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Distributional patterns of †Mawsoniidae (Sarcopterygii: Actinistia)

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ABSTRACT

Mawsoniidae are a fossil family of actinistian fish popularly known as coelacanths, which are found in continental and marine paleoenvironments. The taxon is considered monophyletic, including five valid genera (*Axelrodichthys*, *Chinlea*, *Diplurus*, *Mawsonia* and *Parnaibaia*) and 11 genera with some taxonomical controversy (*Alcoveria*, *Changxingia*, *Garnbergia*, *Heptanema*, *Indocoelacanthus*, *Libys*, *Lualabaea*, *Megalocoelacanthus*, *Moenkopia*, *Rhipis* and *Trachymetopon*). The genera restricted to the Northern Hemisphere (*Diplurus* and *Chinlea*) possess the oldest records (Late Triassic), whereas those found in the Southern Hemisphere (*Mawsonia*, *Axelrodichthys*, and *Parnaibaia*) extend from Late Jurassic to Late Cretaceous, especially in Brazil and Africa. We identified distributional patterns of Mawsoniidae, applying the panbiogeographical method of track analysis, and obtained three generalized tracks (GTs): GT1 (Northeastern Newark) in strata of the Newark Group (Upper Triassic); GT2 (Midwestern Gondwana) in the Lualaba Formation (Upper Jurassic); and GT3 (Itapecuru-Alcântara-Santana) in the Itapecuru-Alcântara-Santana formations (Lower Cretaceous). The origin of Mawsoniidae can be dated to at least Late Triassic of Pangaea. The tectonic events related to the breakup of Pangaea and Gondwana and the evolution of the oceans are suggested as the vicariant events modeling the distribution of this taxon throughout the Mesozoic.

Key words: Mawsoniidae, Mesozoic, evolutionary biogeography, track analysis.

INTRODUCTION

Mawsoniidae are a fossil family of actinistian fish popularly known as coelacanths. The taxon was proposed by Schultze (1993), although until the early 1990's their members were assigned to the family Coelacanthidae Agassiz, 1843 (Wenz 1980, Maisey 1986). Although Mawsoniidae are considered to be monophyletic, there is some controversy regarding their composition. Schultze (1993) only included *Alcoveria*, *Axelrodichthys*, *Chinlea*, *Diplurus* and *Mawsonia* in the family.

Forey (1998) defined Mawsoniidae as comprising *Garnbergia*, *Libys*; *incertae sedis* *Changxingia*, *Heptanema*, *Indocoelacanthus*; *Diplurus*, *Chinlea*; *incertae sedis* *Lualabaea*, *Megalocoelacanthus*, *Moenkopia*; *Mawsonia*, *Axelrodichthys*. Schultze (2004) proposed a new taxonomic composition, as follows: *Alcoveria*, *Chinlea*, *Diplurus*, *Mawsonia*, *Axelrodichthys*, *Libys*, *Trachymetopon*; *incertae sedis* *Heptanema*, *Indocoelacanthus*, *Lualabaea*, *Moenkopia*, and *Rhipis*. Clément (2005) included *Diplurus*, *Chinlea*, *Mawsonia* and *Axelrodichthys* in Mawsoniidae. López-Arbarello et al. (2008) pointed out *Trachymetopon*, *Libys*, *Indocoelacanthus*,

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and *Lualabaea* as Jurassic mawsoniids. Yabumoto (2008) considered *Diplurus*, *Chinlea*, *Mawsonia*, *Axelrodichthys*, and *Parnaibaia* as Mawsoniidae. Miguel and Gallo (2009) assigned *Alcoveria*, *Axelrodichthys*, *Chinlea*, *Diplurus*, *Garnbergia*, *Libys*, *Lualabaea*, *Mawsonia*, *Parnaibaia*, and *Trachymetopon* to the family. Miguel (2011) added *Heptanema*, *Indocoelacanthus*, *Megalocoelacanthus*, *Moenkopia*, and *Rhipis* to Mawsoniidae.

Records of Mawsoniidae are known from continental and marine paleoenvironments (Beltan 1972). This family possesses biogeographical significance due to their extensive temporal range through all the Mesozoic, from the Late Triassic (Carnian) to the Late Cretaceous (Maastrichtian), and their wide geographical distribution in South and North America, Africa, Europe, and Asia (Jain 1974, Schultze 1993, Carvalho and Maisey 2008, Miguel and Gallo 2009). In South America, occurrences are more frequent in northeastern Brazil, being *Mawsonia* the most abundant genus (Carvalho 2002, Carvalho and Maisey 2008, Pinheiro et al. 2011, Silva et al. 2011). The record of *Mawsonia* from the Sanfranciscana Basin, reported by Carvalho and Maisey (2008), represents, until the moment, the single occurrence of the family in southeastern Brazil. *Axelrodichthys* occurs in the Lower Cretaceous of the Araripe Basin, in strata of Crato (Aptian) and Santana (Albian) formations (Maisey 1986, Brito and Martill 1999). Carvalho and Maisey (1999) reported *Axelrodichthys* sp. in the Codó Formation, Albian of the Grajaú Basin. *Parnaibaia* has been found in the Upper Jurassic of the Parnaíba Basin (Yabumoto 2008). In addition to Brazil, there is an uncertain record of Mawsoniidae in the Quebrada Vaquillas Altas locality, Upper Jurassic of Chile (Arratia and Schultze 1999); and more recently, Soto et al. (2011) recorded *Mawsonia* from the Tacuarembó Formation, Kimmeridgian-Hauterivian of Uruguay.

African records of Mawsoniidae include *Mawsonia*, *Axelrodichthys*, *Lualabaea*, and *Rhipis*.

Mawsonia is represented by *M. gigas* in the Ubangi locality, Neocomian of Democratic Republic of Congo (Casier 1961), representing the oldest record of the genus in Africa (Carvalho 2002). In Niger, the genus occurs in the Gadoufaoua, In Gall, and In Abangarit localities. *Mawsonia tegamensis* is the best preserved record in Africa, occurring in the Aptian of Gadoufaoua (Wenz 1975, 1981). *Mawsonia* sp. is found in the Neocomian-Barremian of In Gall (Wenz 1981). *Mawsonia lavocati* occurs in the Albian of In Abangarit (Wenz 1981). In the Albian of Algeria, in the Gara Samani locality, fragments previously assigned to *Mawsonia* (Broin et al. 1971) were later recognized as *M. lavocati* (Wenz 1981). In the Cenomanian of Egypt, in the Baharija locality, numerous bones of *M. gigas* have been described (Weiler 1935, Carvalho and Maisey 2008). In the Albian-Cenomanian of Morocco, in the Kem Kem region, there are records of *M. lavocati* (Tabaste 1963, Wenz 1981). This is the region with the most occurrences of mawsoniids in Africa. Cavin and Forey (2004) reported an indeterminate mawsoniid in the region. More recently, *M. lavocati* was reported by Yabumoto and Uyeno (2005). *Axelrodichthys* is represented in the Early and Late Cretaceous of Africa; Gee (1988) reported it in the In Gall region and Gottfried et al. (2004) pointed out its presence in the Ankazomihaboka Series, Mahajanga Basin, Madagascar, dated with uncertainty as Santonian-Coniacian (Rogers et al. 2000), representing the youngest mawsoniid in Africa, so far. Gottfried et al. (2004) mentioned the similarity between the extrascapular found in the Ankazomihaboka Series and that found in In Gall. Although *Mawsonia* and *Axelrodichthys* also occur in Africa, the specimens found in Brazil are better preserved and are significantly more numerous. *Mawsonia* and *Axelrodichthys* undoubtedly occur from the Jurassic to the Cretaceous of Brazil (Carvalho 1982, 2002, Carvalho and Maisey 2008, Yabumoto 2008) and the Cretaceous of Africa (Wenz 1980, Gottfried et al. 2004), and show biogeographical relevance,

because their history can be related directly to the evolution and final breakup of Western Gondwana (Late Jurassic-Early Cretaceous) and consequently to the opening of the South Atlantic Ocean. *Lualabaea* includes *L. lerichei* and *L. henryi*, from the Tegama region, Stanleyville Formation, Congo Basin, Upper Jurassic (?Kimmeridgian), Democratic Republic of Congo (Saint-Seine 1955, Forey 1998, Myers et al. 2011). *Rhipis* occurs in the Upper Jurassic of the Democratic Republic of Congo, including *R. moorseli* from the Kinko, Luzubi, and Kimbau localities; and *R. tuberculatus* was found only in the Kinko locality (Saint-Seine 1950).

In North America, *Diplurus* and *Chinlea* are the most frequent genera. *Diplurus* occurs in the Carnian of the Boonton, Durham, Westfield, Bergen, Princeton, Gwynedd, and North Wales localities; *Chinlea* occurs in the Norian of San Juan, Montrose, Dolores, and Abiquiu localities, and in the Carnian of Randall (Schaeffer 1948, 1952, 1967, Elliott 1987). More recently, an isolated scale was found in the Pardonet Formation, Norian of Canada, and it was assigned to *Garnbergia* (Yabumoto and Neuman 2004). *Moenkopia* is found in the Moenkopi Formation, Lower Triassic (Anisian), Western United States (Schaeffer and Gregory 1961, Forey 1998). The genus shares similarities with the living latimeriid *Latimeria chalumnae*, although Forey (1998) considered it as Mawsoniidae *incertae sedis*. *Megalocoelacanthus* is found in the Blufftown, Eutaw, and Mooreville formations, Upper Cretaceous (Campanian) of Eastern United States (Schwimmer et al. 1994).

In Europe, *Libys* is assigned only to the Upper Jurassic (Tithonian) of the Solnhofen Formation, West Germany (Forey 1998). The records of *Garnbergia* are scarce although the preservation of the specimens is reasonable (Martin and Wenz 1984). *Alcoveria* is represented by an almost complete specimen from the Middle Triassic (Ladinian) of Spain (Beltan 1972, 1984). It is one of the few genera found in a marine paleoenvironment. Although it was included in the family (Schultze 1993), Forey

(1998) considered it as a Mawsoniidae *incertae sedis*, due to the absence of its synapomorphy (well-developed pleural ribs). *Heptanema* occurs in the Middle Triassic (Ladinian) of Austria and Italy. According to Forey (1998), detailed anatomical studies are lacking, thus, it does not allow for a strict comparison with other coelacanth genera; the pattern of ornamentation of the scales is very similar to that found in *Diplurus*. *Trachymetopon* is known from the Early Jurassic (Sinemurian) of Westphalia, Germany, and has been assigned to Mawsoniidae (Schultze 2004, López-Arbarello et al. 2008). According to Forey (1998), it shares similarities with *Mawsonia* and *Axelrodichthys*.

In Asia, *Changxingia* occurs in the Changxing Formation, Upper Permian of southern China, and includes a well-preserved specimen (Wang and Liu 1981). It represents the single occurrence of Mawsoniidae in the Paleozoic. *Indocoelacanthus* occurs in the Kota Formation, Lower Cretaceous of India (Jain 1974).

Phylogenetic analyses of Mawsoniidae are scarce. Nevertheless, it is consensual that they are comprised of five valid genera: *Diplurus* Newberry, 1878; *Mawsonia* Woodward, 1907; *Chinlea* Schaeffer, 1967; *Axelrodichthys* Maisey, 1986; and *Parnaibaia* Yabumoto, 2008. They also include 11 dubious genera: *Libys* Münster, 1842; *Heptanema* Belloti, 1857; *Rhipis* Saint-Seine, 1950; *Trachymetopon* Hennig, 1951; *Lualabaea* Saint-Seine, 1955; *Moenkopia* Schaeffer and Gregory, 1961; *Alcoveria* Beltan, 1972; *Indocoelacanthus* Jain, 1974; *Changxingia* Wang and Liu, 1981; *Garnbergia* Martin and Wenz, 1984; and *Megalocoelacanthus* Schwimmer et al., 1994 (Cloutier 1991, Cloutier and Ahlberg 1996, Forey 1998, Schultze 1993, 2004, Clément 2005, 2006, Yabumoto 2008, Miguel and Gallo 2009).

Biogeographical studies using fossil taxa have been criticized by some authors (Løvtrup 1977, Nelson and Platnick 1981), being considered as less important than those based on living taxa. Grande (1985) was one of the first authors to emphasize the

relevance of fossils in biogeographical analyses, mainly those showing a fine state of preservation. Yet, according to Grande (1985), fishes were among the first vertebrates used in biogeographical analyses, because of the good quality of their preservation, the abundance, and the high degree of articulation of the specimens, mainly due to paleoenvironmental conditions. Track analysis (Croizat 1958, 1964, Page 1987, Craw et al. 1999, Echeverry and Morrone 2010) allows identification of congruent patterns of geographic distribution and consists basically of plotting locality records of different taxa on maps and connecting them using lines following a criterion of minimum distance, to constitute individual tracks. These tracks correspond to the geographical coordinates of the taxa, the place where their evolution occurred. The coincidence of two or more individual tracks corresponds to a generalized track, which provides a spatial criterion of biogeographical homology (Morrone 2001), and allows the inference of an ancestral biota widespread in the past which was later fragmented by vicariant events. When two or more generalized tracks converge or superimpose in an area, a node is determined, implying that different ancestral biotas interrelated, constituting a composite area (Morrone and Crisci 1995, Craw et al. 1999, Crisci et al. 2003, Heads 2004, Morrone 2009).

Our objective is to apply a track analysis to the geographical distribution of Mawsoniidae, including the valid genera as well as those of controversial systematic position. Several records available for this taxon claim for an explicit biogeographical analysis.

MATERIALS AND METHODS

The analysis was performed using occurrence points (Table SI) (Supplementary material) obtained from literature and, in the case of *Mawsonia* and *Axelrodichthys*, from the labels of specimens deposited in the Paleontological Collections of the Museu de Ciências da Terra (former Divisão de Geologia e Mineralogia/Departamento Nacional

de Produção Mineral-RJ) and the Museu Nacional/ Universidade Federal do Rio de Janeiro, supplemented by the available records of online databases of some scientific institutions (e.g., American Museum of Natural History).

Individual tracks were constructed by plotting their localities on maps with ArcView v3.2 (ESRI 1999) and connecting them through minimum spanning trees (Page 1987) using the Trazos 2004 extension (Rojas 2007). As ArcView works on modern geographic coordinates, the software Point Tracker for Windows (Scotese 2008) was used to calculate paleolatitudes from modern coordinates (decimal latitude and longitude). A “txt” file containing the list of the present-day latitude and longitude of the points (i.e., fossil localities and/or outcrops) is submitted to Point Tracker, it rotates the points back in time to their paleoposition, and the results of the conversion can be read in a GIS software (e.g., ArcGIS) and plotted on maps of the Reconstructed Shapefile Library software (Scotese 2008), which contains about 50 paleoreconstructions (600 millions years before present). We obtained individual tracks for the species and also for the genera by geological periods, in order to incorporate data on species that are still unnamed but can be assigned with confidence to a genus. Generalized tracks were determined by overlapping individual tracks through visual inspection.

RESULTS AND DISCUSSION

We constructed 12 individual tracks. The following species have a single occurrence, so no individual tracks were drawn for them: *Changxingia aspratilis* (Changxing Formation, Upper Permian, China), *Axelrodichthys araripensis* (Crato Formation, Aptian, Brazil), *Axelrodichthys* sp. (Codó Formation, Albian, Brazil), *Axelrodichthys* sp. (Barremian, Africa), *Garnbergia* sp. cf. *ommata* (Pardonet Formation, Norian, North America), *Alcoveria brevis* and *Garnbergia ommata* (Ladinian, Europe), *Lualabaea lerichei* and *L. henryi* (Tegama Series, Kimmeridgian, Africa), *Rhipis tuberculatus* (Kwango Formation,

Kimmeridgian, Africa), *Mawsonia gigas* (Morro do Chaves Formation, Barremian, Brazil), *M. tegamensis* (Aptian, Africa), *Mawsonia* sp. (Barremian, Africa), *Mawsonia* cf. *gigas* (Kem Kem beds, Albian, Africa), *Parnaibaia maranhaoensis* (Pastos Bons Formation, Upper Jurassic, Brazil), *Libys polypterus* and *L. superbis* (Solnhofen Formation, Tithonian, Europe), and *Moenkopia wellsi* (Moenkopi Formation, Anisian, North America).

Although there is no individual track for *A. araripensis* in Aptian, it was included in an individual track from Albian (Santana and Codó formations, Brazil). Also, *Mawsonia gigas* was not included in individual track in Barremian; nevertheless as it is found in more than one geological period, we construct individual tracks from the Berriasian-Hauterivian formations in Brazil and Africa (Candeias, Maracangalha, Morro do Barro, Brejo Santo, Icó, Quiricó, Loia and Kwango), and from Albian-Cenomanian formations in Brazil and Africa (Santana, Itapecuru, Alcântara, Kem Kem, and Baharija) (Figs. 1-11).

The superposition of the 12 individual tracks resulted in three generalized tracks (GTs):

GT1- Northeastern Newark (Fig. 12) is sustained by *Diplurus longicaudatus* and *D. newarki*. It was identified in a region where the nonmarine strata of the Newark Group (Upper Triassic-Lower Jurassic of North America) crop out. Sedimentological features, such as ripple marks, mud cracks, and rain drop prints, as well as ichnofossils such as dinosaur footprints, indicate dry and rainy climate (Schaeffer 1948, Olsen et al. 1996). The paleoichthyofauna of the Newark Group shows a low diversity, represented by members of Redfieldiidae and Semionotidae in addition to *Diplurus* (Schaeffer 1948, Olsen and McCune 1991, McCune 1996).

GT2- Midwestern Gondwana (Fig. 12) is sustained by *Rhipis moorseli* and *Rhipis* sp. It was identified in a region where lacustrine strata of the Lualaba Formation (Upper Jurassic of the Congo Basin, Africa) crop out. It consists primarily

of reddish-brown and greenish-gray mudstones with interspersed limestones and bituminous beds, supporting a lacustrine paleoenvironment with a fluvial contribution (Myers et al. 2011). The paleoichthyofauna of this unit is relatively abundant and diversified, including other mawsoniids (*Lualabaea*), Semionotidae, Lombardinidae, Signeuxellidae, Pleuropholidae, and Teleostei *incertae sedis* (López-Arbarello et al. 2008, Petra and Gallo 2012).

GT3- Itapecuru-Alcântara-Santana (Fig. 12) is sustained by *Mawsonia gigas* and *Axelrodichthys araripensis*. It corresponds to an area of endemism along the Itapecuru-Alcântara-Santana formations, during Albian; the first two units crop out in the São Luís Basin, whereas the Santana Formation crops out in the Araripe Basin.

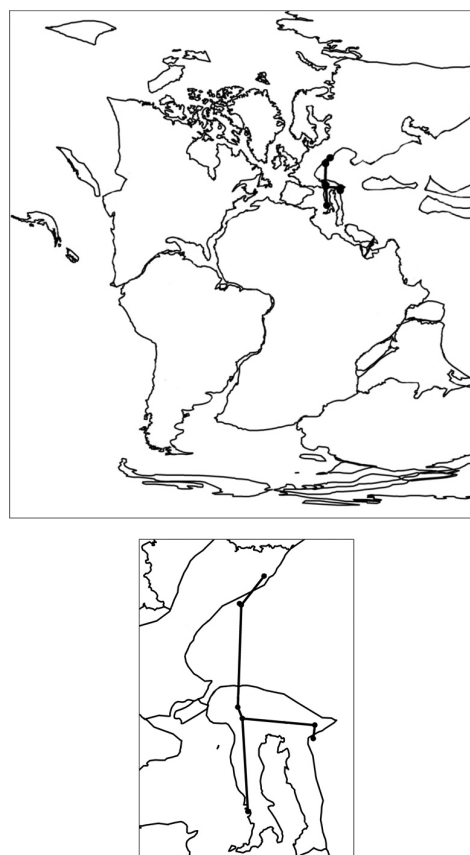


Fig. 1 - Ladinian paleogeographic map showing the individual track of *Heptanema paradoxum*, with a zoom of the occurrences below.

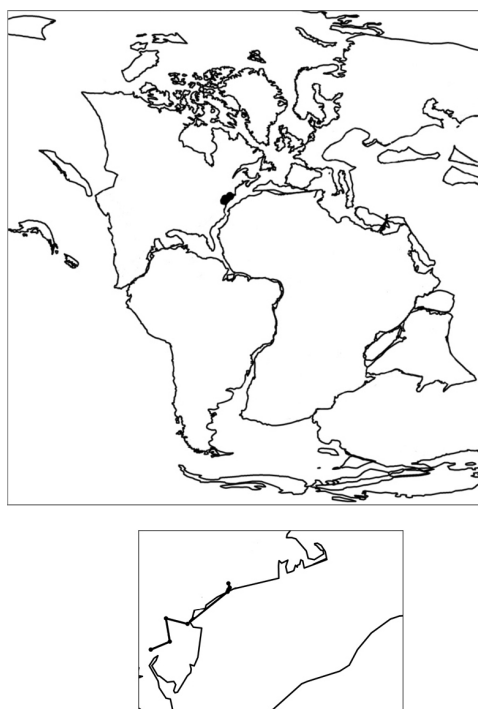


Fig. 2 - Carnian paleogeographic map showing the individual track of *Diplurus longicaudatus*, with a zoom of the occurrences below.



Fig. 4 - Norian paleogeographic map showing the individual track of *Chinlea sorenseni*, with a zoom of the occurrences below.

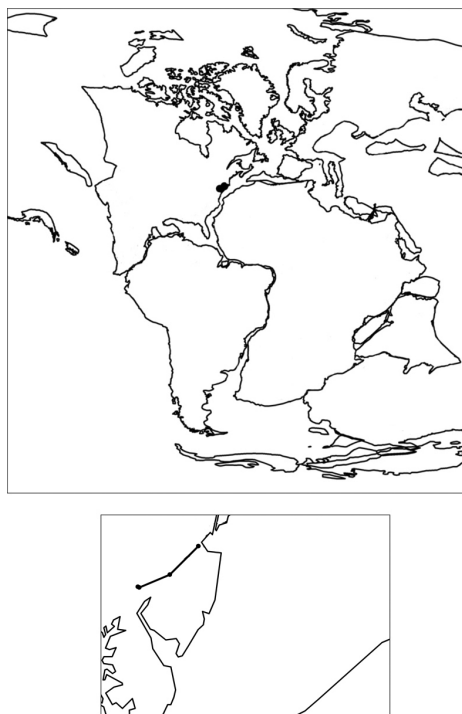


Fig. 3 - Carnian paleogeographic map showing the individual track of *Diplurus newarki*, with a zoom of the occurrences below.

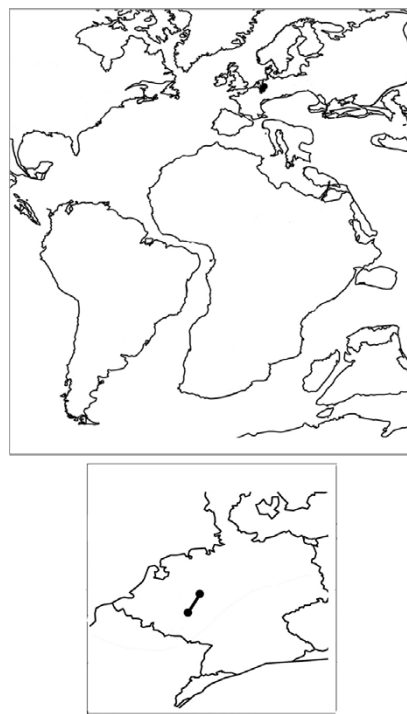


Fig. 5 - Sinemurian paleogeographic map showing the individual track of *Trachymetopon liassicum*, with a zoom of the occurrences below.

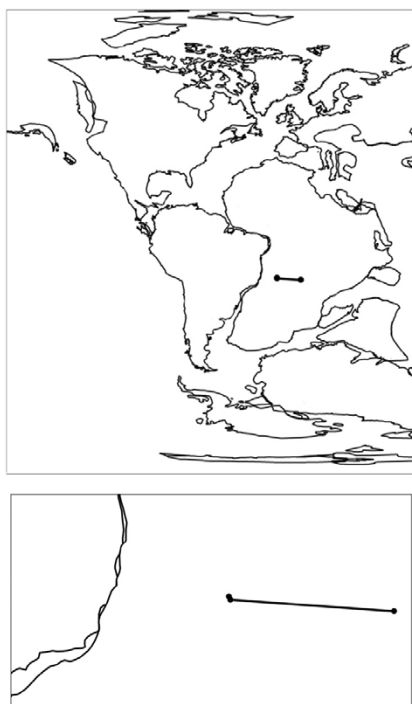


Fig. 6 - Kimmeridgian paleogeographic map showing the individual track of *Rhipis moorseli*, with a zoom of the occurrences below.



Fig. 8 - Paleogeographic map showing the individual track of *Mawsonia gigas* in Berriasian/Hauterivian, with a zoom of the occurrences below.

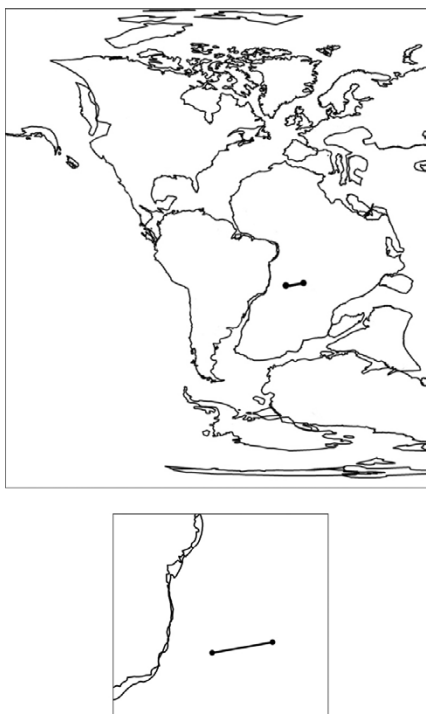


Fig. 7 - Kimmeridgian paleogeographic map showing the individual track of *Rhipis* sp., with a zoom of the occurrences below.

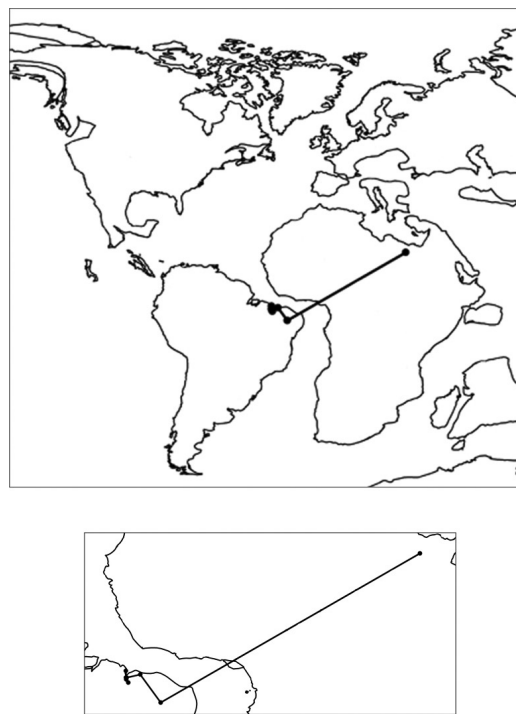


Fig. 9 - Paleogeographic map showing the individual track of *Mawsonia gigas* in Albian/Cenomanian, with a zoom of the occurrences below.

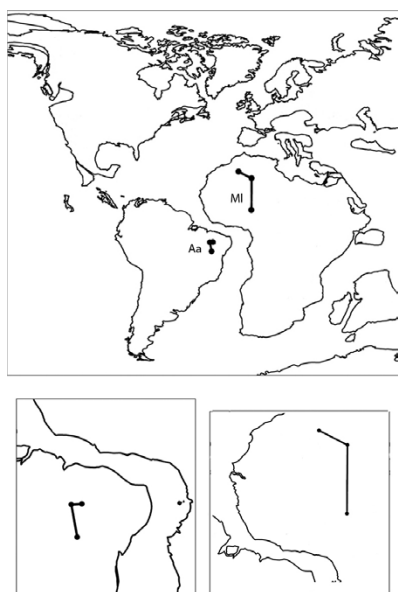


Fig. 10 - Albian paleogeographic map showing individual tracks of *Axelrodichthys araripensis* (Aa) and *Mawsonia lavocati* (MI), with a zoom of the occurrences below.

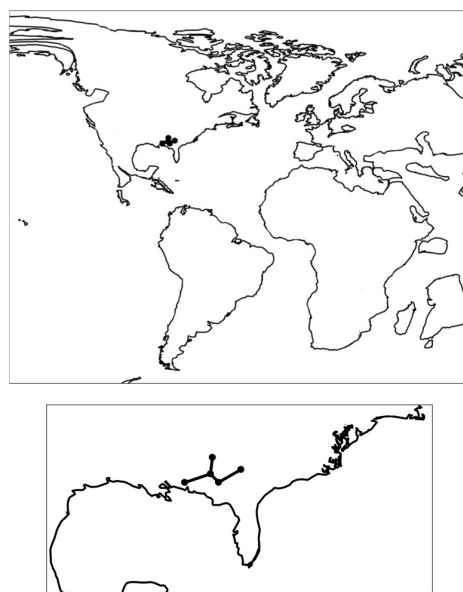


Fig. 11 - Campanian paleogeographic map showing the individual track of *Megalocoelacanthus dobiei*, with a zoom of the occurrences below.

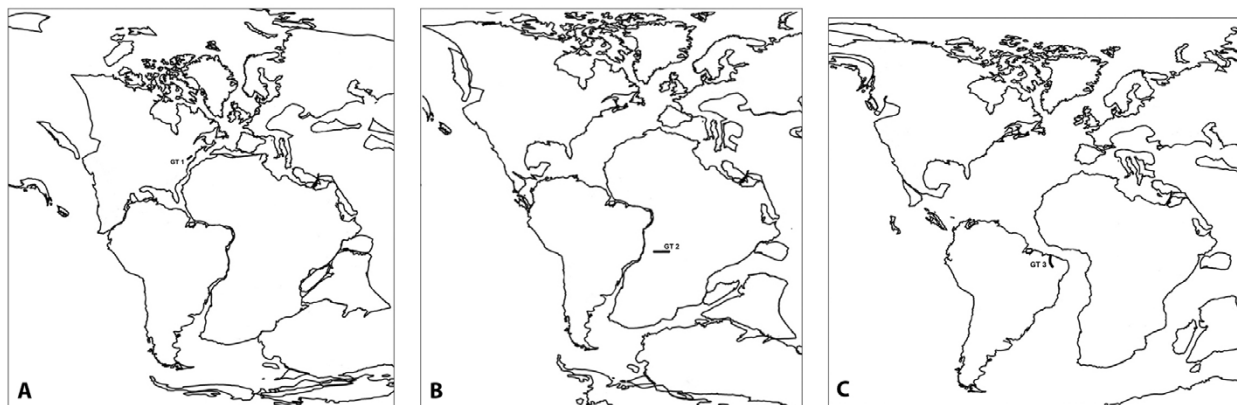


Fig. 12 - Generalized tracks. **A**, GT1 - Northeastern Newark (Upper Triassic); **B**, GT2 - Midwestern Gondwana (Upper Jurassic); **C**, GT3 - Itapecuru-Alcântara-Santana (Lower Cretaceous).

The Itapecuru Formation is characterized as being a meandering fluvial system (Pessoa and Borghi 2005), and its paleoichthyofauna consists of Chondrichthyes (Hybodontidae) and Osteichthyes (Semionotidae, Lepisosteidae, Pycnodontidae, Amiidae, Mawsoniidae, and Ceratodontidae) (Santos and Carvalho 2009). The Alcântara Formation was formed under estuarine to shallow marine conditions, such as coastal plain (Rossetti 2003). Its paleoichthyofauna includes Chondrichthyes

(Hybodontidae, Myliobatidae, and Sclerorhynchidae) and Osteichthyes (Semionotidae, Lepisosteidae, Pycnodontidae, Amiiformes, Mawsoniidae, and Ceratodontidae) (Gallo et al. 2012). The Santana Formation is one of the most important Lagerstätten from the Cretaceous. The sedimentary sequence is diverse, comprising limestones, marls, siltstones, and shales with carbonate concretions. The paleoenvironment is interpreted as being continental with alluvial fans, fluvial systems, and shallow salt lakes

(Silva and Neumann 2003). The paleoichthyofauna of Santana Formation is very abundant and diversified, comprising some Chondrichthyes (Hybodontidae and Rhinobatidae) and numerous Osteichthyes (e.g., Semionotidae, Lepisosteidae, Pycnodontidae, Amiidae, Aspidorhynchidae, Albulidae, Elopidae, and Mawsoniidae).

We did not find any biogeographic node.

Based on the distribution patterns found, the origin and expansion of Mawsoniidae probably occurred in the Late Triassic (or earlier) of western Pangaea, being represented by GT1. If the taxonomic placement of *Changxingia* within Mawsoniidae is confirmed, the age of origin of the group could be assigned to, at least, Upper Permian, in eastern Pangaea (Miguel and Gallo 2012). Also, judging by the distribution pattern of *Diplurus* only in western Pangaea during Late Triassic, the occurrence of a form close to this genus in Vaquillas Altas locality, in the Early Jurassic of Chile (Arratia and Schultze 1999), should be reexamined.

In the Early Jurassic, there are records in western (*Trachymetopon*) and eastern (*Indocoelacanthus*) Pangaea. However, the former was not assigned to any generalized track, whereas the latter does not even form an individual track.

In the Middle Jurassic, Pangaea began to break apart isolating two large landmasses (i.e., Laurasia and Gondwana); there are no records of Mawsoniidae from this period. In the Late Jurassic, the Central Atlantic Ocean separated the two blocks. These tectonic events suggest vicariance as the major feature of Mawsoniidae distribution from the Middle Mesozoic.

Late Jurassic Mawsoniidae show a gondwanic distribution pattern, with occurrences of *Rhipis*, *Lualabaea*, *Mawsonia* and *Parnaibaia* in Western Gondwana, except for *Libys*, which occurs in the Late Jurassic of Laurasia. The occurrence of *Rhipis* is reflected in GT2 (Midwestern Gondwana).

From the Late Jurassic to the Early Cretaceous, Western Gondwana started to break up, finishing its rupture and consequently the opening of the South Atlantic Ocean (SAO) in the Aptian (Arai 2009).

Long-term sea-level fluctuations (from Jurassic to Cretaceous) indicate that Gondwana was occupied by marine environments since Early Mesozoic. The marine transgressions also contributed to the connections between SAO and Tethys Sea across Northern Gondwana during Cretaceous (Gallo et al. 2012). In the Early Cretaceous, there are numerous records of *Mawsonia* and *Axelrodichthys* in Western Gondwana, as shown by GT3. An extensive system of epicontinental seaways was formed during the Aptian between the current South America and Africa (Arai et al. 2007, Maisey 2011), allowing a direct contact of the biotas. Considering the occurrence of *Mawsonia* in the Albion of North Africa and Brazil, as well as of *Axelrodichthys* in the Albion of Brazil, probably the latter also occurred in the Albion of North Africa.

In the Late Cretaceous, Mawsoniidae are represented by marine taxa and their distribution was probably molded by vicariant events related to the evolution of the oceans. The verified occurrences are in the Cenomanian of Brazil and Egypt (*Mawsonia*), Coniacian-?Santonian of Madagascar (*Axelrodichthys*), Campanian of United States (*Megalocoelacanthus*), and Maastrichtian of France (*Mawsonia* or *Axelrodichthys*). Taking into account the distribution pattern of Mawsoniidae during the early and middle Late Cretaceous in northern Brazil and Africa, as well as in Madagascar, possibly new records of the group will occur in southern South America.

GT3 is congruent with previous phylogenetic hypotheses proposed for Mawsoniidae. A comprehensive phylogenetic analysis, however, is necessary in order to verify its composition, due to the controversy related to the validity of several genera.

This analysis emphasizes the potential of the panbiogeographical method for recovering distribution patterns of fossil taxa with a similar applicability in living taxa.

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RESUMO

Mawsoniidae são uma família de peixes actinístios fósseis, conhecidos popularmente como celacanto, os quais são encontrados em paleoambientes continental e marinho. O táxon é considerado monofilético, incluindo cinco gêneros válidos (*Axelrodichthys*, *Chinlea*, *Diplurus*, *Mawsonia* e *Parnaibaia*) e 11 gêneros com alguma controvérsia taxonômica (*Alcoveria*, *Changxingia*, *Garnbergia*, *Heptanema*, *Indocoelacanthus*, *Libys*, *Lualabaea*, *Megalocoelacanthus*, *Moenkopia*, *Rhipis* e *Trachymetopon*). Os gêneros restritos ao Hemisfério Norte (*Diplurus* e *Chinlea*) possuem os registros mais antigos (Triássico Superior), enquanto aqueles encontrados no Hemisfério Sul (*Mawsonia*, *Axelrodichthys* e *Parnaibaia*) estendem-se do Jurássico Superior ao Cretáceo Superior, especialmente no Brasil e África. Nós identificamos padrões de distribuição de Mawsoniidae, aplicando o método pan-biogeográfico de análise de traços, e obtivemos três traços generalizados (TGs): TG1 (Newark Nordeste) nos estratos do Grupo Newark (Triássico Superior); TG2 (Centro-oeste gondwânico) na Formação Lualaba (Jurássico Superior); e TG3 (Itapecuru-Alcântara-Santana) nas formações Itapecuru-Alcântara-Santana (Cretáceo Inferior). A origem de Mawsoniidae pode ser datada, pelo menos, ao Triássico Superior da Pangeia. Os eventos tectônicos relacionados ao rompimento da Pangeia e Gondwana e a evolução dos oceanos são sugeridos como os eventos vicariantes modelando a distribuição deste táxon ao longo do Mesozoico.

Palavras-chave: Mawsoniidae, Mesozoico, biogeografia evolutiva, análise de traços.

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SUPPLEMENTARY MATERIAL

Table SI - Occurrences of Mawsoniidae. NDA = no data available.