

that the rigorous application of appropriate statistical techniques is a crucial concern in quantitative biogeographical analysis.

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## Panbiogeographical study of hagfishes: an anachronistic analysis

### ABSTRACT

In a recent paper by M. J. Cavalcanti and V. Gallo, 'Panbiogeographical analysis of distribution patterns in hagfishes (Craniata: Myxiniidae)' (*Journal of Biogeography*, 2008, **35**, 1258–1268), the authors studied the biogeography of an ancient fish family (Myxiniidae) in the hope that the contemporary distributions of the species would reveal their past history and that of the ocean basins where they reside. In order to accomplish this task, there are several criteria that should have been met: (1) the ages of the taxa utilized (species) would have to be old enough to reflect the history of the areas where they are found, (2) the identification of the species as listed in the databases would have to be accurate, (3) the geographical locations indicated on the figures would have to be consistent with the statements in the text, and (4) the significance of the vicariant patterns would have to depend on evidence pertaining to the ages of such patterns. Unfortunately, it appears that none of these conditions has been met. It seems apparent that faith in an antiquated method of analysis led to neglect of the necessary steps in the analysis. This leaves little justification for publication of the paper, except to show that hagfishes are very widely distributed.

**Keywords** Cladistic biogeography, hagfishes, ocean basins, panbiogeography, vicariance.

In a recent paper published in *Journal of Biogeography*, Cavalcanti & Gallo (2008) chose to analyse the global distribution of

hagfishes (Myxiniidae) using a biogeographical method proposed by Croizat (1958, 1964). For most biogeographers, that method has long been superseded by others. At the American Museum in New York, in the early 1970s, panbiogeography was combined with part of Hennig's phylogenetic method to give birth to vicariance biogeography. After about 10 years, the name was changed to cladistic biogeography and the latter remained the preferred approach by those biogeographers who did not recognize dispersal as an important process in the formation of biogeographical patterns (Briggs, 2007).

Cladistic biogeography was a relatively popular movement until the late 1990s, when an outpouring of work on molecular genetics began to have its effect. In more recent years, it has become obvious that most of the distributions of contemporary clades, which vicariance had attributed to the fractionation of Gondwana, had actually taken place via dispersal in the Tertiary or in more recent times. Cladistic (vicariant) biogeography has declined, primarily because its followers do not recognize the kind of allopatric speciation that takes place when members of a population migrate across a barrier to colonize a new area. The modern approach to biogeography is an eclectic one, recognizing the importance of both vicariance and dispersal, and is based on clues to be found within the relationship of the group concerned and in the history of its territory.

The aim of the authors was to correlate the hagfish distribution patterns with the tectonic history of the ocean basins. Why shouldn't they do this? Granted, Myxiniidae is a very old family extending back some 400 Myr, but does this mean that they could examine the databases for locality records of the *living species*, draw lines between those that occupy certain regions, and come up with information that reflects the history of the ocean basins? Certainly, the ages of the species that have been connected by the lines are critical. The molecular relationship suggests that the split between the two hagfish subfamilies (Myxiniinae and Eptatretinae) took place in the late Cretaceous or early Tertiary (Kuraku & Kuratani, 2006). The phylogeny published by Møller & Jones (2007), based on original and published DNA sequences, clearly indicates that the ages of the genera and species must be considerably younger than those of the subfamilies.

Data on the identification and location of the various species were extracted from portals such as FishBase and Ocean

Biogeographic Information System (OBIS) that, in turn, were compiled from various museum collections. In taxonomically difficult groups such as the hagfishes, unless the specimens have been examined by a person familiar with the group, one cannot be sure that the identifications are correct. This appears to be a general problem in the use of large databases with information on animal distribution.

On the maps provided (Cavalcanti & Gallo, 2008), what is the significance of the lines? Considering that the species concerned are certainly Tertiary in age, and possibly as young as most other extant marine fishes (2–8 Myr), what can they reveal about ocean basins? The authors claim that, because vicariance is a major feature of hagfish distribution, it suggests vicariant distribution of widespread ancestors as the result of sea-floor spreading between continents in connection with ocean formation. However, vicariance as the result of allopatric speciation is a major feature of distribution in almost all groups of marine fishes so, in this respect, hagfishes are no different.

Most of the 'tracks' on the maps indicate that hagfishes occur in the vicinity of shorelines rather than in the deep ocean basins. In fact, many of the species live on the continental shelf or the upper slope (Mok & Chen, 2001). The authors (Cavalcanti & Gallo, 2008) observed that the distributions of the species of *Eptatretus* and *Paramyxine* were clearly associated with the margins of the Pacific Plate, but the locations of the tracks (Figs 4 & 5) do not demonstrate this. They called attention to the trans-Atlantic distribution of *Myxine glutinosa*, saying that it corresponded to a classical track associated with the opening of the Atlantic Ocean during the Cretaceous. But more than 100 fish species have trans-Atlantic distributions, most of them having apparently migrated from west to east (Floeter *et al.*, 2008). They also referred to a northern trans-Pacific disjunction within two genera, but their map (Fig. 2) does not illustrate this.

Considering that this paper does not give evidence for sea-floor spreading and ocean basin formation, what information does it provide? It does illustrate the overall geographical distribution of the family, and suggests that there is a high degree of endemism in several parts of the world. Other than that, it demonstrates an unfortunate choice of an antiquated methodology that is predicated more on faith than on scientific justification. In recent years, hagfishes have become commercially valuable and new species have been described at

a rapid rate. Hopefully it will be possible for someone to use this additional material to investigate the genetics and morphology of the genera and species with the goal of discovering more about the evolutionary and distributional history of the family.

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## The panbiogeography of hagfishes: a reply to Briggs's anachronistic criticism

### ABSTRACT

Briggs's (2009) criticisms of Cavalcanti & Gallo's (2008) panbiogeographical study of hagfishes are shown to be either sup-

portive of the criticized paper's main findings or trivial, arising from an incomplete understanding of the panbiogeographical method and synthesis and of methodological prejudice against this conceptual framework.

**Keywords** Marine biogeography, Myxiniidae, ocean basins, panbiogeography, track analysis, vicariance.

Briggs (2009) has criticized the paper 'Panbiogeographical analysis of distribution patterns in hagfishes (Craniata: Myxiniidae)' by Cavalcanti & Gallo (2008) on the basis that it used what he deemed to be 'an antiquated method of analysis' that therefore would invalidate any findings reported in the paper. In his criticism, Briggs seems to resort more to rhetoric than to plain, sound facts, and shows an incomplete understanding of the basic tenets of the 'antiquated' methodology (panbiogeographical track analysis) he attempts to criticize. Here I will briefly address his criticisms, suggesting that they arise more from Briggs's methodological prejudice than from any fatal flaws of the criticized paper.

Briggs starts by stating that 'most' biogeographers do not use panbiogeography and presents a portrayal of panbiogeography as having been 'superseded' as a result of its combination with Hennig's phylogenetic systematics to give rise to vicariance (cladistic) biogeography. However, many biogeographers (even those not especially tied to Croizat's panbiogeography) recognize that panbiogeography (Croizat, 1958, 1964) stands clearly as an independent research programme (Craw & Weston, 1984; Morrone & Crisci, 1995; Craw *et al.*, 1999), with many contributions, especially over the last decade (see Cavalcanti & Alperin, 2008). In the same context, he claims that 'the modern approach to biogeography is an eclectic one, recognizing the importance of both vicariance and dispersal'; however, 'modern' biogeography has no unique, uniform approach, being instead divided up into a large number of *independent* paradigms and methodological approaches that may indeed characterize a discipline amidst a Kuhnian scientific revolution (Crisci, 2001).

He then criticizes the use of online databases, arguing that the identification of species may not always be correct. However, taxonomic correctness is a general problem with biological databases, affecting even GenBank (Page, 2006, 2008). Notwith-