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Complex origins of the Lusitania biogeographic province and northeastern Atlantic fishes

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Abstract. The Lusitania Province encompasses the warm temperate marine waters between the southern end of the English Channel, in the North, and Cape Juby or Cape Blanco, in the South, including the Mediterranean and the archipelagoes of the Azores, Madeira and the Canary Islands. Briggs and Bowen (2012) proposed that the warm temperate provinces, although retaining their provincial status, should be grouped with the adjacent tropical ones. Thus, they included the Lusitania Province in a warm eastern Atlantic region. We argue that the time elapsed since the Miocene was sufficient to allow the evolution of endemic species, genera and some higher rank taxa, a finding that emphasizes the convenience to avoid the integration of the province in this larger region. The tropicity index for the Lusitania Province is 1.82, indicating a prevalence of warm water over cold water fish. However, this value is strongly biased by the large differences between the Macaronesian archipelagoes (4.08) and the mainland coasts of the Lusitania Province (0.66).

Keywords. Lusitania Province, Atlantic, Mediterranean, ichthyogeography, endemic ichthyofauna

Introduction

The Lusitania Province encompasses the warm temperate marine waters between the southern end of the English Channel, in the North, to Cape Juby (Briggs and Bowen 2012) or Cape Blanco (Spalding et al. 2007) in the South, including the Mediterranean and the archipelagoes of the Azores, Madeira and the Canary Islands.

Recently, Briggs and Bowen (2012) proposed that the warm temperate provinces, although retaining their provincial status, should be grouped with the adjacent tropical ones. Thus, the Lusitania Province would be included in a warm

eastern Atlantic region (EAR). This change in biogeographic classification is supported by two arguments: 1) many warm temperate areas harbor a composite of eurythermic (and other) species shared with the adjacent tropical or boreal provinces; 2) what are now warm temperate areas had a tropical environment in the Miocene and were subjected to a complex cooling process that reached its peak in the Pleistocene glacial cycles (Briggs and Bowen 2012). This short period of a few million years was likely not long enough to allow deep evolutionary changes to occur, thus limiting the distinctiveness of the warm temper-

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ate fauna. As a diverse and well-studied group of marine organisms, coastal fish were the main group analyzed by these authors.

In this paper, we test the hypothesis of Briggs and Bowen (2012) for coastal fishes of the Lusitania Province using distribution data and we attempt to identify the locations of faunal transitions. These results are discussed taking into account a number of phylogenetic and phylogeographic studies. Specifically, we addressed the following questions. 1) Is the Lusitania Province composed by a majority of tropical species? 2) What is the proportion of Lusitania fish fauna that does not occur in tropical and/or boreal habitats? 3) Does the phylogenetic information available provide evidence of *in situ* diversification in the province?

To achieve these goals we compiled presence/absence data for sub-areas of the Lusitania Province and adjacent areas of tropical African and boreal waters to address the first two questions. We also reviewed the phylogenetic literature on eastern Atlantic and Mediterranean fish to address question 3.

A brief outline of the major events that shaped the Lusitania Province

This short description follows Briggs (1995), Floeter et al. (2008) and Briggs and Bowen (2012). In the Miocene, about 20 million years ago (Mya), the collision of the Arabian and African plates closed the Tethys seaway, ending the circumtropical ocean that connected what are now parts of the Atlantic, Indian and Pacific oceans. About 5.0–5.5 Mya the connection between the Atlantic Ocean and the Mediterranean Sea was interrupted generating the Messinian Salinity Crisis (MSC) in the Mediterranean. Most areas of this sea likely lost their marine conditions and were either dry land or lagoons of very diverse salinities, although the geographical extent and chronology of this series of events are still open to debate (e.g., Carnevale et al. 2008, Gironé et al. 2010). In the northeastern part of the Mediterranean, the Alpine orogenesis caused the uplift of terrain that separated a substantial area, called the Paratethys, from the bulk of the Mediterra-

nean. At a second phase, the massive drainage of European freshwaters into the Paratethys drastically reduced its salinity and finally caused a huge freshwater flow into the Mediterranean creating low salinity lacustrine conditions. Marine conditions were probably re-established with the opening of the Strait of Gibraltar (5 Mya), although some studies suggest the existence of marine environments in Italy at an earlier stage (Carnevale et al. 2008). Thus, with the possible exception of some euryhaline lineages, the Mediterranean marine fauna was founded by colonists coming from the Atlantic, which at that latitude was still a tropical ocean.

During the middle Pliocene (3.1–3.5 Mya), the last connection between the tropical Atlantic and Pacific was eliminated, with the closure of the Isthmus of Panama. The Pliocene was a period of large scale cooling, which established a boreal fauna in the Arctic that was connected with the Atlantic but not with the Pacific. The opening of the Bering Strait, about 2.5 Mya, established a contact zone between the Arctic and the Pacific, leading to a massive exchange of species between the Pacific, Arctic and Atlantic oceans. The Pacific, being much more species rich, contributed with more migrants to the Atlantic than the reverse. The cooling trend continued and, about 2 Mya, the Pleistocene glaciations became a dominant climatic feature. Arctic conditions developed and the boreal areas became restricted to the North Atlantic and the North Pacific with a gradual differentiation between the faunas of the different ocean margins. At the last glacial maximum and probably during the peaks of previous glaciations, an ice sheet covered the North Sea and the Baltic Sea. Boreal conditions moved southward several times reaching the southern part of Biscay and northwest Iberia (Dias et al. 1997). The tropical eastern Atlantic also shrank during glacial peaks, to the point that the now tropical Cape Verde Islands lost their tropical character.

Presently, important changes are occurring within the Lusitania Province with the introduction of new species with ballast waters, Lessepsian migrants through the Suez Canal affecting faunal composition in the Mediterranean, and a tropicali-

zation of the warm temperate northeastern Atlantic associated with climatic changes (Bianchi 2007).

Methods

In this paper we restricted our analysis to continental shelf fishes and used the limit of 200 m maximum depth as a criterion for including species in our list. Species that migrate between continental shelves or live in brackish coastal lagoons also were included. Pelagic oceanodromous, deep-water species, Lessepsians and other introduced fish were not considered.

A presence/absence matrix was compiled from faunal lists of specific areas, in which the authenticity and taxonomic validity of the records was checked by the respective authors. Thus the following sources were used: Brito et al. (2002, 2007), Floeter et al. (2008), Wirtz et al. (2008), Bañon et al. (2010), Porteiro et al. (2010). The results of several years of underwater observations and the inspection of specimens collected by local fisherman along the northeastern Atlantic coast resulted in various additions and amendments, especially those of one of the authors (J.F.).

The matrix was subsequently compared with information for the area and ecological conditions included in Froese and Pauly (2012), so that disagreements could be pinpointed and clarified with additional literature. Most taxonomic discordances between sources were solved with the information provided by Catalog of Fishes¹ (Eschmeyer 2012) and the references therein.

For the construction of the matrix, the southern limit of the Lusitania Province was placed in Cape Blanco following Spalding et al. (2007). The subdivisions inside the Lusitania Province follow the proposal of Briggs (1995). In the North, from the southern entrance of the English Channel to northwest Spain in Galicia is what we have designated as Biscay in a broad sense. To the south, we find Atlantic Iberia (Atl. Iberia), western Mediterranean Sea (W Med) and eastern Mediterranean Sea (E Med), Atlantic Morocco (Atl. Morocco) and West Sahara (W Sahara). Offshore, the

archipelagoes of the Azores, Madeira and the Canary Islands (Canary Is.) are also included in the Lusitania Province.

The tropical eastern Atlantic (TEA), encompassing the archipelagoes of Cape Verde and Sao Tome and Principe and the western tropical Continental Africa (W Tropical Cont. Africa) is included only as an external reference group not being analyzed in detail in its internal structure. The Boreal Province was included with the same purpose (but see the discussion section below).

The table with the geographical distribution of each species (see *Supplementary Information*) was used to calculate the species richness and level of endemism for each area.

The relationships among areas were estimated by cluster analysis, using Sorensen similarity coefficient, and unweighted pair group method with arithmetic mean (UPGMA). The statistical significance of each cluster was evaluated using similarity profile permutation tests (SIMPROF), with one thousand permutations. To provide a visual representation of the relationships between areas without constraints imposed by a tree-like structure, we also performed a Multi-Dimensional Scaling (MDS) analysis, with one hundred restarts. These analyses were performed in PRIMER v.6.0 (Clarke and Gorley 2006).

In recent years there has been a debate on the interpretation of classical dissimilarity/beta diversity indices. Baselga (2010) called attention to the fact that dissimilarity between two locations can be decomposed in two components: nestedness, represented by the presence of species in one location that are absent from the other, and turnover, represented by genuine species substitutions, i.e., species that are absent from one locality but are replaced by an equivalent number of other species. Although the best way to quantify the components of beta diversity is still under debate (Almeida-Neto et al. 2012, Baselga 2012, Carvalho et al. 2012), from our point of view the most relevant information is retained in the turnover component. The Sorensen dissimilarity index can be viewed as the sum of

¹ <http://research.calacademy.org/ichthyology/catalog> accessed March 2012

nestedness and turnover which is expressed by the Simpson dissimilarity coefficient. Thus we also present the results of cluster and MDS analyses using the turnover component of beta diversity estimated using the R package Betapart (Baselga 2010).

We computed, for each area, the percentage of species belonging to the following categories: eurythermic species (fish that occur in boreal, temperate and tropical waters), cold water species (fish that occur in boreal and temperate waters but are absent from tropical areas), warm water species (fish that occur in tropical and tem-

perate waters but are absent from boreal region) and Lusitania endemic fish. The category 'other species' was created to include fish with more complex distributions, mainly outside the eastern Atlantic. A rough tropicality index was obtained by dividing the number of warm water species by that of cold water ones for each area.

Results

In Table 1 species richness and the level of endemism are presented for each area in the eastern Atlantic Ocean and Mediterranean Sea. Considering the continental shores of Africa and

Province	Region	Species		Genera		Tropicality index
		Total	% Endemism	Total	% Endemism	
Boreal		189	1.6	134	0.7	-
Lusitania	Biscay	231	0	156	0	0.41
	Atlantic Iberia (Atl. Iberia)	308	0	189	0	1.13
	W Mediterranean Sea (W Med)	348	1.1	200	0.5	1.62
	E Mediterranean Sea (E Med)	300	5.3	171	1.2	1.55
	Mediterranean Sea	370	15.4	207	3.9	1.6
	Atlantic Morocco (Atl. Morocco)	262	0	169	0	1.95
	West Sahara (W Sahara)	225	0.4	148	0	3.68
	Azores	148	1.4	114	0	3.45
	Madeira	186	0	136	0	3.85
	Canary Islands (Canary Is.)	258	0	170	0	5.56
	Macaronesia	292	2.4	190	0	4.08
	Lusitania	519	25.2	281	6.4	1.8
Tropical E Atlantic	Cape Verde	303	5.6	194	1.0	-
	Sao Tome and Principe	286	2.4	185	0	-
	Western Tropical Continental Africa	473	13.1	269	2.6	-
	Tropical E Atlantic (TEA)	554	33.6	297	6.1	-
Lessepsian taxa		79		70		-
Introduced taxa		4		4		-
Total number of taxa		844		408		-

Table 1. Number of taxa and percentage of endemic taxa in each region of the Lusitania Province considered in this study, together with comparative data for the adjacent Boreal (North) and Tropical Eastern Atlantic (South) Provinces. An index of tropicality, obtained by dividing the number of warm water species by that of cold water species for each area, is shown. Combined datasets of specific groups of regions were also analyzed (the Mediterranean Sea includes data from the eastern and western Mediterranean Sea; Macaronesia includes data from the Azores, Madeira and the Canary Islands and Lusitania includes data from the province as a whole) and the results are shown in bold. The number of Lessepsian and introduced taxa in the Lusitania Province is also presented.

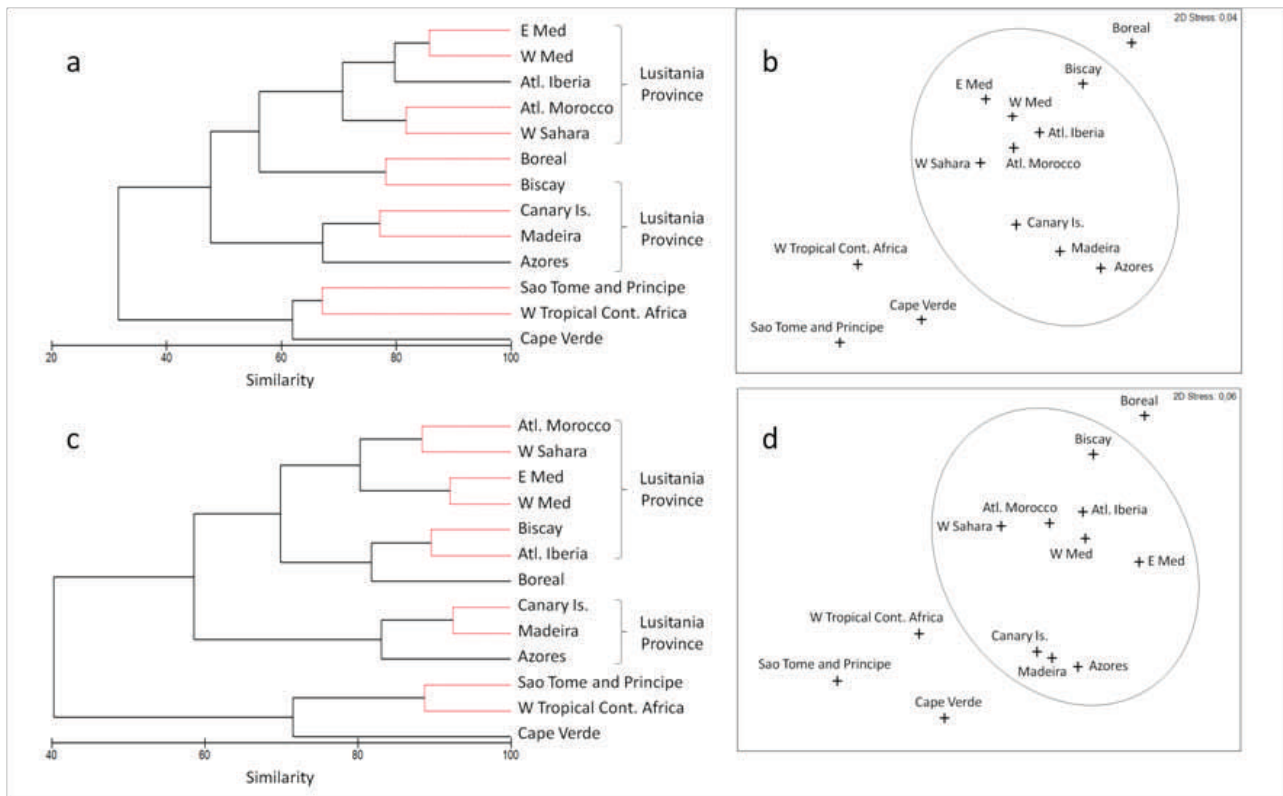


Figure 1. Similarity between areas was estimated by cluster (UPGMA) and multi-dimensional scaling (MDS) analyses. The statistical significance of each cluster estimated by the similarity profile permutation tests (SIMPROF) and non-significant results are shown in purple. Species diversity was analyzed separately with Sorensen (total beta diversity) (figures a and b) and Simpson (turnover component of beta diversity) similarity coefficients (figures c and d) (see methods section for further details). The Lusitania Province is outlined in each figure to depict its close relationship with the Boreal Province and its distinctiveness from the tropical eastern Atlantic Province.

Europe, species richness has a peak at the tropical region (473 species). Northward this peak is followed by a sharp decline in the West Sahara region (225 species) with species richness increasing in the Mediterranean Sea (370 species) and declining continuously northward of Atlantic Iberia.

The eastern Atlantic displays low levels of endemism except for two distinct areas: the TEA (33.6%) and the Mediterranean Sea (15.5%). Generic richness and percent of endemic genera followed a similar trend to the one described above for species, with endemic genera restricted to the TEA and the Mediterranean Sea.

The Macaronesian Islands show decreasing richness, from the Canary Islands northward to Madeira and the Azores, and a very low level of endemism for all archipelagos (Canary Islands 0%, Madeira 0% and Azores 1.4% increasing to 2.4% when we consider the three archipelagos together). The same trend was found for genera with decreasing richness from the Canary Islands

to the Azores and no endemic genera even if we consider the three archipelagos together.

Species richness in the Lusitania Province totals 519 species, 25.2% of which are endemic (see Table 1). Because the Mediterranean Sea emerges as the peak of a group of adjacent areas with high species richness, we computed the corresponding values for the group Mediterranean Sea + Atlantic Iberia + Atlantic Morocco and obtained a total of 414 species, with 19.8% being endemics. Only 5.1% endemic genera were identified in the same group of areas and no endemic families were found for the entire Lusitania Province.

The cluster (Figure 1a) and MDS (Figure 1b) analyses indicate: 1) a significant separation between the TEA and a group formed by Lusitania and boreal fish; 2) Macaronesian islands split from mainland coast with an internal structure where Madeira and the Canary Islands are closer to each other than to the Azores; 3) the two remaining

branches correspond to Biscay and the Boreal Province, on one hand, and the Mediterranean Sea, Atlantic Iberia, Atlantic Morocco and West Sahara, on the other. This last branch splits once again separating Atlantic Morocco and West Sahara from the Atlantic Iberia and the Mediterranean Sea.

When the cluster and MDS analyses were performed with the species turnover component (removing nestedness) the results are similar (Figures 1c and 1d), with the important difference that Atlantic Iberia no longer clusters with the Mediterranean Sea, but rather with Biscay and Boreal Province.

In Figure 2 we show, for each area, the percentages of eurythermic species, cold water species and warm water species. Eurythermic species correspond to percentages that range from 9.4% in the tropical eastern Atlantic, 10.0% in the Lusitania Province to 27.5% in Boreal waters. The tropicity index decreases from South to North, with different latitudinal profiles within Macaronesia and along the mainland coast. On the continental coast values greater than 3 are found only in West Sahara, while values in Macaronesia are consistently greater than 3, reaching 5 in the Canary Islands and decreasing northward from the Canary Islands to the Azores. While in Atlantic Iberia the index is still greater than 1 (more warm water than cold water species) the situation is reversed in Biscay.

Discussion

A given marine biogeographic area displays a fauna that is the product of historical events and present day connections with other areas. We will structure this discussion in two sections. First, we outline the major findings of this paper. Second, we discuss the phylogenetic information that historically shaped the province and comment on some hydrographic features that likely are operating at present.

Main conclusions

Our four major findings are as follows. First, the level of endemism for the Lusitania Province (25.2%) is higher than the threshold of 10% that is

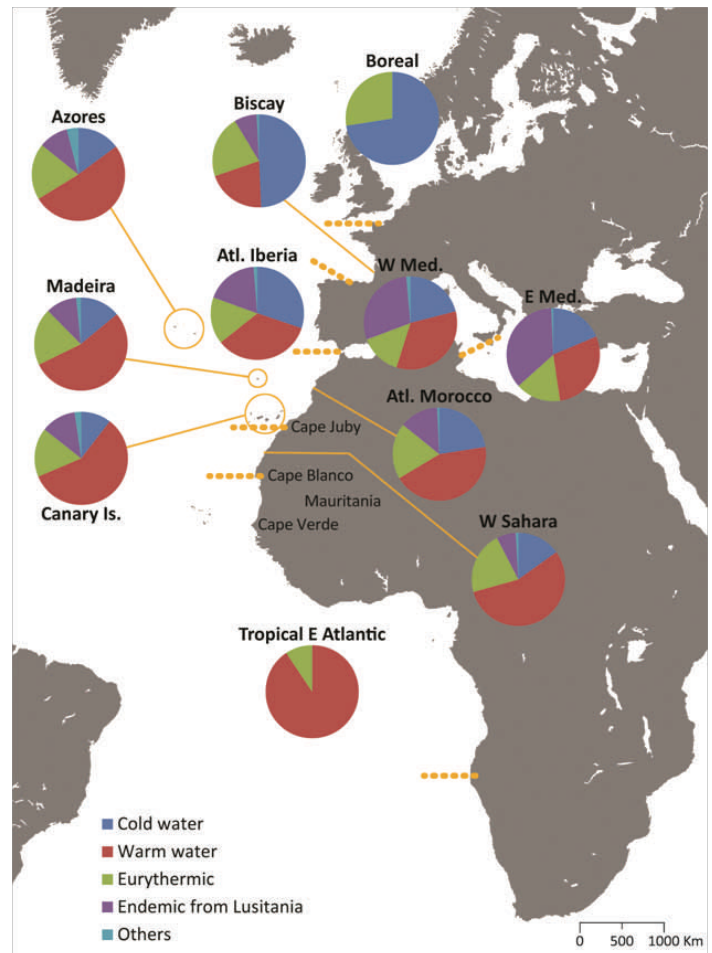


Figure 2. Relative percentages of species belonging to the following categories: eurythermic species (green), cold water species (blue), warm water species (red), and Lusitania endemic species (purple). The category “others” (light blue) includes mainly species outside the eastern Atlantic. Frontiers between provinces or regions within Lusitania are represented by dashed orange lines.

normally used to recognize provincial status for a given geographic area (e.g., Briggs 1995).

Second, both species richness and endemism display a peak in the Mediterranean Sea. Given the history of the region, the high endemic rate in the Mediterranean Sea was probably higher in recent historical times. Considering the warming period initiated with the end of the last Pleistocenic glaciation and the probable range expansion of some warm water species, it is likely that some species previously restricted to the Mediterranean Sea are no longer endemic to this sea basin. This hypothesis is supported by the fact that some species widely distributed along the Mediterranean shores are also found in the adja-

cent Atlantic regions of Iberia and Morocco, often with very restricted ranges in the Atlantic (e.g. only southwest Spain and south Portugal).

Third, the Lusitania Province is divided in two major structural units. One is Macaronesia (the archipelagoes of the Azores, Madeira and the Canary Islands) and the other encompasses the mainland shores of Europe and northwest Africa, with the already mentioned peak of diversity in the Mediterranean Sea. Both cluster and MDS analyses support this pattern. When nestedness is removed and dissimilarity is expressed as species turnover (*sensu* Baselga 2010), the topologies are similar, although some changes occur within groups, namely the grouping of Atlantic Iberia with Biscay and Boreal Province, instead of the Mediterranean Sea. Both multivariate analysis, with or without nestedness, agree in that while the southern boundary of the province is very well defined, the northern boundary is not well defined, suggesting a gradual change northward of Atlantic Iberia. Macaronesia, in turn, presents very low levels of endemism, which is probably related with the distance between these archipelagoes and mainland Africa and Europe, the recent Miocene origin of the islands (Feraud et al. 1981 but see Fernández-Palacios et al. 2011) and the hydrography of the region. For a discussion of possible affinities among these archipelagoes and that of Cape Verde see Llori et al. (1991) and Brito et al. (2007).

Finally, the tropicality index of 1.8 for the Lusitania Province falls to 0.66 when Macaronesia is removed from the analyses. Macaronesian islands display a level of tropicality (T.I. = 4.08) similar to that of the African continental coast at lower latitudes. Thus the variation of the tropicality index reflects the large difference between Macaronesia and mainland shores and not a larger affinity of the Lusitania Province with the tropics. The fact that the Lusitania Province does not include a majority of tropical species, combined with its high level of endemism and species richness argues against the inclusion of this province in a warm eastern Atlantic region (*sensu* Briggs and Bowen 2012).

Historical and oceanographic context

Several published phylogenies on Lusitania fish show that genera, or clades that include several genera, are endemic to the area (e.g., Hanel et al. 2002, Almada et al. 2005, Carreras-Carbonell et al. 2007). In a comprehensive study involving 62% of Mediterranean teleost fish Meynard et al. (2012) showed that many basal lineages, at the level of orders and families, arose in the Cretaceous well before the closure of the Tethys Sea. With the closure of the Mediterranean Sea in the east, new diversifications together with regional extinctions continued afterwards, contributing to the formation of Atlantic Ocean and Mediterranean Sea faunas. These phylogenetic results and the levels of endemism, especially in the Mediterranean Sea and adjacent areas, point to diversification processes that took place basically *in situ* (Meynard et al. 2012), although other phylogenies clearly point to processes that probably originated in tropical Africa (e.g., *Diplodus* spp., Summerer et al. 2001).

On the mainland coast of North Africa there is a long stretch where upwelling is especially intense, bringing cold water to the surface (e.g., Barton et al. 1998). At the Bank of Arguin, immediately to the South of Cape Blanco, in Mauritania, not far from the tropics, mean annual sea surface temperature (SST) is rather low, around 17 °C. These oceanographic conditions mean that as latitude decreases along the African coast SSTs increase at a slower rate than offshore, strengthening the barrier separating tropical and warm temperate species. This likely explains why there are several sister taxa with species in the Mediterranean Sea and tropical Africa, being absent between these regions (e.g., Domingues et al. 2006, 2008, Levy et al. 2011).

In the North, Biscay displays a tropicality index lower than one, meaning that cold water species prevail. Biscay harbored boreal to sub-polar waters during the last glaciation, until about 10,000 years ago (CLIMAP 1981), and, together with Atlantic Iberia and the Mediterranean Sea, acted as glacial refugia for many species of the North and Baltic seas (Maggs et al. 2008). The situation was probably similar in the penultimate glaciation. Thus, the Lusitania Province acted his-

torically as an area from which many boreal species recolonized the North and Baltic seas.

Contrary to other warm temperate areas with less complex coasts, the Lusitania Province has a major East-West mid-latitude expanse stretching some thousands of kilometers to the East, the Mediterranean Sea. This sea remained mostly ice-free during glaciations and had SSTs some degrees higher than the adjacent Atlantic (e.g., CLIMAP 1981, Thiede 1978). The presence of this large warm temperate sea, spared from the extremes of glaciations, may have acted to promote the Lusitania biodiversity, as proposed by Almada et al. (2001) with reference to the family Blenniidae. It was likely a sheltered sea that allowed the survival of many thermophilic groups, promoted local evolution of many clades and functioned as a refuge during glaciations.

In the interglacials, like the present one, the warming of the surrounding Atlantic in Iberia and Morocco allowed the movement of species out of the Mediterranean Sea, enriching the warm temperate Atlantic Ocean.

The situation is different for several warm water species from Macaronesia. Phylogeographic and biogeographic studies of warm water fish in these islands point to their colonization from West African sources, with the Canary Islands and Madeira representing intermediate steps that allowed some fish to reach the Azores. The main current in this region is the Canary Current, which flows southward along the southwest European and northwestern African coasts. However, gyres and eddies form frequently and flow in opposite directions, so that there is a complex two-way system of connection among archipelagoes (Stramma 1984). Santos et al. (1995) provided evidence for transport mechanisms along this route and both their own studies and several molecular studies (e.g., Almada et al. 2005, Domingues et al. 2006) support this scenario for warm water fish.

As stated above, we think that it is a better strategy to keep the warm temperate Lusitania Province distinct from the eastern Atlantic warm region (*sensu* Briggs and Bowen 2012). Although we agree with Briggs and Bowen (2012) on the importance of tropical lineages in the formation of

the Lusitania ichthyofauna, it seems also well documented that, especially after the Miocene, a true warm temperate fauna evolved in the area. In the future our hypothesis needs wider testing with as many groups of organisms as possible.

Acknowledgments

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