
CRPI
GERR
LAMP
BATH
UMBR
SAUR
CARG
NEOB
TRIP
DION
GADL
OCYU
HAEM
ALBU
SPAR
BENT
POLY
DIPL
PRAS
CALA
LOBI
PPI
1.0
0.5
0.0
-0.5
-1.0
PC2 20.7%
-1.0
-0.5
0.0
0.5
1.0
PC1 31.9%


PPE
PYTH
PLOT
ECHI
OCYU
DINE
CONG
SAUR
BOTH
CLUP
CHER
OPHD
LONC
MYCT
OTOP
SYAC
COEL
DIAP
HAEM
PRTO
APOG
CITH
GADL
PORI
SYMP
BROT
GOBI
PRAS
ARIO
BREG
POLY
LEPO
NEBRI
LARI
OPHI
ARIU
ISOP
EPE
PARL
CYNO
MICR
CHIL
JPE
VPE
RHYG
PCON
PROT
ALBU
EUCI
CETN
STEI
ANCH
LUTJ
CALA
OGIB
BENT
NEOB
OPIG
CRPE
1.0
0.5
0.0
-0.5
-1.0
PC2 23.9%
-1.0
-0.5
0.0
0.5
1.0
1.5
PC1 62.2%


1
2
3
4
5
6
7
8
9
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12
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16
17
18
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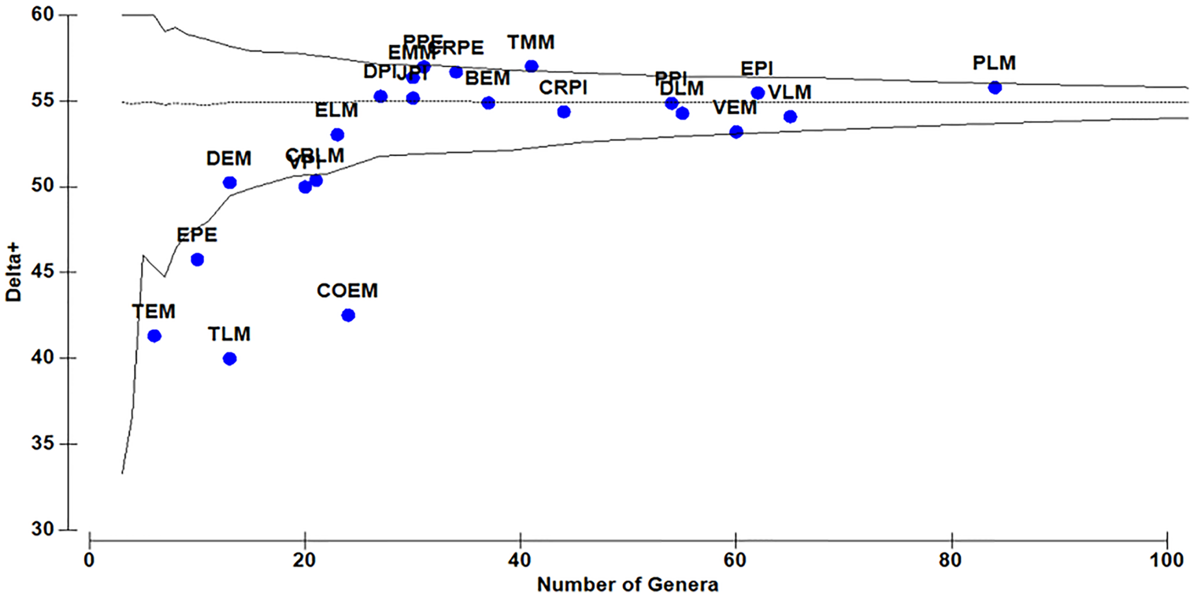
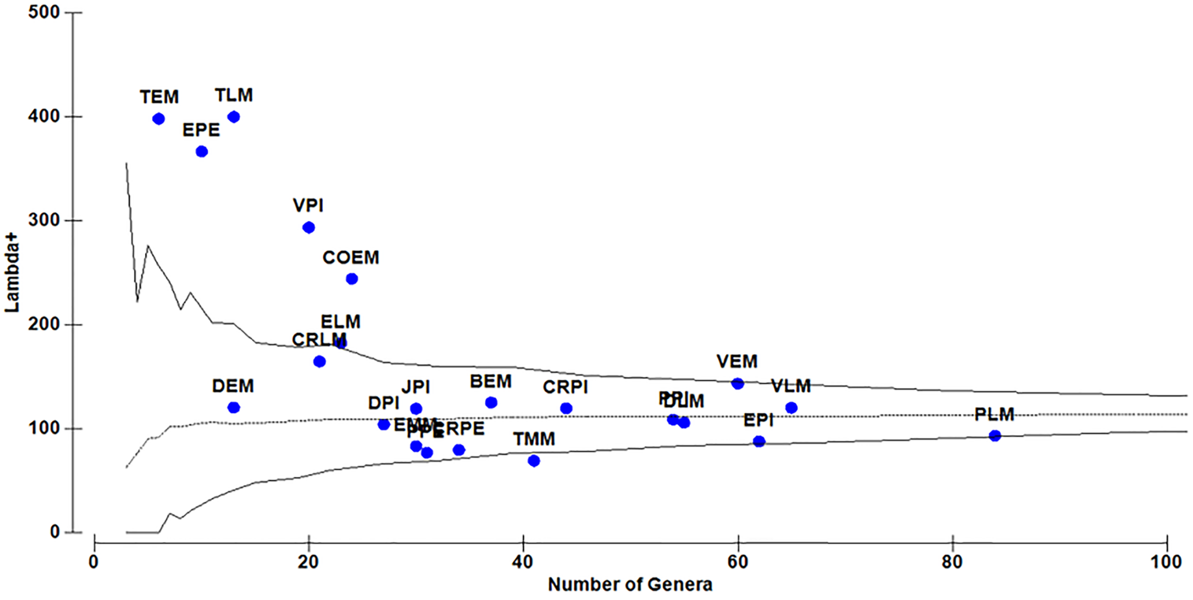
20
21
22
23
24
25
26
27

1.


60
55
50
45
40
35
30
Delta+
0
20
40
60
80
100
Number of Genera
PPE
EMM
ERPE
TMM
DPI
JPI
BEM
CRPI
PPI
DLM
EPI
VLM
VEM
PLM
ELM
DEM
CRLM
VPI
EPE
COEM
TEM
TLM

2.


500
400
300
200
100
0
Lambda+
0
20
40
60
80
100
Number of Genera
TEM
TLM
EPE
VPI
COEM
ELM
CRLM
VEM
DEM
JPI
BEM
CRPI
PPI
DLM
VLM
DPI
EMM
PPE
ERPE
TMM
EPI
PLM

Highlights

- Review of Teleostean fossil otoliths from tropical America
- Paleobiogeographic analyses of Neogene fish assemblage
- Fish otoliths may be used as geochronoindicators

The authors of the entitle manuscript “AMPHI-AMERICAN NEOGENE TELEOSTEAN TROPICAL FISHES ” **have no competing interests to declare**.

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