Fishes and the Break-up of Pangaea: an introduction

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Abstract: There is general agreement that a tight relationship exists between evolutionary histories of living lineages and the shifting geography of the Earth during the Phanerozoic, but how to depict that link has been much disputed in recent decades. The issue is fundamental, as it involves two supposedly-irreconcilable paradigms for how we interpret past and present distributions: the Darwin–Wallace biogeographic paradigm that involves dispersal from centres of origin, and the vicariance paradigm. When dealing with extinct organisms, for which we have only sparse and fragmentary fossil remains, the limit between the two paradigms becomes blurred. Here, all available data about time (stratigraphy) and space (palaeogeography) need to be gathered in order to detect biogeographical signals.

Because of the incompleteness of the fossil record, the analyses may lead to storytelling style descriptions of biogeographic scenarios (phylogenies are often weakly supported, datings are frequently vague and occurrences are sparse). But these scenarios are always open to refutation if new fossils are found and, accordingly, are genuine scientific hypotheses. The Darwin–Wallace biogeographic paradigm and the vicariance paradigm have been described as the extreme points of a pendulum; in this book, examples of relationships between the evolutionary history of fish clades and the break-up of Pangaea are described using approaches that lie between these extreme points of the pendulum.

There have been many studies which construct biogeographic scenarios on the basis of Recent fish distributions. They deal mainly with primary freshwater fish faunas (Ribeiro 2006) or clades, such as osteoglossomorph subgroups (Nelson 1969; Kumazawa & Nishida 2000) or otophysans (Saitoh *et al.* 2003; Briggs 2005), because primary freshwater fishes are supposedly firmly confined to their continental environments. Distributions of marine fishes may also provide meaningful, although sometimes controversial, biogeographic patterns, as exemplified by the phylogenetic and biogeographic studies of notothenioids (Bargelloni *et al.* 2000) or cirrhitoids (Burridge 2000) for instance. Fossils are rarely included in these research programs, except as milestones providing minimum divergence ages by which to calibrate phylogenies. This caution comes from the weak reliability that most workers attribute to the fossil record, a criticism already put forward by Darwin some 150 years ago. But although some workers complain about the quality of the fossil record, others discover and describe new fossil fish occurrences and new taxa. Although much work remains to be done on the phylogenetic relationships of Recent and extinct fish clades, and to get better sampling of fossil fishes in Mesozoic and Cenozoic deposits worldwide, the amount of meaningful data is rapidly growing and the general picture is now better than ever. This volume aims at gathering together much of this available information on a large number of fish groups. However, far from exhausting the subject, our aim is to contribute to the furtherance of the debate.

In the Triassic, the close association of continental blocks allowed terrestrial and freshwater organisms to spread easily. **Richter & Toledo** show that a lungfish genus was widespread in the Triassic across most Southern continents and extended into Europe, and they suggest that its dispersal ability was determined by palaeoclimatic changes. At the infancy of the break-up of Pangaea, Laurasia split from Gondwana forming a marine route between the Tethys and the Pacific Ocean. **Arratia** finds evidence of this marine connection in the Late Jurassic by resolving the phylogenetic relationships of marine crossognathiforms. This reveals a sister-area relationship between Chile and Cuba, which together are the sister area of Germany. **Kriwet & Klug** suggest that shark assemblages were quite uniform in Europe in the Late Jurassic. Their analyses indicate that both vicariance and dispersal are required to explain the biogeographic pattern of Late Jurassic neoselachians. Marine vicariant events also affect coastal fishes, living on the

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continental shelf, when they are tightly constrained by physical barriers. Barriers preventing fish dispersal include: marine currents, surface gradients of temperature and salinity, great water depths, and freshwater and sediment outflows from rivers. Examples of Early Cretaceous marine vicariance events involving ophiopsid taxa from the northern margin of the Gondwana and taxa from the southern margin of Laurasia in Western Tethys are detected by **Brito & Alvarado-Ortega**, a pattern also found for aspidorhynchids. The Early Cretaceous was a period when freshwater taxa were diversifying in biogeographical provinces that were becoming increasingly isolated from each other. This is the case for freshwater hybodonts in SE Asia, as **Cuny** shows, but also for a stem-group of Osteoglossomorpha in Eastern Asia, as **Wilson & Murray** show, and for an endemic Asian family of halecomorphs, the sinamiids. The late Early Cretaceous is also the time of the opening of the South Atlantic, and several freshwater or brackish fish taxa were clearly affected by this event: mawsoniid coelacanths, lepidosirenid lungfishes, a halecomorph and a paraclupeid among others. In the Late Cretaceous, both dispersal and vicariance events are detected. **Otero *et al.*** suggest that occurrences of characiforms in the Late Cretaceous of Europe may be the result of dispersals from Africa, and the same may be true for mawsoniid coelacanths. The Late Cretaceous witnessed connections between Eastern Asia and North America fresthwater fishes as shown in polyodontids and in several lineages of osteoglossomorphs (although it remains difficult to discriminate between vicariance and dispersal events as pointed out by **Wilson & Murray**). In the Palaeogene, there are new examples of connections (dispersal or vicariances) between Asia and North America as **Chang & Chen** show with the catostomids. **Bonde** describes several marine osteoglossomorph taxa from the Palaeogene of Denmark, which makes the palaeobiogeographical scenario of this otherwise mainly freshwater lineage more complex.

The general pattern brought out (by analysing the relationships between evolutionary histories of fish lineages and the evolution of the geographical frameworks) using the fossil record does not differ significantly from the pattern that can be deduced from phylogenetic and distributional studies of Recent taxa. Inclusion of fossils provides a more colourful picture and unveils unexpected issues that would have been otherwise overlooked.

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