Historical patterns of distribution in Pycnodontiform and Amiiform fishes in the context of moving plates

Hugo MARTÍN-ABAD & Francisco José POYATO-ARIZA

Universidad Autónoma de Madrid, c/ Darwin, 2, Cantoblanco, 28049-Madrid, Spain.
E-mail : hugo.martin@uam.es, francisco.poyato@uam.es

ABSTRACT. Amiiformes and Pycnodontiformes are non-teleostean actinopterygians that were key members of most Mesozoic fish assemblages, appearing often associated throughout their fossil record. Their phylogenetic and biogeographic patterns, however, are strikingly different. For pycnodonts, whose record extends from around 215 to 40 million years ago, up to seven out of 12 palaeobiogeographical events correspond to dispersals from the Tethys Sea. This was their center of radiation and their final refuge in their expanding-contracting distribution pattern. In turn, the distribution of amiiforms (195 million years ago to recent), although also initially associated with the Tethys sea, follows a mostly vicariant pattern; five main vicariant events out of a total of 15 events, which also include dispersal and radiation events, define their palaeobiogeography, in contrast with no vicariant event detected for pycnodonts. Ecologically, both appear closely associated with coastlines and continents, reaching an almost cosmopolitan distribution; they often occur associated in the same localities. This indicates that their dispersal during the same time intervals are not determined by moving plates alone. Data suggest that their taxonomic diversity and ecomorphological disparity may have played an important role in their dissimilar biogeographical patterns. Pycnodontiforms present a higher diversity and disparity, with variable body-fin shape and dentition; amiiforms are less diversified, with rather uniform body shape and dentition, their disparity being, then, quite low. This was a key factor of their different capacities to compete with teleosts, which would dominate fish faunas since the Late Cretaceous on. Therefore, internal factors play a crucial role to explain the historical patterns of distribution in these organisms.

KEYWORDS: Ambientalism, Actinopterygii, biogeography, dispersal, Fossil Record, internalism, time-slices, vicariance.

1. Introduction

1.1. Conceptual framework

Comparative biogeography has been extensively used to explain the present distribution of extant taxa around the world. By comparing the distribution of the different elements of biotas, a series of patterns, defined by common causes or processes, can be established, and thus their ecological relationships comprehended. These patterns, however, acquire a new interpretation when the temporal dimension is included into the analysis. The combination of time with phylogenetic and geographic data permits the detection of the successive events that lead to the present distribution of a taxon (Hunn & Upchurch, 2001); that is, its biogeographical history. Going a step further, as a result of comparing the biogeographical histories of different taxa common patterns arise, which can show the correlation between environment and evolution (Cavin et al., 2007a). We may add that, as a logical consequence, when differences in these patterns are detected, they must be explained by factors involved in the particular evolutionary history of the corresponding groups.

The inclusion of this temporal dimension into biogeographic studies, however, has not been that extensive, for it requires both a good fossil record and a well-established phylogenetic framework; these two requisites rarely occur together. Nonetheless, as discussed by Cavin et al. (2007a), actinopterygian fishes constitute a potentially good case study, having, among vertebrates, a reasonably good and widespread fossil record, both temporarily and spatially.

1.2. Study taxa

The present paper focuses on the distribution of two actinopterygian orders, the Pycnodontiformes and the Amiiformes, two groups that were prominent members of most fish assemblages, especially during the Mesozoic. A recent analysis of the fossil record of these two groups (Poyato-Ariza & Martín-Abad, 2013) has revealed significant differences in their patterns of diversity and disparity. The pycnodontiforms present a higher taxonomic diversity and larger ecomorphological disparity than the amiiforms. Although both groups often appear together in the same localities, analyses of their phylogenies for comparing their patterns of distribution were not available so far.

The order Pycnodontiformes is a group of neopterygian fishes without Recent representatives; their record known from well-established remains (e.g., Poyato-Ariza, 2005) ranges from the Late Triassic (Norian) to the Eocene (Lutetian-Ypresian). The

systematics of the group (Fig. 1) shows a phylogenetic history of continuous diversification of genera and small families at the base, plus a large derived clade, the Pycnodontidae (see further details in Poyato-Ariza & Wenz, 2002, fig. 43). For example, basal forms are branches formed either by single genera or very small families, such as the Mesturidae and the Brembodontidae. The most inclusive or derived group is the family Pycnodontidae, with very high diversity and distribution. It constitutes the superfamily Pycnodontoidea together with its sister group, the Coccodontidae, less diversified and geographically very restricted. Pycnodonts are mostly marine, typically coastal, but purely continental forms are also known (Poyato-Ariza et al., 1998; Poyato-Ariza, 2005). Both the basal forms and the Pycnodontidae are known from extensive geographic areas (i.e., worldwide except Antarctica and Australia), with the Western Tethys as their initial center of radiation as well as final refuge (Poyato-Ariza & Martín-Abad, 2013).

Amiiforms are an order of halecomorph fishes that had a widespread distribution, being especially diversified during the Mesozoic. They are relatively large, mostly ichthyofagous predators that initially inhabited marine systems, typically coastal. The most derived groups are found in mixed or fully freshwater environments (i.e., Grande & Bemis, 1998). Their oldest reliable evidence dates from the Early Jurassic (Sinemurian), and their biostratigraphic range extends to the Recent, with a single extant species, *Amia calva*. The order (Fig. 2) is divided into two superfamilies, Caturoidea (Caturidae plus Liodesmidae) and Amioidea (Amiidae plus Sinamiidae). The family Amiidae, which was the group of study by Grande & Bemis (1998), is further subdivided into four subfamilies (Amiopsinae, Solnhofenamiinae, Vidalamiinae, and Amiinae) plus the Amiidae *incertae sedis Nipponamia* (Yabumoto, 1994). Finally, Vidalamiinae is divided in two tribes, Vidalamiini and Calamopleurini. The interrelationships of the order are relatively well-resolved, especially for the family Amiidae, at least at generic-level (Fig. 2).

The palaeobiogeography of pycndontiforms and amiiforms has been previously examined; Nursall (1996) discussed the distribution of the pycnodonts, although the lack of a phylogenetic hypothesis at the time prevented a detailed biogeographic analysis. Grande & Bemis (1998) explored the phylogeny and historical biogeography of the family Amiidae. Cavin et al. (2007a) studied the correlation between several environmental indicators and the evolution of ray-finned fishes during the Late Mesozoic, revealing that the diversity of some groups vary along with factors such as the sea temperature. More recently, Cavin

(2008) reviewed the palaeobiogeography of Cretaceous bony fishes, including pycnodontiforms and amioids, suggesting that the entire autoecology of the fishes is a very significant parameter affecting their dispersal ability. Fishes from both orders are found from marine coastal and continental environments (e.g., Nursall, 1996; Grande & Bemis, 1998; Poyato-Ariza, 2005); they are usually related to land masses and, as a consequence, constitute an ideal choice to study distribution in the context of moving of plates.

1.3. Objectives

The present paper aims to compare and contrast the distribution of the Pycnodontiformes and Amiiformes in time and in space. The data will be contrasted with the most comprehensive phylogenetic hypotheses available to identify types of allopatric speciation. Their patterns of evolution and distribution will be compared and discussed with regard to plates movement. Their distribution will be presented graphically and shown in a series of palaeogeographic maps (Figs. 3-7); from the Late Triassic, when pycnodonts first appeared, to the Recent, when the living representative of amiiforms, *Amia calva*, can still be found. We test the hypotheses that vicariant events played a role in forming phylogenetic relationships of pycnodontiforms and amiiforms.

2. Palaeobiogeography: material and methods

Since our aim is to analyze the distribution of these fish groups in relation with the moving plates, we will not perform any standard comparative biogeography analysis based on sister-group relationships of areas (e.g., Cecca et al., 2011). We will rather use the available phylogenetic hypotheses to identify dispersal and/or vicariance events (e.g., Cavin, 2008). Dispersal and vicariance are defined as two types of allopatric speciation,

which briefly means that the speciation process takes place by geographical isolation, and thus the resulting species do not occur together (Mayr, 1942). Vicariance is assumed when a cladogenetic event coincides in time with the separation of the area inhabited by sister taxa; or, in other words, when two sister taxa or two taxa situated in a pectinated position in the phylogeny occur contemporaneously in two different formations (Cavin et al., 2007; Cavin, 2008). Dispersal happens when a younger taxon occurs in a different location than the more basal and more derived clades in a pectinated position, or than the reconstructed location of the common ancestor of a sister group (Cavin, 2008). In addition, radiation events are assumed when several taxa within a clade occur in the same geographic area in a short period of time, even if their interrelationships are not perfectly known (Cavin, 2008). Although these concepts refer to the origination of new species, they can be applied to higher-level taxa as well (e.g., Cavin et al., 2007); in the present paper they are mainly applied at generic level. This will reveal more closely the relationships of pycnodonts and amiiforms with the moving plates by inferring the spatial movements of these fishes throughout time.

For pycnodontiforms, (Fig. 1) we will adapt the tree by Poyato-Ariza & Wenz (2002) including all genera of the order known at the time; subsequent phylogenetic analyses are incomplete, including only the Pycnodontidae (e.g., Poyato-Ariza & Wenz, 2004; Machado & Brito, 2006). For Amiiformes (Fig. 2), we use the most inclusive tree by Grande & Bemis (1998, appendix F) with the accepted interrelationships of amiids (Grande & Bemis, 1998, appendix C), plus those taxa that have been confirmed not to modify the relationships reflected in it, according to the literature.

In order to examine their geographic record in time slices (Figs. 3-7), only reliably identified taxa have been considered; they usually correspond to complete, articulated specimens.
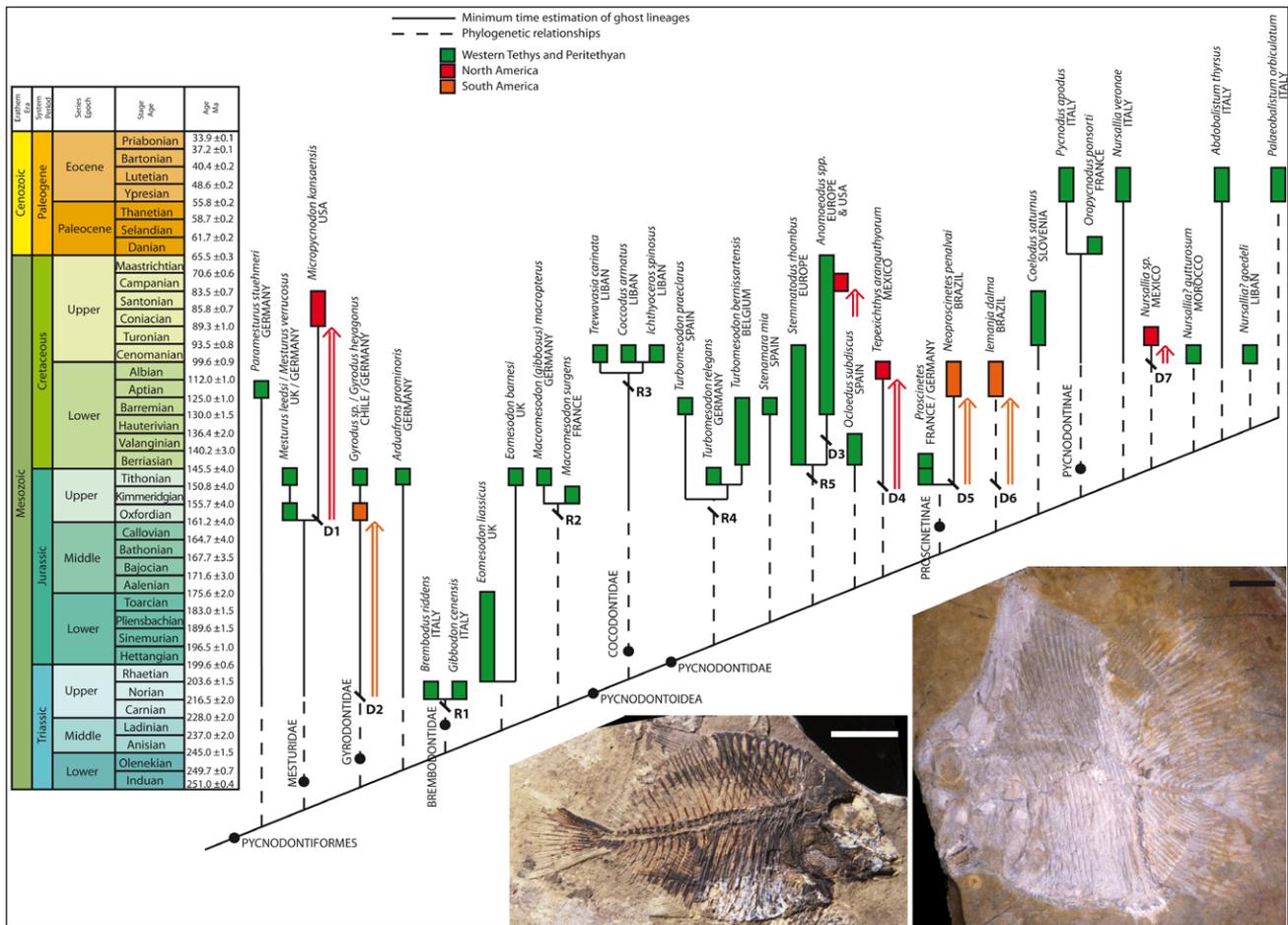

Figure 1. Cladogram showing interrelationships of Pycnodontiformes, modified from Poyato-Ariza & Wenz, 2002. Arrows and D1-4 indicate dispersal events; R1-6 indicate radiation events. Below: photos of *Stemmatodus* (left; specimen MNHN JRE 39, photo D. Serrette) from the Early Cretaceous of Italy and of *Macromesodon* (right; specimen Musée de Lyon, ML 15660, photo D. Serrette, courtesy S. Wenz), from the Early Jurassic of France. Scale bars equal 1 cm.
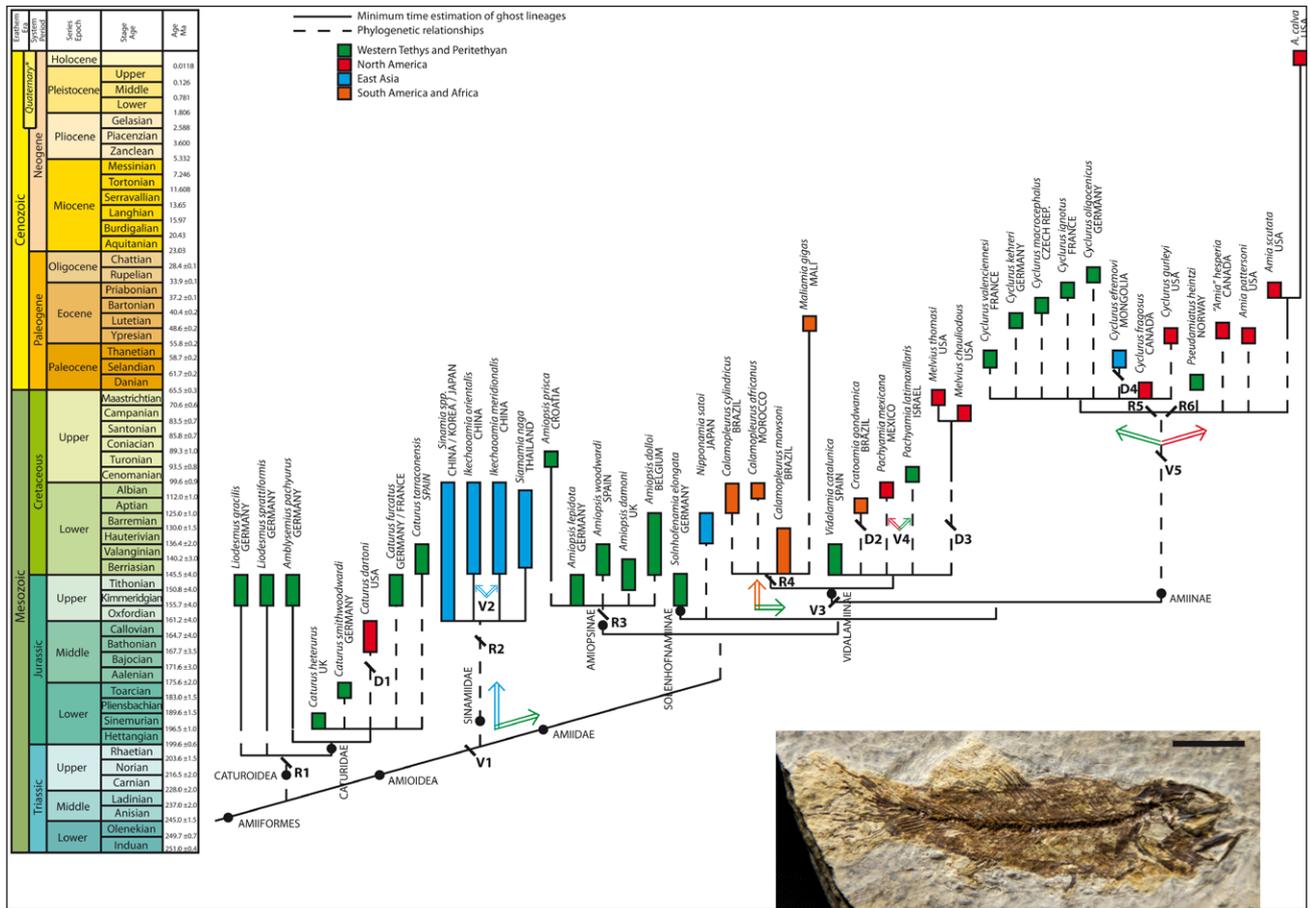
Figure 2. Cladogram showing interrelationships of Amiiformes, modified from Grande & Bemis, 1998. V1-5 indicate vicariant events (double arrows in angle indicate large vicariant events); D1-4 indicate dispersal events; R1-6 indicate radiation events. Below, *Amiopsis* (specimen MCCM-LH 23062a, photo A. Martín-Abad) from the Early Cretaceous of Spain. Scale bar equals 1 cm.

Incomplete or isolated material (usually teeth) is taken into account only when it reveals additional geographic or temporal data about any of the groups. Regarding pycnodonts, most of the information has been extracted from Nursall (1996), Poyato-Ariza & Wenz (2002), and Poyato-Ariza (2005). Additional data come from Tanimoto & Takata (1998), Tanimoto & Fujimoto (2001), Taverne (2003), Kriwet (2004), Kriwet & Schmitz (2005), Rana & Kumar (2005), Machado & Brito (2006), Capasso (2007), Everhart (2007), Alvarado-Ortega et al. (2009), Cavin et al. (2009), Poyato-Ariza & Bermúdez-Rochas (2009), Shimada & Everhart (2009), Poyato-Ariza (2010), Martill et al. (2011), Friedman (2012), Koerber (2012), and Poyato-Ariza (2013). For amiiforms, most of the information was collected by Grande & Bemis (1998). Additional data comes from Schaeffer & Patterson (1984), Forey & Grande (1998), Lambers (1999), Grande et al. (2000), Liu et al. (2002), Friedman et al. (2003), Gaudant et al. (2005), Yabumoto (2005), Yabumoto et al. (2006), Forey & Patterson (2006), Cuny et al. (2006), Cavin et al. (2007b), Arratia & Schultze (2007), López-Arbarello et al. (2008), Brito et al. (2008), Cavin et al. (2009), Cuny et al. (2010), Bogan et al. (2010), Chang et al. (2010), Sullivan et al. (2011), and Cavin & Giner (2012).

The data are presented graphically on palaeocoastline maps for a more comprehensive appreciation. We use "time-slicing" (Upchurch & Hunn, 2002), which permits identification of geographical congruence but avoids superimposition of past biogeographical histories by more recent events (for further discussion, see Cecca et al., 2011). The maps illustrate the geographic record of Pycnodontiformes and Amiiformes in time slices; each caption provides details on the particular taxa known from the corresponding regions. Maps were modified from illustrations and information from Stanley (2005) plus the Palaeogeography Library (2012) and Kerbtier.de (2012).

Temporal information is grouped mostly according to the standard biostratigraphical series; other time-slices were selected according to the diversity and geographical distribution of the

taxa, so that artifacts (e.g., relative diversity) would not obscure biogeographical events. For this reason, Early and Middle Jurassic, with a diversity that is too low to establish any logical biogeographical pattern, are represented together. In turn, the Late Cretaceous is subdivided into two time slices, since its diversity is too high to be coherently represented in a single figure. This way, we define a "Late Cretaceous 1" ranging from Cenomanian to Coniacian and a "Late Cretaceous 2" ranging from Santonian to Maastrichtian. Additionally, this subdivision reveals that the decrease in diversity of both groups after the K/Pg boundary is an artifact of considering the Late Cretaceous record as whole, because, in fact, such a decrease actually occurs within the Late Cretaceous (Poyato-Ariza & Martín-Abad, 2013). The palaeocoastline maps depict the spatial movements of the pycnodontiform and amiiform taxa as inferred from their phylogenetic relationships (Figs. 1 & 2). Incidentally, we prefer to use "dispersal" rather than "migration" because the latter, in the case of fishes, also refers to the relocation from sea to continent or vice versa during the life span of an individual (e.g., eels, salmons).

3. Palaeobiogeographical events

3.1. Pycnodontiformes

The known record of pycnodontiform fishes is clearly centered in the Western Tethys region (Fig. 1). The first, last, and most of the pycnodontiform record stem consistently from the Tethys, and particularly from its Western part. For this reason, all movements predicted by combining their phylogeny with their temporal and geographical distribution do begin in the Tethys (Figs. 1, 3-5).

The oldest known pycnodont remains are the Brembodontidae, from the Late Triassic of Italy; since they are not the most basal pycnodonts, more primitive forms like the Mesturidae and Gyrodontidae are predicted to be ghost lineages at least since the Late Triassic (Fig. 1). Within Mesturidae, there is dispersal
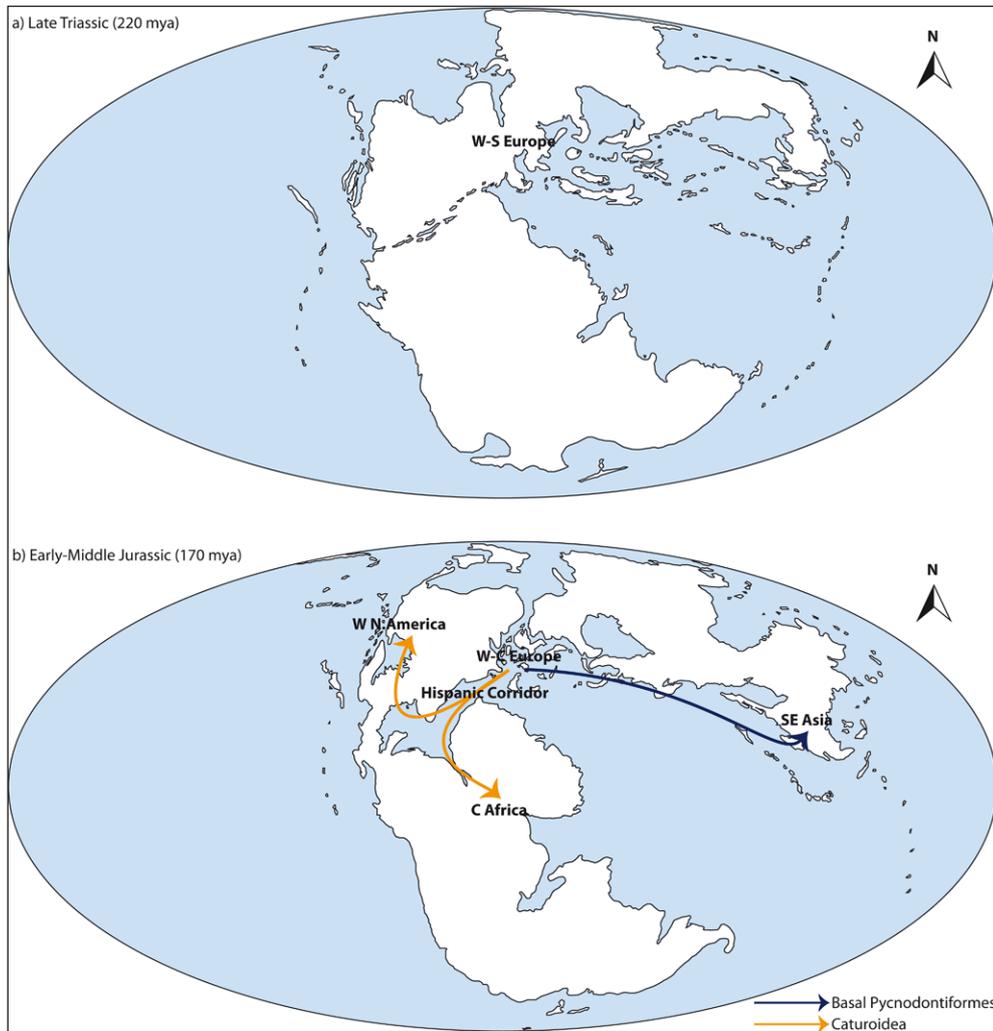
Figure 3. Palaeocoastline maps of the Earth showing the distribution of Pycnodontiformes and Amiiformes during: **a)** the Late Triassic (220 mya); Western-South Europe: *Brembodus*, *Gibbodon*, "*Eomesodon*" *hoeferi*, Pycnodontiformes indet.; and **b)** the Early-Middle Jurassic (170 mya); Western-Central Europe: *Eomesodon liassicus*, cf. *Proscinetes*, *Mesturus leedsi*; *Caturus heterurus*, *Caturus smithwoodwardi*, *Amblysemius*, *Eurypoma grande*. Central Africa: *Caturus*. Western North America: *Caturus*. Southeast Asia: cf. *Gyrodus*.

from the Western Tethys to the Pacific coast of South America some time during the Late Jurassic, after the first European record appears. *Gyrodus*, one of the most basal pycnodonts, moved from Europe to South America before the Late Jurassic. The European record of the genus is younger than the Mesturidae, which represent a more basal clade. A more derived clade than *Gyrodus* is *Arduafrons* from Europe, so the most parsimonious hypothesis is the origination of *Gyrodus* in Europe.

Other than local radiation events (see below), the phylogenetic pattern that reflects the movements of pycnodontiforms in relation with the moving plates is dispersal rather than vicariance; up to seven dispersal events can be traced on their phylogeny (Fig. 1). Apart from *Gyrodus* (D2 in Fig. 1), six genera dispersed to the Americas; within the Mesturidae, *Micropycnodon* (or ancestor; D1 in Fig. 1, Fig. 5a) dispersed to North America; already within the Pycnodontidae, *Anomoeodus* (D3 in Fig. 1, Fig. 5a) and *Tepexichthys* (or ancestor; D4 in Fig. 1, Fig. 4b) dispersed to North America; then *Neoproscinetes* (D5 in Fig. 1) and *Iemanja* (D6 in Fig. 1) (or corresponding ancestors) separately, to South America (Fig. 4b), and finally, *Nursallia* (D7 in Fig.1, Fig. 5a) to North America. These fishes used the Hispanic Corridor, which was the shortest route between Europe and the Americas (e.g., Smith, 1983; Arias, 2006). A partial phylogeny including only Pycnodontidae (Machado & Brito, 2006, fig. 4B) corroborates the interpretation of independent passage to South America for *Potiguara* as well (see Maisey, 1993 and 2000 for additional data on the biogeography of Gondwana fishes). Genera like *Mercediella* in South America or *Tibetodus* in Asia are of unknown affinities, so the phylogeny cannot predict their origins. However, it is most likely that they came from the Western Tethys as well, since the vast majority of the Pycnodontidae are European; that is why some routes are proposed, pending phylogenetic confirmation (e.g., revision of *Mercediella*). The Asian record of pycnodonts is interesting, because, in addition to *Tibetodus*, it includes two undetermined pycnodontids from the Early

(Hauterivian; Tanimoto & Takata, 1998) and Late Cretaceous (Maastrichtian; Tanimoto & Fujimoto, 2001) of Japan. These are based on very fragmentary material; their taxonomic assignation is uncertain, especially in the case of the specimens from the Hauterivian. But, together with the indeterminate pycnodonts from India and Thailand, they clearly show previously unknown Asian diversification of the group, at least during the Cretaceous. Unfortunately, the very fragmentary nature of all this material prevents their inclusion in the phylogeny, so it remains unknown whether they came from the Western Tethys via different passages, like the American forms, or if there was a true Asian radiation. The discovery of more complete material could be used to test these hypotheses.

Radiation events are relatively common in the pycnodont record. Up to five can be confirmed by the data analyzed in the present study (Fig. 1): the Brembodontidae present two genera in the Norian of Italy (R1 in Fig. 1); different species of *Macromesodon* appeared at the end of the Jurassic in Europe (R2 in Fig. 1); a local radiation of the Coccodontidae occurred in the interior of the Tethys (R3 in Fig. 1; see also Cavin, 2008); three different species of *Turbomesodon* appeared in the Upper Jurassic-Lower Cretaceous of Europe (R4 in Fig. 1); finally, *Stemmatodus* and *Anomoeodus* are sister genera whose ranges overlap during the Cretaceous of Europe (R5 in Fig. 1). In addition, new taxa described in recent years suggest diversification of derived pycnodontids during the Late Cretaceous in the Western Tethys region with genera like *Tergestinia*, *Polazzodus*, and *Sylvienodus*. This suggests a possible local radiation of the Pycnodontinae or of derived Pycnodontidae, but only their inclusion in the phylogeny will permit testing this hypothesis (Poyato-Ariza, work in progress).

In summary, 12 main events in pycnodontiform palaeobiogeography have been identified. Seven of them are dispersals (58%) and the remaining five correspond to radiations (42%); no vicariant event has been detected (0%).

Figure 4. Palaeocoastline maps of the Earth showing the distribution of Pycnodontiformes and Amiiformes during: **a)** the Late Jurassic (150 mya); Western-Central Europe: *Macromesodon surgens*, *Proscinetes* spp., *Arduafrons*, *Gyrodus*, *Mesturus*, *Macromesodon gibbosus*, *Proscinetes elegans*, *Turbomesodon relegans*, *Mesturus* sp., *?Eomesodon barnesi*, *?Eomesodon depressus*; *Eurypoma grande*, *Eurypoma egertoni*, *Amblysemius*, *Amiopsis*, *Caturus*, *Solnhofenamia*, *Liodesmus*. S. America: *Gyrodus* sp.; caturid-like remains. Northern China: *Sinamia*, *Ikechaoamia*; and **b)** the Early Cretaceous (120 mya); Western-Central Europe: *Stemmatodus*, *Ocloedus subdiscus*, *Turbomesodon bernissartensis*, *Arcodonichthys*, *Gyrodus*, *Anomoeodus nursalli*, *Stenamara*, *Turbomesodon praeclarus*, *Paramesturus*; *Amiopsis*, *Caturus*, *Vidalamia*, *Tomognathus gigeri*. Northern Africa: *Caturus* sp., *Calamopleurus africanus*. Southern North America: *Nonaphalagodus*, *Paramicrodon*, *Tepexichthys*; *Pachyamia mexicana*. South America: *Iemanja*, *Neoproscinetes*, *Mercediella*; *Calamopleurus mawsoni*, *Calamopleurus cylindricus*, *Cratoamia*. Northern China: *Sinamia*, *Ikechaoamia*. Eastern Asia: cf. *Anomoeodus*, *Tibetodus*, Pycnodontidae indet.; *Caturus*, *Siamamia*, *Sinamia*, *Ikechaoamia*, *Nipponamia*.
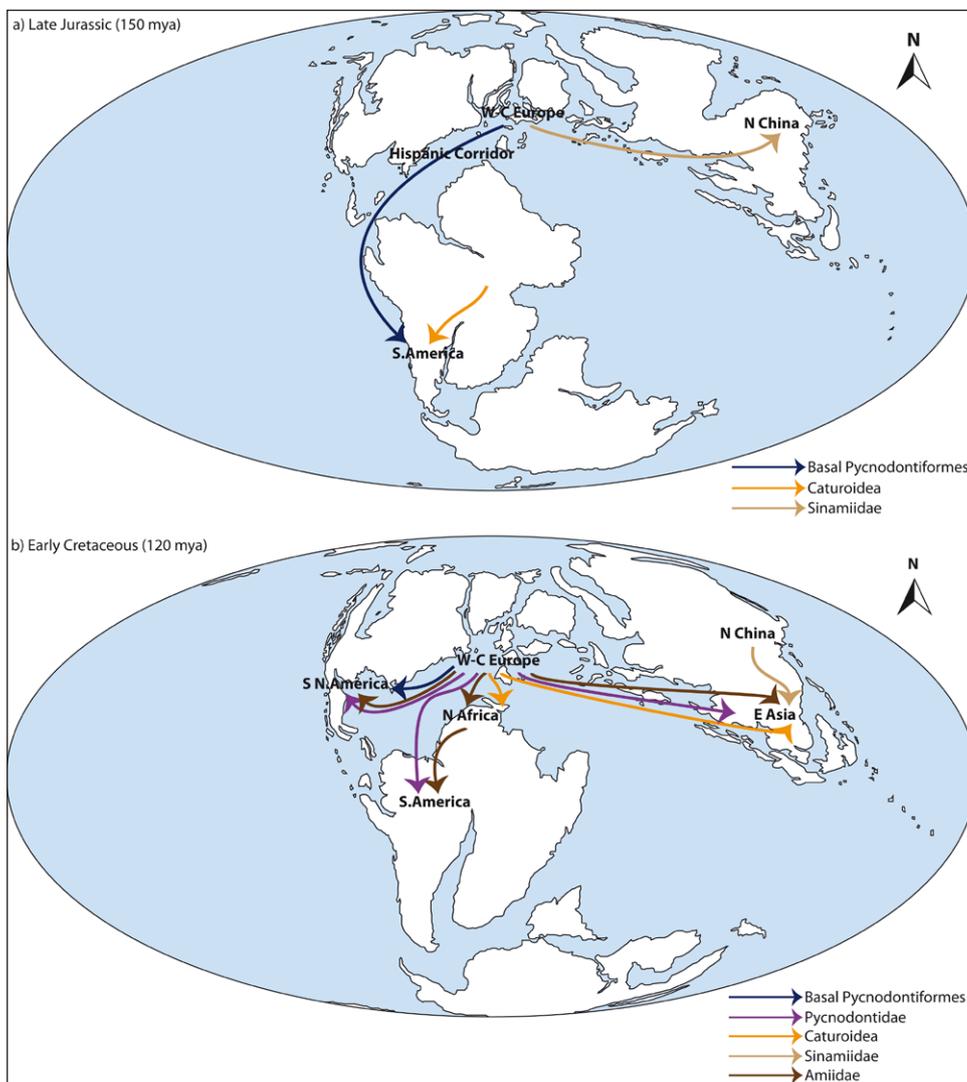
3.2. Amiiformes

3.2.1. Caturoidea

The first well-known caturid is Sinemurian in age (Fig. 2). However, liodesmids, the sister group to caturids, are considered more primitive; their oldest record is Kimmeridgian in age, involving they were a ghost lineage at least from the Sinemurian. Additionally, undetermined caturoids have been cited from Triassic deposits (e.g., Cartanyà, 1995, 1999). In any case, all well-recognized caturoids, and thus the oldest amiiforms, radiated within the Western Tethys Ocean (R1 in Fig. 2). The only exception is the North American, Middle Jurassic *Caturus dartoni* (D1 in Fig. 2), which constitutes the first inferred dispersal of amiiform fishes through the Hispanic Corridor (Fig. 3b). The last reliable record of caturoids is Valanginian in age, although a few undetermined caturids have been cited up to the Aptian-Albian in Tunisia (Cuny et al., 2010) and Thailand (Cuny et al., 2006; Cavin et al., 2009). Being undetermined, their biogeographic movements cannot be tested.

3.2.2. Sinamiidae

All sinamiids known so far are endemic from East and Southeast Asia (China, Japan, Korea, and Thailand) (Fig. 2). The pectinated branches immediate to sinamiids, more basal (Caturoidea) and more derived (Amiidae), are from the Western Tethys (at least the oldest amiids); this strongly suggests a vicariant event taking place very close to the origin of the superfamily Amioidea (V1 in Fig. 2, Fig. 4a). According to Cavin et al. (2007b), sinamiids are involved in another vicariant event that resulted on the occurrence of different species of *Sinamia* and *Ikechaoamia* in Early Cretaceous faunas from North and South China (V2 in Fig. 2). This vicariant event can be explained by the presence of

the Qinling Mountain Belt between them. Apart from this, other sinamiid species radiated through Asia as well (R2 in Fig. 2).

3.2.3. Amiidae

The oldest record of the Amiidae comes from Solnhofen, Germany: it includes the only representative of Solnhofenamiinae, *Solnhofenamia elongata*, and the first reliable record of the Amiopsinae, a subfamily that successfully radiated during the Early Cretaceous (R3 in Fig. 2). Both subfamilies were sympatric, along with other halecomorph groups (Grande & Bemis, 1998), and endemic of Western and Central Europe.

The monospecific *Nipponamia*, recovered from Early Cretaceous deposits in Japan, poses an intriguing problem in amiid palaeobiogeography. Its systematic position within the family remains indeterminate, and it is consequently difficult to ascertain whether it corresponds to an event of vicariance or of dispersal. It is, nonetheless, the only non-amiine amiid to have reached Eastern Asia (Fig. 4b).

The oldest records of the Vidalamiinae are from the Berriasian of both Brazil and Spain. Each of these two records corresponds to a different tribe, the Calamopleurini and the Vidalamiini, respectively. Calamopleurins inhabited the Southern Hemisphere, reaching only the Northern Hemisphere as the African Plate shifted northwards (Fig. 4b). The distribution of vidalamiins extended through the Tethys Sea and the Cretaceous Seaway of North America (Fig. 4b), which were connected by the North American Atlantic Coast during the Early Cretaceous (Grande & Bemis, 1998). Recently, a vidalamiin from Brazil, *Cratoamia gondwanica*, has been described (Brito et al., 2008). A common ancestor to the two tribes dispersed into the Southern Hemisphere about 170 million years ago (mya) and its range was subdivided by an opening between North and South America
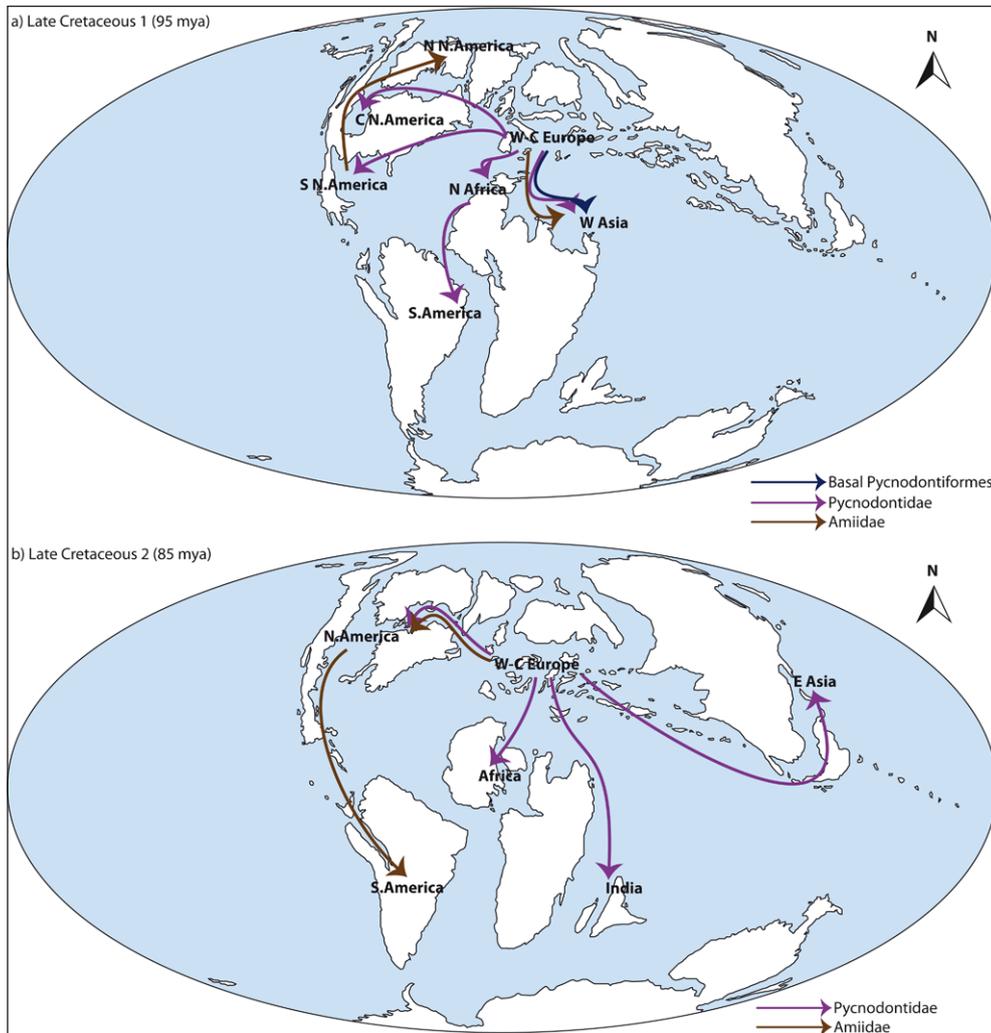
Figure 5. Palaeocoastline maps of the Earth showing the distribution of Pycnodontiformes and Amiiformes during: **a)** the Late Cretaceous 1 (Cenomanian-Coniacian; 95 mya); Western-Central Europe: *Anomoeodus willetti*, *Nursallia*, *Coelodus saturnus*; *Tomognathus mordax*, *Amiopsis prisca*. Northern Africa: *Nursallia gutturosum*, cf. *Pycnodus* sp. Northern North America: undetermined Vidalamiinae. Central North America: *Micropycnodon*; *Paraliodesmus*. Southern North America: Pycnodontidae indet., *Nursallia* sp. South America: *Potiguara rosadoi*, *Nursallia flavellatum?*. Western Asia: *Akromystax*, *Hensodon*, *Nursallia? goedelii*, *Proscinetes*, *Coccodus*, *Ichthyoceros*, *Trewavasia*; *Pachyamia latimaxillaris*; and **b)** the Late Cretaceous 2 (Santonian-Maastrichtian; 85 mya); Western-Central Europe: *Polazzodus*, *Pseudopycnodus*, *Anomoeodus subclavatus*, cf. *Anomoeodus* spp., cf. *Paramicrodon*. Africa: cf. *Gyrodus*, cf. *Ocloedus*. North America: *Anomoeodus* cf. *A. barberi*, *Melvius hauliodous*, *Melvius thomasi*, *Cyclurus*. South America: *?Amia*. Eastern Asia: Pycnodontidae indet. India: cf. *Pycnodus*.

around 150 mya (Grande & Bemis, 1998; Cavin, 2008). After this vicariant event (V3 in Fig. 2), calamopleurins radiated through the Southern Hemisphere (R4 in Fig. 2) possibly by small, additional vicariant events involving the South American and the African species of *Calamopleurus*, and between *Calamopleurus* and *Maliamia* (Cavin et al., 2007a; see also Maisey, 1993 and 2000 for more details on Gondwana amiids). Among vidalamiins, another vicariant event can be detected between the Western and Eastern Tethyan species of *Pachyamia* (V4 in Fig. 2; Fig. 5a). *Cratoamia* (or ancestor) dispersed into the Southern Hemisphere (D2 in Fig. 2; Fig. 4b), and *Melvius* into North America (D3 in Fig. 2; Fig. 5b).

The Amiinae include numerous well-known species (Fig. 2). Their interrelationships, however, are currently unresolved, so it is difficult to establish their palaeobiogeographical history. The first remains assigned to the Amiinae come from the Cenomanian of Uzbekhistan (not represented in Fig. 2 because it is considered Amiinae *nomen dubium*), suggesting a possible linkage with central Europe, which had permanently been inhabited by amiids. In any case, amiines (Figs. 5-7) were separated by another vicariant event (V5 in Fig. 2) at some point, as several species radiated in Europe (R5 in Fig. 2) and others inhabited North America (R6 in Fig. 2). *Cyclurus efremovi* dispersed to Mongolia (D4 in Fig. 2, Fig. 6a). All well-known species of *Amia* come from North America, although older *nomen dubium* remains have been reported from Argentina (Fig. 5b; Bogan et al., 2010) and France (Grande and Bemis, 1998). Taking into account the occurrence of its sister taxon, *Cyclurus*, in older North American deposits, a North American origin for the genus could be hypothesized.

As a summary, 15 main events that shaped the palaeobiogeographical pattern of amiiforms have been detected in their phylogeny. Five of them are vicariant events (33%), while only four correspond to dispersals (27%); the other six are radiations (40%).

4. Discussion

4.1. Pycnodontiformes

Their record is centered in and around the Tethys, where their diversity is always very high. There could be historic reasons for this, since the European localities have been exploited for a longer time; however, the discovery of numerous localities more recently known from all over the world certainly limits the effects of a potentially unequal sampling. The dispersal pattern inferred for basal pycnodonts supports the hypothesis by Cavin (2008) that their diversity is the result of a steady, particularly favorable environment rather than of a radiation event. The general distribution of land masses and their associated marine platforms in and around the Tethys would provide such an environment for quite a long time during the Mesozoic and early Cenozoic, contributing to the continuously increasing diversity of pycnodonts in the Western Tethys. This would explain why the expansion events of the group, as predicted by their phylogenetic relationships, consistently occur from the Tethys to other parts of the globe. Such events were always minor in scale, due to particular movements of individual taxa; no vicariance or major radiation events are ever detected in this group. Minor radiations inside the Tethys did occur, as hypothesized by Cavin (2008) for the Coccodontidae from the Late Cretaceous of the Lebanon, and maybe for the Pycnodontinae or related forms from Southern Europe and Morocco (Poyato-Ariza, work in progress). However, pycnodont diversity in the Tethys is primarily explained as the result of a very long evolutionary history in a fairly constant, favorable environment, primarily provided by the land masses, coastlines and associated marine platforms in and around the Western Tethys. As a whole, their biogeographical history is better explained as an expansion-contraction pattern (compare maps in Figs. 3-5), in which particular taxa of the group sporadically

Figure 6. Palaeocoastline maps of the Earth showing the distribution of Pycnodontiformes and Amiiformes during: **a)** the Paleocene (65 mya); Central Europe: *Tergestinia, Oropycnodus*; *Amia, Cyclurus*. Northern Europe: *Pseudamiatus*. Africa: cf. *Pycnodus*. Northern North America: *Cyclurus, Amia*. Eastern Asia: *Cyclurus*; and **b)** the Eocene (50 mya); Central Europe: *Nursallia veronae, Palaeobalistum, Pycnodus apodus*, cf. *Pycnodus*; *Cyclurus*. Africa: cf. *Pycnodus*; *Maliama*. North America: *Cyclurus, Amia, "Amia" hesperia*. Central Asia: *Cyclurus*. Eastern China: *Cyclurus*.
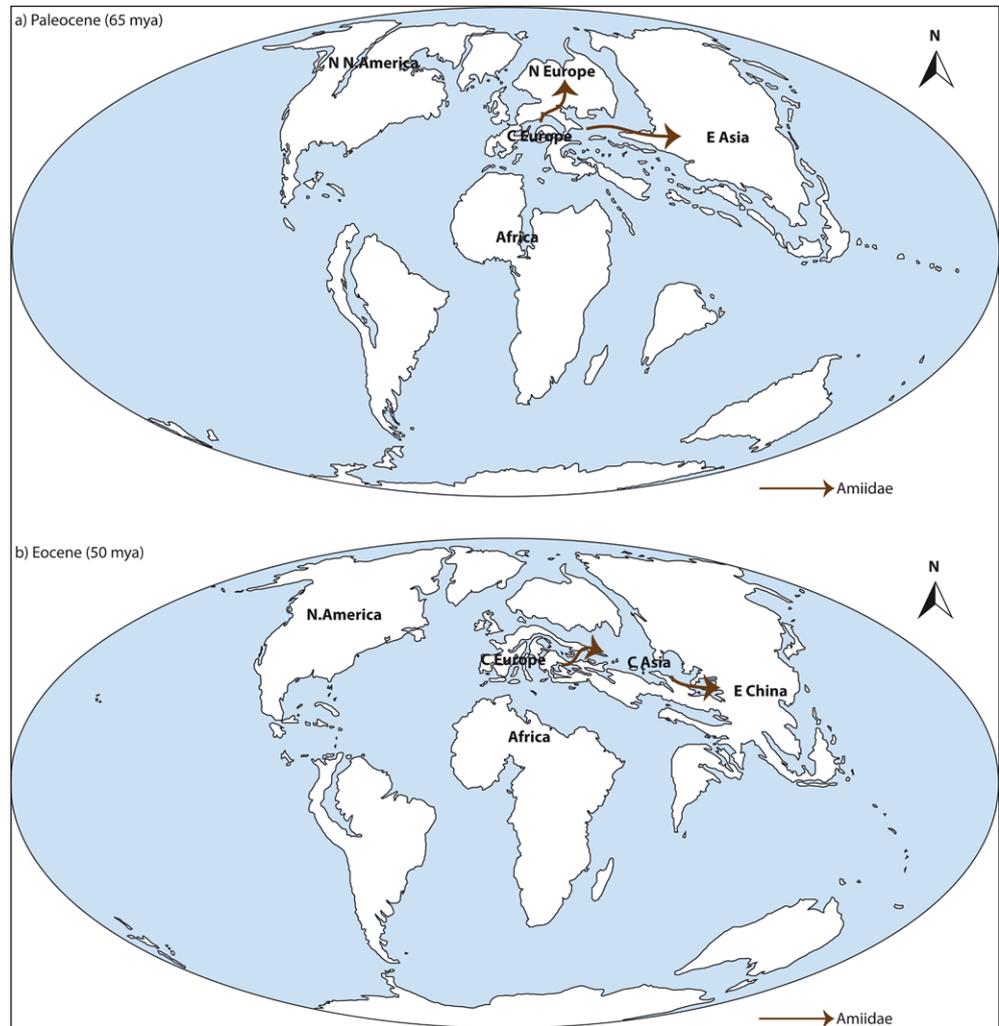
move from the Western Tethys to other areas; their disappearance from those other areas is also slowly progressive. Finally, their extinction occurred after the closing of the Tethys, which acted, therefore, as the center of both the expansion and the contraction in this pattern.

4.2. Amiiformes

They exhibit a very different palaeobiogeographical pattern from that of pycnodontiforms, in which vicariance is the key process to explain their distribution. According to the fossil record, three major vicariant events affecting relatively large clades can be detected (V1, V3, and V5 in Fig. 2). The first of them, the one affecting sinamiids (V1), is related with the transition from marine to freshwater environments, since both the caturids and the more primitive amiids inhabited marine environments, but all known sinamiids are from freshwater deposits (Grande and Bemis, 1998). The vicariant event between the two tribes of Vidalamiinae (V3) is determined by the connection, during the Early Cretaceous, between the Tethys Sea and the Cretaceous Seaway of North America, through the North American Atlantic Coast. As for the third main vicariant event (V5), the distribution of amiines throughout North America and Europe was probably associated again to a transition from marine to freshwater environments, since non-amiine amiids were, at least in origin, marine, whereas all known amiines are considered freshwater fishes. As with pycnodontiforms, amiiforms have constantly inhabited the Tethys, at least until the Oligocene. This sea acted as the center for dispersal and from where the different vicariant events took place. As for any other group, the environment played a key factor in the evolution and distribution of amiiform fishes. For example, Cavin et al. (2007a) cite several physical parameters that can determine the vicariance of marine coastal fishes (marine currents, surface gradients of temperature and salinity, great depths, freshwater and sediment outflows from rivers); within

amiiformes, these factors probably influenced specially the more local vicariant events of vidalamiines. For freshwater taxa, radiations can form species flocks, as is the case of sinamiids and amiines, rapidly spreading among adjacent areas.

4.3. Comparison

Since both groups are primarily related with coastal marine and continental environments, their distribution is closely linked to the position of the land masses (Figs. 3-7), that is, to moving plates. For instance, the opening of the Hispanic Corridor facilitated these fish faunas to move westwards during the Early-Middle Jurassic; the insular Cretaceous Tethys acted as a center of origin and dispersal of new groups (Cavin et al., 2007a; present paper, Figs. 4 & 5); and the opening of the South Atlantic during the Early-Late Cretaceous (Fig. 5a) permitted passage between South America and Africa, for instance for the tribe Calamopleurini (*Calamopleurus* and *Maliamia*, Fig. 2).

In summary, the biogeographical patterns of pycnodonts and amiiforms show the following features in common: 1) they lived in the same environments (although they occupied different niches), linked to coastlines and continents; 2) a similar temporal range; and 3) a very similar general geographical distribution, including frequent simultaneous occurrences (e.g., Solnhofen, Las Hoyas, Santana Formation). Within this common frame, however, their palaeogeographic patterns are remarkably different: radiation largely explains the distribution of pycnodonts; in turn, vicariance is crucial to understand the distribution of amiiforms, whereas it has not been detected in pycnodonts at all. This strongly suggests that other factors were essential to explain this difference.

A recent study (Poyato-Ariza & Martín-Abad, 2013) showed that Pycnodontiformes and Amiiformes had very different ecomorphological plasticity, much higher in the former. This might be one of the factors determining their different potential
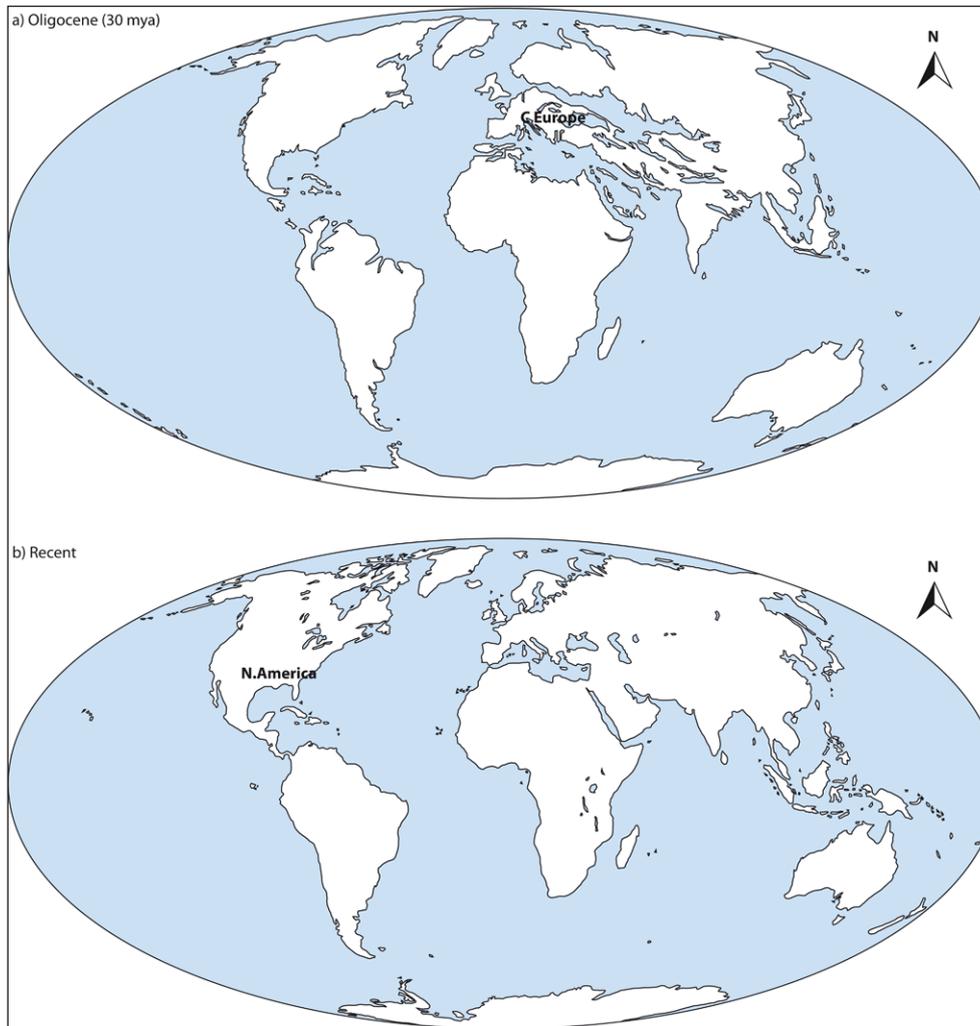
Figure 7. Palaeocoastline maps of the Earth showing the distribution of Pycnodontiformes and Amiiformes during: **a)** the Oligocene (30 mya); Central Europe: pycnodont-like; *Cyclurus oligocenicus*; and **b)** the Recent; North America: *Amia calva*.

for biogeographical movements. It would be very interesting to test how such plasticity is linked to their distribution patterns in detail, since this was a key factor in their competition with teleosts throughout most of the Mesozoic. Pycnodonts were more ecomorphologically plastic in body-fin shape and dentition; they kept teleosteans from durophagous and related niches for a very long time. Only major environmental changes, such as large transgressions, allowed teleosteans to displace pycnodonts from those specialized niches; for instance, pycnodonts disappear from the Americas after the opening of the Atlantic at the beginning of the Late Cretaceous (Fig. 5). In contrast, amiiforms are less ecomorphologically plastic, as shown by their very uniform general body-shape and dentition, corresponding to an ichthyofagous niche (see also Poyato-Ariza & Martín-Abad, 2013). This low plasticity may have restricted their ability for ecological competition, and thus their distribution was more tightly linked to coastlines. As a matter of fact, only the adaptation to freshwater environments seems to have allowed them to persist today, and exclusively in North America.

5. Conclusions

The data presented herein reveal that pycnodontiforms and amiiforms present striking differences in their biogeographic history. All palaeobiogeographical events in the history of pycnodontiforms are dispersal (58%, accounting for their large-scale distribution) or radiation (42%, involving only small-scale, local distribution), with a 0% of vicariant events. In the case of the amiiforms, vicariant events (33%) are more abundant than dispersals (27%) and explain the main large-scale patterns of distribution, while radiations (40%) explain the local diversification of species. As a consequence, the distribution of Pycnodontiformes is essentially explained by a pattern of dispersal, whereas that of Amiiformes is essentially explained by

a pattern of vicariance. This indicates that their movements and ability to disperse, during the same time slices, are not determined by moving plates alone. We suggest that an additional factor involved in the distribution patterns of pycnodonts and amiiforms may be their difference in ecomorphologic plasticity, which largely determined their relationships with the environment. Such plasticity is higher in pycnodonts, which led them to be able to disperse all throughout their evolutionary history. This conclusion is consistent with Cavin (2008), who claimed that fish autoecology is a significant parameter affecting the ability for dispersal. Furthermore, it shows that internal factors are crucial to properly comprehend the palaeobiogeographical pattern of a group. Such factors, namely the morphological plasticity and the subsequent ability for ecologic competition, would strongly affect their capacity for expansion within any particular historic and/or geographic frame.

6. Acknowledgements

7. References

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