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Vicariance and dispersal in southern hemisphere freshwater fish clades: a palaeontological perspective

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ABSTRACT

Widespread fish clades that occur mainly or exclusively in fresh water represent a key target of biogeographical investigation due to limited potential for crossing marine barriers. Timescales for the origin and diversification of these groups are crucial tests of vicariant scenarios in which continental break-ups shaped modern geographic distributions. Evolutionary chronologies are commonly estimated through node-based palaeontological calibration of molecular phylogenies, but this approach ignores most of the temporal information encoded in the known fossil record of a given taxon. Here, we review the fossil record of freshwater fish clades with a distribution encompassing disjunct landmasses in the southern hemisphere. Palaeontologically derived temporal and geographic data were used to infer the plausible biogeographic processes that shaped the distribution of these clades. For seven extant clades with a relatively well-known fossil record, we used the stratigraphic distribution of their fossils to estimate confidence intervals on their times of origin. To do this, we employed a Bayesian framework that considers non-uniform preservation potential of freshwater fish fossils through time, as well as uncertainty in the absolute age of fossil horizons. We provide the following estimates for the origin times of these clades: Lepidosireniformes [125–95 million years ago (Ma)]; total-group Osteoglossomorpha (207–167 Ma); Characiformes (120–95 Ma; a younger estimate of 97–75 Ma when controversial Cenomanian fossils are excluded); Galaxiidae (235–21 Ma); Cyprinodontiformes (80–67 Ma); Channidae (79–43 Ma); Percichthyidae (127–69 Ma). These dates are mostly congruent with published molecular timetree estimates, despite the use of semi-independent data. Our reassessment of the biogeographic history of southern hemisphere freshwater fishes shows that long-distance dispersals and regional extinctions can confound and erode pre-existing vicariance-driven patterns. It is probable that disjunct distributions in many extant groups result from complex biogeographic processes that took place during the Late Cretaceous and Cenozoic. Although long-distance dispersals shaped the distributions of several freshwater fish clades, their exact mechanisms and their impact on broader macroevolutionary and ecological dynamics are still unclear and require further investigation.

Key words: historical biogeography, vicariance, long-distance dispersal, freshwater fishes, evolutionary timescales, palaeontology, fossil record.

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I. INTRODUCTION

Freshwater fishes are a fundamental component of the biosphere, constituting more than 20% of living vertebrate species (Nelson, Grande & Wilson, 2016). Extant freshwater fish clades with intercontinental, disjunct distributions have long been model systems in historical biogeography, as seas and oceans represent a relatively strong barrier to their dispersal (Lundberg, 1993).

Continental vicariance driven by Mesozoic breakup of Pangaea is a widely cited explanation for these disjunct distributions (e.g. Novacek & Marshall, 1976; Parenti, 1981; Greenwood, 1983; Chakrabarty, 2004; Sparks & Smith, 2005; Inoue *et al.*, 2009). Alternative scenarios involve more recent long-distance dispersals, *via* land (through transient land bridges or after continental collision) or sea. Despite obvious challenges, trans-oceanic dispersal has been increasingly proposed as the probable mechanism underlying the intercontinental distributions of several terrestrial and freshwater groups (e.g. de Queiroz, 2005; Poux *et al.*, 2006; Pramuk *et al.*, 2008; Samonds *et al.*, 2012), including some freshwater fish clades (Lundberg, 1993; McDowall, 2002; Bonde, 2008; Friedman *et al.*, 2013). Time is the critical variable in testing whether distributions matching those predicted by vicariance arose by this mechanism (Upchurch & Hunn, 2002; Donoghue & Moore, 2003). Vicariance can be ruled out if lineages with a disjunct distribution are too young to have been influenced by the corresponding geologic event (e.g. breakup between South America and Africa for a clade inhabiting both continents).

Traditionally, fossils and their stratigraphic context have been the only source of information on evolutionary timescales relevant to vicariance hypotheses. In the last 20 years, advances in molecular clock methods have revolutionized the field of evolutionary biology (Ho & Duchêne, 2014), and construction of a molecular time-calibrated tree is now the conventional approach for timing evolutionary events. However, fossils remain the principal source of time calibration for molecular trees, requiring a thorough understanding of the fossil record in order to select calibrations and appropriate parameters properly for timetree analysis (Parham *et al.*, 2012). Alternative methods for estimating the time of origin of a group rely only on palaeontological and stratigraphic data (Strauss & Sadler, 1989; Marshall, 1997; Hedman, 2010), but are used less frequently than molecular clocks.

Herein, we consider existing fossil and molecular evidence for the evolutionary timescale of freshwater fish clades with a widespread disjunct distribution that includes southern hemisphere landmasses. We use phylogenetic and palaeobiogeographic information to infer possible biogeographic patterns for these clades, and to evaluate whether vicariance associated with the Mesozoic breakup of Gondwana, dispersal, or both shaped their geographic distribution. We excluded taxa with a distribution limited to the northern hemisphere, as during the Mesozoic and Cenozoic North America and Eurasia were often connected by transient land bridges (e.g. the Beringian and Thulean land bridges; Brikiatis, 2014, 2016). Biotic exchanges between former Laurasian landmasses were relatively common in the late Mesozoic and Cenozoic and involved several freshwater fish taxa (see Cavin, 2017), including sturgeons (Choudhury & Dick, 1998), bowfins (Grande & Bemis, 1998), cypriniforms (Imoto *et al.*, 2013) and pikes (Grande, 1999).

While we cover both extant taxa with no (or limited) fossil record (Section II.1) and extinct taxa known only from the fossil record (Section II.2), particular attention is given to seven extant freshwater fish clades with more extensive fossil records: Lepidosireniformes (South American and African lungfishes), Osteoglossomorpha (bonytongues and allies), Characiformes (characins and allies), Galaxiidae, Cyprinodontiformes (killifishes), Channidae (snakeheads) and Percichthyidae (Southern temperate perches). Most of these groups (with the notable exceptions of galaxiids and cyprinodontiforms) are usually classified as primary division freshwater fishes (Myers, 1938), an ecological term indicating low tolerance to salinity. Although widely used, Myers' (1938) classification of freshwater fishes is purely qualitative, has no bearing on ancestral environmental adaptations (i.e. whether a group of freshwater fishes derives from freshwater or marine ancestors) and does not necessary reflect the dispersal abilities of a fish clade.

For the seven focal clades listed above, we used the temporal distribution of their fossil record quantitatively to estimate their origin times, building upon the theoretical framework developed by Marshall (1997). This method utilizes an empirically derived fossil preservation potential function to assess, for a given taxon, the plausible extent of an early evolutionary history undetected by its fossil record (in other words, how much older than its oldest known fossil can a taxon plausibly be). By so doing, it accounts for non-uniform fossil preservation in time. Furthermore, we modified the method to consider uncertainty in the absolute age of fossil-bearing deposits. The origin-time estimates derived with this method were then compared with the timescale of Gondwanan fragmentation to test for vicariant scenarios, and with published molecular estimates to check for congruency or discrepancy.

II. FRESHWATER FISH CLADES WITH INTERCONTINENTAL DISTRIBUTIONS

(1) Extant taxa with disjunct distributions and no (or limited) fossil record

Biogeographic hypotheses for clades with limited palaeontological records are generally assessed through phylogenies that are time-calibrated with fossils of other groups. Many freshwater fish clades with disjunct distributions fall under this category.

(*a*) *Mordaciidae and Geotriidae*

Southern hemisphere lampreys inhabit southern South America and southern Oceania. The four species in these groups are either anadromous or secondarily restricted to freshwater (Potter *et al.*, 2015), suggesting high dispersal potential. Indeed, the monotypic *Geotria* inhabits river systems throughout southern South America, New Zealand and southern Australia, making it one of the most widespread freshwater fishes (Berra, 2007). The unresolved phylogenetic position of *Geotria* relative to mordaciids and northern hemisphere lampreys (Potter *et al.*, 2015) and the lack of published timetrees for lampreys preclude further testing of biogeographic scenarios.

(*b*) *Atheriniformes*

Within atheriniforms (silversides), the Malagasy Bedotiidae is closely aligned to an Australasian group including Melanotaeniidae, Pseudomugilidae and Telmatherinidae. This relationship has been interpreted as evidence of Cretaceous vicariance between Indo-Madagascar and Austro-Antarctica (Sparks & Smith, 2004). However, fossil-calibrated phylogenies identify an Eocene divergence between bedotiids and Australasian taxa (Campanella *et al.*, 2015), contradicting the vicariant hypothesis. Many silverside clades show repeated freshwater invasions by marine ancestors, and the last common ancestor of bedotiids and the Australasian clades was likely marine or at least euryhaline. Marine dispersal followed by freshwater invasion better explains the biogeographic pattern seen in this group (Campanella *et al.*, 2015).

(*c*) *Synbranchidae*

Swamp eels occur in fresh and brackish waters of Central and South America, West Africa, East Asia, Indo-Malaysia and northern Oceania. Many synbranchids show broad salinity tolerance, and air breathing allows extensive survival out of water (Graham, 1997). Relationships within synbranchids are poorly known (Rosen & Greenwood, 1976). Nonetheless, a latest Cretaceous divergence of synbranchids from their closest living relatives (Near *et al.*, 2013) and the intercontinental distributions of *Monopteros* and *Ophisternon* (Rosen & Greenwood, 1976) imply multiple long-distance dispersal events.

(*d*) *Mastacembelidae*

Spiny eels inhabit Indo-Malaysia and Africa, with one species restricted to the Middle East. Phylogenetic analyses support an Indo-Malayan origin for mastacembelids, followed by dispersal to the Middle East and from there to Africa during the Miocene (Day *et al.*, 2017). This is congruent with the African invasion of several Asian mammals starting around 18 million years ago (Ma) (Koufos, Kostopoulos & Vlachou, 2005).

(*e*) *Anabantidae*

Climbing gouramies contain the Indo-Malayan *Anabas* and three African genera. *Anabas* can tolerate long periods of air exposure, move on land, and traverse small obstacles (Davenport & Abdul Matin, 1990; Graham, 1997). A single fossil anabantid, *Eoanabas thibetana*, is known from late Oligocene deposits of central Tibet (Wu *et al.*, 2017). The basal position of *Eoanabas* and *Anabas* within anabantids, as well as their affinity to several freshwater clades endemic to Southeast Asia (Betancur-R *et al.*, 2017), implies an Indo-Malayan origin. Anabantid dispersal from Asia to Africa probably occurred during the second half of the Paleogene (Rüber, Britz & Zardoya, 2006).

(*f*) *Polycentridae*

Polycentrids include African and South American leaffishes. Collins, Britz & Rüber (2015) resolved the South American leaffishes as a clade within African leaffishes. There is no time-calibrated phylogenetic analysis targeting polycentrids, but more inclusive timetrees suggest an Eocene divergence between South American leaffishes and the African *Polycentropsis* (Near *et al.*, 2013). This would imply transoceanic dispersal from Africa to South America in the Paleogene, paralleling the well-known cases of monkeys and caviomorph rodents (Poux *et al.*, 2006).

(*g*) *Gobioidei*

Among gobies, multiple lineages with marine ancestors colonized freshwater environments. Some of these (e.g. Milyeringidae, Butidae, Eleotridae, Sicydiinae) display disjunct intercontinental distributions. The fossil record of gobies extends to the early Eocene (Bannikov & Carnevale, 2016). However, the uncertain systematic position of early fossil gobies prevents an accurate estimate of the goby evolutionary timescale based exclusively on fossils (Bannikov & Carnevale, 2016). Molecular clock estimates indicate that crown gobies are Late Cretaceous–Paleocene in age (Alfaro *et al.*, 2018; Li *et al.*, 2018). Among goby lineages with intercontinental distribution in freshwater environments, butids and eleotrids can thrive in a wide range of salinities, with some species inhabiting coastal marine habitats (Berra, 2007). Thus, marine dispersal is a likely explanation for their widespread distribution. Sycidiines have an amphidromous life cycle. Molecular data suggest a late Miocene origin in the western Pacific Ocean and arrival in Africa and the New World through current-driven westward marine dispersal (Keith *et al.*, 2011). The most striking case is that of the blind cave gobies belonging to Milyeringidae, which includes two genera of obligate troglobic fishes: the Malagasy *Typhleotris* and Australian *Milyeringa* (Chakrabarty, Davis & Sparks, 2012). Chakrabarty *et al.* (2012) proposed a vicariant scenario with an Early Cretaceous origin of this group, but their molecular estimate for the divergence between *Typhleotris* and *Milyeringa* ranges from the Early Cretaceous to the Eocene. An Early Cretaceous origin for a goby subclade is in stark contrast not only with the known fossil record of gobies, but also with the fossil record of acanthomorphs as a whole (Patterson, 1993). More recent studies place the origin of milyeringids firmly within the Cenozoic (Li *et al.*, 2018). Although a recent milyeringid origin would imply at least one long-distance dispersal event between Madagascar and Australia, such an event seems highly unlikely for troglobites with marked physiological limitations and very restricted habitat (Chakrabarty *et al.*, 2012). The possibility of two independent invasions of the subterranean environment from extinct marine or brackish ancestors, followed by independent acquisition of characters typical to troglobic organisms (loss of functional eyes, loss of pigmentation, and so on), cannot be excluded and could explain the striking biogeographic pattern displayed by milyeringids. However, the lack of milyeringid fossils precludes further assessment of this hypothesis.

(2) Fossil taxa with disjunct distributions

Several cases of disjunct distributions in freshwater fishes are known exclusively from the fossil record. These fall into two broad categories: widespread extinct clades; or extant clades with present distribution restricted to only one landmass, but for which fossils are found on multiple continents. Most cases discussed here are associated with the opening of the South Atlantic, as Mesozoic and early Cenozoic freshwater deposits of South America and Africa are much better sampled than those of other southern landmasses.

(*a*) *†Mawsoniidae*

Mawsoniids represent a primarily continental radiation of Mesozoic coelacanths. †*Mawsonia* and †*Axelrodichthys* have been found in South American and African deposits spanning from the Early Cretaceous to the Cenomanian (de Carvalho & Maisey, 2008). Persistence of these mawsoniid genera in South America and Africa during opening of the South Atlantic suggests vicariance. Post-Cenomanian mawsoniids are known only from Europe and Madagascar (Gottfried, Rogers & Rogers, 2004; Cavin, Valentin & Garcia, 2016), hinting at possible dispersals from Africa in the Late Cretaceous. Cretaceous mawsoniids are often found in brackish deposits and thus they could have had relatively high salinity tolerance and long-distance dispersal potential.

(*b*) *Polypteridae*

Bichirs are an exclusively freshwater clade of early diverging actinopterygians that today occurs only in Africa, where their fossil record extends back to the Cenomanian (Gayet, Meunier & Werner, 2002; Grandstaff *et al.*, 2012; Cavin *et al.*, 2015; Cavin, 2017). Fragmentary polypterid remains from the Maastrichtian and Paleocene of Bolivia reveal a more widespread distribution of this group in the past (Gayet *et al.*, 2002). Undescribed polypterid material from the Albian–Cenomanian Alcântara Formation of Brazil (Candeiro *et al.*, 2011) suggests polypterid presence in South America pre-dating South America–Africa breakup. However, the lack of a phylogenetic framework for fragmentary fossil polypterids precludes a reliable reconstruction of their biogeographic history. The recent recognition of scanilepiforms – known from Triassic freshwater deposits of North America and Eurasia – as stem polypterids (Giles *et al.*, 2017) suggests a Pangean distribution in the early Mesozoic, followed by vicariance and regional extinctions.

(*c*) *Lepisosteidae*

Gars, like the only other extant holostean lineage (the bowfin *Amia*), are now restricted to North America. Lepisosteids have a broad Late Cretaceous distribution, with North American, South American, European, Central Asian, African, Malagasy and Indian deposits yielding gar fossils of this age (Grande, 2010). The majority of the Late Cretaceous lepisosteid material is fragmentary and diagnostic only to family, so biogeographic scenarios are difficult to reconstruct. While extant gars are mainly freshwater fishes and most fossils are found in continental deposits, some living species are occasionally found in brackish and coastal marine environments (notably *Atractosteus tristoechus*, the Cuban gar; Grande, 2010). Moreover, the discovery of early lepisosteids in Late Jurassic marine deposits from Mexico (Brito, Alvarado-Ortega & Meunier, 2017) suggests that high salinity tolerance might be primitive for the group. Marine dispersal probably played a major role in the widespread distribution of lepisosteids during the Cretaceous.

(*d*) *†Obaichthyidae and other lepisosteoids*

Obaichthyids are the sister taxon to Lepisosteidae and consist of two Aptian–Cenomanian genera: †*Obaichthys* and †*Dentilepisosteus*. Like mawsoniid coelacanths, both genera are present in Brazilian and Moroccan continental and transitional deposits (Grande, 2010), suggesting vicariance during late stages of the opening of the South Atlantic. A similar pattern can be inferred for the basal lepisosteoids †*Araripelepidotes* and †*Pliodetes* from the Aptian of Brazil and Niger, respectively, which might be sister lineages (Cavin, 2010).

(*e*) *†Vidalamiinae*

Vidalamiins are a Cretaceous–early Paleogene clade of amiids closely related to the extant bowfin *Amia*. Within vidalamiins, †Calamopleurini occurs only in western Gondwana while †Vidalamiini has a broader distribution including North America, South America, Europe and the Middle East (Grande & Bemis, 1998; Brito, Yabumoto & Grande, 2008). While the geographic and temporal distribution of calamopleurine fossils is consistent with vicariance related to the rifting of South America and Africa, the biogeographic history of Vidalamiini appears more complex and likely involved marine dispersals. Vidalamiin fossils derive from continental and coastal marine deposits, and several species were likely euryhaline (Grande & Bemis, 1998).

(*f*) *†Archaeomenidae and †Luisiellidae*

Archaeomenids and luisiellids are poorly known freshwater stem teleost groups with a southern Gondwanan distribution (Sferco, López-Arbarello & Báez, 2015; Bean, 2017). The age of these taxa (†Archaeomenidae: Early Jurassic–Early Cretaceous; †Luisiellidae: Late Jurassic–Early Cretaceous) is consistent with a continuous Jurassic range encompassing South America, Antarctica and Australia [but see Su (1994) for a putative archaeomenid from the Early Jurassic of China].

(*g*) *†Cladocyclidae*

Cladocyclids include freshwater, brackish and coastal forms belonging to the primarily marine ichthyodectiforms, a clade of predatory stem teleosts. †*Cladocyclus* and †*Chiromystus* are both known from the Early–middle Cretaceous of South America and Africa (Martill *et al.*, 2011; Cavin, Forey & Giersch, 2013), paralleling the pattern seen in mawsoniids, obaichthyids and vidalamiins. Additionally, †*Cladocyclus* is known from Albian continental deposits of Australia (Berrell *et al.*, 2014) and possibly Italy (Signore *et al.*, 2006). As cladocyclids are often found in lagoonal and coastal marine deposits, at least some species were probably euryhaline. Thus, their palaeobiogeographic distribution may have been shaped by a combination of dispersal and vicariance.

(*h*) *Chanidae*

Milkfishes, an ostariophysan clade, include the living marine *Chanos chanos* and several extinct species, with some found in continental and transitional deposits. †*Dastilbe* and †*Parachanos* are of particular interest. These are found in Aptian–Albian deposits of Brazil and Central Africa, respectively (Fara, Gayet & Taverne, 2010), and could be sister taxa (Near, Dornburg & Friedman, 2014). †*Dastilbe batai* from the Aptian–Albian of Equatorial Guinea is poorly preserved and may belong to the genus †*Parachanos* (Dietze, 2007). Thus, the palaeobiogeographic distribution of †*Dastilbe* and †*Parachanos* at the end of the Early Cretaceous is consistent with vicariance associated with opening of the South Atlantic. Notably, †*Parachanos* is also known from Late Cretaceous deposits of Italy and Croatia (Fara *et al.*, 2010); long-distance dispersal from Africa could explain the post-Albian European distribution of this taxon, similar to mawsoniid coelacanths. Another freshwater chanid, †*Nanaichthys* from the Aptian of Brazil, reveals a possible trans-Tethyan dispersal event during the Early Cretaceous, as this genus appears to be closely related to the Berriasian–Barremian †*Rubiesichthys* and †*Gordichthys* from Spain (Amaral & Brito, 2012).

(3) Extant taxa with disjunct distributions and known fossil record

Evolutionary timescales, and associated biogeographic scenarios, for geographically widespread extant clades can be assessed by both molecular timescales and the temporal and geographic distribution of their fossils. Seven of these clades are covered in detail herein: Lepidosireniformes, Osteoglossomorpha, Characiformes, Galaxiidae, Cyprinodontiformes, Channidae and Percichthyidae (Fig. 1). For these taxa, we reviewed their fossil record focusing on biogeographically relevant fossils. Then, we used the stratigraphic distribution of their fossils to infer times of evolutionary origin in a Bayesian framework. Finally, biogeographic scenarios involving vicariance and dispersal were evaluated on the basis of our fossil-based estimates and published molecular timetrees.

We did not include three clades prominently featured in the historical biogeography literature: Dipnoi, Siluriformes and Cichlidae. These groups (and the reasons for exclusion from this review) will be briefly discussed here.

Dipnoi (crown lungfishes) includes Lepidosireniformes (South American *Lepidosiren* and African *Protopterus*) and Ceratodontiformes (the Australian *Neoceratodus*). Crown lepidosireniforms are discussed below in the context of the split between South America and Africa, but the early biogeographic history of crown lungfishes has been linked to vicariance and the progressive fragmentation of Gondwana (Cavin *et al.*, 2007). The relationships of several Mesozoic lungfish genera relative to extant ones are still debated, leading to considerable uncertainty for the age of the dipnoan crown. Some phylogenetic studies recover all extinct Mesozoic genera as stem lungfishes, placing the origin of crown lungfishes in the Late Jurassic (Schultze, 2004). By contrast, other analyses find several early Mesozoic genera (e.g. †*Ceratodus*, †*Arganodus*, †*Asiatoceratodus* and †*Gosfordia*) within the lungfish crown (Cavin *et al.*, 2007; Longrich, 2017). It has even been suggested that Permian lungfishes like †*Gnathorhiza* may be more closely related to Lepidosireniformes than to *Neoceratodus* (Kemp, Cavin &

Guinot, 2017), placing the minimum age for the origin of crown lungfishes to around 300 Ma. The identification of Triassic or Permian lungfishes as stem lepidosireniforms, coupled with their widespread geographic distribution, would strongly suggest a Gondwanan (if not Pangean) distribution of early crown lungfishes, followed by a series of vicariant events and local extinctions (Cavin *et al.*, 2007). Little effort has been put into the development of a precise timescale for lungfish evolution from a molecular clock perspective, with recent estimates for crown lungfishes ranging from the Permian to the Late Jurassic (Irisarri *et al.*, 2017). Because of the uncertain affinities of early Mesozoic lungfish genera, we do not estimate the age of crown lungfishes using quantitative biostratigraphical models here. However, lepidosireniforms are considered in this framework below.

Siluriformes (catfishes) is a major clade of globally distributed otophysans that includes several thousand species. While phylogenetic analyses strongly support the South American endemics Loricarioidei and Diplomystidae as the earliest branching lineages in the siluriform tree (implying a South American origin for the group), deep-level relationships among other siluriforms – collectively grouped in Siluroidei – remain largely unknown (Betancur-R *et al.*, 2017). It is therefore not easy to identify biogeographically relevant nodes in the siluriform phylogeny (i.e. nodes corresponding to disjunct intercontinental distributions). The siluriform fossil record extends to the Late Cretaceous of South America (Gayet, 1990). However, these early fossils are fragmentary and cannot be confidently assigned to any extant lineage. Because of the uncertainties in siluriform systematics and in the affinities of the earliest siluriform fossils, we refrain from discussing the siluriform fossil record and biogeography in detail here. However, there are indications of long-distance dispersal in siluriform evolutionary history. First, several lineages of catfishes are adapted to high-salinity environments, with Ariidae and Plotosidae including mostly coastal marine species (Berra, 2007). Specifically, ariids recolonized freshwater environments after marine dispersal several times during their history, achieving a worldwide distribution in tropical fresh waters (Betancur-R, 2010). More remarkably, molecular phylogenetics resolves the recently discovered *Lacantunia enigmatica* from Mexico as deeply nested within a diverse group of African catfishes (the ‘Big Africa’ clade) with strong statistical support (Lundberg *et al.*, 2007). Molecular clock studies place origin of the ‘Big Africa’ clade during the Late Cretaceous (Lundberg *et al.*, 2007). Thus, the presence of a member of this radiation in Mexico requires a biogeographic scenario that involves complex dispersal routes (Lundberg *et al.*, 2007). A better understanding of siluriform historical biogeography will depend on the resolution of their deep-level phylogeny and on further analysis of the early fossil record of catfishes.

Cichlidae (cichlids) is a model system for several fields in evolutionary biology, including historical biogeography. The ‘Gondwanan’ geographic distribution of cichlids (which includes the Neotropics, Africa, Madagascar and the Indian subcontinent) has been the focus of considerable attention among biogeographers. The topological congruence between cichlid phylogeny and Gondwanan fragmentation (with the Malagasy and Indian lineages branching first and the African clade being sister group to the South American one) has been often interpreted as evidence for vicariance (Chakrabarty, 2004; Sparks & Smith, 2005). However, this argument does not take into account the timescale of cichlid evolution, which would be necessary to test a vicariant hypothesis. Topological patterns that appear to be consistent with a vicariant scenario may arise from dispersal events, a phenomenon called pseudo-congruence (Donoghue & Moore, 2003). Most recent molecular-clock studies agree on a Late Cretaceous–Paleocene origin of crown cichlids, inconsistent with the vicariant scenario (Friedman *et al.*, 2013; Matschiner *et al.*, 2017). Matschiner (in press) reviews more than 15 years of cichlid molecular-clock studies and their implications for the group's biogeographic history. The oldest cichlid fossils are relatively recent, from middle Eocene deposits of Africa and South America (Murray, 2000*a*; Malabarba, Malabarba & López-Fernández, 2014). However, their derived anatomy suggests that a long portion of the early cichlid fossil record might be missing. Friedman *et al.* (2013) estimated the timing of cichlid origin based on the temporal distribution of their fossil record, using a comparable methodology to that applied here (see Section III). They found that, even when accounting for non-uniform fossil preservation through time, the estimated time of origin only extends to the Late Cretaceous (Campanian), around 77 Ma. While Friedman *et al.* (2013) refer to this estimate as the age for crown cichlids, it more conservatively marks divergence between South American and African cichlids, as every known cichlid fossil belongs to either Cichlinae (the Neotropical cichlid clade) or Pseudocrenilabrinae (the African cichlid clade). Nonetheless, even a Campanian age for the split between cichlines and pseudocrenilabrines would reject the hypothesis of vicariance and suggest a transatlantic dispersal event in the early history of cichlids. Because of the amount of literature discussing vicariance and dispersal in cichlid biogeography under several different approaches, we do not consider this group in more detail here.

III. MATERIALS AND METHODS

(1) Estimation of origin times of focal clades using their fossil occurrences

We derived fossil-based estimates of the dates of origin for the seven fish groups mentioned above (Lepidosireniformes, Osteoglossomorpha, Characiformes, Galaxiidae, Cyprinodontiformes, Channidae and Percichthyidae) and for some of their sub-clades. Our method is based on the number and distribution through time of known stratigraphic horizons that yielded fossils belonging the group of interest. This approach builds upon the theoretical framework developed by Marshall (1997), which accounts for non-uniform fossil preservation and recovery through time by using an empirically derived function of recovery potential. We combined this framework with the Bayesian probability estimate for the extension of observed stratigraphic ranges developed by Strauss & Sadler (1989) to calculate 95% credibility intervals (CIs) for the origin times of focal clades.

(*a*) *Bayesian probability estimate for the extension of observed stratigraphic ranges*

Strauss & Sadler (1989) were the first to propose a Bayesian estimate for stratigraphic CIs for a given focal group. They derived the posterior density function of the endpoint θ of a stratigraphic range given the data x as:

$$h(\theta|x) = \frac{(n-2)[(\theta-y)^{-n+1} - \theta^{-n+1}]}{u_n} \qquad [1]$$

where y is the age of the last observed fossil (last appearance datum), n is the number of fossil horizons and u_n is a factor calculated by the equation:

$$u_n = (z-y)^{-n+2} - (1-y)^{-n+2} - z^{-n+2} + 1 \qquad [2]$$

with z being the age of the first observed fossil (first appearance datum). The posterior density function given above is valid for each θ larger than z and smaller than a prior upper bound; θ, y and z are rescaled to have the prior upper bound equal to 1. This formula assumes a uniform prior distribution of the fossil horizons bounded between 0 and 1, a condition that is almost always violated by the empirical fossil record.

The Bayesian point estimator of θ [that is, the mean of Equation (1)] is given by:

$$\frac{(n-2)u_{n-1}}{(n-3)u_n} + \frac{y[(z-y)^{-n+2} - (1-y)^{-n+2}]}{u_n} \qquad [3]$$

(*b*) *Extension to non-random distributions of fossil horizons*

In order to relax the strong assumption of uniform distribution of fossil horizons, we utilized the logical framework, introduced by Marshall (1997), of a preservation and recovery potential function. Marshall (1997) extended the use of stratigraphic confidence intervals for non-random distributions of fossil horizons by reframing the problem in terms of recovery potential rather than time. Given a function representing preservation and recovery potential over time, the area under this function between the age of the first observed fossil and the age of the last observed fossil corresponds to the duration of the focal clade (in units of preservation potential). The confidence limit for the origin time of this clade is the point at which the area under the preservation potential function between the first appearance and that point is equal to the duration of the lineage in units of preservation potential multiplied by a scaling factor that reflects the number of distinct fossil occurrences and the desired level of confidence.

Friedman *et al*. (2013) applied this framework to Strauss & Sadler's (1989) Bayesian estimate to account for heterogeneity through time in the fossil record of freshwater fishes. They measured θ, y and z of Equations (1–3) in terms of summed preservation potential and not in terms of time. In order to calculate the area under the preservation potential function easily, geological time was divided into time bins, with each bin being assigned a value equal to the proportion between the number of fossil horizons that yielded fossils of the group of interest and the total number of fossil horizons. Doing this, a uniform distribution of fossil horizons is assumed only within each time bin, and not throughout the entire fossil record. Posterior distributions, Bayesian point estimates and 95% CIs were then calculated in terms of accrued preservation potential, and later converted in terms of absolute time in light of their empirical function for preservation potential.

Herein, we applied the same method employed in Friedman *et al*. (2013) with a few adjustments. We corrected the script of Friedman *et al*. (2013) by adding a term that was missing in their calculation of u_n [Equation (2)]. However, we ascertained that this had no significant effect on the results, as that term is several orders of magnitude smaller than the resulting origin time estimate. We also employed a different empirical preservation potential function, the main difference being the use of time bins of 1 million years (Myr) each rather than corresponding to chronostratigraphic epochs (see Section III.3). Finally, we considered uncertainty in the absolute age of fossil horizons.

(*c*) *Extension to uncertain absolute age of fossil horizons*

Uncertainty in the absolute age of fossil horizons was considered by generating 1000 replicates for each Bayesian time-estimate analysis. In each replicate, every horizon was assigned an age randomly drawn from a uniform distribution bounded by minimum and maximum age of the chronostratigraphic stage (or stages) corresponding to that horizon. The absolute ages for chronostratigraphic epochs and stages were taken from the ICS International Chronostratigraphic Chart (v. 2016/12). Median and two-tailed 95% confidence intervals for the Bayesian estimates on origin times (summarized by their 95% CIs) were then calculated among the replicates.

(2) Assembly of fossil occurrence data sets

Fossil occurrences for the seven focal clades were compiled through a comprehensive literature search (see online Supporting information, Tables S1–S7). Different stratigraphic formations (or localities in cases of no formalized stratigraphy) were treated as different sampling horizons. The age of each horizon (to stage level, when possible) was assigned according to the literature. Marine fossil occurrences of the focal clades were pruned from the analysis, as accounting for marine deposits throughout the fossil record could heavily bias the recovery potential function.

(3) Estimation of the empirical recovery potential function

The recovery potential function used to account for non-uniformity in fossil preservation and recovery through time was derived empirically using a list of stratigraphic horizons (formations and/or localities) with the potential to yield fossils belonging to the group of interest. For every freshwater fish clade analysed here, this criterion was satisfied by non-marine deposits that yielded fish fossils. A list of non-marine deposits that yielded fish fossils was compiled through a literature search and implemented with records from the Paleobiology Database (PBDB; https://paleobiodb.org). The beginning of the Permian (around 299 Ma) was chosen as the upper limit for the age of fossil horizons: this represents the prior upper bound on the Bayesian estimates for the origin times of the focal clades. This is a conservative prior, as it does not artificially exclude vicariance scenarios; moreover, the oldest fossils belonging to the analysed clades come from the Middle Jurassic (around 167 Ma). Although some molecular clock estimates place the origin of total-group Osteoglossomorpha in the Carboniferous (e.g. Inoue *et al.*, 2009), a Carboniferous origin for any crown-teleost clade is in strong disagreement with the fossil record (Arratia, 2015; Friedman, 2015).

The list of non-marine fossil fish deposits comprised a total of 935 unique horizons, ranging from the early Permian to the Holocene (Table S8). Fossil horizons were subdivided into seven broad, continental-scale geographic areas (North and Central America; South America; Europe and Western Asia; Africa and Arabian Peninsula; Northeastern Asia; Indo-Malaya; Oceania). For each clade, only fossil horizons from relevant geographic areas (i.e. areas in which the clade is either present today or was present in the past according to the fossil record) were included (Table 1). The discrete recovery potential function was built by dividing geologic time into bins of 1 Myr each, with every bin being assigned a value equal to the total number of fossil horizons present in that time interval. In so doing, uniform recovery potential was assumed within each time bin.

All calculations were performed in R version 3.4.1 (R Core Team, 2017). The script is available as Appendix S1.

IV. RESULTS AND DISCUSSION

Table 2 summarizes the ages of origin of the freshwater fish clades considered here, as estimated from the stratigraphic distribution of fossil occurrences. Range estimates encompass uncertainty in fossil horizon age (i.e. they span from the lower confidence interval of the lower CI of the posterior distribution to the upper confidence interval of the upper CI of the posterior distribution).

Results for seven focal clades are discussed below in the context of their fossil record and geographic distribution. Comparisons with molecular timescales permit a comprehensive view of the biogeographic history for each group at a continental scale.

(1) Lepidosireniformes (South American and African lungfishes)

Lepidosireniformes (*sensu* Otero, 2011) includes two living genera, the South American *Lepidosiren* (one extant species) and the African *Protopterus* (four extant species). Molecular and morphological data support monophyly of the group (e.g. Betancur-R *et al.*, 2013; Criswell, 2015). Lepidosireniform fossils comprise mainly tooth plates and jaw fragments, with some exceptions (Table S1) (Silva Santos, 1987). Crown lepidosireniforms are distinguished on the basis of tooth plate characters (Otero, 2011; Longrich, 2017). Like modern species, fossils of the group are restricted to South America and Africa (Fig. 2). The oldest fossils of *Lepidosiren* derive from the Late Cretaceous El Molino Formation (Maastrichtian of Bolivia; Schultze, 1991) and Vilquechico Formation (?Coniacian–Maastrichtian of Peru; Arratia & Cione, 1996). †*Protopterus nigeriensis* from the Cenomanian Wadi Milk Formation of Sudan might represent the oldest African crown lepidosireniform (Claeson *et al.*, 2014). However, Longrich (2017) did not find conclusive evidence for assigning this species or other Late Cretaceous–Eocene African fossils to *Protopterus*, and it is not clear whether they belong within the lepidosireniform crown. Leaving aside possible polyphyly of the genus (when including fossils), *Protopterus* is represented in the African record by up to eight different species (six extinct) and hundreds of specimens without specific attribution, ranging from the Late Cretaceous to the Holocene (Otero, 2011).

Extant *Protopterus* and *Lepidosiren* are strictly freshwater (Berra, 2007) and deposits yielding fossils of these genera are generally freshwater or estuarine (Cavin *et al.*, 2007). Past work cites these environmental associations as supporting a vicariant model for the South American–African distribution of Lepidosireniformes (Lundberg, 1993; Otero, 2011). The early Late Cretaceous age of the first crown lepidosireniform fossils is consistent with vicariance. Some Mesozoic (and many Paleozoic) lungfishes outside Lepidosireniformes are known from marine deposits, leading some to hypothesize primitive marine habits and independently acquired freshwater adaptations among the living lungfish genera (Schultze, 1991). However, most (if not all) of the marine Mesozoic fossils probably represent remains of freshwater animals that have been reworked into marine deposits (Cavin *et al.*, 2007).

(*a*) *Fossil-based estimate of origin times*

The origin of crown Lepidosireniformes is hereby estimated to occur between the Aptian and the Cenomanian (124.9–95.1 Ma; median point estimate: 103.5 Ma); this overlaps with fragmentation of Western Gondwana (South America + Africa; Heine, Zoethout & Müller, 2013). Our fossil-based age estimate is consistent with molecular divergence times between *Protopterus* and *Lepidosiren* (estimates centered around 112–96 Ma; Broughton *et al.*, 2013; Giles *et al.*, 2017). The limited suite of dental characters used for the systematics of extinct lepidosireniforms results in some ambiguity in the placement of some fossil remains. The possible exclusion of Late Cretaceous taxa like †*Protopterus nigeriensis* from the genus *Protopterus* (Longrich, 2017) could strongly impact the fossil-based estimate of the age of origin for the group, making it substantially younger. Nonetheless, the currently known timescale for lepidosireniform origin and evolution (based on fossil and molecular data) does not reject the vicariance hypothesis. The disjunct distribution of extant Lepidosireniformes can probably be considered as the genuine product of an ancient vicariant event.

(2) Osteoglossomorpha (bonytongues and allies)

Osteoglossomorpha is one of the earliest diverging lineages of modern teleosts (Arratia, 1999; Near *et al.*, 2012), comprising 246 living species distributed across the Americas, Africa, the Indo-Malayan region and Australia (Nelson *et al.*, 2016). The osteoglossomorph fossil record is rich (Table S2), with more than 80 extinct species, and expands the present distribution of the group to Europe and Northeastern Asia (Wilson & Murray, 2008) (Fig. 3).

Morphological and molecular data strongly support osteoglossomorph monophyly, but interpretations of intrarelationships (reviewed in Hilton, 2003) have changed considerably over time. Current classifications recognize six main lineages (Nelson *et al.*, 2016): Hiodontiformes (the sister group to all other living osteoglossomorphs; Hilton, 2003), Pantodontidae, Notopteridae, Gymnarchidae, Mormyridae and Osteoglossidae (grouped together as Osteoglossiformes).

The oldest articulated osteoglossomorph fossils belong to †*Paralycoptera* and derive from the Late Jurassic Lai Chi Chong Formation of Hong Kong and Fenshuiling Formation of Shandong, China (Tse, Pittman & Chang, 2015). The phylogenetic placement of †*Paralycoptera* is uncertain. Some analyses place it on the osteoglossomorph stem (Wilson & Murray, 2008) and others recover it as a crown osteoglossiform (Li & Wilson, 1999; Zhang, 2006). Fossil squamules from the Anoual Formation of Morocco could push back the earliest osteoglossomorph occurrence in the fossil record to the Middle Jurassic (early Bathonian; Haddoumi *et al.*, 2016). The otolith-based genus †*Archaeglossus* (Schwarzhans, 2018) from the marine Middle–Late Jurassic of England might also represent an early osteoglossomorph. The presence of early Mesozoic osteoglossomorphs in marine sediments would not be completely unexpected, as crown teleosts probably originated in marine environments (Betancur-R, Ortí & Pyron, 2015). Early Cretaceous deposits from Northeastern Asia (Russia, Mongolia, China, Korea and Japan) yield numerous early osteoglossomorphs (Wilson & Murray, 2008). Many of these fossils belong to the abundant †*Lycoptera* or closely related stem osteoglossomorphs (Li & Wilson, 1999). However, some of these Asian genera (e.g. †*Huashia*, †*Kuntulunia*, †*Xixiaichthys*) are unstable in phylogenetic analyses (Li & Wilson, 1999; Zhang, 2006; Wilson & Murray, 2008).

The oldest definitive crown osteoglossomorph is †*Yanbiania wangqinica*, a hiodontiform from the Aptian–Albian Dalazi Formation of China (Li & Wilson, 1999). Fossil hiodontiforms are also known from Late Cretaceous deposits in North America and Asia (Newbrey *et al.*, 2013;

Brinkman, Newbrey & Neuman, 2014), but extant *Hiodon* is restricted to North America. Among Osteoglossiformes, pantodontids, gymnarchids and mormyrids are endemic to Africa, and have a meagre fossil record in African Cenozoic deposits (Wilson & Murray, 2008). Notopterids show a disjunct distribution, with two African and two Indo-Malayan genera. Notopterid fossils are limited to otoliths from the latest Maastrichtian of India (Nolf, Rana & Prasad, 2008) and a few articulated specimens from the Eocene–Oligocene of Sumatra (Sangkarewang Formation; Sanders, 1934; de Smet & Barber, 2005). †*Palaeonotopterus greenwoodi* from the early Late Cretaceous (Cenomanian) Kem Kem Beds of Morocco was originally interpreted as a notopterid (Forey, 1997), but it probably represents a basal member of the clade that groups together Notopteridae, Mormyridae and Gymnarchidae (Wilson & Murray, 2008). Nonetheless, †*Palaeonotopterus* demonstrates that key divergences within crown osteoglossiforms had occurred by 100 Ma.

Extant osteoglossids comprise two sub-clades, each with an intercontinental distribution: Arapaiminae (*sensu* Forey & Hilton, 2010) inhabits South America (*Arapaima*) and Africa (*Heterotis*), while Osteoglossinae is distributed across South America (*Osteoglossum*), Southeast Asia and northern Australia (*Scleropages*). Osteoglossid fossils are known from every continent (except Antarctica) and show a higher diversity of the group in the past. †*Chanopsis lombardi* from the late Early Cretaceous (Aptian–Albian) Loia and Bokungu formations of the Democratic Republic of Congo (DRC) could represent the oldest member of Osteoglossidae (Taverne, 2016). Although †*Chanopsis* shows features characteristic of some osteoglossid sub-groups (e.g. lateral expansion of the anterior end of the frontal) it lacks definitive osteoglossid synapomorphies (Forey & Hilton, 2010) and has never been included in a formal phylogenetic analysis. Other putative early osteoglossids include †*Laeliichthys* from the Aptian of Brazil and †*Paradercetis* from the Late Cretaceous of DRC; both taxa have been assigned to Arapaiminae and feature prominently in discussions about the biogeography of the clade (Taverne, 1979; Lundberg, 1993). However, characters suggesting a relationship between *Laeliichthys* and Arapaiminae might be plesiomorphies or homoplasies (Forey & Hilton, 2010), while †*Paradercetis* is known from a poorly preserved skull roof without any clear osteoglossomorph features (A. Capobianco, personal observation of MRAC RG 10.970). It is advisable to exclude these taxa from discussions about osteoglossid evolution and biogeography pending further study. †*Laeliichthys* and †*Paradercetis* aside, jaw fragments from the Maastrichtian El Molino Formation of Bolivia could represent the oldest arapaimines (Gayet *et al.*, 2001). Osteoglossine fossils are rare, but articulated specimens of *Scleropages* from the early–middle Eocene of China (Xiawanpu and Yangxi formations; Zhang & Wilson, 2017) lie outside the current geographic range of the genus. Perhaps unexpectedly, worldwide marine deposits of Paleocene–early Eocene age yield the highest diversity of fossil osteoglossids (e.g. †*Brychaetus*, †*Furichthys*, †*Heterosteoglossum*, †*Magnigena*, †*Opsithrissops*; Bonde, 2008; Forey & Hilton, 2010). Taverne (1979) grouped some of the marine osteoglossids with the freshwater *Phareodus* in Phareodontinae. However, †*Magnigena* and †*Opsithrissops* do not seem to be closely related to †*Brychaetus* (Forey & Hilton 2010), implying multiple marine invasions. Reexamination of early Cenozoic osteoglossids (including marine forms) is necessary to untangle the complex evolutionary and biogeographic history of Osteoglossidae.

Extant osteoglossomorphs are restricted to fresh waters, with notopterids occasionally found in brackish environments (Berra, 2007). Thus, their distribution (encompassing all southern landmasses except for Antarctica) has been the subject of various biogeographic hypotheses (Nelson, 1969; Greenwood, 1973; Lundberg, 1993; Wilson & Murray, 2008). Africa has been proposed as the osteoglossomorph centre of origin (in a dispersalist scenario) due to the presence of every major extant osteoglossomorph lineage (except Hiodontidae; Darlington, 1957). However, the fossil record shows the highest diversity of Late Jurassic–Early Cretaceous osteoglossomorphs in northeastern Asia. Whether this pattern is due to an Asian origin or to geographical bias in the continental sedimentary record is not clear. Another scenario (Kumazawa & Nishida, 2000) involves a widespread Pangaean distribution during the Permian–Triassic for which there is no palaeontological evidence despite a wealth of fossil fishes of this age (Romano *et al.*, 2016). Cavin (2017) proposed a Laurasia–Gondwana vicariant event during the Jurassic corresponding to the divergence between the Laurasian Hiodontiformes and the Gondwanan Osteoglossiformes. The highly unstable phylogenetic position of several basal osteoglossomorphs (and possibly osteoglossiforms) from the Cretaceous and early Paleogene of North America and Asia (Murray *et al.*, 2018) makes this hypothesis difficult to evaluate at present.

The cosmopolitan distribution (encompassing North and South America, Africa, Europe, continental Asia, Indo-Malaya and Australia) of marine osteoglossomorphs and †*Phareodus*-like freshwater osteoglossids in the early Paleogene suggests a role for long-distance marine dispersal (Bonde, 2008; Wilson & Murray, 2008). Thus, the disjunct modern distribution of Arapaiminae and Osteoglossinae could be explained by marine dispersal followed by colonization of freshwater environments.

(*a*) *Fossil-based estimate of origin times*

The fossil-based estimate for total-group Osteoglossomorpha ranges from the Late Triassic to the Middle Jurassic (Rhaetian–Bathonian: 206.9–167.0 Ma; median point estimate: 182.4 Ma), suggesting an early ghost lineage extending for up to 40 Myr. The time of origin of total-group Osteoglossomorpha is closely linked to the origin of the teleost crown, as either osteoglossomorphs or elopomorphs (or a clade including both) represent the sister group to all other living teleosts (Arratia, 2010; Dornburg *et al.*, 2014; Hughes *et al.*, 2018). The age discordance between the oldest crown-teleost fossils, found in Late Jurassic deposits (except for some very fragmentary Middle Jurassic remains; Haddoumi *et al.*, 2016), and molecular clock estimates, which range from the Late Carboniferous to the Late Triassic (Near *et al.*, 2012; Broughton *et al.*, 2013; Dornburg *et al.*, 2014), has been called the ‘teleost gap’ (Near *et al.*, 2012). It represents one of the most striking differences between fossil and molecular timescales that still remains partially unexplained. Incompleteness of the fossil record and failure to recognize early crown-teleost fossils are not sufficient explanations for this phenomenon (Sallan, 2014), and specific choices of calibration points for molecular phylogenies play some role (Friedman, 2015; Giles *et al.*, 2017). The fossil-based estimate derived here for total-group Osteoglossomorpha partially bridges that gap, possibly extending the origin of this group as far back as the latest Triassic. Still, a significant difference of at least 15–40 Myr remains, suggesting the need for a revision of molecular clock studies focused on broad-scale teleost relationships.

While total-group Osteoglossomorpha is old enough to have been affected by the breakup of Gondwana (and even Pangea), the abundance of basal osteoglossomorphs in areas not occupied by living lineages (northeastern Asia) or with low present-day diversity (North America) suggests a complex history where dispersal and/or local extinction might have played a fundamental role. Moreover, at least three subclades that are deeply nested within Osteoglossomorpha (Notopteridae, Osteoglossinae, Arapaiminae) show disjunct distributions. The sparse fossil record of notopterids indicates that the group was already present in the Indian subcontinent by the end of the Cretaceous, but it cannot be used to derive an informative estimate for its time of origin. Molecular estimates of divergence between African and Asian notopterids show considerable variation (from the Late Jurassic to the Late Cretaceous; Inoue *et al.*, 2009; Lavoué, 2016). Thus, neither an Africa–India vicariance scenario nor a sweepstakes dispersal from Africa to India across the Mozambique Channel can be confidently rejected on the basis of the present evidence.

The fossil record of Arapaiminae and Osteoglossinae gives a minimum latest Cretaceous and early Eocene age for these two clades, respectively. However, derivation of probabilistic fossil-based estimates of their origin times is complicated by inadequate understanding of the relationships of fossil osteoglosssids (Forey & Hilton, 2010). Nonetheless, it is possible to estimate an age for Osteoglossidae as a whole. The fossil-based estimate for osteoglossid origin varies greatly depending on the inclusion or exclusion of †*Chanopsis*: Early Cretaceous and even the latest Jurassic (Tithonian–Albian: 154.4–103.2 Ma; median point estimate: 124.0 Ma) with †*Chanopsis*, or most of the Late Cretaceous (Aptian–Campanian: 113.0–72.1 Ma; median point estimate: 82.8 Ma) excluding this genus. It is clear that the phylogenetic placement of †*Chanopsis* has broad implications on the reconstruction of the early evolutionary history of the group, and a phylogenetic reassessment of this taxon is badly needed. Despite the differences in the fossil-based origin times inferred here relative to the position of †*Chanopsis*, both estimates are approximately consistent with molecular dates for crown Osteoglossidae (Early Cretaceous; Broughton *et al.*, 2013). These dates are old enough to allow for a significant role of continental vicariance, particularly involving South America–Africa drift and the fragmentation of the South America–Antarctica–Australia block, in the biogeographic history of the clade. However, the complex distributional pattern of extant and fossil osteoglossids (Wilson & Murray, 2008; Lavoué, 2016) and the presence of marine forms in the fossil record strongly suggest that dispersal has been a fundamental process during osteoglossid evolution.

(3) Characiformes (characins and allies)

Characiformes is a major clade of otophysans containing more than 2000 species, making it one of the most diverse freshwater fish lineages (Nelson *et al.*, 2016). Extant characiforms are restricted to freshwater environments of Africa and South and Central America, with one species in the southwestern USA (Fig. 4).

Numerous morphological characters support characiform monophyly (Wiley & Johnson, 2010), including the presence of multicuspid teeth in the jaws (lost in predators like *Hepsetus* and *Salminus*; Fink & Fink, 1981). The species-poor African Citharinoidei and species-rich Neotropical and African Characoidei represent the principal characiform lineages. Surprisingly, some molecular work questions characiform monophyly (Chen, Lavoué & Mayden, 2013; Chakrabarty *et al.*, 2017), but other analyses suggest these results are spurious (Arcila *et al.*, 2017).

Isolated teeth are the most common characiform fossils (Table S3) (Malabarba & Malabarba, 2010; Gaudant, 2014). These are sufficiently diagnostic to support a characiform attribution but often inadequate for more precise placements. The oldest putative characiform fossil teeth come from the Cenomanian of Morocco (Ifezouane Formation; Dutheil, 1999) and Sudan (Wadi Milk Formation; Werner, 1994). These occurrences would demonstrate presence of the group in Africa shortly after tectonic separation from South America. However, their attribution to characiforms has been challenged and they might instead represent ginglymodian multicuspid teeth, common in Cretaceous continental deposits of Africa, India and China (Cavin, 2017). The

African record also yields the oldest articulated characiform, †*Eocitharinus macrognathus* from the middle Eocene Mahenge Formation (Lutetian of Tanzania; Murray, 2003*b*; this is also the earliest known citharinoid). Alestidae, an African subclade of Characoidei, has a relatively abundant fossil record that spans the Cenozoic. Teeth of *Hydrocynus* appear in late Paleocene–early Eocene deposits of Algeria (Hammouda *et al.*, 2016). Possible alestid fossils from the Oligocene Baid Formation of Saudi Arabia (Micklich & Roscher, 1990) and Eocene and middle Miocene deposits of southwestern Europe (Gaudant, 2014) indicate a broader distribution of this clade in the past. Fragmentary material from the Maastrichtian Maevarano Formation of Madagascar has been tentatively referred to Characiformes (Ostrowski, 2012), but requires further study.

The Maastrichtian El Molino Formation of Bolivia is the oldest horizon yielding characiform fossils in South America, which today is home to the greatest diversity of characiforms (Gayet, 1991). Various tooth morphologies are present in these latest Cretaceous Bolivian deposits, indicating that the diversification of modern lineages (characids, serrasalmids and possibly acestrorhynchids) was underway by the end of the Late Cretaceous (Gayet *et al.*, 2001, 2003). Complete fossils of South American characiforms (including bryconids, curimatids, triportheids and several characid lineages) are known from the Eocene–Oligocene Entre-Corregos Formation and the Oligocene Tremembé Formation of southeastern Brazil (Malabarba, 1998; Weiss, Malabarba & Malabarba, 2014).

The recent discovery of putative characiform dentaries and vertebral centra from late Campanian North American deposits (Dinosaur Park and Kaiparowits formations) greatly extends the known geographic range of the group and implies an elaborate biogeographic scenario (Newbrey *et al.*, 2009; Brinkman *et al.*, 2013). Although the dentaries show an interdigitating hinge joint at the symphysis (a character thought to be unique to characiforms), these identifications should be approached with caution given the limited material. Characiforms also appear in the European fossil record by the end of the Cretaceous, with teeth found in Maastrichtian deposits in France and Romania (Grigorescu *et al.*, 1985; Otero, Valentin & Garcia, 2008). There are no extant European characiforms, but fossils are found throughout the Cenozoic (including articulated specimens; Gaudant, 1980), with the youngest examples from the latest Miocene (Gaudant, 2014).

Extant characiforms are strictly freshwater (with isolated brackish records; Lundberg, 1993), and all known fossils come from freshwater or at most brackish deposits. However, marine Early and Late Cretaceous fossils from Europe and South America (†*Salminops*, †*Sorbinicharax* and †*Santanichthys*) have been aligned with characiforms in the past (Gayet, 1985; Taverne, 2003; Filleul & Maisey, 2004), leading to hypotheses of a marine origin for Characiformes and of better dispersal abilities in early characiforms than might be predicted from modern forms (Calcagnotto, Schaefer & DeSalle, 2005; Otero *et al.*, 2008). Restudy of †*Salminops* and †*Sorbinicharax* failed to find evidence that these genera are even otophysans (Mayrinck, Brito & Otero, 2015; Mayrinck *et al.*, 2017). †*Santanichthys* is better interpreted as a basal member of

Otophysi or Ostariophysi rather than a stem characiform (Malabarba & Malabarba, 2010). Thus, a marine origin of Characiformes is not supported by palaeontological and phylogenetic data.

Two factors further complicate attempts to reconstruct characiform biogeographic history. First, extant African characiforms belong to three distinct clades (Citharinoidei, Alestidae and the monotypic Hepsetidae). Second, characiform fossils are found in areas outside their present distribution (Fig. 4). Several non-mutually exclusive hypotheses have been formulated to explain the presence of three different characiform lineages in Africa: a single vicariant event between Africa and South America when characiforms were already diversified, followed by extinction of several African lineages to account for the rarity of sister pairs between extant American and African clades; multiple vicariant events associated with the diachronous split between South America and Africa; and trans-oceanic dispersal events from South America to Africa, usually associated with the questionable hypothesis of a marine ecology in early characiforms (Lundberg, 1993; Malabarba & Malabarba, 2010). Evaluating these proposals without a well-supported phylogenetic framework for Characiformes is prohibitive; in fact, apart from the basal split between Citharinoidei and Characoidei, there is no agreement across different analyses about the relationships among major characiform lineages (see Dahdul, 2010). Arcila *et al.* (2017) recently recovered a single African characoid clade, with a strongly supported sister-group relationship between Hepsetidae and Alestidae. Given the low support for most other basal nodes within Characoidei, an alternative hypothesis with a diverse South American characoid clade nested within an African radiation cannot be excluded *a priori*. Under this scenario, only one event (either a pre-drift dispersal, or a post-drift oceanic dispersal, or a vicariant event) would be necessary to explain the current distribution of characiforms. Characiform fossils found in Europe and North America are difficult to interpret in a biogeographic framework, as their phylogenetic affinities are unclear. It has been proposed that European characiforms, which are mainly found in Maastrichtian, early Eocene, Oligocene and middle Miocene deposits, are the result of multiple waves of immigration, presumably from Africa, instead of a single colonization of the continent (Gaudant, 2014). The North American Campanian fossils, if confirmed as characiforms, hint at possible dispersals from South America or Europe (there is evidence for both routes from early Campanian terrestrial vertebrates; Newbrey *et al.*, 2009; Cavin, 2017). The widespread distribution of characiforms in the latest Cretaceous may suggest multiple long-distance dispersal events during the biogeographic history of the clade.

(*a*) *Fossil-based estimate of origin times*

The fossil-based divergence time estimate for characiforms depends heavily on the inclusion or exclusion of the Cenomanian fossil teeth from northern Africa. When including these putative characiform occurrences, our estimate is consistent with a vicariant scenario involving the South America–Africa split, as the origin of the clade is estimated as Albian–Cenomanian (119.8–95.1 Ma; median point estimate: 102.5 Ma). This is generally congruent with molecular clock estimates for the age of crown Characiformes (mostly ranging from 120 to 80 Ma; Near *et al.*, 2012; Betancur-R *et al.*, 2015). Without Cenomanian occurrences, our estimate shifts forwards in time by around 20 Myr to the Late Cretaceous (Cenomanian–Campanian: 97.3–75.1 Ma; median point estimate: 83.4 Ma), rejecting the vicariant scenario. Thus, a careful taxonomic reassessment of the Cenomanian multicuspid teeth from the Ifezouane and Wadi Milk formations could substantially impact the reconstruction of characiform biogeographic history. Particular caution should be applied when interpreting these results for two main reasons besides uncertainty on Cenomanian occurrences: the phylogenetic position of most early characiform fossils is unknown, so placement in the crown rather than on the stem is not assured; and the divergence between Citharinoidei and Characoidei may not correspond to a South America–Africa split, if South American characoids are nested within an African radiation. In this last case, the divergence between South American and African characiforms would have occurred later than the citharinoid–characoid split. Considering these two factors, together with the inclusion of Cenomanian fossils, our older estimate is more likely to be a conservative test of the vicariant scenario (i.e. it is likely to be an overestimate of true divergence time rather than underestimate). If we exclude the doubtful Cenomanian fossils, some of the oldest known characiforms – from Maastrichtian and Paleocene deposits – are unambiguous members of modern lineages that are deeply nested within characiform phylogeny (Gayet *et al.*, 2001, 2003). Hence, our younger estimate is more likely to be an underestimate of the true age of characiform origin. The apparent absence in the fossil record of early crown characiforms and the sudden appearance of several derived lineages in the Maastrichtian–Paleocene could be the result of different phenomena, which are not mutually exclusive: an early evolutionary history characterized by low diversification rates, followed by rapid diversification from the Maastrichtian onwards; the lack of appropriate depositional settings in the fossil record to recover Late Cretaceous characiforms; or a high degree of endemism before a rapid geographic expansion at the end of the Late Cretaceous (less likely under a vicariant scenario).

The fossil-based estimate for the origin of the African Alestidae could at most extend to the latest Cretaceous (Maastrichtian–Ypresian: 72.1–53.1 Ma; median point estimate: 60.4 Ma), significantly postdating the separation of South America and Africa. A stable phylogenetic placement of alestids (and of the other African characoid taxon, Hepsetidae) is needed before interpreting this result in light of a biogeographic scenario. Nonetheless, the timescale of alestid evolution is consistent with the emergence of modern characiform lineages during the Maastrichtian–Paleocene. The fossil record of characiforms in Europe hints at multiple dispersals of alestids from Africa during the Cenozoic, a pattern found in other non-marine vertebrates (Koufos *et al.*, 2005; Tabuce & Marivaux, 2005).

(4) Galaxiidae (galaxiids)

Galaxiidae includes more than 50 species of freshwater and diadromous fishes inhabiting temperate regions of the southern hemisphere (southern South America, South Africa, Australia, New Zealand and New Caledonia) (Fig. 5). Both morphological and molecular phylogenies strongly support galaxiid monophyly (McDowall & Burridge, 2011; Burridge *et al.*, 2012).

The galaxiid fossil record is restricted to Miocene lacustrine deposits of New Zealand (Table S4) (McDowall & Pole, 1997; Lee, McDowall & Lindqvist, 2007). The earliest examples belong to †*Galaxias effusus* from the early Aquitanian Foulden Hills Diatomite (Lee *et al.*, 2007). The Maastrichtian †*Stompooria rogersmithi* from freshwater deposits of South Africa was originally described as a galaxiid (Anderson, 1998). Although these specimens are articulated, subsequent study indicates they are too poorly preserved to permit precise taxonomic identification (Wilson & Williams, 2010). Significantly, †*Stompooria* differs from living galaxiids in several features, including the presence of scales (McDowall & Burridge, 2011).

Because of their peculiar distribution and the complex life cycle of some species, galaxiids have been at the centre of a long-standing debate concerning the relative contributions of vicariance and sweepstakes dispersal [see McDowall (2010) for a review]. While most galaxiids are exclusively freshwater, at least 11 species are diadromous (i.e. they migrate between fresh waters and sea during their life cycle; McDowall, 2007). Some diadromous species show broad distributions (e.g. *Galaxias maculatus* occurs in Australia, New Zealand, Chatham Islands, southern South America and Falkland Islands; McDowall, 1972), implying that open seaways are not a barrier to their dispersal. Diadromy has been lost many times during galaxiid evolution, indicated by phylogenetic studies and by the existence of landlocked populations of otherwise diadromous species (Allibone & Wallis, 1993; Waters & Wallis, 2001). Time-calibrated total evidence analyses imply a complex scenario of vicariant events associated with the early divergences followed by multiple marine dispersals since the Oligocene (Burridge *et al.*, 2012).

Moreover, ancestral life-history reconstructions show that diadromy cannot be rejected as the ancestral state for most of the nodes corresponding to disjunct geographic distributions (Burridge *et al.*, 2012).

(*a*) *Fossil-based estimate of origin times*

The fossil-based estimate for the origin time of galaxiids is extremely broad and spans the whole Mesozoic and most of the Cenozoic (235.0 – 21.2 Ma; median point estimate: 97.1 Ma), failing to give insight into their biogeographic history. This is a consequence of the very low number of distinct stratigraphic horizons in which galaxiid fossils have been found (only four when excluding †*Stompooria*). Published timetrees place the origin of crown Galaxiidae in the Late Cretaceous–early Paleogene, with a very long stem lineage extending to the Early Cretaceous (Burridge *et al.*, 2012; Betancur-R *et al.*, 2017).

Fossil *Galaxias* from the early Miocene of Otago show that galaxiids were present there shortly after the Oligocene 'drowning' event that almost completely submerged New Zealand [Cooper & Cooper, 1995; Landis *et al.*, 2008; see Sharma & Wheeler (2013) for a critique of this scenario]. This is consistent with the total-evidence analysis of Burridge *et al.* (2012), which indicates that the earliest New Zealand galaxiid clades diverged from their sister groups around the Oligocene–Miocene boundary. Thus, the presence of several lineages of galaxiids in New Zealand is better explained through multiple long-distance dispersal events.

(5) Cyprinodontiformes (killifishes and allies)

Cyprinodontiformes comprises more than 1200 species occurring in the Americas, the Mediterranean region, Africa and Southeast Asia and living predominantly in freshwater and brackish environments. Cyprinodontiform monophyly – and its division into two subclades with approximately equal modern diversity: Aplocheiloidei and Cyprinodontoidei – is strongly supported by morphological and molecular studies (Parenti, 1981; Setiamarga *et al.*, 2008). However, phylogenetic relationships among major killifish lineages (especially within Cyprinodontoidei) differ wildly across studies, with recent molecular phylogenies challenging the monophyly of long-standing taxa like Cyprinodontidae and Poeciliidae (Pohl *et al.*, 2015).

European and North American cyprinodontoids dominate the cyprinodontiform fossil record (Table S5). Very few fossil occurrences are known from Africa and South America, and none from Madagascar, India and Southeast Asia (Fig. 6). The oldest fossils referred to Cyprinodontiformes come from the Maastrichtian El Molino Formation of Bolivia (Gayet, 1991). These articulated, poorly preserved specimens do not exhibit typical cyprinodontiform synapomorphies of the caudal skeleton (Arratia & Cione, 1996). The El Molino fossils could represent a very basal lineage of killifishes or small-bodied freshwater fishes unrelated to killifishes. Undescribed material from the middle Eocene Lumbrera Formation of Argentina was listed as an indeterminate poeciliid by Arratia & Cione (1996). The earliest definitive cyprinodontiform fossils come from early Oligocene (Rupelian) deposits of Europe (Spain, France, Switzerland and Germany) and are represented by articulated specimens (Gaudant, 1982;

Frey, Maxwell & Sánchez-Villagra, 2016). Numerous killifish species were present in Europe by the end of the Oligocene, probably representing every major living lineage of Old World cyprinodontoids (*Aphanius*-like cyprinodontids, valenciids and procatopodine poeciliids; Costa, 2012). The European genera *Aphanius* and *Valencia* have fossil records that extend to the early and middle Miocene, respectively (Reichenbacher & Kowalke, 2009; Gaudant *et al.*, 2015). Killifishes also appear in the Oligocene of North America (Coatzingo Formation of Mexico; Guzmán, 2015), and the genus *Fundulus* is first found in early Miocene (Burdigalian) deposits of Nevada (Lugaski, 1977). Other extant killifish genera (*Cyprinodon* and several goodeids) have been found in Pliocene and Pleistocene deposits of the southern USA and Mexico (Smith, 1981; Miller & Smith, 1986). Only one fossil aplocheiloid species has ever been formally described (†*Kenyaichthys kipkechi* from the late Miocene Lukeino Formation of Kenya; Altner & Reichenbacher, 2015). Several fossil aplocheiloid specimens are also known from the Oligocene Daban Formation of Somalia (Van Couvering, 1982), but remain undescribed. These two cases represent the only examples of fossil killifishes in Sub-Saharan Africa.

Several killifishes live in brackish environments, and some fundulids and cyprinodontids inhabit coastal marine settings (Berra, 2007). Nonetheless, the widespread distribution of cyprinodontiforms has been interpreted as a 'reduced Pangaean' distribution by Parenti (1981, p. 534), who argued that the origin of Cyprinodontiformes should extend to the Late Triassic. Similarly, the origins of both cyprinodontids and aplocheiloid killifishes have been hypothesized to have occurred in the Late Jurassic–Early Cretaceous based on modern geographic distributions

(Parker & Kornfield, 1995; Murphy & Collier, 1997). Others emphasized the high salinity tolerance shown by several cyprinodontiforms in arguing for marine dispersal, with a South American origin and successive dispersals to Africa during the Late Cretaceous to early Paleogene (Lundberg, 1993; Briggs, 2003).

Traditional classifications place Old World cyprinodontoids in three unrelated lineages, but molecular phylogenies resolve them as a clade nested within an American radiation (Pohl *et al.*, 2015). This topology implies only one event (either vicariance or long-distance dispersal) to explain the presence of cyprinodontoids on both sides of the Atlantic.

Recent phylogenies of Aplocheiloidei indicate that African and Indo-Malayan cyprinodontoids are sister lineages (Furness *et al.*, 2015; Pohl *et al.*, 2015), contradicting a hypothesized South American and African clade (Murphy & Collier 1997). The branching order of major clades within Aplocheiloidei is incongruent with the sequence of Gondwanan breakup, suggesting that a purely vicariant scenario is overly simplistic. Unfortunately, the scant aplocheiloid fossil record provides few temporal and biogeographic constraints.

(*a*) *Fossil-based estimate of origin times*

Cyprinodontiformes (with the inclusion of the El Molino fossils) is estimated to originate during the Late Cretaceous (Campanian–Maastrichtian: 80.0–67.0 Ma; median point estimate: 70.7 Ma), whereas its major sub-clade Cyprinodontoidei probably appeared during the early-middle Eocene (Ypresian–Lutetian: 54.8–42.0 Ma; median point estimate: 46.3 Ma).

The fossil-based time estimate for Cyprinodontiformes rejects the vicariant hypothesis for this group, as South America, Africa and the Indo-Malagasy block were already separated from each other by seaways during the Campanian–Maastrichtian (Ali & Aitchison, 2008; Granot & Dyment, 2015). This timescale agrees with recent molecular studies that put the origin of killifishes in the Late Cretaceous (Near *et al.*, 2013; Matschiner *et al.*, 2017). However, this result should be treated with caution for two reasons. First, the fossil-based estimate is strongly reliant on the Maastrichtian El Molino Formation material, whose cyprinodontiform affinity is dubious at best; the next oldest occurrence is around 20 Myr younger than the El Molino fossils. Additionally, the taxonomic distribution of fossil cyprinodontiforms among the two main sub-clades – Cyprinodontoidei and Aplocheiloidei – is extremely uneven, so that the two aplocheiloid occurrences in the Oligocene–Miocene do not contribute to the time estimate derived here. Thus, a time estimate focused only on the cyprinodontoid fossil record may be more reliable than a cyprinodontiform estimate.

The estimated age for Cyprinodontoidei strongly rejects the vicariant hypothesis by placing cyprinodontoid origin in the early–middle Eocene. This is congruent with some molecular estimates (Near *et al.*, 2013; Betancur-R *et al.*, 2017), but significantly younger than others (Matschiner *et al.*, 2017). In any case, a latest Cretaceous–early Paleogene origin for this transatlantic clade strongly suggests a key role of long-distance dispersal in its biogeographic history.

A higher probability of long-distance dispersal events in killifishes compared to other freshwater fishes should be expected on the basis of remarkable physiological, behavioural and life-history traits, including not only high salinity tolerance, but also a facultative amphibious lifestyle, desiccation-resistant eggs and developmental diapause, that are present in at least some members of this group (Turko & Wright, 2015; Furness, 2016). In this regard, killifishes could represent a valuable biogeographic model system to study the timing and directionality of rare biotic exchanges among geographically separated landmasses during the last 80 Myr.

(6) Channidae (snakeheads)

The freshwater, predatory Channidae includes two extant genera: *Parachanna* (Western and Central Africa) and *Channa* (Indo-Malayan region and East Asia) (Fig. 7). Together with anabantoids (gouramies and allies), snakeheads are labyrinth fishes (Anabantiformes = Anabantoidei + Channoidei; Wiley & Johnson, 2010). This group is characterized by the presence of the suprabranchial organ, an accessory air-breathing apparatus (Wiley & Johnson, 2010). Channid monophyly is supported by numerous morphological synapomorphies (Wiley & Johnson, 2010; Murray, 2012) and molecular phylogenetic analyses (e.g. Li, Musikasinthorn & Kumazawa, 2006).

The earliest snakehead fossils come from middle Eocene (Lutetian) deposits of Indo-Pakistan and consist mainly of cranial material (Table S6) (Khare, 1976; Murray & Thewissen, 2008). The channid affinity of these middle Eocene fossils is clear, but their exact relationships to modern lineages is unclear. Fragmentary fossils of *Parachanna* appear in late Eocene (early–middle Priabonian) formations of Egypt and Libya (Murray *et al.*, 2010*a*; Otero *et al.*, 2015). More complete cranial remains and isolated vertebrae are known from the latest Eocene–earliest Oligocene Jebel Qatrani Formation in the Fayum Depression (Murray, 2012). Fossil snakeheads are also found in early–middle Miocene deposits of Europe and Central Asia, areas with no extant channids (e.g. Gaudant & Reichenbacher, 1998; Kordikova, Heizmann & Pronin, 2003). Better-preserved specimens are needed to determine whether European fossils belong to *Parachanna* or *Channa* (Gaudant, 2015). The range expansion of *Channa* into East Asia appears to have happened relatively recently, as the oldest snakehead remains in this region come from early Pleistocene deposits of China (Liu & Su, 1962).

Snakeheads are currently restricted to freshwater environments, although at least one species (*Channa punctata*) has moderate salinity tolerance and can thrive in brackish waters (Dubey *et al.*, 2016). Fossil snakeheads are usually found in freshwater deposits, although some of the earliest representatives of the group come from estuarine/transitional deposits (Subathu and Birket Qarun formations of India and Egypt, respectively; Khare, 1976; Murray *et al.*, 2010*a*). Channids are facultatively amphibious, can survive outside of water for days in a humid environment and are capable of short bursts of overland movement (Chew *et al.*, 2003). Thus, channids probably have good dispersal potential over the mainland, but they are limited by other environmental factors including water salinity and atmospheric humidity. It has been hypothesized that the geographic distribution of channids has been strongly controlled by climatic variables (precipitation and temperature), and that their presence in Europe and Central Asia during the early–middle Miocene and recent invasion of East Asia reflect broad-scale changes in Eurasian atmospheric circulation patterns (Böhme, 2004).

Two biogeographic scenarios have been proposed for channids. The first involves an origin in the Indo-Malayan region, followed by dispersal to Africa (Briggs, 1995). Although a late Miocene–early Pliocene age has been previously hypothesized for this dispersal event (Böhme, 2004), *Parachanna* fossils in late Eocene–early Oligocene deposits of northern Africa set a minimum age of around 40 Ma (Murray, 2012). The second scenario postulates a vicariant event between the Indo-Malagasy block and the rest of Gondwana during the Late Jurassic–Early Cretaceous (Li *et al.*, 2006).

Regardless of scenario, the fossil record of channids implies dispersal to Europe by 20 Ma. Gaudant (2015) proposed Africa as the source of immigration on the basis of palaeobiogeographic affinities between Europe and Africa during the early–middle Miocene. Specifically, European fossil channids have been found in association with specimens of alestid characiforms, a group now restricted to Africa. However, a phylogenetic appraisal of the European channids is needed to distinguish between African and Asian origins.

(*a*) *Fossil-based estimate of origin times*

The fossil-based estimate for the origin of Channidae ranges from the Late Cretaceous to the Eocene (Campanian–Lutetian: 78.7–43.1 Ma; median point estimate: 53.2 Ma), long after the separation of the Indian subcontinent from continental Africa. Thus, it rejects the hypothesis of Early Cretaceous vicariance associated with the *Parachanna–Channa* divergence. Instead, this date is consistent with the hypothesis of origin in the Indian (or Indo-Malagasy) subcontinent, followed by dispersal into Africa before the late Eocene. Although the exact timing of initial collision between India and continental Asia is still debated (ranging between 50 and 35 Ma; Ali & Aitchison, 2008; Najman *et al.*, 2010), the fossil record of terrestrial mammals shows a strong signal of biotic exchange between Southeast Asia and Africa in the middle Eocene (Tabuce & Mariveaux, 2005). It is possible that channid dispersal to Africa was coeval with this mammalian exchange.

Because of ambiguities concerning Eocene fossils from Indo-Pakistan, it is unclear whether our estimate pertains to the channid crown or total group. We therefore compare our results to molecular estimates for both clades. Only studies that used mitochondrial data and/or calibrations based on vicariance hypotheses found origin times significantly older than the fossil-based estimate (Li *et al.*, 2006; Wang & Yang, 2011). Other studies provide relatively broad estimates that overlap with the fossil-based one and are consistent with a dispersal-to-Africa scenario (e.g. Adamson, Hurwood & Mather, 2010; Matschiner *et al.*, 2017). Surprisingly, none of these molecular timetrees has sufficient scope to estimate the origin time of channids accurately, as they are either focused on channids with sparse outgroup sampling, or they encompass the whole teleost tree and include only few channid species. A time-calibrated phylogeny focused on Anabantaria (the clade comprising synbranchiforms and anabantiforms;

Betancur-R *et al.*, 2017) would be needed to assess the timescale of anabantiform – and channid – origin and diversification properly. Because most anabantarian lineages are endemic to the Indo-Malayan region, it is possible that this clade originated in the isolated Indian subcontinent during the Late Cretaceous. An anabantarian timetree would be necessary to test this hypothesis.

(7) Percichthyidae (South American and Australian temperate perches)

Percichthyidae includes more than 20 species of perch-like freshwater fishes, distributed across Australia and southern South America (Fig. 8). Molecular phylogenies show that Percichthyidae *sensu* Johnson (1984) is polyphyletic, with the catadromous *Percalates* distantly related to other percichthyids (e.g. Near *et al.*, 2013; Lavoué *et al.*, 2014). Thus, we use the term Percichthyidae to contain members of the group as historically construed minus *Percalates* (i.e. *sensu* Betancur-R *et al.*, 2017). *Percalates* and percichthyids share several morphological features, to the point that *Percalates* has been synonymized to the percichthyid genus *Macquaria* in the past (MacDonald, 1978); consequently, the fossil record of percichthyids is difficult to evaluate. New morphological studies are needed to identify percichthyid synapomorphies permitting correct taxonomic identification of perch-like fossil fishes found in freshwater sediments of southern continents. In fact, various fossil specimens reported in the literature as percichthyids have been referred to the non-percichthyid *Percalates* (Hills, 1934).

The Maastrichtian El Molino Formation of Bolivia yields the oldest putative percichthyid fossils (Table S7), including the articulated anterior half of a skeleton referred to the genus

Percichthys (Gayet & Meunier, 1998). Other articulated percichthyid specimens have been found in deposits from the early–middle Eocene of Argentina and the Oligocene of Brazil, and in the early Miocene Río Pedregoso Formation of Chile (originally interpreted as late Paleocene in age; Arratia, 1982; Pedroza *et al.*, 2017). These fossils show a broader distribution of percichthyids in South America, where they are today restricted to the southernmost tip of the continent. Percichthyid fossils are also found in Australia, with the oldest examples being at least early–middle Miocene in age (Hills, 1946; Turner, 1982). Two scales from the early Miocene Bannockburn Formation of New Zealand show some similarities with those of percichthyids (McDowall & Lee, 2005). Although the material is too scant for precise taxonomic identification, none of the extant freshwater fishes of New Zealand shows a comparable scale morphology, suggesting the existence of an extinct lineage of perch-like fishes in New Zealand.

Berra (2007) assigned Percichthyidae to Myers' 'peripheral division' of freshwater fishes. However, this classification stemmed from the inclusion of the catadromous *Percalates* in the group. Excluding *Percalates* from Percichthyidae, extant percichthyids occur almost exclusively in freshwater environments (with a few species rarely recorded in estuaries; Arratia, 1982). Additionally, percichthyid fossils are only found in freshwater deposits. Chen *et al.* (2014) recovered an antitropical clade of temperate freshwater fishes, named Percichthyoidea, uniting the North American centrarchids and elassomatids, the East Asian sinipercids, and percichthyids. They proposed a freshwater origin for percichthyoids and a complex biogeographic history to account for its distribution. However, other studies place marine taxa (like *Enoplosus*) as deep branches within this broader clade (Near *et al.*, 2013; Betancur-R *et al.*, 2017), hinting at a marine origin followed by freshwater invasions: one in the northern hemisphere and another in the southern hemisphere, leading to percichthyids.

(*a*) *Fossil-based estimate of origin times*

Because of the relatively poor percichthyid fossil record, our fossil-based time estimate for percichthyid origin spans most of the Cretaceous, from the Barremian to the Maastrichtian (127.4–69.1 Ma; median point estimate: 87.6 Ma). Strikingly, it is significantly older than molecular clock estimates, which indicate a Paleocene–Oligocene origin for crown Percichthyidae (Near *et al.*, 2013; Chen *et al.*, 2014; the oldest known percichthyid fossils predate the upper bound of this range). Moreover, the South American clade including the genera *Percichthys* and *Percilia* appears to be nested within the Australian radiation (Lavoué *et al.*, 2014). This is in contrast with the early appearance of South American percichthyids, including extinct species attributed to *Percichthys*. Two hypotheses can be proposed to explain this discrepancy. First, published molecular-clock analyses underestimate the divergence times of the main lineages within Centrarchiformes (like Percichthyidae), due to the inadequate fossil calibrations. Second, the early South American fossil percichthyids may not be percichthyids at all, but rather more closely related to *Percalates* or to another lineage of perch-like fishes. Detailed anatomical studies of percichthyids and their relatives are needed to identify diagnostic characters for determining the relationship of these fossils.

Although circum-Antarctic deep water circulation was established only around 31 Ma (Lawver & Gahagan, 2003), geophysical and palaeopalynological evidence suggest that the seaway between east Antarctica and Australia formed by the beginning of the Paleocene (Woodburne & Case, 1996; Bowman *et al.*, 2012). Thus, the Maastrichtian age of the Bolivian percichthyid fossils would suggest that early percichthyids would have been able to disperse overland between South America and Australia *via* Antarctica. It is possible that the *Percichthys* + *Percilia* clade diverged from other percichthyids because of a vicariant event caused by submersion of the South Tasman Rise and the separation of Australia from Antarctica during the Paleocene.

V. HISTORICAL BIOGEOGRAPHY OF WIDESPREAD FRESHWATER FISH CLADES

(1) Biogeographic patterns and the origin of modern geographic distributions

General patterns concerning the biogeographic history of widespread freshwater fishes can be gathered from the individual study cases presented here. Continental vicariance cannot be rejected for some of these clades: lepidosireniforms, osteoglossomorphs, characiforms and percichthyids (Fig. 9). However, osteoglossomorphs and characiforms are probably characterized by a complex biogeographic history that involved several long-distance dispersals as well as continental vicariance and that has been partially concealed by regional extinctions. In fact, the fossil record of these two groups greatly expands their present geographic distribution, highlighting the importance of palaeontological data in reconstructing the biogeographic history of extant organisms. While the fossil record of galaxiids does not capture their early evolutionary history, molecular clock studies suggest a similar pattern of early vicariance followed by long-distance dispersals, although on a more recent timescale. Among all the extant clades examined here, crown lepidosireniforms are probably the only group whose continental geographic distribution has been driven purely by a strict vicariant event: separation of South American and African landmasses. By contrast, cyprinodontiforms and channids are likely much younger than any major continental breakup that might have affected their geographic distribution. Thus, their intercontinental distribution is probably the result of multiple dispersal events, either overland (channids) or transoceanic (cyprinodontiforms).

There is no doubt that the progressive breakup of Gondwana had a massive impact on the geographic distribution of terrestrial and freshwater organisms living at the time of these geologic events. However, it seems that, at least for freshwater fishes, the pre-existing background of vicariance-driven distributions has been progressively eroded through time by extinctions and intercontinental dispersals. In fact, while the separation of South America and Africa corresponds to several vicariant events that can be inferred from the Aptian–Cenomanian fossil record of these continents (involving mawsoniids, lepisosteoids, amiids, cladocyclids and chanids; see Section II.2), lungfishes are the only freshwater fishes inhabiting both continents today for which the same process can be confidently identified as the primary cause of their present disjunct distribution. Together, the evidence presented here strongly suggests that rare intercontinental dispersals can have a significant effect on biogeographic patterns across continents. The relevance of long-distance dispersals in freshwater fish biogeography highlighted here parallels a growing literature supporting a prominent role of these events in the biogeographic history of a wide variety of terrestrial and freshwater organisms (de Queiroz, 2005; Gamble *et al.*, 2011; Pyron, 2014; Rota, Peña & Miller, 2016; Scheben *et al.*, 2016).

(2) Oceanic dispersal in freshwater fishes

While in some cases marine intercontinental dispersal of freshwater organisms could be explained by marine ancestry (e.g. osteoglossids), there is no evidence for past adaptations to open marine environments in several freshwater clades for which an oceanic dispersal event likely happened (e.g. cichlids, killifishes, synbranchids). The exact mechanisms by which transoceanic dispersal of freshwater fishes could happen are difficult to evaluate because this kind of dispersal is rare and relatively improbable (although it becomes almost inevitable over geological timescales). Proposed mechanisms (not mutually exclusive) include formation of giant freshwater plumes following catastrophic events like typhoons or tropical river floods; rafting of large chunks of soil and vegetation [see Houle (1998) for dispersal of terrestrial vertebrates, but these 'floating islands' might include puddles of fresh water as well]; 'stepping-stone' dispersal across island arches (Gilpin, 1980; however, this mechanism may be unfeasable for freshwater organisms); or bird-mediated zoochory of fish eggs (Hirsch *et al.*, in press). Strikingly, most freshwater fish taxa for which transoceanic dispersal has been inferred possess peculiar physiological or behavioural adaptations (e.g. high salinity tolerance, drought-resistant eggs, air-breathing and amphibious lifestyle) that might have increased their chance of surviving such an improbable journey. A similar pattern is also seen in terrestrial vertebrates for which sweepstakes dispersal has been inferred. For example, small body size, arboreal habits and heterothermy are common features of mammals that survived transoceanic journeys (Kappeler, 2000; Nowack & Dausmann, 2015), while drought- and salinity-resistant eggs and adhesive fingers are probably some of the adaptations that allowed geckos to disperse multiple times across oceans and to colonize oceanic islands (Gamble *et al.*, 2011). In this sense, while long-distance dispersals have a stochastic nature, we would expect a strong phylogenetic component for these events, which should be clustered within clades possessing those traits mentioned above. Among freshwater fishes examined here, the only exception to this general pattern seems to be represented by the poorly studied polycentrid leaffishes (see Section II.1), thus encouraging further investigation of this clade's natural history.

(3) Congruence and discrepancy between the fossil record and molecular divergence-time estimates

The fossil-based age estimates inferred herein for several clades of widespread freshwater fishes are generally congruent with molecular timescales published in the last 10 years (Fig. 10). This is a striking result, as these two different approaches draw upon semi-independent data: although time calibration of molecular phylogenies commonly employs fossil data, these are usually limited to a very small subset of the known fossil record of a clade (Parham *et al.*, 2012). Moreover, molecular timescales of some taxa are often estimated using exclusively external fossil calibrations – that is, fossils belonging to other, closely related taxa. As a result, there is very minor overlap between the data informing our fossil-based age estimates and the data informing evolutionary timescales in molecular phylogenies. Yet, for several taxa (Lepidosireniformes, Osteoglossidae, Characiformes, Cyprinodontiformes, Cyprinodontoidei, Channidae), the fossil-based timescales inferred in this study are not significantly different from published molecular ones, providing support for the evolutionary timescales presented here.

Deviations are worth discussing, as they might highlight problematic issues in either of these approaches for estimating evolutionary timescales. The origin of Percichthyidae estimated here is significantly older than corresponding molecular estimates; this may be due to the misidentification of some articulated specimens from the Maastrichtian El Molino Formation as belonging to the genus *Percichthys* (see Section IV.7). The most striking discrepancy is represented by the age that we derived for total-group Osteoglossomorpha (latest Triassic–Middle Jurassic), which is significantly younger than most recent molecular estimates. This relates to a broader discrepancy between the oldest crown teleost fossils (Middle–Late Jurassic) and the age of crown teleosts inferred by molecular clock studies: the so-called 'teleost gap' (Near *et al.*, 2012). While the use of rapidly evolving molecular markers and misidentified fossil calibrations can yield unrealistically old estimates for the crown teleost radiation, correcting for these factors still results in an inferred Permo-Triassic origin of crown teleosts (Dornburg *et al.*, 2014; Giles *et al.*, 2017). The wealth of stem teleosts found in Middle Triassic–Middle Jurassic formations (Arratia, 2015; López-Arbarello & Sferco, 2018) suggests that it should not be impossible (at least theoretically) to find crown teleost fossils in deposits of that age. Incompleteness of the fossil record can only partially account for this gap. According to our fossil-based estimates, even when accounting for non-uniform fossil preservation potential through time it would be very unlikely to find any stem osteoglossomorph fossils older than 207 Ma. However, it should be noted that this estimate is based on the temporal distribution of non-marine deposits, which is likely not appropriate when trying to derive age estimates for the earliest divergences in the teleost tree, as the early evolutionary history of teleosts probably occurred in marine environments (Betancur-R *et al.*, 2015; Guinot & Cavin, 2018). In summary, the gap between the earliest molecular divergence estimates within crown teleosts and the oldest crown teleost fossils can be only partially explained by an incomplete fossil record or by failure to recognize crown teleosts among known Triassic fossils. It is possible that high heterogeneity in the rates of molecular evolution at the base of the teleost radiation or biased effective calibration prior densities are responsible for pushing molecular estimates towards older dates, but more studies about the impact of prior specification on the molecular timescale of early teleost evolution are needed to test these hypotheses.

(4) Limitations of the stratigraphic approach to infer origin times and test biogeographic hypotheses

The stratigraphic approach utilized here presents several limitations. Firstly, at least 15–20 distinct fossil horizons are needed in order to obtain an informative range of age estimates, meaning a range that is precise enough not to encompass several geologic periods and to provide some insight on evolutionary timescales. Several clades have a very limited fossil record and are often concentrated in a few distinct fossil horizons, as in the cases of galaxiids and percichthyids. Additionally, many of the estimates derived here rely heavily on the correct taxonomic identification of the oldest known representatives of a clade. This can be particularly problematic when the oldest putative fossils of a clade are very fragmentary (e.g. teeth, scales or isolated otoliths, as in lepidosireniforms, osteoglossomorphs and characiforms) or when, even with better preserved articulated fossils, their phylogenetic affinities are dubious (e.g. El Molino cyprinodontiforms and percichthyids, or of the putative osteoglossid *Chanopsis*). While a possible solution to the former could be to restrict the analysis to articulated fossils only, with the preservation potential function based upon fossil horizons that can yield articulated specimens (Friedman *et al.*, 2013), this approach ignores considerable information coming from microfossil assemblages and, more importantly, drastically lowers the number of distinct stratigraphic horizons from which the focal clade is known.

Another possible issue stems from the phylogenetic interpretation of the results of this type of analysis – in other words, the phylogenetic node to which an age estimate pertains. We believe that it is more appropriate to refer this estimate to the least inclusive clade containing all the fossils considered in the analysis (see Section II.3 for an example involving cichlids).

While we used the estimated origin time of widespread freshwater fish clades as a test of a simple vicariant scenario for each of these clades, it is clear that our approach is very limited in scope and can only test whether the evolutionary timescale of the group of interest is compatible with the timescale of relevant continental breakups. Model-based biogeographic analyses that include fossil taxa in a phylogenetic framework, allow for heterogeneity in dispersal rates through time, and constrain vicariant events to the known timescales of underlying geologic events are needed to reconstruct the biogeographic history of these clades in more detail. While significant progress has been made towards the development of complex biogeographic models [Ronquist & Sanmartín, 2011; Matzke, 2014; but see Ree & Sanmartín, 2018 for a critique of the Dispersal–Extinction–Cladogenesis + Jump dispersal (DEC+J) model], two major challenges remain: the inclusion of fossil taxa in a 'total-evidence' phylogeny (Ronquist, Lartillot & Phillips, 2016), which requires the collection of morphological data for both extant and extinct taxa – a complex and time-consuming task that requires high levels of taxon-specific expertise; and the lack of models accounting for taphonomic biases and the incomplete nature of the fossil record in phylogeny-based biogeographic reconstruction software. It is worth noting that fragmentary fossil specimens that can be assigned to broad clades but are not sufficiently diagnostic to permit finer taxonomic resolution can often provide invaluable geographic and temporal information. These specimens have very few informative morphological characters, so they will likely be ignored in any phylogeny-based biogeographic reconstruction [although see Silvestro *et al.* (2016) for a way to estimate biogeographic parameters using fossil data without phylogenies, and Cau (2017) for an approach towards specimen-level phylogenetics in palaeontology]. Consequently, even a qualitative assessment of the geographic and temporal distribution of fossils belonging to a certain clade – including fragmentary specimens – has the potential to greatly improve our understanding of its biogeographic history.

(5) Future directions

Stressing the importance of the fossil record in biogeographic reconstruction, we hope that further attention will be directed towards ways of integrating fossil data into analytically explicit biogeographic reconstructions. Ultimately, a better understanding of the early biogeographic history of freshwater fishes will come from detailed morphological studies able to solve the systematics of some key fossil taxa. For example, the Maastrichtian El Molino Formation in Bolivia records the first occurrence of several freshwater fish lineages that still occur in South American freshwater environments (Gayet, 1991; Gayet *et al.*, 2001), and thus represents one of the oldest fossil fish assemblages with a modern taxonomic composition in southern landmasses. Moreover, it is one of the very few freshwater fish communities known from around the Cretaceous–Paleogene boundary in the southern hemisphere. Yet, despite the biogeographic and palaeoenvironmental importance of these fossils, the systematic position of the El Molino fishes (including those for which articulated specimens are known) is still highly uncertain.

Time-calibrated phylogenetic trees based mainly (if not exclusively) on molecular data will remain, for the foreseeable future, the primary way to derive evolutionary timescales for a group of organisms and thus test alternative biogeographic hypotheses. Accuracy and precision of molecular timescales strongly depend on the choices made for time calibration (Duchêne, Lanfear & Ho, 2014). The fossil-based estimates derived here for the origin of widespread freshwater fish taxa could be used in future studies as calibration priors for the relevant nodes, with the advantage that soft maximum bounds were objectively inferred from the temporal distribution of the fossil record and not arbitrarily decided (as often happens in node calibrations; Bromham *et al*., in press). The use of analytically derived calibration distributions removes a layer of subjectivity in the process of molecular dating and can potentially yield timescales that better reflect what we know from the palaeontological record [see also Hedman (2010) and Matschiner *et al.* (2017) for different approaches to deriving fossil-based origin time distributions].

Comparing separate molecular evolutionary timescales across freshwater fish taxa can be problematic because available analyses are usually focused on specific clades. These commonly differ in the methods employed, in the kind of data analysed and in prior assumptions – which, in the case of Bayesian dating, include priors on distribution of node times, branch-rates and calibration distributions, among others. Thus, it might be expected that different studies do not show comparable timescales, making the task of building a comprehensive timescale of biogeographic evolution in freshwater fishes particularly challenging. While substantial progress has been made towards the reconstruction of a fish timetree encompassing every major fish lineage (Near *et al*., 2012; Betancur-R *et al*., 2017), these studies are not targeted towards the reconstruction of intercontinental biogeographic patterns and so they lack several key taxa and internal nodes. A possible solution could be to perform a 'fish-wide' time-calibrated phylogenetic analysis that specifically targets every biogeographically relevant freshwater taxon, in order to derive a unified timescale of continental-scale biogeographic events across freshwater fishes.

Finally, among freshwater fishes, descendants of past long-distance dispersals play a fundamental role in freshwater communities and can be subject to spectacular radiations, as in the cases of cichlids in the Neotropics, galaxiids in New Zealand and killifishes in Africa. Several recent studies suggest that ecological opportunity through invasion of new adaptive zones – including colonization of new geographic areas – can influence diversification patterns (e.g. Burbrink & Pyron, 2010; Burress & Tan, 2017). However, the impact of long-distance dispersal events on macroevolutionary dynamics – including diversification rates and modes – and continental-scale biotic assemblages is still largely unexplored.

VI. CONCLUSIONS

(1) Vicariance and dispersal both played crucial roles in structuring the distribution of modern freshwater fishes. However, even when clades are old enough to have experienced continental vicariance, the pre-existing vicariance-driven distribution is often confounded and eroded through time by successive dispersals and regional extinctions during the Late Cretaceous and Cenozoic. The only known examples of present-day disjunct intercontinental distributions

consistent with pure vicariance are South American and African lungfishes (Lepidosireniformes) and, possibly, Southern temperate perches (Percichthyidae).

(2) The evidence presented here shows that oceanic long-distance dispersal likely happened in several freshwater fish taxa. This complements recent studies stressing the importance of long-distance dispersal in terrestrial lineages. However, the means by which oceanic dispersal by freshwater fishes is achieved, and the impact of these rare events on macroevolutionary dynamics are still relatively unknown and could represent important future areas of investigation in biogeographic research.

(3) Fossils can provide invaluable temporal, geographic and environmental information that can be used to reconstruct the biogeographic history of a clade. Specifically, fossil data can expand the present geographic distribution of a clade and reveal past dispersal or vicariant events that have been obscured by regional extinction. Moreover, fossils can show that extinct members of a clade had environmental tolerances differing from modern species. For example, while all living osteoglossomorphs are restricted to freshwater habitats, several fossil osteoglossomorphs were found in marine deposits of Paleocene–early Eocene age all over the world, suggesting a substantial role of marine dispersal in the past (if not present) geographic distribution of the group.

(4) Methods to infer origin times using the temporal distribution of the known fossil record of a clade complement time-calibrated molecular phylogenies as means to establish evolutionary timescales. Fossil-based estimates can be compared with molecular estimates and, when conflicts

between the two arise, can point out problematic issues in either evaluation of the fossil record or the methods used to infer molecular timetrees. Fossil-based age ranges can be also used to calibrate relevant nodes on molecular phylogenies, avoiding the necessity to specify user-defined, subjective calibration parameters.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1. Detailed list of known fossil Lepidosireniformes (Sheet1) and list of horizons (formations or localities) yielding lepidosireniform fossils (Sheet2).

Table S2. Detailed list of known fossil Osteoglossomorpha (Sheet1) and list of horizons (formations or localities) yielding osteoglossomorph fossils (Sheet2).

Table S3. Detailed list of known fossil Characiformes (Sheet1) and list of horizons (formations or localities) yielding characiform fossils (Sheet2).

Table S4. Detailed list of known fossil Galaxiidae (Sheet1) and list of horizons (formations or localities) yielding galaxiid fossils (Sheet2).

Table S5. Detailed list of known fossil Cyprinodontiformes (Sheet1) and list of horizons (formations or localities) yielding cyprinodontiform fossils (Sheet2).

Table S6. Detailed list of known fossil Channidae (Sheet1) and list of horizons (formations or localities) yielding channid fossils (Sheet2).

Table S7. Detailed list of known fossil Percichthyidae (Sheet1) and list of horizons (formations or localities) yielding percichthyid fossils (Sheet2).

Table S8. List of post-Carboniferous non-marine horizons (formations or localities) yielding fish fossils.

Appendix S1. R script estimating origin times based on the number and distribution through time of fossil occurrences.

	North and Central America	South America	Europe and Western Asia	Africa and Arabian Peninsula	North-Eastern Asia	Indo-Malaya	Oceania
Lepidosireniformes		X		X			
Osteoglossomorpha	X	X	X	X	X	X	X
Osteoglossidae	X	X	X	X	X	X	X
Characiformes	X	X	X	X			
Alestidae			X	X			
Galaxiidae		X		X			X
Cyprinodontiformes	X	X	X	X		X	
Cyprinodontoidei	X	X	X	X			
Channidae			X	X	X	X	
Percichthyidae		X					X

Table 1. Biogeographic areas selected for each of the analysed clades to build their empirical preservation potential function. X indicates areas in which the clade is either present today or was present in the past according to the fossil record.

	Replicates lower 95%	**Median point estimate**	**Replicates upper 95%**
Lepidosireniformes			
	95.05	103.51	124.93
Total-group Osteoglossomorpha			
	167.03	182.44	206.89
Osteoglossidae (without *Chanopsis*)			
	72.07	82.85	112.96
Osteoglossidae (with *Chanopsis*)			
	103.22	123.96	154.42
Characiformes (with Cenomanian occurrences)			
	95.08	102.47	119.84
Characiformes (without Cenomanian occurrences)			
	75.07	83.40	97.30
Alestidae			
	53.13	60.37	72.10
Galaxiidae			
	21.15	97.13	235.02
Cyprinodontiformes			
	67.02	70.72	79.97
Cyprinodontoidei			
	42.02	46.27	54.77
Channidae			
	43.08	53.19	78.70
Percichthyidae			
	69.10	87.59	127.39

Table 2. Fossil-based estimates for the time of origin of widespread freshwater fish clades considered in this study. Columns indicate lower 95% confidence interval of the lower credibility interval (CI) of the Bayesian posterior distribution, median point estimate, and upper 95% confidence interval of the upper CI of the Bayesian posterior distribution, respectively. Values result from 1000 replicates accounting for uncertainty in absolute age of fossil horizons. All numbers are in units of million years ago (Ma).

Figure legends

Fig. 1. Family-level time-calibrated molecular phylogeny of extant non-tetrapod Osteichthyes (bony fishes), modified from Betancur-R *et al.* (2015). The seven clades of widespread freshwater fishes that represent the focus of this review are highlighted in orange, while other extant clades with a disjunct distribution in the southern hemisphere that are discussed in the text are highlighted in aquamarine. Coloured bands indicate the timeframe of the Western–Eastern Gondwana break-up and the South America–Africa break-up.

Fig. 2. Histogram showing the temporal distribution of distinct stratigraphic horizons bearing fossils of crown Lepidosireniformes. Each time bin is 5 million years (Myr) in width. The inset displays the present-day geographic distribution of Lepidosireniformes (in blue), as well as the main localities in which lepidosireniform fossils have been found (orange dots). Extant geographic ranges for Figs 2–8 were taken from Berra (2007). Photograph of West African lungfish (*Protopterus annectens*) from Wikimedia Commons.

Fig. 3. Histogram showing the temporal distribution of distinct stratigraphic horizons bearing fossils of total-group Osteoglossomorpha. Each time bin is 5 million years (Myr) in width. The inset displays the present-day geographic distribution of Osteoglossomorpha (in blue), as well as

the main localities in which osteoglossomorph fossils have been found (orange dots). Photograph of Lokundi mormyrid (*Hippopotamyrus castor*) modified from Sullivan *et al.* (2016).

Fig. 4. Histogram showing the temporal distribution of distinct stratigraphic horizons bearing fossils of Characiformes. Each time bin is 5 million years (Myr) in width. The hatched rectangle represents the doubtful occurrences of characiforms teeth in Cenomanian deposits of Africa. The inset displays the present-day geographic distribution of Characiformes (in blue), as well as the main localities in which characiform fossils have been found (orange dots). Photograph of striped headstander (*Anostomus anostomus*) by J. Armbruster from Wikimedia Commons.

Fig. 5. Histogram showing the temporal distribution of distinct stratigraphic horizons bearing fossils of Galaxiidae. Each time bin is 5 million years (Myr) in width. The inset displays the present-day geographic distribution of Galaxiidae (in blue), as well as the main localities in which galaxiid fossils have been found (orange dots). Photograph of spotted galaxias (*Galaxias truttaceus*) by N. Litjens from Wikimedia Commons.

Fig. 6. Histogram showing the temporal distribution of distinct stratigraphic horizons bearing fossils of Cyprinodontiformes. Each time bin is 5 million years (Myr) in width. The inset displays the present-day geographic distribution of Cyprinodontiformes (in blue), as well as the

main localities in which cyprinodontiform fossils have been found (orange dots). Photograph of an African killifish (*Nothobranchius kilomberoensis*) from Wikimedia Commons.

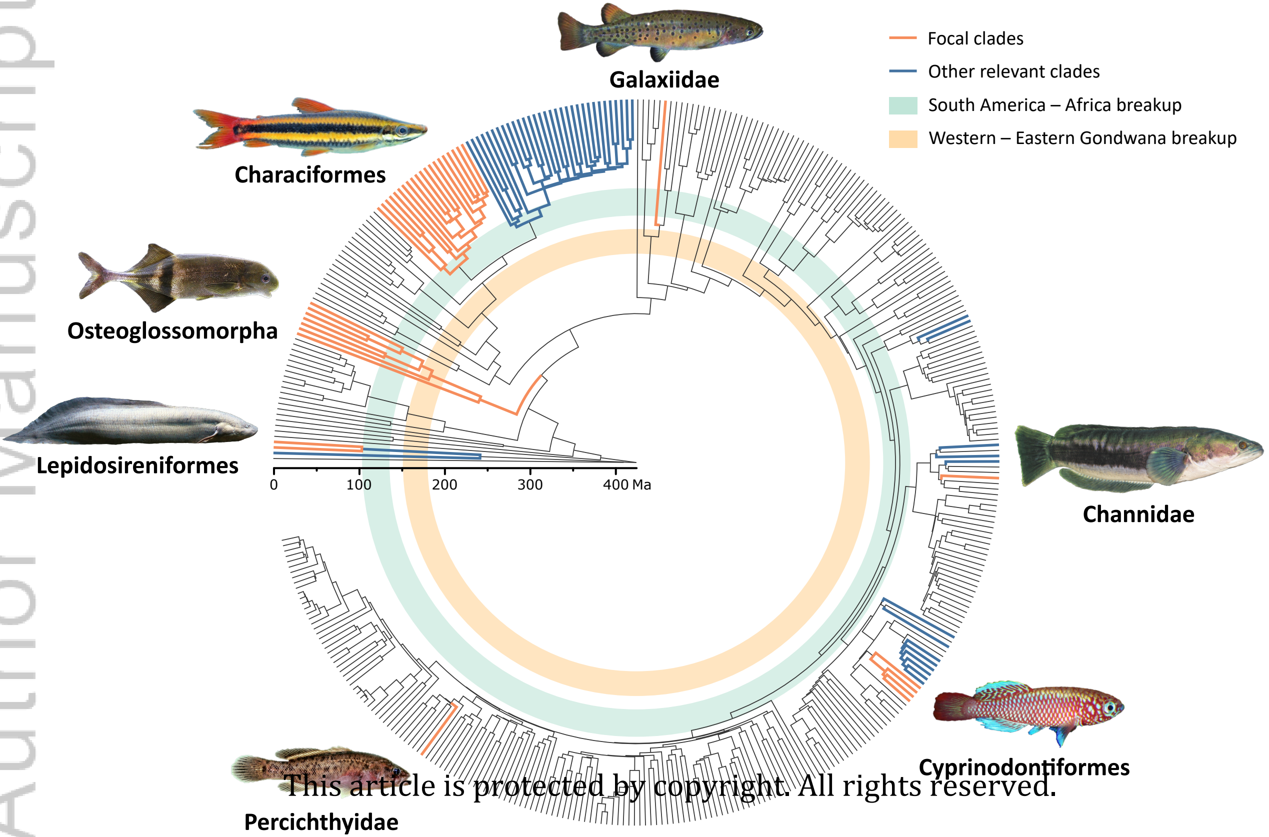
Fig. 7. Histogram showing the temporal distribution of distinct stratigraphic horizons bearing fossils of Channidae. Each time bin is 5 million years (Myr) in width. The inset displays the present-day geographic distribution of Channidae (in blue), as well as the main localities in which channid fossils have been found (orange dots). Photograph of giant snakehead (*Channa micropeltes*) from Wikimedia Commons.

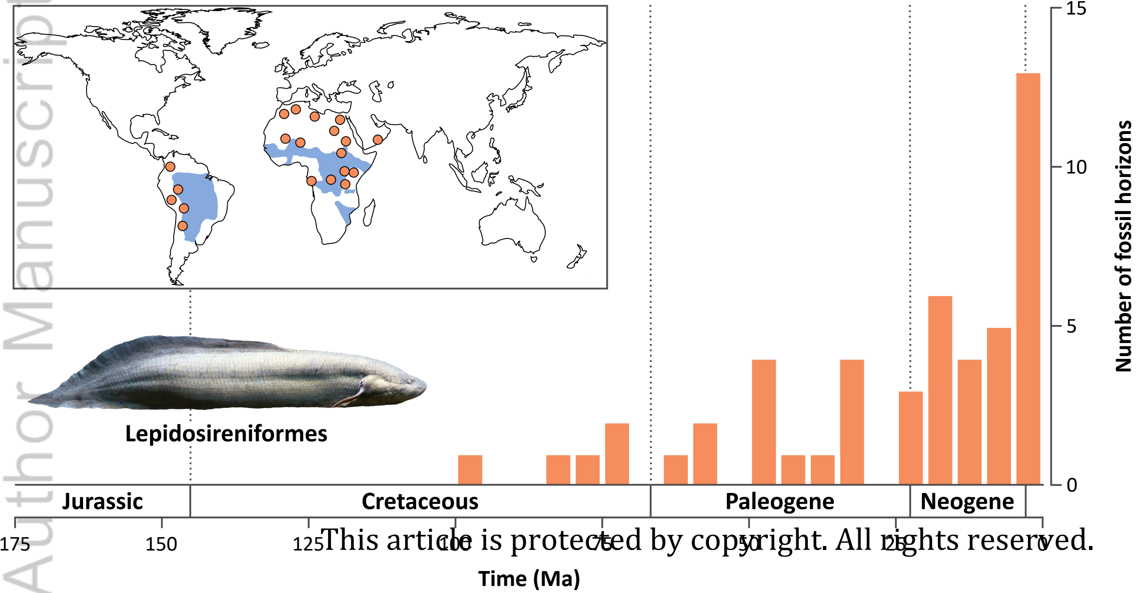
Fig. 8. Histogram showing the temporal distribution of distinct stratigraphic horizons bearing fossils of Percichthyidae. Each time bin is 5 million years (Myr) in width. The inset displays the present-day geographic distribution of Percichthyidae (in blue), as well as the main localities in which percichthyid fossils have been found (orange dots). Photograph of nightfish (*Bostockia porosa*) by the Australian Museum from Wikimedia Commons.

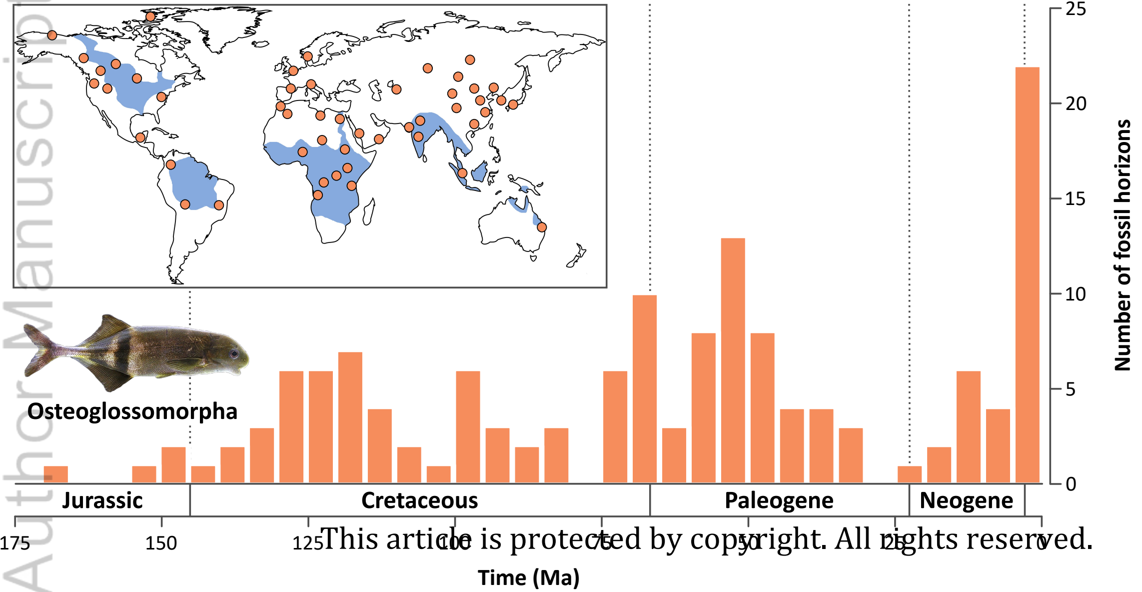
Fig. 9. Fossil-derived timescale for the origin of the focal clades considered in this review. Galaxiidae is not included because its estimate was not informative (see Section IV.4). The timescale for characiform origin shown here and in Fig. 10 is the older estimate from this study (i.e. including Cenomanian occurrences; see Section IV.3). The dot indicates the median point estimate, while the bar encompasses the range of estimates when accounting for both non-

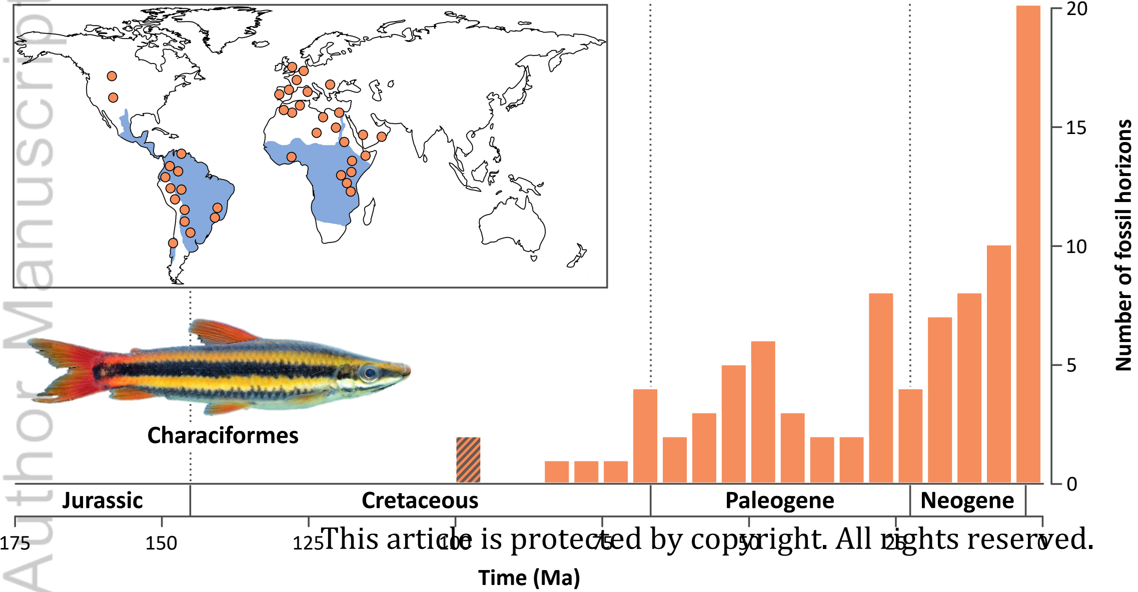
uniform distribution of the fossil record and uncertainty in the age of fossil horizons. As in Fig. 1, coloured bands indicate the timeframe of the Western–Eastern Gondwana breakup (in light ocre) and the South America–Africa breakup (in light green). The horizontal axis represents time, with scale provided in million years ago (Ma). Paleogeographic maps are taken from Scotese (2014). Blue boxes refer to the age of the palaeogeographic reconstructions relative to the timescale.

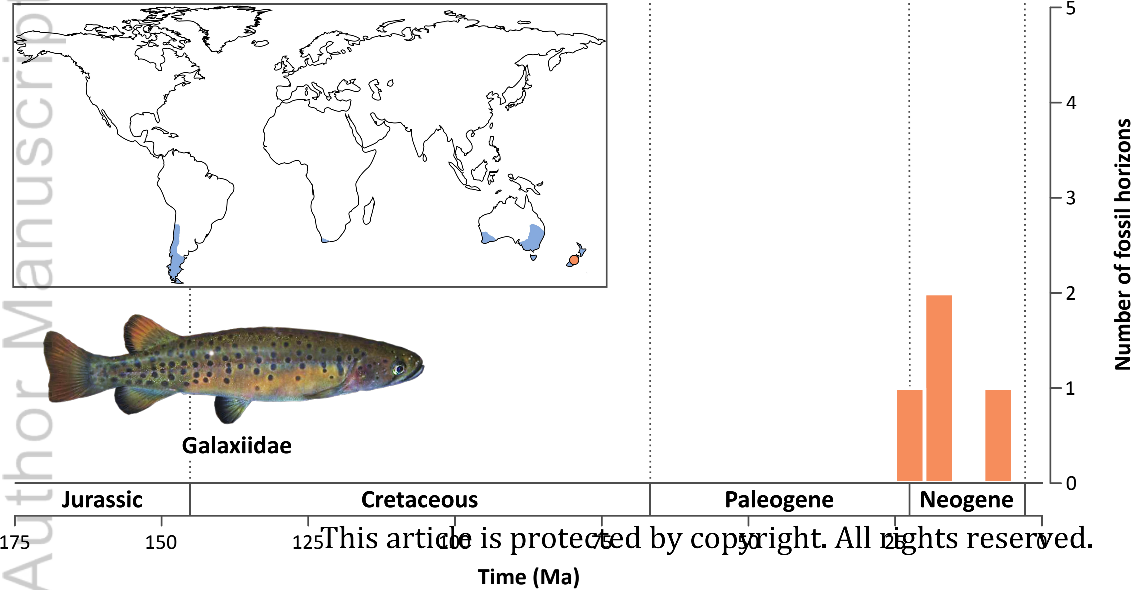
Fig. 10. Comparison between fossil-derived estimates (in orange) and recently published molecular estimates (in grey) for the origin times of: 1, Lepidosireniformes; 2, total-group Osteoglossomorpha; 3, Characiformes; 4, Cyprinodontiformes; 5, Channidae; 6, Percichthyidae. Molecular estimates for channids refer to stem Channidae (see Section IV.6). Galaxiidae is not included because its fossil-based estimate was not informative (see Section IV.4). The dot indicates the point estimate, while the bar (when present) encompasses 95% confidence or credibility interval. The horizontal axis represents time, with scale provided in million years ago (Ma).


Focal clades
Other relevant clades
South America – Africa breakup
Western – Eastern Gondwana breakup
Galaxiidae
Characiformes
Osteoglossomorpha
Lepidosireniformes
Channidae
Cyprinodontiformes
Percichthyidae
0
100
200
300
400 Ma

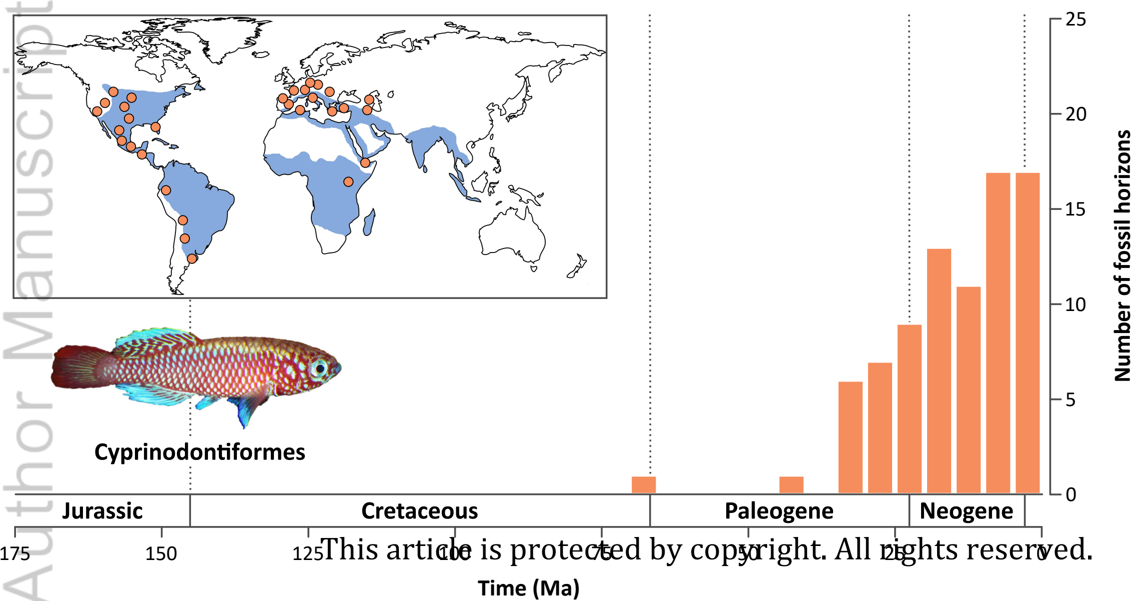

Lepidosireniformes
15
10
5
0
Number of fossil horizons
Jurassic
Cretaceous
Paleogene
Neogene
175
150
125
100
75
50
25
0
Time (Ma)

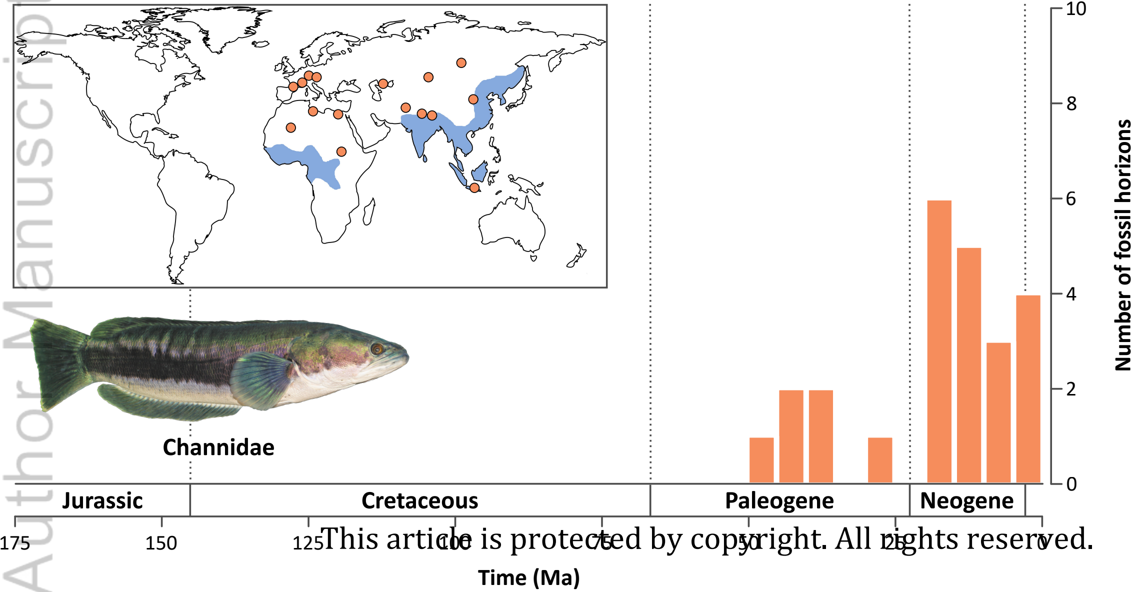

Osteoglossomorpha
Jurassic
Cretaceous
Paleogene
Neogene
175
150
125
100
75
50
25
0
Time (Ma)
0
5
10
15
20
25
Number of fossil horizons

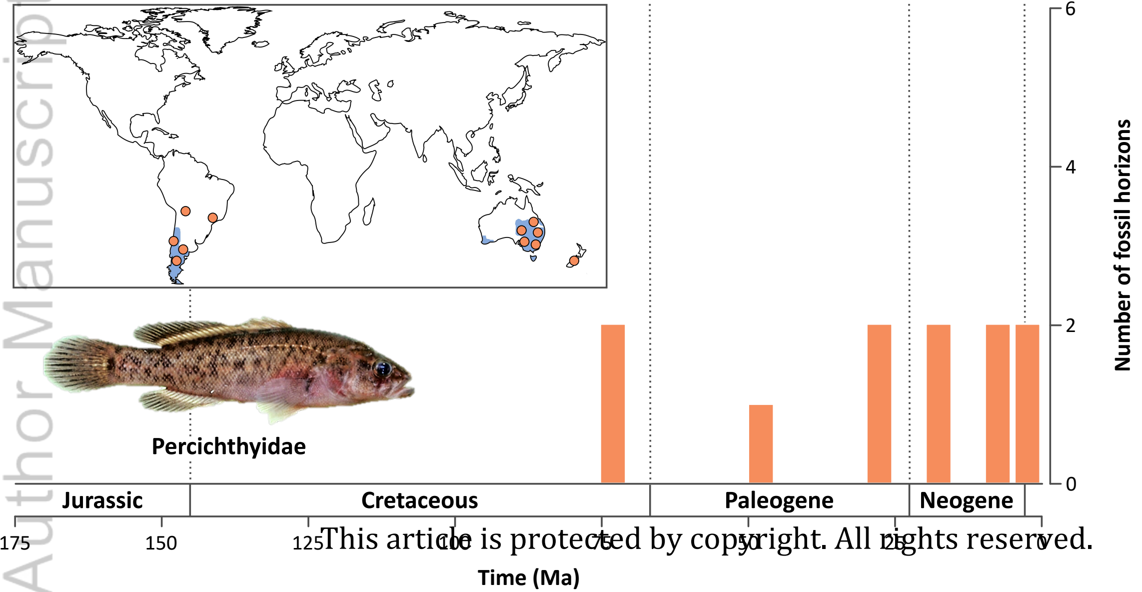

Characiformes
Jurassic
Cretaceous
Paleogene
Neogene
175
150
125
100
75
50
25
0
Time (Ma)
Number of fossil horizons
0
5
10
15
20

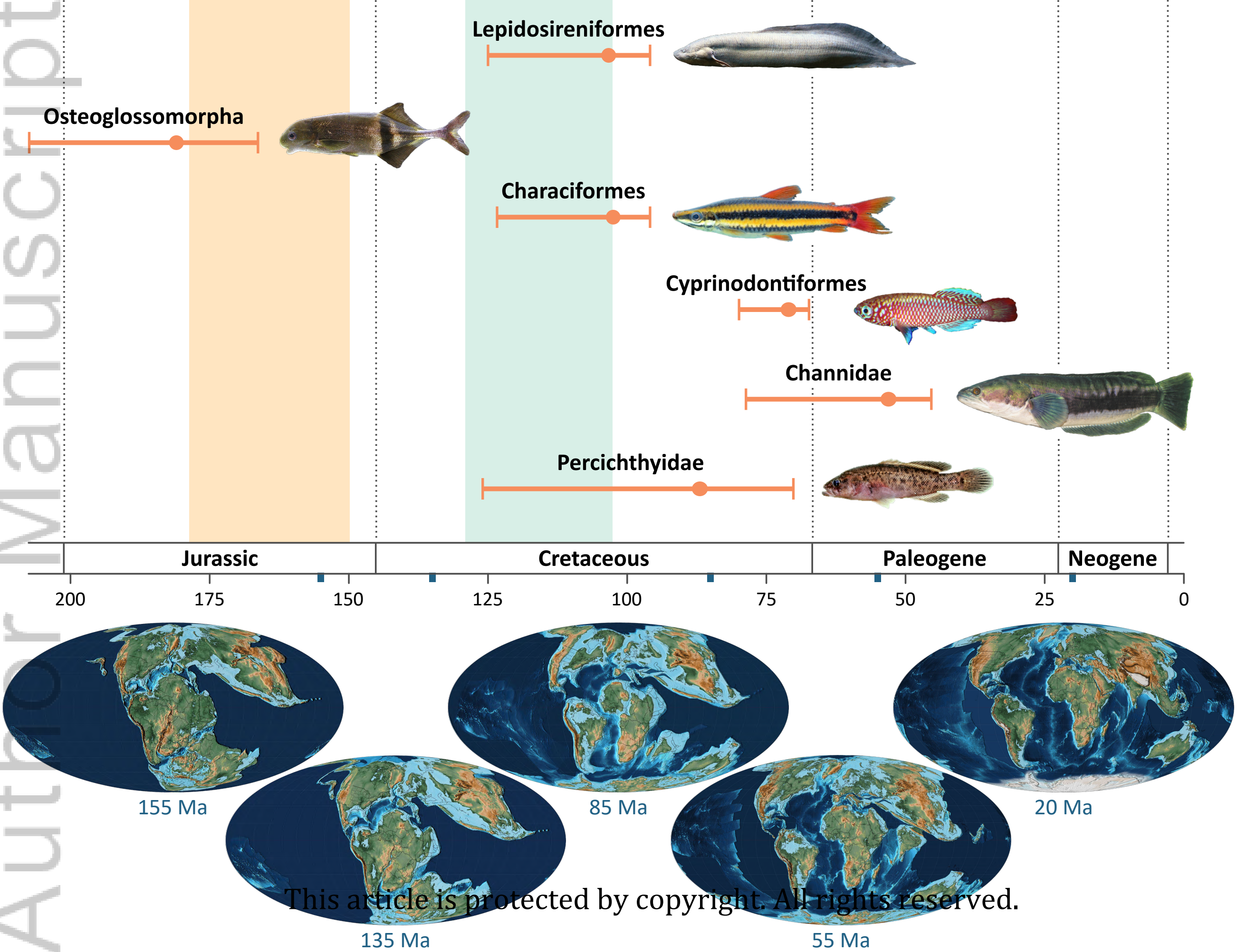


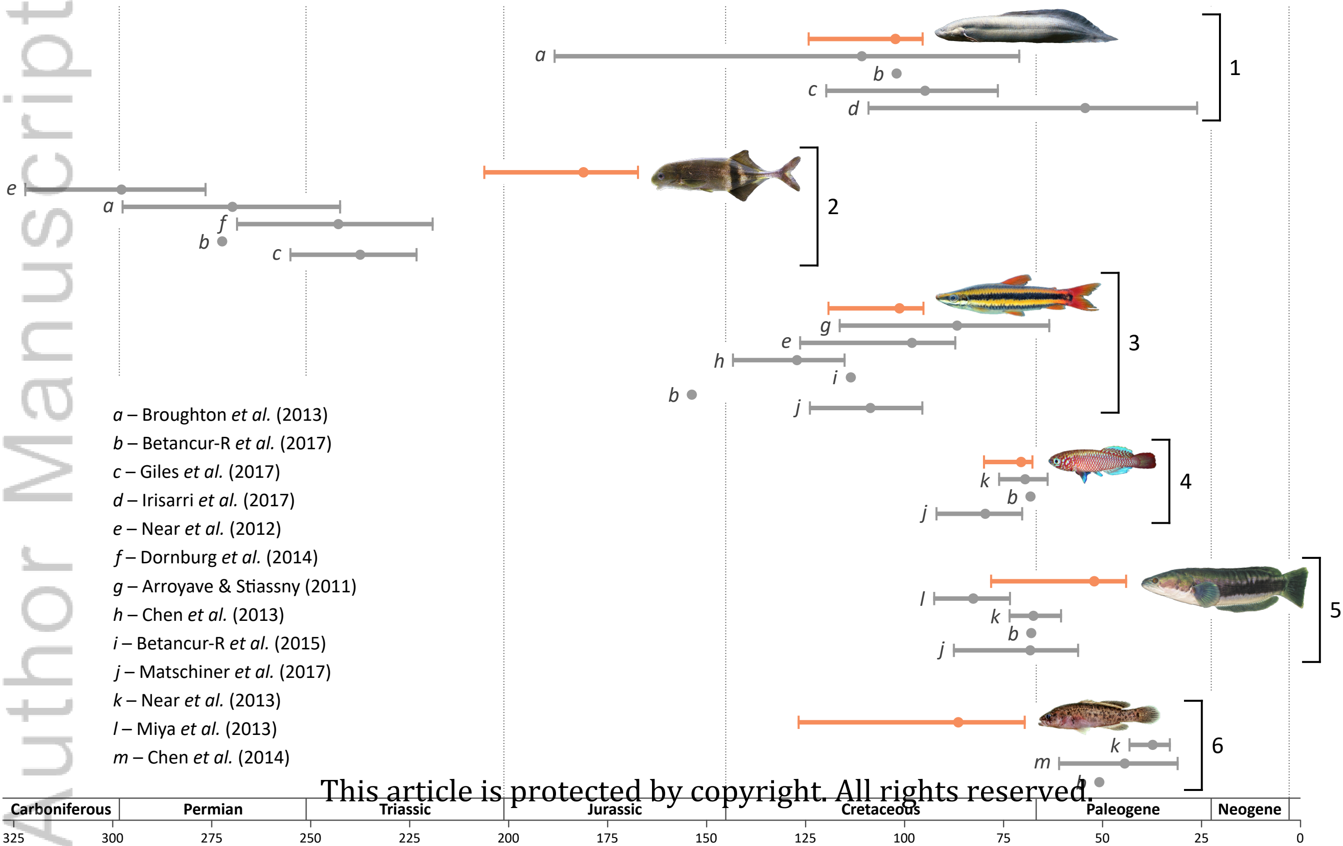
Galaxiidae
Jurassic
Cretaceous
Paleogene
Neogene
175
150
125
100
75
50
25
0
Time (Ma)
Number of fossil horizons
0
1
2
3
4
5


Cyprinodontiformes
Jurassic
Cretaceous
Paleogene
Neogene
175
150
125
100
75
50
25
0
Time (Ma)
Number of fossil horizons
25
20
15
10
5
0


Channidae
Jurassic
Cretaceous
Paleogene
Neogene
175
150
125
100
75
50
25
0
Time (Ma)
Number of fossil horizons
10
8
6
4
2
0


6
4
2
0
Number of fossil horizons
Percichthyidae
Jurassic
Cretaceous
Paleogene
Neogene
175
150
125
100
75
50
25
0
Time (Ma)


Lepidosireniformes
Osteoglossomorpha
Characiformes
Cyprinodontiformes
Channidae
Percichthyidae
Jurassic
Cretaceous
Paleogene
Neogene
200
175
150
125
100
75
50
25
0
155 Ma
135 Ma
85 Ma
55 Ma
20 Ma


1
2
3
4
5
6
a
b
c
d
e
f
g
h
i
j
k
l
m
a – Broughton et al. (2013)
b – Betancur-R et al. (2017)
c – Giles et al. (2017)
d – Irisarri et al. (2017)
e – Near et al. (2012)
f – Dornburg et al. (2014)
g – Arroyave & Stiassny (2011)
h – Chen et al. (2013)
i – Betancur-R et al. (2015)
j – Matschiner et al. (2017)
k – Near et al. (2013)
l – Miya et al. (2013)
m – Chen et al. (2014)
Carboniferous
Permian
Triassic
Jurassic
Cretaceous
Paleogene
Neogene
325
300
275
250
225
200
175
150
125
100
75
50
25
0