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Review Article

150 million years of freshwater fish biogeography: vicariance or dispersal?

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Abstract - Freshwater fishes are supposedly good case studies to test palaeobiogeographical models because they are attached to land masses, at least primary freshwater fishes, which are unable to cross marine barriers. In this study, I review the literature about the fossil record and about the phylogeny of various freshwater fish groups in order to address, in a qualitative way, the biogeographic scenarios proposed to explain their modern distribution. At the intercontinental scale, vicariant events seem to have played a minor role in the distribution of main freshwater fish clades, except for some during the first phases of the break-up. Most of the biogeographical events that shaped the modern distribution of freshwater fish clades are likely dispersals events that occurred in the Late Cretaceous and in the Palaeogene.

Keywords: Actinopterygii, Sarcopterygii, Mesozoic, Cenozoic, Pangaea

1. Introduction

Freshwater fishes are supposedly good case studies to test palaeobiogeographical models because they are attached to land masses, at least primary freshwater fishes, which are unable to cross marine barriers. More specifically, it is expected that the comparison of phylogenetic patterns together with the modifications of the geographical frame caused by tectonic motions allows distinguishing vicariant events from dispersal events. The Mesozoic witnessed the break-up of Pangeae and the diversification of several freshwater fish clades, which have a recent global distribution. This situation makes vicariant scenarios plausible to explain their distribution. Such scenarios have indeed been proposed for several major freshwater fish clades, such as the osteoglossiforms, the cypriniforms, the siluriforms, the characiforms and the cichlids among other.

2. Material and methods

In this study, I review the literature about the fossil record and about the phylogeny of various freshwater fish groups in order to address, in a qualitative way, the biogeographic scenarios proposed to explain their modern distribution. Vicariant and dispersals events are difficult to distinguish and to recognize in the fossil record. I consider here the likely occurrence of a vicariant event when a phylogenetic split can be associated with a geographical barrier, and when the fossil records of both sister taxa are approximately isochronous. This study develops some conclusions published by Cavin (2017).

3. Results

3.1. Split of Laurasia and Gondwana at the origin of vicariant events

The first break in Pangea provoked the split between Gondwana in the south and Laurasia in the north (Fig. 1, left). The survey of the data indicates that for freshwater fishes, few vicariant events can be associated to this split. The fossil record of osteoglossomorphs, together with the recent-most molecular phylogenies, indicate that vicariant events probably played minor role in the modern distributions of lineages (Lavoué, 2016), contrary to the former prevailing view. The oldest fossils of bony tongues are from the Early Cretaceous of Asia and from the Late Cretaceous of North America. They are generally regarded as stem osteoglossomorphs, but their phylogenetic relationships are labile according to studies. Among the crown osteoglossomorphs the hiodontiforms, restricted now to North America are regarded as the sister group to all other osteoglossomorphs. If Asian and North-American Cretaceous osteoglossomorphs would revealed to be stem hiodontiforms rather than stem osteoglossomorphs (as it is the case, for instance, for *Jiaohichthys* according to Zhang, 2006), then the phylogenetic pattern of osteoglossomorphs corresponds well to a vicariant event between the hiodontiforms in Laurasia and the osteoglossiforms in Gondwana. The oldest osteoglossiform from Gondwana is the Early Cretaceous *Laeliichthys* from Brazil and the early Late Cretaceous *Palaeonotopterus* from Morocco, i.e. two occurrences only slightly younger than the occurrences of osteoglossomorphs in Laurasia. More

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anatomical and phylogenetic studies are necessary to test this issue, but this vicariant split at the base of the osteoglossomorph tree might be the only vicariant event in the history the group.

Another probable vicariant event associated with the split of Gondwana and Laurasia is the separation of the cypriniforms in Laurasia from other otophysans (the characiphysi) in Gondwana (Chen *et al*., 2013). One difficulty with this pattern is that the origin of cypriniforms is often located in SE Asia (Saitoh *et al*., 2011), an area that hardly fit with a vicariant event with the Gondwana. Some recent phylogenies resolved the suckers as the sister group of all other cypriniforms (for instance Hirt *et al*., 2017). This pattern is a clue that the vicariant event may have occurred between South America and a large land mass, which includes North America (or possibly only its western part, the Lauramidia) together with East Asia. The modern distribution of cypriniforms in Eurasia and Africa is regarded as the result of westwards dispersals from East Asia during the Cenozoic.

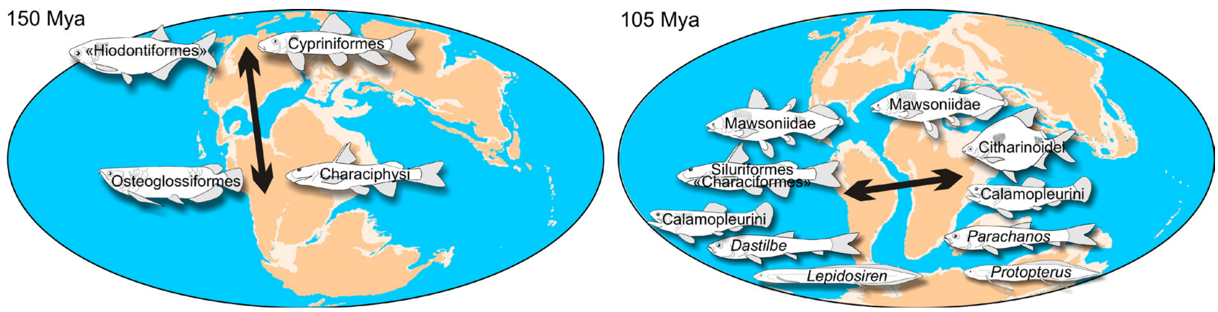

Figure 1. Examples of vicariant events related to the split of Pangeae between Laurasia and Gondwana (left) and related to the split of Western Gondwana between South America and Africa (right). Times in million of years are only indicative.

3.2. Split of South America and Africa at the origin of vicariant events

The opening of South Atlantic during the Early Cretaceous is commonly associated with vicariant events. Survey of literature shows, however that this event affected mostly taxa of low taxonomic rank (Fig. 1, right). Among characiphysi, the citharinoidei likely split from siluriforms plus other characiforms (citharinoidei are not part of characiforms any more) during this vicariant event (Chen *et al*., 2013). Other potential groups affected by this event are chanids (*Parachanos* and *Dastilbe*), calamopleurini (*Calamopleurus*), lepisosteiforms (*Pliodetes* and *Araripelepidotes*) and sarcopterygian fishes such as the mawsoniid coelacanths and the lepidosirenid lungfishes.

3.3. Dispersals

Except the few vicariant events described above, examination of the fossil record together with available phylogenies indicates that the modern distribution of freshwater fish groups is mostly the results of dispersals events. Route of dispersals are either continental (Fig. 2) or marine (Fig. 3). An important land connection between continents is Beringia, which regularly connected Asia and North America during the Cretaceous and in the Cenozoic and was taken by the polyodontids, acipenserids, catostomids, freshwater ellimmichthyiforms among others. In Eurasia, several lineages moved across this large landmass, mostly from east to west. These dispersals concern several clades of cypriniforms such as the cobitiids, the gobionids, the cyprinids and the leuciscinids. Several of these families also moved towards Africa, such as the cyprinids and the cobitiids, but also non-cypriniforms moved towards Europe and Africa (Böhme, 2004), such as the channids.

Marine routes taken during dispersals are difficult to draw, but marine episodes can be detected in the evolutionary history of fish clades based on the sedimentary context of fossil finds. For instance, the worldwide distribution of osteoglossids in the Palaeogene and the occurrence of fossils in marine sediment clearly indicate that some osteoglossid species inhabited marine environments, and this suggests the possibility of inter-continental marine dispersals. The dispersal of characoidei (characiforms minus citharinoids) from South America to Africa, where alestids and hespetids thrive today, is illustrated by occurrences of isolated characiform remains in the Late Cretaceous of North America (Newbrey *et al*., 2009) and in the Late Cretaceous (Otero *et al*., 2008) and Cenozoic of Europe (Gaudant, 2014). This distribution indicates likely marine dispersal, at least sporadically, for some characiforms in the Late Cretaceous.

The biogeographical history of siluriforms is difficult to reconstruct because the Mesozoic fossil record is poor and the phylogenies have remained uncertain and poorly resolved. Recent studies (Sullivan *et al*., 2006; Kappas *et al*., 2016), however, clearly pointed out an origin in South America and at least two big diversifications in both Asia and Africa ("Big Africa" clade and "Big Asia" clade). The pattern does not fit well with a series of vicariant events related to the break-up of Pangaea, but better favors a series of dispersals that occurred in the Late Cretaceous and in the Palaeogene.

The recent distribution of cichlids have long been regarded as the result of a succession of vicariant events because the splits observed in the phylogeny of the clades corresponds well to the splits of land masses inhabited by the different lineages (see for instance Sparks and Smith

(2005) for a strong defense of this scenario). However, the analysis of the fossil record and of the biology of cichlids, whose species tolerate brackish and salt coastal waters, provides good evidence that the modern distribution is mostly the result of Cenozoic dispersals via brackish or marine routes (Murray, 2001, Friedman *et al*., 2013).

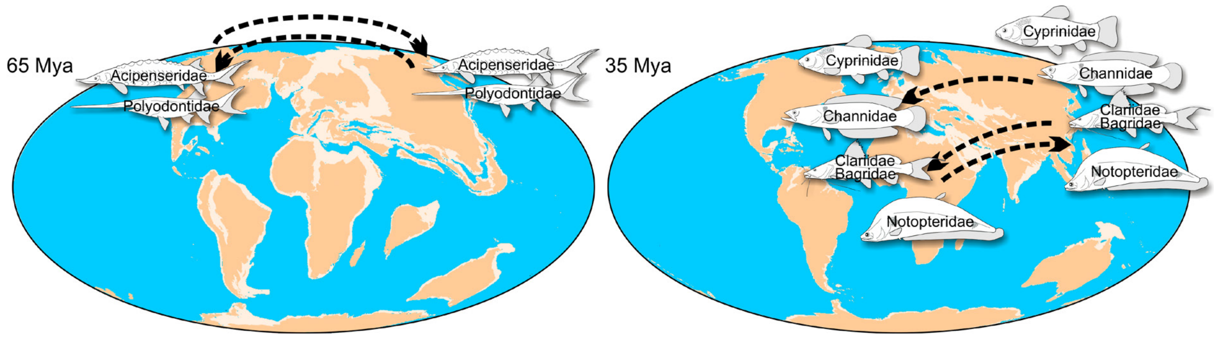

Figure 2. Examples of continental dispersals through Beringia (left) and across Eurasia and Africa (right). Times in million of years are only indicative.

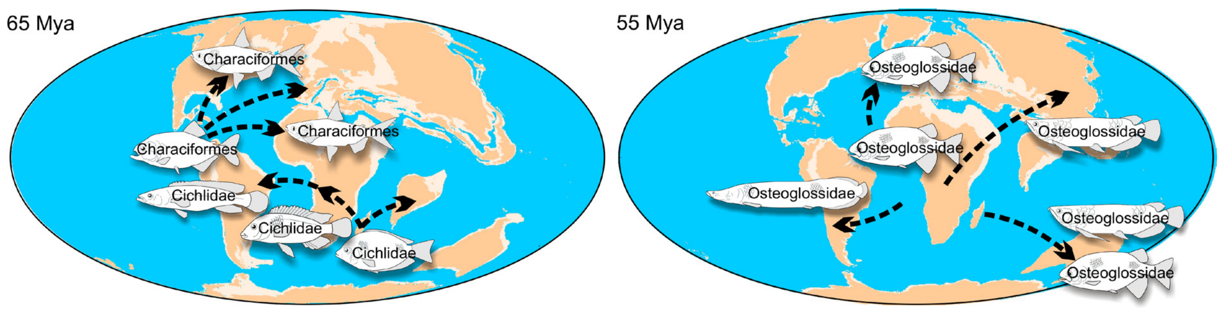

Figure 3. Examples of marine dispersals. Times in million of years are only indicative.

4. Discussion and conclusions

At the intercontinental scale, vicariant events seem to have played a minor role in the distribution of main freshwater fish clades, except for some during the first phases of the break-up. Most of the biogeographical events that shaped the modern distribution of freshwater fish clades are likely dispersals events that occurred in the Late Cretaceous and in the Palaeogene.

Marine dispersals may appear to be a highly improbable phenomenon for freshwater fishes, especially for those of the primary section. However, this consideration should be reassessed if we consider that the distinction between continental versus marine aquatic environments does not fit exactly the distinction between freshwater versus salt waters, in particular during periods with sea level either higher or lower than today. On the one hand salinity of large continental bodies of water may be high, thus preventing dispersals of freshwater fishes and, on the other hand, closed oceanic basin may have low salinity content and thus, promotes dispersals. High sea level probably favors the formation of brackish environments on or around continental masses, which make more complex the analysis of fish dispersals routes since these environments may vary very quickly in time. It seems that it has been the case with a brackish Arctic Ocean during the Eocene (Waddell and Moore, 2008). Sea level also directly affects the degree of fragmentation of land by creating barriers for many freshwater fishes. Low sea level, on the other hand, increases the surface of the low-lying areas and permit freshwater fishes to spread from one hydrographic basin to another. In 1952, Schaeffer already proposed different ways to explain dispersals of freshwater fishes. One of them "tongues of fresh water discharged into the sea by large rivers (e.g., Amazon) and deflected along the coast by off-shore currents as far as the mouths of other rivers (Schaeffer, 1952)" may well have played an important role in the dispersal of freshwater fishes along coasts. This kind of dispersals may occur between landmasses that have previously split apart and, if they occurred in the same sequence as the continental splits, may mimic vicariant events, but with a delay of tens of millions years. This pattern would apply well to the biogeographic history of cichlids for instance.

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