



Panbiogeographical analysis of distribution patterns in hagfishes (Craniata: Myxinidae)

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ABSTRACT

Aim To analyse the worldwide distribution patterns of hagfishes using panbiogeographical track analysis, and to attempt to correlate these patterns with the tectonic history of the ocean basins.

Location Atlantic and Pacific oceans.

Method The distributions of 47 out of 70 species of hagfish (in the genera *Eptatretus*, *Myxine*, *Nemamyxine*, *Neomyxine*, and *Paramyxine*) were studied by the panbiogeographical method of track analysis. The analysis was performed using distributional data obtained from the collections included in the Ocean Biogeographic Information System (OBIS, <http://www.iobis.org>) and FishBase (<http://www.fishbase.org>), with additional records from the literature. Individual tracks were obtained for each species by plotting localities and connecting them by minimum-spanning trees. Generalized tracks were determined from the spatial overlap between individual tracks.

Results Six generalized tracks were found: in the Gulf of Mexico, Caribbean Sea, South-eastern Atlantic, Western Pacific, North-eastern Pacific and South-eastern Pacific.

Main conclusions The distribution patterns of myxinids are marked by a high degree of endemism and vicariance, and are correlated with the tectonic features involved in many of the events that led to the development of oceanic basins. The main massing of the group is around the Pacific Basin. In the Atlantic Ocean, the distribution of *Myxine glutinosa* seems to correspond to a classic trans-oceanic track and vicariance resulting from the opening of the Atlantic Ocean during the Cretaceous. In the Pacific Ocean, the distribution of the *Eptatretus* and *Paramyxine* species is clearly associated with the margins of the Pacific tectonic plate. The generalized tracks of hagfishes are shared by several other groups of marine organisms, including many from shallow tropical waters, implying a common history for this marine biota. Overall, vicariance is a major feature of hagfish distribution, suggesting vicariant differentiation of widespread ancestors as a result of sea-floor spreading between continents in connection with ocean formation.

Keywords

Agnathans, Atlantic Ocean, historical biogeography, Myxiniformes, Pacific Ocean, panbiogeography, track analysis.

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INTRODUCTION

The family Myxinidae comprises seven genera and about 70 species of small to middle-sized agnathans known as hagfishes (Nelson, 2006). They are entirely marine forms, usually found in burrows on soft bottoms of the continental shelf and the upper

continental slope in tropical, temperate, and cold waters from all oceans (Mincarone, 2000, 2001; Mok & Chen, 2001; Fernholm, 1998, 2002; Møller *et al.*, 2005).

The oldest fossil hagfish, *Myxinikela siroka*, dates from the Carboniferous (Pennsylvanian) of Illinois (about 320 Ma) (Bardack, 1991). The similarity to modern hagfishes is

striking, and suggests that this is a morphologically conservative group.

It has been proposed that hagfishes are the sister group of all other vertebrates, living and fossil (Gess *et al.*, 2006). Phylogenetic hypotheses for the family Myxinidae (Janvier, 1997; Kuo *et al.*, 2003; Chen *et al.*, 2005; Møller & Jones, 2007) suggest that the status of some genera is questionable and the phylogenetic relationships among the species are still under debate. A hypothesis of phylogenetic relationships among the genera of hagfishes was first proposed by Janvier (1997), based on morphological data, depicting *Myxine* + *Neomyxine* as a monophyletic group, whereas the relationships between *Eptatretus* and *Paramyxine* remain uncertain. Recently, Kuo *et al.* (2003) analysed partial sequences of the 16S rRNA gene of 14 species of *Eptatretus*, *Myxine*, and *Paramyxine*. Their molecular phylogeny supports both *Myxine* and *Eptatretus*, but the relationships between *Eptatretus* and *Paramyxine* are not clear. The monophyly of *Paramyxine* is assured if *P. cheni* is excluded from the tree. At the level of genus, the molecular phylogeny supports the hypothesis of Janvier (1997). Recently, Møller & Jones (2007) produced a phylogenetic analysis based on molecular 16S rRNA data, which shows *Eptatretus* as a monophyletic taxon with *E. strickrotti* as the most basal member. Furthermore, their analysis suggests that *Paramyxine* should be synonymised with *Eptatretus*. Together, these hypotheses provide a framework for studying the geographical distribution patterns of these groups, which in turn may offer further insights into the evolution of hagfishes.

Despite their widespread distribution, there have been few biogeographical studies on hagfishes, and some have been spatially restricted (Adam & Strahan, 1963; Martini *et al.*, 1997; Mincarone & Soto, 2001; Mok, 2001; Mok & Chen, 2001), so the worldwide distribution patterns of many species remain largely unknown.

Panbiogeography was developed by Croizat (1958, 1964), and later expanded and quantified by New Zealand researchers (e.g. Page, 1987; Craw, 1989; Henderson, 1989; Craw *et al.*, 1999). The panbiogeographical method of track analysis consists of plotting locality records of various taxa on maps and connecting them using lines following a criterion of minimum distance. These lines are named individual tracks and correspond to the geographical coordinates of the taxon, or the place in the sector of geographical space where the evolution of this taxon occurred. The coincidence of individual tracks of several groups corresponds to a generalized track, implying a common history for the entire biota. The panbiogeographical method emphasizes the relevance of the geographical distributions as direct objects of analysis. Although in recent years panbiogeography has become one of the main research programmes in historical biogeography (Morrone & Crisci, 1995; Craw *et al.*, 1999; Crisci, 2001; Morrone, 2004), so far the panbiogeographical method has rarely been applied to the analysis of marine biotas (Chin *et al.*, 1991; Hajdu, 1998; Aguilar-Aguilar & Contreras-Medina, 2001; Heads, 2005).

In this paper, the worldwide distribution of 47 selected species of hagfishes from the genera *Eptatretus* Cloquet (ex

Duméril, 1819; *Myxine* Linnaeus, 1758; *Nemamyxine* Richardson, 1958; *Neomyxine* Richardson, 1953; and *Paramyxine* Dean, 1904 was studied using panbiogeographical track analysis to identify possible common patterns that could be correlated with the tectonic history of ocean basins.

MATERIALS AND METHODS

The analysis was performed using 3797 distributional records (occurrence points) obtained from the collections included in the Ocean Biogeographic Information System (OBIS, <http://www.iobis.org>; Grassle, 2000), OBIS-Brazil (BROBIS, <http://obissa.cria.org.br>), and FishBase (<http://www.fishbase.org>) as well as data from the literature. Distribution data were compiled from all known species of Myxinidae, but only 47 species belonging to five genera were included in this study (Table 1). These species were selected on the basis of the availability of at least two locality records for each species. The species not included in the panbiogeographical analysis because of insufficient data are listed in Table 2.

Individual tracks were constructed for each species by plotting their localities of occurrence on maps with the ARCVIEW 3.2 software (ESRI, 1999) and connecting them by minimum-spanning trees using the TRAZOS2004 extension (Rojas, 2004). Geographical outliers (i.e. records showing obvious geo-referencing errors) were detected and excluded from the data using the SPOUTLIER software tool developed by the SpeciesLink Project of Centro de Referência em Informação Ambiental (CRIA, 2004).

To construct generalized tracks, all the individual track maps were printed and then superimposed. Generalized tracks were determined from the areas of overlap of individual tracks, and correlated with the main geological features of ocean basins (lithospheric plates, mid-oceanic ridges, and deep-sea trenches) by visual inspection.

The main massing (geographical concentration of diversity) was assessed by counting numbers of species in each of the major oceanic divisions (Western and Eastern Atlantic, Western and Eastern Pacific).

RESULTS

Based on the coincidence of the individual tracks for each species, six generalized tracks were found (Figs 1 & 2). These are defined as follows: (a) Gulf of Mexico (including *Eptatretus minor* and *E. springeri*); (b) Caribbean Sea (including *E. multidentis*, *M. mccoskeri* and *M. robinsonum*); (c) South-eastern Atlantic (including *E. hexatrema*, *E. profundus* and *M. capensis*); (d) Western Pacific (including *E. burgeri*, *E. strahani*, *M. formosana*, *M. kuoi*, *P. atami*, *P. cheni*, *P. fernholmii*, *P. sheeni*, *P. taiwanae* and *P. yangi*); (e) North-eastern Pacific (including *E. deani* and *E. stoutii*); (f) South-eastern Pacific (including *M. circifrons* and *M. hubbsi*). Individual tracks for the species supporting most of these generalized tracks are shown in Figs 3–5.

Table 1 Geographic distribution, sample size, and bathymetric ranges of myxiniid species included in this study. Primary sources of distributional and bathymetric data for each species are provided.

| Species | Geographic range | Number of records | Minimum depth (m) | Maximum depth (m) | Source |
|---|---|-------------------|-------------------|-------------------|--------------------------------------|
| <i>Eptatretus burgeri</i> (Girard, 1855) | North-west Pacific: Sea of Japan and eastern Japan to Taiwan | 28 | 10 | 270 | FishBase |
| <i>E. carlinhubbsi</i> McMillan & Wisner, 1984 | Pacific Ocean: Wake Island, Guam, and Hawaii | 4 | 481 | 1574 | FishBase |
| <i>E. cirrhatus</i> (Forster, 1801) | Western Pacific: southern and eastern Australia and New Zealand | 39 | 386 | 456 | OBIS |
| <i>E. deani</i> (Evermann & Goldsborough, 1907) | Eastern Pacific: south-eastern Alaska to central Baja California, Mexico | 45 | 165 | 1262 | OBIS |
| <i>E. fritzi</i> Wisner & McMillan, 1990 | Eastern Pacific: Guadalupe Island, Mexico | 2 | 512 | – | FishBase |
| <i>E. grouseri</i> McMillan, 1999 | Eastern Pacific: known only from the Galápagos Islands | 2 | 722 | – | FishBase |
| <i>E. hexatrema</i> (Müller, 1836) | South-east Atlantic: known only from Walvis Bay, Namibia to Durban, South Africa | 9 | 10 | 400 | OBIS, FishBase |
| <i>E. laurahubbsae</i> McMillan & Wisner, 1984 | South-east Pacific: Chile (Juan Fernandez Islands) | 3 | 2400 | – | FishBase |
| <i>E. mcconnaugheyi</i> Wisner & McMillan, 1990 | Eastern Central Pacific: off southern California and in lower Gulf of California | 3 | 43 | 415 | FishBase |
| <i>E. mccoskerii</i> McMillan, 1999 | Eastern Pacific: known only from the Galápagos Islands | 2 | 215 | – | FishBase |
| <i>E. mendozai</i> Hensley, 1985 | Western Atlantic: Caribbean Sea | 3 | 720 | 1100 | FishBase |
| <i>E. menezesi</i> Mincarone, 2000 | South-west Atlantic: Brazil | 6 | 250 | 470 | OBISSA, Mincarone (2000) |
| <i>E. minor</i> Fernholm & Hubbs, 1981 | Western Central Atlantic: Gulf of Mexico | 3 | 300 | 400 | FishBase |
| <i>E. multidentis</i> Fernholm & Hubbs, 1981 | Western Atlantic: Caribbean Sea and off French Guiana including north-eastern Brazil | 7 | 239 | 770 | FishBase, Mincarone & Sampato (2004) |
| <i>E. nana</i> Wisner & McMillan, 1988 | South-east Pacific: off Chile | 2 | 170 | 270 | FishBase |
| <i>E. polytrema</i> (Girard, 1855) | South-east Pacific: Chile (from Coquimbo to Puerto Montt) | 2 | 240 | 270 | FishBase |
| <i>E. profundus</i> (Barnard, 1923) | South-east Atlantic: known only from the holotype taken off Cape Point, South Africa | 8 | 490 | 1150 | OBIS |
| <i>E. sinus</i> Wisner & McMillan, 1990 | Eastern Central Pacific: Gulf of California | 2 | 207 | – | FishBase |
| <i>E. springeri</i> (Bigelow & Schroeder, 1952) | Western Central Atlantic: North-eastern Gulf of Mexico | 7 | 300 | 730 | OBIS |
| <i>E. stoutii</i> (Lockington, 1878) | Eastern Pacific: south-eastern Alaska to Bahia San Pablo, central Baja California, Mexico | 77 | 37 | 834 | OBIS |
| <i>E. strahani</i> McMillan & Wisner, 1984 | Western Central Pacific: Philippines | 6 | 189 | – | OBIS |

Table 1 Continued

| Species | Geographic range | Number of records | Minimum depth (m) | Maximum depth (m) | Source |
|--|--|-------------------|-------------------|-------------------|------------------------------------|
| <i>E. wisneri</i> McMillan, 1999 | Eastern Pacific: known only from the Galápagos Islands | 2 | 563 | – | FishBase |
| <i>Myxine affinis</i> Günther, 1870 | South-west Atlantic: Straits of Magellan, southern Chile and southern Argentina | 12 | 4 | 150 | FishBase, Wisner & McMillan (1995) |
| <i>M. australis</i> Jenyns, 1842 | Southern Ocean: Tierra del Fuego and southern coasts of Chile and Argentina | 24 | 4 | 146 | OBIS, Wisner & McMillan (1995) |
| <i>M. capensis</i> Regan, 1913 | South-east Atlantic: Namibia and South Africa | 21 | 88 | 480 | OBIS |
| <i>M. circifrons</i> Garman, 1899 | Eastern Pacific: off southern California; also Peru and Chile | 18 | 732 | 1860 | FishBase, Wisner & McMillan (1995) |
| <i>M. fernholmii</i> Wisner & McMillan, 1995 | South-east Pacific and South-west Atlantic: known only from the type material, off southern Chile and off the Falkland Islands | 5 | 135 | 1480 | FishBase |
| <i>M. formosana</i> Mok & Kuo, 2001 | North-west Pacific: Taiwan | 2 | 753 | – | FishBase |
| <i>M. glutinosa</i> Linnaeus, 1758 | North-east Atlantic: Murmansk to the Mediterranean Sea; absent in eastern Mediterranean and Black Sea | 3255 | 44 | 1167 | OBIS |
| <i>M. hubbsi</i> Wisner & McMillan, 1995 | South-east Pacific: off the west coast of North and South America (northern Peru to Gulf of Panama) | 12 | 114 | 2440 | FishBase, Wisner & McMillan (1995) |
| <i>M. hubbsoides</i> Wisner & McMillan, 1995 | South-east Pacific: known only from type material off central Chile | 3 | 735 | 880 | FishBase, Wisner & McMillan (1995) |
| <i>M. ios</i> Fernholm, 1981 | Eastern Atlantic: south-west off Ireland and Iceland, off Western Sahara | 48 | 614 | 1694 | OBIS |
| <i>M. jespersanae</i> Møller, Feld, Poulsen, Thomsen & Thormar, 2005 | North Atlantic: off West Greenland, in the eastern Davis Strait; Denmark Strait, Reykjanes Ridge, and South East of Iceland | 19 | 772 | 1556 | Møller <i>et al.</i> (2005) |
| <i>M. knappi</i> Wisner & McMillan, 1995 | South-west Atlantic: known only from the type material near the Falkland Islands | 4 | 630 | 650 | FishBase, Wisner & McMillan (1995) |
| <i>M. kuoi</i> Mok, 2002 | North-west Pacific: Taiwan | 2 | 595 | – | FishBase |
| <i>M. itmosa</i> Girard, 1859 | Western Atlantic: Davis Strait; south to Florida; including Campeche Bank, Gulf of Mexico | 42 | 75 | 1006 | FishBase, Wisner & McMillan (1995) |
| <i>M. mcoskeri</i> Wisner & McMillan, 1995 | Western Central Atlantic: southern Caribbean Sea | 7 | 100 | 1174 | FishBase, Wisner & McMillan (1995) |
| <i>M. memillanae</i> Hensley, 1991 | Western Central Atlantic: Puerto Rico and Virgin Islands | 3 | 700 | 1500 | FishBase |
| <i>M. robinsorum</i> Wisner & McMillan, 1995 | Western Central Atlantic: southern Caribbean Sea | 3 | 783 | 1768 | FishBase, Wisner & McMillan (1995) |
| <i>Nemamyxine krefftii</i> McMillan & Wisner, 1982 | South-west Atlantic: off Argentina and southern Brazil | 2 | 80 | 800 | FishBase |
| <i>Neomyxine biniplicata</i> (Richardson & Jowett, 1951) | South-west Pacific: New Zealand | 2 | 73 | – | FishBase |

Table 1 Continued

| Species | Geographic range | Number of records | Minimum depth (m) | Maximum depth (m) | Source |
|---|---|-------------------|-------------------|-------------------|-----------------------------|
| <i>Paramyxine atami</i> Dean, 1904 | North-west Pacific: Japan | 3 | 300 | 536 | FishBase |
| <i>P. cheni</i> Shen & Tao, 1975 | North-west Pacific: south-west of Taiwan (northern South China Sea) | 7 | 156 | 268 | FishBase, Mok & Chen (2001) |
| <i>P. fernholmii</i> Kuo, Huang & Mok, 1994 | North-west Pacific: Taiwan | 2 | 330 | 384 | FishBase |
| <i>P. sheni</i> Kuo, Huang & Mok, 1994 | North-west Pacific: off south-western Taiwan | 7 | 150 | 619 | OBIS, Mok & Chen (2001) |
| <i>P. taiwanae</i> Shen & Tao, 1975 | North-west Pacific: north-eastern and south-western parts of Taiwan | 13 | 120 | – | OBIS, Mok & Chen (2001) |
| <i>P. yangi</i> Teng, 1958 | North-west Pacific: Taiwan and the South China Sea | 19 | 120 | 547 | OBIS, Mok & Chen (2001) |

Some of the species occur sympatrically, although not constituting any generalized track: *Eptatretus mendozai* and *E. macmillanae* in the Caribbean Sea (Puerto Rico), and *Myxine affinis* and *M. australis* in southernmost South America (Patagonia).

The most widespread genus is *Eptatretus*, occurring in the North and South Atlantic as well as in the Western and Eastern Pacific. Not surprisingly, this is also the most diverse genus, comprising more than 30 species from a total of about 70 (Nelson, 2006), of which 14 were included in this study. The main massing of the Myxinidae is located around the Pacific Basin, an area encompassing 31 of the species studied, with local massings in the Eastern Pacific (19 species) and Western Pacific (12 species).

Only seven out of 3797 (0.18%) records retrieved from OBIS/BROBIS were positively identified as geographical outliers (inland records: Mali, Mauritania, and Czech Republic) by the SP-OUTLIER algorithm. All outliers were restricted to the locality records of a single species, *Myxine ios*.

DISCUSSION

Several of the species analysed show a locally endemic distribution. This is supported by the observation of Martini *et al.* (1997) that hagfishes are not generally good dispersers, but rather tend to live and breed locally. This is not surprising, given that there is a general consensus that hagfishes do not have a larval stage (Walvig, 1963).

Overall, vicariance is a major feature of hagfish distribution, suggesting vicariant differentiation of widespread ancestors (Heads, 1985). The spatial correlations between the distribution of myxinids and tectonic features point to a shared geological and biological history as the key to understanding the evolution of this group both around the Pacific and in the Atlantic.

In the Atlantic Ocean, the distribution of *Myxine glutinosa* corresponds to a classical trans-oceanic track associated with the vicariant event resulting from the opening of the Atlantic Ocean during the Cretaceous (Croizat, 1958, 1964). However, according to Wisner & McMillan (1995) and Fernholm (2002), the nominal species *M. glutinosa* in the Western Atlantic deserves a separate status as *M. limosa*, with *M. glutinosa* restricted to the Eastern Atlantic form (but see Martini *et al.*, 1998, for a different opinion). In West Greenland, *M. glutinosa* occurs sympatrically with *M. jespersanae*, although with a rather limited overlap in their bathymetric distributions (64–782 m vs. 772–1556 m), but there is no documented capture of both species in the same trawl haul or trap (Møller *et al.*, 2005).

Populations of *Myxine australis* present a disjunct distribution in the southernmost part of South America (Mincarone & Soto, 2001), which may indicate species-level differences among the populations of the Atlantic and Pacific oceans. Although Mincarone & Soto (2001) stated that there are no significant differences in body proportions among the specimens from those populations, they pointed out, however, a marked difference with regard to the number of cusps. In the

Table 2 Geographic distribution and bathymetric ranges of myxinid species not included in this study. Primary sources of distributional and bathymetric data for each species are provided.

| Species | Geographic range | Minimum depth (m) | Maximum depth (m) | Source |
|--|---|-------------------|-------------------|--------------------------------------|
| <i>Eptatretus bischoffii</i> (Schneider, 1880) | South-east Pacific: off Chile | – | – | FishBase |
| <i>E. caribbeaus</i> Fernholm, 1982 | Western Central Atlantic: Caribbean Sea | – | – | FishBase |
| <i>E. chinensis</i> Kuo & Mok, 1994 | Western Pacific: South China Sea | – | – | FishBase |
| <i>E. eos</i> Fernholm, 1991 | South-west Pacific: Tasman Sea, west of New Zealand | 900 | 1013 | FishBase |
| <i>E. fernholmi</i> McMillan & Wisner, 2004 | Western Pacific: known only from the type locality in the Philippines | 563 | – | FishBase |
| <i>E. goliath</i> Mincarone & Stewart, 2006 | South-west Pacific: known only from the holotype, off the north-east North Island, New Zealand | 811 | – | FishBase, Mincarone & Stewart (2006) |
| <i>E. indrambaryai</i> Wongratana, 1983 | Indian Ocean: Andaman Sea | – | – | FishBase |
| <i>E. lakeside</i> Mincarone & McCosker, 2004 | South-east Pacific: Galápagos Islands | – | – | FishBase |
| <i>E. octatrema</i> (Barnard, 1923) | South-east Atlantic: known from the holotype taken from the Agulhas Bank, South Africa | – | – | FishBase |
| <i>E. okinoseanus</i> (Dean, 1904) | North-west Pacific: Taiwan and southern Japan | – | – | Ohta & Kim (2001) |
| <i>E. strickrotti</i> Møller & Jones, 2007 | Eastern Pacific: East Pacific Rise, near Sebastian's Steamer hydrothermal vent | 2211 | – | FishBase |
| <i>E. wayuu</i> Mok, Saavedra-Diaz & Acero, 2001 | Western Atlantic: known only from the Guajira coast near Puerto Bolivar, Colombia, Caribbean Sea | 306 | – | FishBase |
| <i>Myxine debueni</i> Wisner & McMillan, 1995 | South-east Pacific: ranging eastwards to the Straits of Magellan in the South-west Atlantic | – | – | FishBase |
| <i>M. dorsum</i> Wisner & McMillan, 1995 | South-west Atlantic: known only from two specimens | 115 | – | FishBase |
| <i>M. garmani</i> Jordan & Snyder, 1901 | North-west Pacific: Japan | 308 | – | FishBase |
| <i>M. paucidens</i> Regan, 1913 | North-west Pacific: known only from the Sagaminada Sea, Japan | – | – | FishBase |
| <i>M. pequenoi</i> Wisner & McMillan, 1995 | South-east Pacific: known only from the type material off Valdivia, Chile | – | – | FishBase |
| <i>M. sotoi</i> Mincarone, 2001 | South-west Atlantic: Brazil | 810 | – | FishBase |
| <i>Nemamyxine elongata</i> Richardson, 1958 | South-west Pacific: New Zealand. Known only from type specimen; another specimen was caught in 2000 off South Island, New Zealand | 132 | – | Mincarone & Stewart (2006) |
| <i>Notomyxine tridentiger</i> (Garman, 1899) | South-east Pacific and South-west Atlantic: southern coasts of South America | 115 | – | FishBase |
| <i>Paramyxine ancon</i> (Mok, Saavedra-Diaz & Acero, 2001) | Western Central Atlantic: off La Punta de los Remedios, Caribbean Sea | 488 | – | FishBase |
| <i>P. moki</i> McMillan & Wisner, 2004 | North-west Pacific: Japan | – | – | FishBase |
| <i>P. nelsoni</i> Kuo, Huang & Mok, 1994 | North-west Pacific: south-west Taiwan | 190 | – | FishBase |

Table 2 Continued

| Species | Geographic range | Minimum depth (m) | Maximum depth (m) | Source |
|---|--|-------------------|-------------------|----------|
| <i>P. walkeri</i> McMillan & Wisner, 2004 | North-west Pacific: Japan | – | – | FishBase |
| <i>P. wisneri</i> Kuo, Huang & Mok, 1994 | North-west Pacific: south-east of Taiwan | – | – | FishBase |

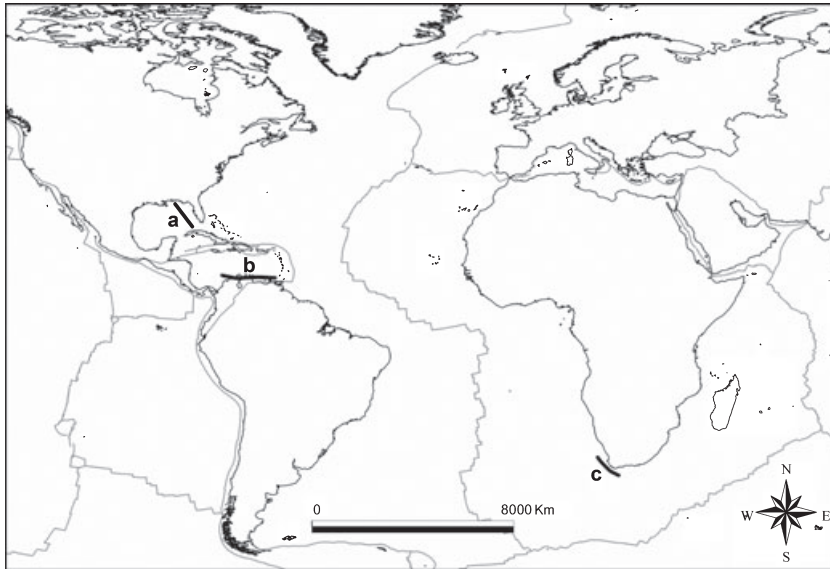


Figure 1 Generalized tracks obtained in the analysis: a, Gulf of Mexico track; b, Caribbean Sea track; c, South-eastern Atlantic track. Dashed lines indicate margins of major lithospheric plates, mid-oceanic ridges, and deep-sea trenches.

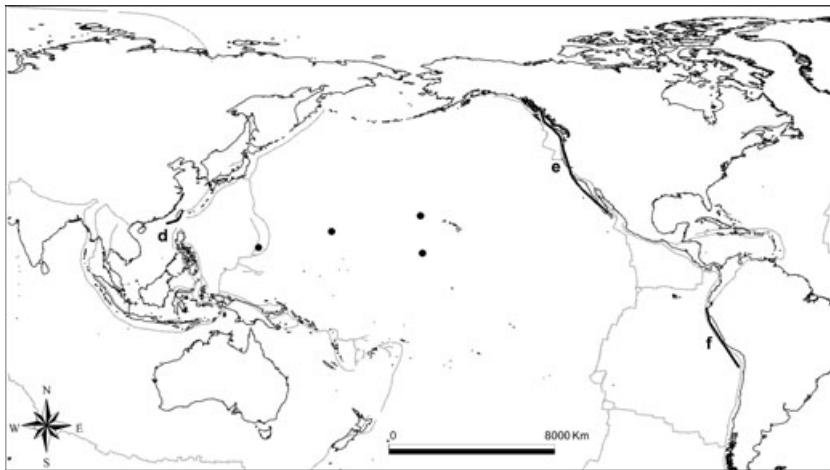


Figure 2 Generalized tracks obtained in the analysis: d, Western Pacific track; e, North-eastern Pacific track; f, South-eastern Pacific track. Dots show the distribution of *Eptatretus carlhubbsi*. Dashed lines indicate margins of major lithospheric plates, mid-oceanic ridges, and deep-sea trenches.

present study, this disjunct distribution was also observed in *M. affinis*.

A distinct distribution pattern observed for some species is a replacement in space, with one species substituting another one in contiguous areas. This can be seen for *Eptatretus menezesi* and *Nemamyxine krefftii* in the South-western Atlantic (Brazil), and for *E. deani* and *E. mcconnaugheyi* in the North-eastern Pacific (California).

Myxine is largely vicariant with *Eptatretus*, overlapping only in the Caribbean Sea (*E. caribbeaus*, *E. multidentis*, *E. mendozai*,

E. wayuu, *M. mccoskeri*, and *M. robinsorum*), south-western Cape (*M. capensis* and *E. profundus*), and central California (where *M. circifrons* and *M. hubbsi* overlap with *E. deani* and *E. stouti*). The overlap of these genera in the Caribbean region is most interesting, as that region represents a former geological connection between the Pacific and Atlantic (Ekman, 1953). It is interesting that *Myxine* is peripheral to the Caribbean whereas *Eptatretus* is found throughout it. *Myxine circifrons* has a disjunction pattern also widely seen in terrestrial organisms (for which these patterns have been

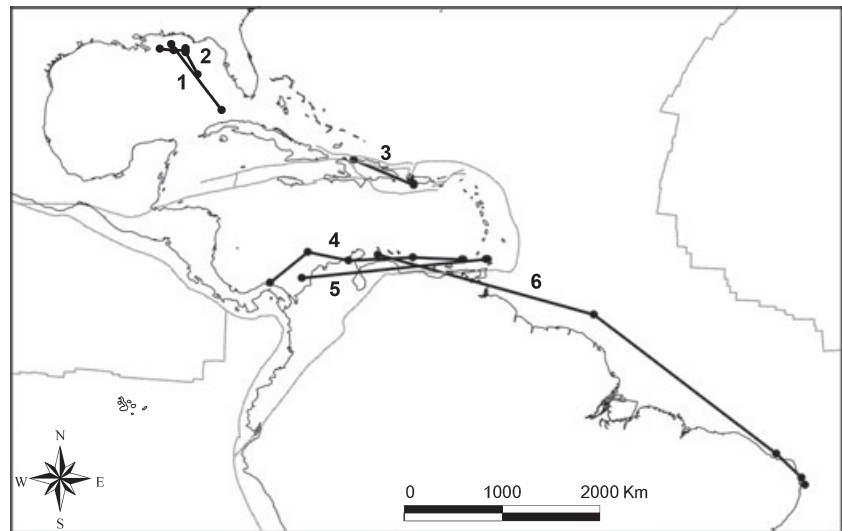


Figure 3 Individual tracks of the species included in the generalized tracks a and b: 1, *Eptatretus mendozai*; 2, *E. minor*; 3, *E. multidentis*; 4, *E. springeri*; 5, *Myxine mccoskeri*; 6, *M. robsorum*.

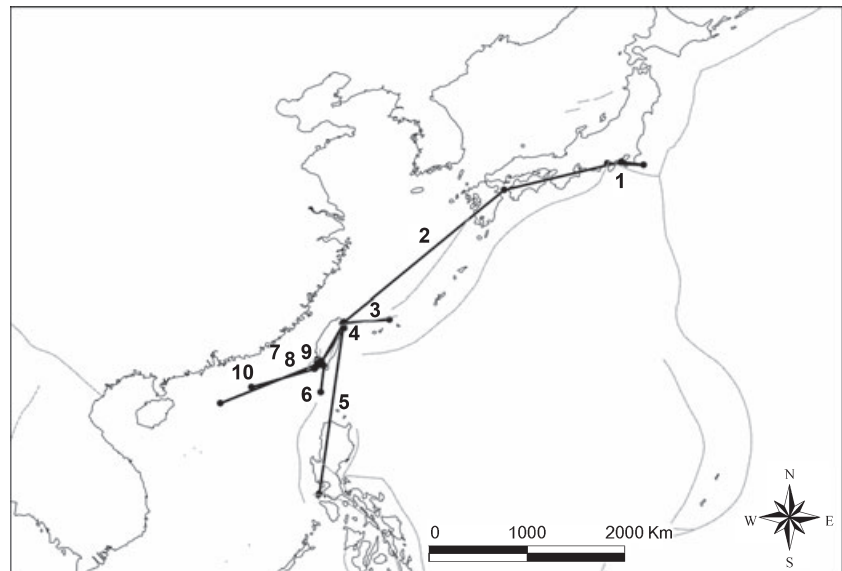


Figure 4 Individual tracks of the species included in the generalized track d: 1, *Eptatretus burgeri*; 2, *E. strahani*; 3, *Myxine formosana*; 4, *M. kuoi*; 5, *Paramyxine atami*; 6, *P. cheni*; 7, *P. fernholmi*; 8, *P. sheni*; 9, *P. taiwanae*; 10, *P. yangi*.

conventionally attributed to long-distance dispersal caused by recent bird transport: Carlquist, 1981). The Atlantic range of *Eptatretus* involves the Caribbean and eastern South America, a pattern found with some other organisms (Grehan, 2001). It is interesting to note that a large number of species of *Eptatretus* (five), including the newly described species *E. strickrotti* from the East Pacific Rise (Møller & Jones, 2007), have been recorded from a comparatively small area around or near the Galápagos Islands (McMillan, 1998), an important biogeographical node (Grehan, 2001). The range of *E. carlhubsii* is shared with that of many terrestrial organisms (Springer, 1982; Stoddart, 1992). Interestingly, only one species of Myxinidae (*E. indrambaryai* Wongratana, 1983) has been recorded from the Indian Ocean, although it remains to be seen if this constitutes a real absence of the group in this region or just a result of differential sampling effort.

In the Pacific Ocean, the distribution of the species of *Eptatretus* and *Paramyxine* is clearly associated with the

margins of the Pacific Plate. Moreover, *Eptatretus carlhubsii* (Fig. 2) seems to be a Pacific Plate endemic (*sensu* Springer, 1982). These distribution patterns are shared by several other groups of marine organisms, including many from shallow tropical waters (coral reef fishes: Springer, 1982; marine algae: Chin *et al.*, 1991; marine mammals: Aguilar-Aguilar & Contreras-Medina, 2001), and may imply a common history for this marine biota.

The generalized tracks found in the Pacific (Western and Eastern) indicate a northern trans-Pacific disjunction of *Eptatretus* and *Paramyxine* in that geographical sector of the Earth. This trans-Pacific distribution pattern is also observed in many other groups of circum-Pacific, poorly dispersing taxa, including terrestrial plants (Heads, 1999; Grehan, 2007) and shallow-water marine organisms (Glasby, 1999; O'Foighil *et al.*, 1999). The results of the present study add the deep-water, ancient myxinids to these trans-Pacific disjunctions. The classical plate tectonics model for the Pacific Ocean requires

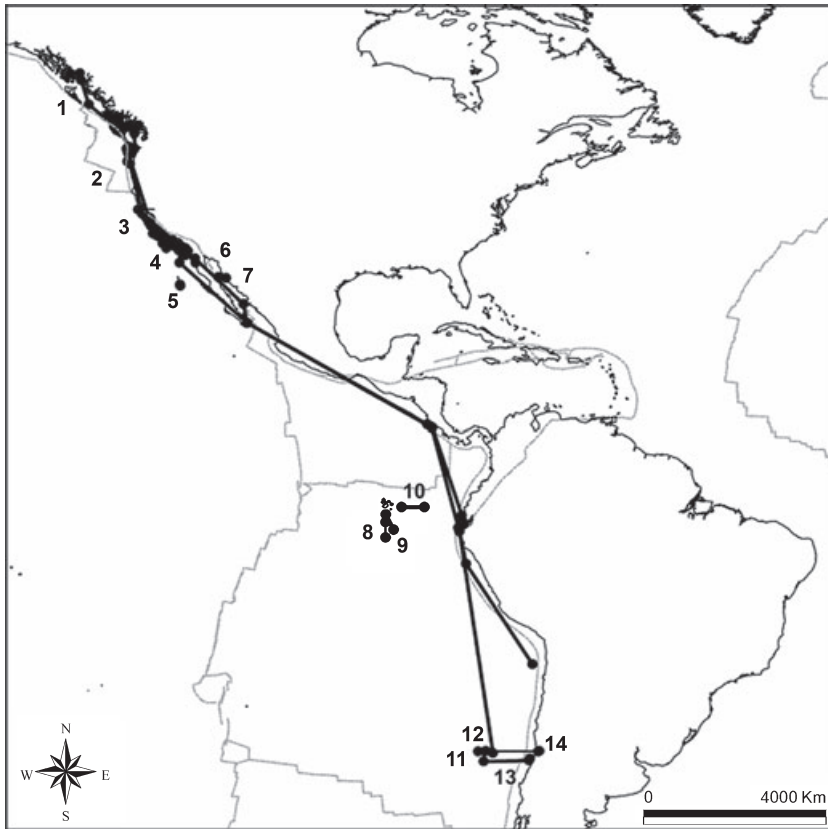


Figure 5 Individual tracks of the species included in the generalized tracks e and f: 1, *Eptatretus deani*; 2, *E. fritzi*; 3, *E. grouseri*; 4, *E. laurahubbsae*; 5, *E. mccoonaugheyi*; 6, *E. mccooskeri*; 7, *E. nanii*; 8, *E. polytrema*; 9, *E. sinus*; 10, *E. stoutii*; 11, *E. wisneri*; 12, *Myxine circifrons*; 13, *M. hubbsi*; 14, *M. hubbsoides*.

the former existence of a pre-Pacific superocean (Panthalassa), but this hypothesis is difficult to reconcile with the many disjunct taxa of narrow ranges and limited dispersal ability that show a circum-Pacific distribution, including the Myxinidae studied here. This group is of Pangean origin, and its current distribution patterns are most parsimoniously explained by the fragmentation and subsequent differentiation of widespread ancestors as a result of a single vicariant event, the opening of the Pacific Basin in Mesozoic times.

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