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REVIEW

Origins of Afrotropical freshwater fishes

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The Afrotropics house a diverse freshwater ichthyofauna with > 3000 species, almost all of which are endemic. Recent progress in dated phylogenetics and palaeontology of several groups of Afrotropical freshwater fishes (AFFs) has allowed the testing of palaeoecology- and palaeogeography-based hypotheses explaining their early presence in Africa. Seven hypotheses were tested for 37 most-inclusive monophyletic groups of AFFs. Results indicated that ten lineages originated from direct, but asynchronous, marine-to-freshwater shifts. These lineages contribute < 2% to the current AFF species richness. Eleven lineages colonized the Afrotropics from the Orient after the Afro-Arabian plate collided with Eurasia in the early Oligocene. These lineages contribute ~20% to the total diversity. There are seven sister relationships between Afrotropical and Neotropical taxa. For only three of them (4% of the species diversity), the continental drift vicariance hypothesis was not rejected. Distributions of the other four younger trans-Atlantic lineages are better explained by post-drifting long-distance dispersal. In those cases, I discuss the possibility of dispersal through the Northern Hemisphere as an alternative to direct trans-Atlantic dispersal. The origins of ten AFF lineages, including the most species-rich Pseudocrenilabrinae (> 1100 species), are not yet established with confidence.

ADDITIONAL KEYWORDS: Africa – ancestral area reconstruction – biogeography – phylogeny.

INTRODUCTION

Freshwater organisms are generally considered to be good models for studying intercontinental biogeography relative to tectonic, geographical and climatic changes over geological time, because of their physiological intolerance of salinity and their restricted dispersal capacities necessitating physical connections among freshwater systems. However, it is not well known from where, when and how these organisms originated in each continental region, because either there are conflicts between observed patterns and hypothesized processes or there is a lack of study. Such information is relevant from a historical biogeographical perspective and for studying post-invasion consequences, such as adaptations to new environments and diversification dynamics. In this work, I used information in the recent literature on phylogeny, palaeontology and geology to test common biogeographical hypotheses on the origins of the diverse Afrotropical freshwater fish (AFF) fauna in order to reveal general patterns of origin and infer their causes.

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FRESHWATER FISHES

The ray-finned fishes (Actinopterygii) comprise > 33 000 described and valid species (Fricke *et al.*, 2018), representing more than half of total vertebrate diversity. About half of ray-finned fishes live in freshwater environments, which comprise < 1% of the surface of the total aquatic environment but represent highly fragmented and complex physical environments suitable for diversification and speciation (Nelson *et al.*, 2016). As a corollary, the freshwater-fish fauna is geographically well structured, often with a high level of regional and continental endemism, especially in tropical regions.

The ecology of early aquatic vertebrates, including the ancestors of ray-finned fishes, has been debated, although there is a consensus that they were marine adapted, or

at least able to endure some degree of salinity (Halstead, 1985; Griffith, 1987; Betancur-R *et al.*, 2015). This means that strictly freshwater-adapted fishes originated later, from at least one complete evolutionary transition from a marine environment to a freshwater environment. Given that freshwater ray-finned fishes do not form a monophyletic group, being widely scattered throughout the phylogenetic tree of fishes, more than one marine-to-freshwater event must be hypothesized to explain the total diversity of freshwater fishes, combined with possible (reverse) freshwater-to-marine events (Vega & Wiens, 2012; Betancur-R *et al.*, 2015). However, it is not known with precision how many habitat transitions occurred (and where and how those transitions occurred) in the course of ray-finned fish evolution. Recent work on some subgroups of the Teleostei that contain both freshwater and marine species showed that, in general, evolutionary transitions from a marine to a freshwater environment (and vice versa) are relatively rare events on a geological time scale (Yamanoue *et al.*, 2011; Bloom & Lovejoy, 2012; Davis *et al.*, 2012; Lavoué *et al.*, 2013; Conway *et al.*, 2017), but there are some complex situations, such as those found in Atheriniformes and Beloniformes, with multiple complete and incomplete ecological transitions needed to explain the observed habitat preference patterns (Campanella *et al.*, 2015). The rarity of such marine–freshwater habitat transitions might be attributable to the necessity of both physiological adaptations to a new environment (e.g. osmoregulation system adaptation) and ecological opportunities (e.g. a new environment with low selective pressures). Such a general evolutionary trend is called 'phylogenetic niche conservatism', in which descendants tend to maintain the ecological preferences of their ancestors (Wiens & Graham, 2005; Donoghue, 2008; Losos, 2008; Crisp *et al.*, 2009).

The Afrotropical region

Following Sclater (1858), Wallace (1876) divided the continental lands (including their freshwater systems) into six zoogeographical regions based on overall tetrapod (i.e. mammals, birds and non-avian reptiles) faunistic similarities: Nearctic, Palaearctic, Australian (= Australasian), Neotropical, Oriental and Ethiopian (now called Afrotropical [Crosskey & White, 1977]) regions. This division scheme is still largely accepted today, with only a few refinements (Holt *et al.*, 2013; Kreft & Jetz, 2013), such as recognition of regions of transition (owing to secondary biotic contact between two distinct biogeographical regions) (Fig. 1). Three main determinants were recently recognized separating these regions: oceanic areas through tectonic movements, climate through temperature and mountain ranges through elevation (Ficetola *et al.*, 2017). However, this scheme provides little information on the origin and evolution of their faunas and on intercontinental faunistic exchanges that have occurred.

Geological context: African tectonics from the Early Cretaceous to the end of the Miocene

By the Late Jurassic (163–145 million years ago [Mya]), the supercontinent Pangaea became fragmented into a southern continent, called Gondwana, which included

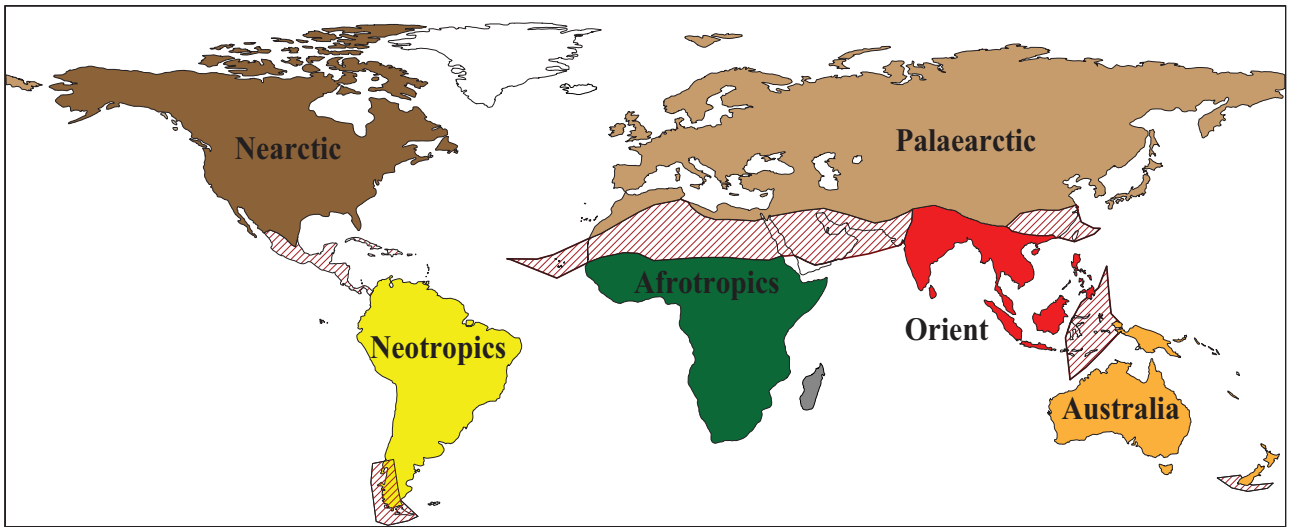

Figure 1. Schematic world map, on which the six main terrestrial–freshwater biogeographical regions are indicated (i.e. the Nearctic, Palaearctic, Oriental, Neotropical, Australian and Afrotropical regions). Transition zones between these biogeographical regions are hatched. Modified from Wallace (1876) and Kreft *et al.* (2013).

Africa, and a northern continent, called Laurasia (Scotese, 1991; Lawver *et al.*, 2007; Matthews *et al.*, 2016; Muller *et al.*, 2016; Torsvik and Cocks, 2016) (Fig. 2). In the Early Cretaceous, Gondwana divided further into two: West Gondwana, comprising Africa and South America, and East Gondwana, including Madagascar, India, Antarctica and Australia. Yet, land connections existed between the southernmost regions of South America, Antarctica and Australia until the early Cenozoic (Scotese, 1991; Smith *et al.*, 1994; Lawver *et al.*, 2007; Muller *et al.*, 2016; Torsvik and Cocks, 2016). Africa and South America then gradually began to separate from each other, and contact between the two continents definitively ended ~105–100 Mya (in the middle Albian), when a continuous north–south seaway separated the two landmasses (Granot & Dyment, 2015; Müller *et al.*, 2016). This seaway subsequently expanded longitudinally to become the Atlantic Ocean. During the next ~70–80 million years (Myr), from the mid-Cretaceous (105 Mya) to, at least, the very late Eocene (~35 Mya; see Allen & Armstrong, 2008) or, at the latest, the early Miocene (23 Mya; see Meulenkamp & Sissingh, 2003), Africa was mostly surrounded by marine environments and, consequently, its freshwater fauna must have been largely isolated from those of other continental landmasses (Smith *et al.*, 1994; Lawver *et al.*, 2007; Müller *et al.*, 2016). Such isolation (in some ways, comparable to the South America splendid isolation concept of Simpson, 1980) explains the high level of endemism of Afrotropical organisms, especially freshwater fishes, with several higher-level taxa of fish unique to this continental region, such as the families Mormyridae and Gymnarchidae (Osteoglossiformes), Kneriidae and Phractolaemidae (Gonorynchiformes),

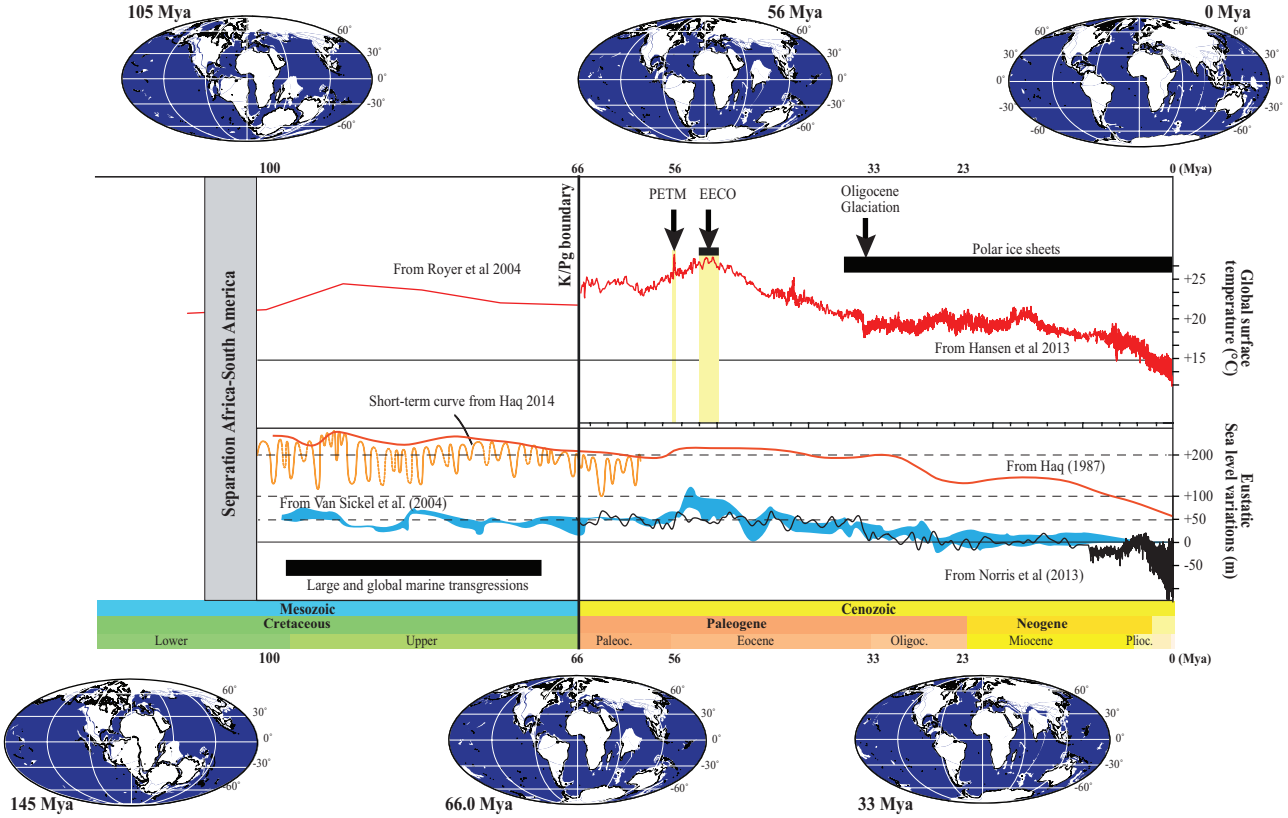

Figure 2. Selected world palaeogeographical reconstructions along with global sea-level and temperature variations during the last 105 Myr (i.e. after the final separation of Africa and South America). World plate tectonic map reconstructions are shown at 145 (separation of Laurasia and Gondwana), 105 (separation of Africa and South America), 66 [the Cretaceous–Palaeogene (K/Pg) boundary], 56 [Palaeocene–Eocene thermal maximum (PETM)], 33 (Oligocene glaciation) and 0 Mya (present); maps were created at www.odsn.de with data from Hay *et al.* (1999). Continental plates and continental fragments are shown in white. The Cenozoic temperature variation curve is modified from Hansen *et al.* (2013). Two major climatic events are indicated: the PETM and the early Eocene climate optimum (EECO). Three different long-term sea-level variation estimations during the late Mesozoic and Cenozoic are shown: the blue curve is from Van Sickel *et al.* (2004), the black curve is from Norris *et al.* (2013), and the red curve is from Haq (1987). Short-term sea level variations are from Haq (2014).

Citharinidae and Distichodontidae (Characiformes), Malapteruridae and Mochokidae (Siluriformes).

Nonetheless, this isolation was not total, as evidenced by the fossil record and by the presence of Africa-related freshwater and terrestrial organisms in some late Mesozoic and early and middle Cenozoic deposits of Europe (Murray, 2001a; Cavin *et al.*, 2005; Otero *et al.*, 2008; Costa, 2012; Gaudant, 2013; Rage, 2013; Gaudant, 2014). Cavin *et al.* (2005) reported a Cretaceous (90 Mya) coelacanth from non-marine deposits of Europe having Gondwanan affinities; Otero (2008) mentioned characid fishes (similar to African alestins) from the Late Cretaceous (Maastrichtian) of Transylvania, Romania, and fossil cyprinodontoids were excavated from Europe (Oligocene–Miocene; Costa, 2012; Gaudant, 2013). These fish fossils, along with some terrestrial tetrapod fossils, suggest that trans-Tethyan freshwater and terrestrial dispersals between Africa and western Europe through sporadic routes pre-dated the Miocene (Gheerbrant & Rage, 2006). This led, in part, to the Late Cretaceous–early Cenozoic palaeoprovince concept of Eurogondwana, comprising southern Europe and north Africa (Le Loeuff, 1991).

Towards the end of the Oligocene (~25–23 Mya), an eastern biogeographical route is better documented from geological data (Meulenkamp & Sissingh, 2003). At that time, the African plate, in its slow northward motion, eventually collided with the Eurasian plate, causing closure of the Tethys Sea and the formation of a permanent terrestrial connection between the northeastern African region (through the Arabian plate) and both the southwestern Palaearctic and western Oriental regions. This terrestrial connection provided opportunities for continental interchanges, which may have been limited only by prevailing climatic conditions in the region. These continental interchanges between Africa and the Orient, from the late Oligocene–early Miocene, are documented for several freshwater, semi-aquatic and terrestrial organisms (Menon, 1951; Greenwood, 1974; Van Couvering, 1977; Otero, 2001; Stewart, 2001; Murray, 2006).

Global sea-level changes from the Late Cretaceous to mid-Cenozoic

Global sea levels varied through geological time, and these variations are important parameters in terrestrial/freshwater historical biogeography, because they alternately exposed and closed oversea connections. Alternatively, they may also have provided opportunities for marine-adapted organisms to invade freshwater environments during marine transgressions on continental landmasses (Bloom & Lovejoy, 2017). The Late Cretaceous–early Cenozoic sea level was 50–120 m above the present sea level (Van Sickel *et al.*, 2004; Miller *et al.*, 2005; Norris *et al.*, 2013) (Fig. 2). The maximal sea level, perhaps as high as 170 m above the present, occurred in the early Eocene and slowly receded through the Eocene and Oligocene (Van Sickel *et al.*, 2004; Norris *et al.*, 2013). The overall amplitude of the sea-level curves estimated by Van Sickel *et al.* (2004) and Norris *et al.* (2013) (Fig. 2) conflict with those of Haq *et al.* (1987) and Haq (2014), which are ~100 m higher. Van Sickel *et al.* (2004) provided possible reasons explaining the difference observed between their results and those of Haq *et al.* (1987). A eustatic cause for these sea-level changes is likely, given their remarkable similarities in timing and amplitude in different locations (Sahagian *et al.*, 1996; Miller *et al.*, 1998). From the late Eocene (< 33 Mya), the sea-level amplitude slowly decreased to reach the present level through glacioeustatic control (Miller *et al.*, 1998).

High sea levels that occurred in the Late Cretaceous, Palaeocene and Eocene may have contributed to accentuating the physical isolation of several continental regions by covering lowland areas with salt water. During this period, large marine transgressions covered large parts of several continental regions, including west-central Africa (Giresse, 2005; Barnett-Moore *et al.*, 2017) (Fig. 2). These transgressive episodes are hypothesized to have played key roles in the distribution of some marine fish groups, but their effects on the biogeography of AFFs are not yet known.

Global temperatures and palaeoclimates during the Cenozoic

In contrast to the present day, the Late Cretaceous–early Cenozoic period was characterized by strikingly much warmer mean global temperatures (up to 12 °C higher than those of the present day), along with poles with reduced and not permanent ice sheets and, importantly, a reduced latitudinal temperature gradient (Fig. 2) (Zachos *et al.*, 2001, 2008; Hansen *et al.*, 2013).

During this period, large fluctuations in temperature occurred. This was particularly notable during the early Cenozoic, with periods of intense warming. The two most extreme cases are the Palaeocene–Eocene thermal maximum (PETM), a 200 000-year-long period that occurred ~56 Mya, and the early Eocene climatic optimum (EECO) between 53 and 51 Mya, when global temperatures reached a maximum (Fig. 2). After the EECO, global temperatures gradually decreased until the limit of the Eocene–Oligocene (at ~33.9 Mya). Then, a sharp decrease in global temperatures ended the greenhouse conditions, which gave rise to icehouse conditions and the formation of permanent polar ice sheets (Zachos *et al.*, 2008; Eldrett *et al.*, 2009) (Fig. 2).

Warm periods were also characterized by shifts in the distribution and intensity of precipitation (Bowen *et al.*, 2004). In particular, climates of regions in high latitudes were wetter, with increased precipitation events and massive flooding (Zachos *et al.*, 2008),

fostering widespread boreotropical forests (Zachos *et al.*, 2008; Hansen *et al.*, 2013; Herold *et al.*, 2014). These forests enabled expansion of tropical biota in northern regions (Wolfe, 1975; Harrington *et al.*, 2012; Herold *et al.*, 2014; Kooyman *et al.*, 2014).

After the Eocene, the rapid decrease in global temperatures drove the extinction of warm-adapted organisms from most Nearctic and Palaearctic regions and definitively closed any pre-Oligocene Holarctic routes for tropical organisms (Prothero & Berggren, 1992).

Diversity and affinities of Afrotropical freshwater fishes

The AFF fauna is taxonomically highly diversified (Roberts, 1975; Lowe-McConnell, 1988; Skelton & Swartz, 2011), and it represents one of the three continental-scale tropical freshwater faunas, with the Neotropical one (Albert, 2011; Reis *et al.*, 2016) and the Oriental one (Kottelat, 2013). More than a decade ago, Lévêque *et al.* (2008) listed 48 families (15 endemic) and 2945 species of AFFs.

The early evolution of AFFs first attracted the attention of biogeographers because of the similarity of some elements of this fauna to that of the Neotropics, which was noted more than a century ago (Eigenmann, 1912; Regan, 1922), well before the theory of continental drift of Wegener (1915) transformed the field of biogeography (Hallam, 1967; Gosline, 1975; Patterson, 1975). Intercontinental distribution patterns observed among some Afrotropical–Neotropical fishes are similar to those of some other faunistic and floristic organisms [e.g. rodents (Coster *et al.*, 2010), blindsnakes (Vidal *et al.*, 2010), amphisbaenians (Longrich *et al.*, 2015) and angiosperm family Malpighiaceae (Davis *et al.*, 2004)], leading to the conclusion that common causes could explain such recurrent distribution patterns.

The repeated sister-group relationships between Afrotropical and Neotropical lineages have therefore fuelled discussions of the importance of continental drift-mediated vicariance relative to post-drift dispersal (Myers, 1938; Schaeffer, 1952; Gosline, 1975; Roberts, 1975; Novacek & Marshall, 1976; Goldblatt, 1993; Lundberg, 1993; Maisey, 2000; Briggs, 2005; Cavin *et al.*, 2008; Albert, 2011; Cavin, 2017; McIntyre *et al.*, 2017). Even though continental drift vicariance is the best explanatory hypothesis, recent time-calibrated molecular phylogenetic trees showed that some trans-Atlantic divergences post-dated separation of Africa and South America (Lundberg *et al.*, 2007; Chen *et al.*, 2013; Friedman *et al.*, 2013; Lavoué, 2016; Matschiner *et al.*, 2017). In those cases, alternative hypotheses involving marine dispersal and/or freshwater dispersal (e.g. through geodispersal; see Wiley & Lieberman, 2011) must be considered instead of only vicariance associated with continental fragmentation (de Queiroz, 2005; Upchurch, 2008). Thus, both vicariance and dispersal processes are important in explaining distributions of trans-Atlantic freshwater fishes, but their relative importance is unknown. Although molecular dating studies documented necessary long-distance dispersal between Africa and South America after their separation, the mechanistic hypotheses that explain how fishes dispersed from one continent to the other are rarely discussed.

Another characteristic of the AFF fauna is its even closer similarity at the familial and generic levels to the (tropical) Oriental fauna. This is probably attributable to post-Oligocene faunistic exchanges between Africa and the Orient facilitated by the establishment of a permanent land connection between these two regions (e.g. Menon, 1951; Greenwood, 1974; Roberts, 1975; Van Couvering, 1977; Otero & Gayet, 2001; Meulenkamp & Sissingh, 2003; Oliver *et al.*, 2015). However, the number and direction of these dispersal events are still not fully known, and it is also not known whether this land connection explains all Afrotropical–Oriental freshwater fish relationships.

Afrotropical freshwater fossil record

Fossils are the only direct evidence for the past presence of a taxon at a given time and place. Fossils can also inform us about the dynamics of origination and extinction of a taxonomic group and its ecological evolution through habitat preferences of its early members (Grande, 1985b). The fish fossil record of continental African waters provides a wealth of information regarding the taxonomic composition of fish assemblages through geological time, as evidenced by the recent (i.e. the last two decades) work of L. Cavin, A. M. Murray, O. Otero and K. M. Stewart, among other pre-eminent palaeontologists. However, for some taxonomic groups (e.g. Pellonulini, Synbranchidae and Aplocheiloidei), some geological periods (e.g. the Palaeocene) and some African regions (e.g. central Africa), fish fossils are rare or absent. Despite these limitations, the study of the AFF fossil record reveals a faunal turnover that occurred between the middle Cretaceous, at the time of the separation of Africa and South America, with a rather primitive fauna with many non-teleost fish lineages and few primitive-looking teleosts, and the middle Eocene, with a fauna dominated by modern teleost fish lineages (reviewed by Greenwood, 1974; Van Couvering, 1977; Murray, 2000b; Stewart, 2001; Otero, 2010; Cavin *et al.*, 2010, 2015).

Middle to Late Cretaceous

The continental (freshwater and brackish) middle Cretaceous (i.e. Cenomanian, 100.5–93.9 Mya) fish

assemblages from north Africa (specifically, from Morocco and Egypt) are relatively well studied (Cavin *et al.*, 2010, 2015), and they consistently reveal the presence of several groups of non-teleost fishes. These include the sarcopterygian dipnoi (i.e. lungfish of the Ceratodontidae and Neoceratodontidae, with both families now extinct in Africa) and actinistian (i.e. coelacanths of the Mawsoniidae, extinct), the non-teleost actinopterygian Cladistia (Polypteridae), Holostei Amiiformes (including the Amiidae; extinct in Africa and with only one extant species of *Amia calva* Linnaeus, 1766 restricted to North America) and Holostei Semionotiformes–Lepisosteiformes [including freshwater Lepisosteidae; extinct in Africa, and with only a few extant species restricted to North and Central America, Nearctic (Cavin *et al.*, 2010; Grande, 2010)], and teleost Ichthyodectiformes (extinct), Tselfatiiformes (extinct), Notopteroidei (with †*Palaeonotopterus greenwoodi* Forey, 1997) and some undetermined characiform remains along with some possible remains of Siluriformes. This fauna shows strong affinities with that of South America at that time (Cavin *et al.*, 2010, 2015).

Early to middle Cenozoic (Palaeocene and Eocene)

The Cretaceous–Palaeogene (K/Pg; 66 Mya) transition is marked by exceptional volcanic activities and the collision of a large extraterrestrial bolide in the Caribbean region (Schulte *et al.*, 2010). This led to the last [not mentioning the ongoing one (e.g. Ceballos *et al.*, 2017)] major biological mass extinction on earth, sometimes referred as to the Fifth Extinction). This mass extinction event was not taxonomically uniform, with some groups of organisms being more impacted than others. Although the freshwater fish fauna is considered to have been less disturbed than was marine fauna by the K/Pg extinction event, the fossil record of the AFF fauna reveals important changes, with the complete or partial extinctions of several non-teleost groups of fishes (e.g. Actinistia, Amiiformes, Lepisosteidae) and the nascent diversification of the Teleostei, with early records of several teleost subgroups. Freshwater-fish fossils are rare in the aftermath of the K/Pg extinction event [except for the earliest record of the Claroteidae, †*Nigerium gadense* White, 1935 and †*Nigerium wurnoense* White, 1935 (Longbottom, 2010)] and the earliest and most renowned palaeontological locality after this event is the Mahenge site (Tanzania) of middle Eocene age (46–45 Mya), where fish fossils are abundant, well preserved and very diversified (Murray, 2000a; Kaiser *et al.*, 2006). At this site, palaeontologists documented the first record (and sometimes the only one) of several groups of extant Afrotropical teleosts, such as the Denticipitidae with †*Paleodenticeps tanganikae* Greenwood, 1960, Pantodontidae with †*Singida jacksonoides* Greenwood & Patterson, 1967 and †*Chaulioparei on mahengeense* Murray & Wilson, 2005, Alestidae with †*Mahengecharax carrolli* Murray, 2003, the Kneriidae+Phractolaemidae lineage with †*Mahengichthys singidaensis* Davis, Arratia & Kaiser, 2013, Citharinoidei with †*Eocitharinus macrognathus* Murray, 2003 and Cichlidae with five species of †*Mahengechromis* (Greenwood, 1960; Murray, 2000a, 2001b; Murray & Wilson, 2005; Davis *et al.*, 2013; Lavoué, 2016).

In addition, other, often more-recent, Eocene localities in North Africa, such as the late Eocene Birket Qarun Formation, Fayum, Egypt (Murray *et al.*, 2010), the middle Eocene Dur At-Talah site from Libya (Otero *et al.*, 2015) and the late Eocene/Oligocene Jebel Qatrani Formation, Fayum, Egypt (Murray, 2004) have revealed the presence of a gymnarchid (†*Gymnarchus* sp., 37 Mya), a claroteid (†*Nigerium tamaguelense* Longbottom, 2010, 56–41 Mya), an alestid (†*Hydrocynus* sp., 56–41 Mya; Hammouda *et al.*, 2016), a latid (†*Lates qatraniensis* Murray & Attia, 2004, 33.9 Mya), a channid (†*Parachanna fayumensis* Murray, 2006, 37–36 Mya) and a freshwater clupeid (†*Chasmoclupea aegyptica* Murray, Simons & Attia, 2005, 33 Mya) that seem to have no close relationship with the Afrotropical freshwater tribe Pellonulini and, possibly, remains of the catfish families Mochokidae and Schilbeidae, and Cichlidae along with remains of older but still living freshwater lineages, such as the Protopteridae and Polypteridae.

Late Cenozoic (Oligocene and Miocene)

According to palaeontologists, Oligocene and upper Miocene deposits with freshwater fish are relatively infrequent in Africa, but these rare deposits indicate one further step towards the building of the modern AFFs, with the first documented presence of Oriental-derived groups, such as Bagridae (†*Bagrus* sp., 30 Mya; but see Gayet & Otero, 1999), Clariidae (†*Clarias* sp., 30 Mya) and Cyprinidae (Otero, 2001), along with continuous records of Mochokidae, Cichlidae, Alestidae, Protopteridae and Polypteridae (Otero & Gayet, 2001). Additionally, Otero *et al.* (2017) described an ichthyological fauna from the late Oligocene locality of Lokone, Kenya (~28 Mya), that includes †*Protopterus* sp., †*Polypterus* sp., †*Heterotis* sp., †*Gymnarchus* sp., †*Hydrocynus* sp., one species of the extinct alestid genus †*Sindacharax*, along with other possible remains of alestids, a claroteid, a cichlid and †*Distichodus* sp. As inferred, the palaeoenvironmental conditions of north Africa and the Arabic region during the Oligocene–Miocene must have been warm and humid, possibly similar to the present climatic conditions found in much of tropical Africa.

Objectives of this study

The relative contributions of direct marine-to-freshwater shifts, vicariance events and dispersal events to construction of the AFF fauna have not recently been evaluated critically. Herein, I attempted to provide a time-calibrated phylogenetic test to determine the multiple evolutionary origins of the AFF fauna. Data on these lineages are based on a literature review of their diversity, habitat preferences, phylogenetic relationships, time divergence and fossil records. Recent morphology-based and molecular-based phylogenetic works provide the backbone of this study: (1) of identifying most-inclusive monophyletic groups of AFFs (a few of them secondarily extended their distribution to another continental region); (2) of identifying the closest outgroups of each of these lineages, including their sister group (= their phylogenetic position); (3) of inferring the ecological preferences (relative to salinity) of their most ancient common ancestors by outgroup comparisons and maximum-likelihood (ML) criterion; (4) of inferring the geographical origins of their most ancient common ancestors using ancestral range estimation methods; (5) of estimating the age (within maximal and minimal limits when available) of the evolutionary events (regarding the salinity preference and continental distributions) leading to the initial presence of each Afrotropical freshwater group; and (6) of comparing these ecological distribution patterns against geology, palaeoclimate and sea-level fluctuations to uncover possible common processes.

MATERIAL AND METHODS

The limits of the Afrotropical region and the list of its freshwater fish taxa

The region examined corresponds to the freshwater systems of the Afrotropical region as identified by Alfred Russel Wallace (1876), with the exclusion of those of Madagascar, but the inclusion of those of the most southern region of Africa, the Cape region and the entire Nile River basin. The arid and xeric northern African and Arabian regions are excluded, because these are currently considered transitional regions between the Afrotropics, Palaearctic and Orient (Doadrio, 1994; Kreft & Jetz, 2013) (Fig. 1). Moreover, in the absence of large perennial freshwater habitats, these northern African and Arabian regions are the home of a few freshwater fish species that are generally of recent origins (Doadrio, 1994; Lévêque, 1990).

At the family level, a list of AFF taxa (including non-actinopterygian fish taxa) was compiled from Berra (2007) and cross-checked using Lévêque *et al.* (2008) and the online database *Faunafri* (Paugy *et al.*, 2008). I chose to follow the revised classification of Wiley & Johnson (2010), with some modifications made by Eschmeyer & Fong (2011), Nelson *et al.* (2016), Betancur-R *et al.* (2017) and Tan & Ambruster (2018).

The AFF list was trimmed to exclude most taxa that are not strictly confined to freshwater habitats, because of their presupposed marine dispersal abilities owing to their salinity tolerance (Whitfield, 2005). However, to confirm this assumption I briefly reviewed the origins of these euryhaline (including diadromous species) and brackish taxa. Whitfield (2005) established a list of sub-Saharan fish species living in or transiting the estuaries that he classified into seven guilds according to how they use this habitat (see Elliott *et al.*, 2007; Potter *et al.*, 2015). Two of these guilds (marine immigrants and stragglers) deal with marine fish species that I will not consider further (they include all species of Antennariidae, Belonidae, Carangidae, Carcharhinidae, Drepanidae, Gerreidae, Haemulidae, Lutjanidae, Monodactylidae, Moronidae, Mugillidae, Polynemidae, Pristidae, Pristigasteridae, Sciaenidae and Serranidae). Two other guilds (freshwater immigrants and stragglers) deal with freshwater lineages that are already examined in this study (e.g. Cichlidae, Clariidae). The last three guilds deal with estuarine residents and migrants and with catadromous migrants, for which I commented on their origins. Only subtropical and tropical species are considered.

Searching for Afrotropical lineages

To examine the origins of the AFF fauna, I considered only the most-inclusive monophyletic lineages of AFFs (i.e. AFF groups having their earliest common ancestors in the Afrotropical freshwaters, with only few of them, later, dispersed out of Africa). I did not consider any formal taxonomic ranks, such as family, because, although useful to classify organisms, they are arbitrary and provide only incomplete information on the early evolution of their members. For example, the origins of the families Gymnarchidae, Mormyridae and Notopteridae were not considered separately, because they form a group of Afrotropical fishes (Lavoué & Sullivan, 2004). These three families evolved from a common and exclusive Afrotropical freshwater ancestor. In contrast, the Afrotropical cyprinids form a polyphyletic group within the worldwide-distributed family Cyprinidae (*sensu* Tan & Armbruster, 2018). The Afrotropical cyprinids comprise several phylogenetically independent lineages that have invaded the Afrotropics separately. In this case, I specifically examined the origin of each of these Afrotropical cyprinid lineages.

From a literature survey of recent phylogenetic works, I identified 37 most-inclusive monophyletic lineages of AFF (Table 1; Figs 3–5). The online version of the *Catalog of Fishes* (Fricke *et al.*, 2018; consulted

Table 1. List of the 37 Afrotropical freshwater fish lineages ('M', 'G', 'V' and 'U') examined in this study along with the three or four lineages ('O') that dispersed from the Afrotropics

Afrotropical freshwater fish lineage	Afrotropical diversity	Living non-Afrotropical sister group	Maximal age (stem group; Mya)	Minimal age (crown group; Mya)	Ancestral habitat	Biogeographical process inferred
M1: Afrotropical freshwater *Fontitrygon*	Two species	Unresolved	115	5?	Marine	Marine-to-freshwater transition
M2: *Denticeps clupeoides*	One species	Clupeoidei	145	45 (strict)	Marine	Marine-to-freshwater transition
M3: Pellonulini	22 species	*Ethmalosa fimbriata*	60	17 (older?)	Marine	Marine-to-freshwater transition
M4: Kneriidae + Phractolaemidae	30 species	Chanidae	> 150	107 Mya	Marine	Marine-to-freshwater transition
M5: *Arius brunellii*	One species	Unresolved	19	5?	Marine	Marine-to-freshwater transition
M6: *Carlarius gigas*	One species	Unresolved	19	5?	Marine	Marine-to-freshwater transition
M7: Afrotropical freshwater *Tetraodon*	Five species	*Chelonodon*	17	7	Marine	Marine-to-freshwater transition
M8: Afrotropical freshwater *Lates*	Seven species	*Psammoperca wiagensis*	62.5	33.9	Marine?	Marine-to-freshwater transition
M9: *Dagetichthys lakdoensis*	One species	Rest of *Dagetichthys*	30	5?	Marine	Marine-to-freshwater transition
M10: *Kribia*	Four species	*Oxyeleotris nullipora*?	40	5?	Brackish water?	Marine-to-freshwater transition
O1: Notopterinae	Eight species	Xenomystinae	105	60	Fresh water	Afrotropics to Orient dispersal
G1: Afrotropical chedrins	50 species	Oriental *Raiamas*	28	14.5	Fresh water	Orient to Afrotropics dispersal
G2: Afrotropical small barbs clade	220+ species	*Systomus*	30.5	23	Fresh water	Orient to Afrotropics dispersal
G3: Afrotropical *Labeobarbus*	125 species	Middle East taxa	9.5	4.6	Fresh water	Orient to Afrotropics dispersal

Table 1. *Continued*

Afrotropical freshwater fish lineage	Afrotropical diversity	Living non-Afrotropical sister group	Maximal age (stem group; Mya)	Minimal age (crown group; Mya)	Ancestral habitat	Biogeographical process inferred
G3′: *Labeobarbus habereri*	One species	Afrotropical *Labeobarbus* + Middle East taxa	13?	4.6	Fresh water	Orient to Afrotropics dispersal?
G4: Afrotropical *Garra*	17 species	Oriental *Garra rufa*	9	5	Fresh water	Orient to Afrotropics dispersal
G5: Afrotropical *Labeo*	60 species	Some Oriental *Labeo*	20	18	Fresh water	Orient to Afrotropics dispersal
G6: *Afronemacheilus*	Two species	*Nun*?	48?	5	Fresh water	Orient to Afrotropics dispersal
G7: Afrotropical clariids	80 species	Oriental clariids	35	30	Fresh water	Orient to Afrotropics dispersal
G8: *Bagrus*	Ten species	*Hemibagrus*	40	30	Fresh water	Orient to Afrotropics dispersal
G9: Afrotropical anabantids	32 species	*Anabas testudineus*	43	23	Fresh water	Orient to Afrotropics dispersal
G10: *Parachanna*	Three or four species	*Channa*	48	36	Fresh water	Orient to Afrotropics dispersal
G11: Afrotropical *Mastacembelus*	41 species	*Mastacembelus mastacembelus*	27	12	Fresh water	Orient to Afrotropics dispersal
G12: Big Africa catfish clade	450+ species	Pangasiidae?	80	58	Fresh water	Orient to Afrotropics dispersal
V1: Protopteridae	Four species	*Lepidosiren paradoxa*	> 150	94	Fresh water	South America–Africa vicariance
V2: Polypteridae	14 species	Actinopteri	> 150	94	Fresh water	South America–Africa vicariance
V3: Citharinoidei	110 species	Characoidei	145	105	Fresh water	South America–Africa vicariance
G13: Afrotropical characoids	114 species	Unresolved (Neotropical)	76	55	Fresh water	Neotropics to Afrotropics dispersal
O2: Cichlinae	≥ 500 species	Pseudocrenilabrinae	55	48 (strict)	Fresh water	Afrotropics to Neotropics dispersal
O3: *Lacantunia enigmatica*	One species	Claroteidae	60	5?	Fresh water	Afrotropics to Nearctic dispersal

Table 1. *Continued*

Afrotropical freshwater fish lineage	Afrotropical diversity	Living non-Afrotropical sister group	Maximal age (stem group; Mya)	Minimal age (crown group; Mya)	Ancestral habitat	Biogeographical process inferred
U1: *Heterotis niloticus*	One species	*Arapaima*	80	28 (strict)	Fresh water	Unresolved but post-dating the South America–Africa fragm.
U2: *Pantodon buchholzi*	One species	Rest of Osteoglossiformes	> 150	57	Fresh water?	Unresolved
U3: Afrotropical Notopteroidei	≥ 220 species	Osteoglossidae (excluding *Pantodon*)	> 150	94 (strict)	Fresh water	Unresolved but pre-dating the South America–Africa fragm.
U4: Nothobranchiidae	280 species	Aplocheilidae	60	45	Fresh water	Unresolved but post-dating the South America–Africa fragm.
U5: *Pantanodon stuhlmanni*	One species	Rest of Cyprinodontoidei	60	5?	Fresh water/ brackish water	Unresolved but post-dating the South America-Africa fragm.
U6: Procatopodinae + Aplocheilichthyinae	80 species	*Aphanius* plus *Valencia*	60	33	Fresh water	Unresolved but post-dating the South America–Africa fragm.
U7: Afrotropical polycentrids	Two species	Unresolved	95	25	Fresh water?	Unresolved but post-dating the South America–Africa fragm.
O4?: Neotropical polycentrids	Three species	*Polycentropsis abbreviata*	40	30	Fresh water	Unresolved but post-dating the South America–Africa fragm.
U8: Afrotropical *Monopterus*	Two species	(*Monopterus indicus*, *Monopterus fossorius*, *Monopterus cuchia*)	> 75	5?	Fresh water	Unresolved but post-dating the South America–Africa fragm.
U9: *Ophisternon afrum*	One species	Unresolved	> 75	5?	Fresh water	Unresolved but post-dating the South America–Africa fragm.
U10: Pseudocrenilabrinae	≥ 1100 species	Cichlinae	64	48 (strict)	Fresh water	Unresolved but post-dating the South America–Africa fragm.

Abbreviations: fragm., fragmentation; G, dispersal to Afrotropics; M, marine origin; O, dispersal from Afrotropics; U, unresolved; V, continental drift vicariant origin.

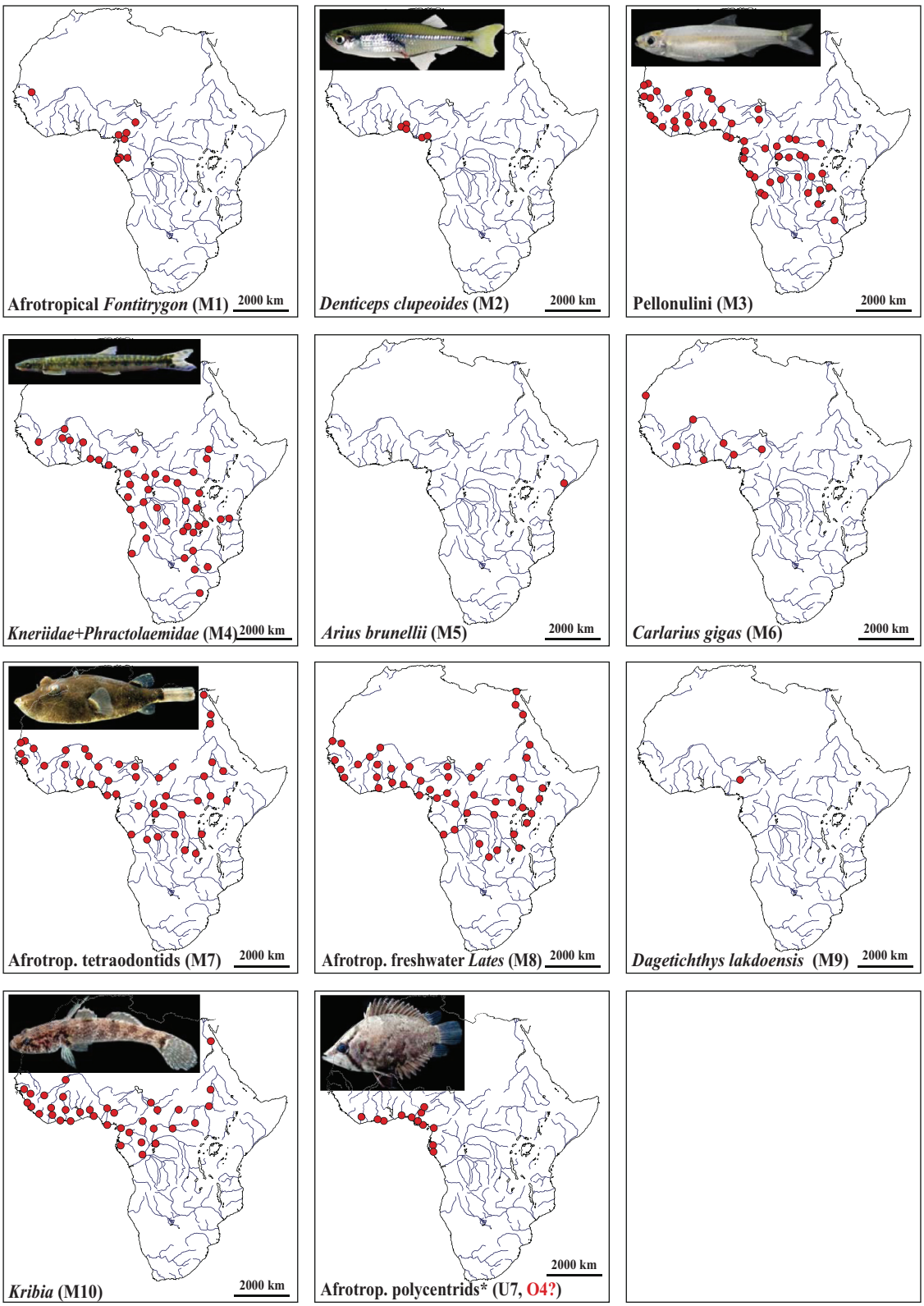

Figure 3. Schematic maps of African main freshwater systems, on which are shown separately the distributions (with red-filled circles) of 11 lineages of Afrotropical freshwater fishes (* indicates a subsequent range extension out of Africa of one sublineage). The photograph of *Kribia* has been flipped horizontally. Distributional data are from *Faunafri* (Paugy *et al.*, 2008).

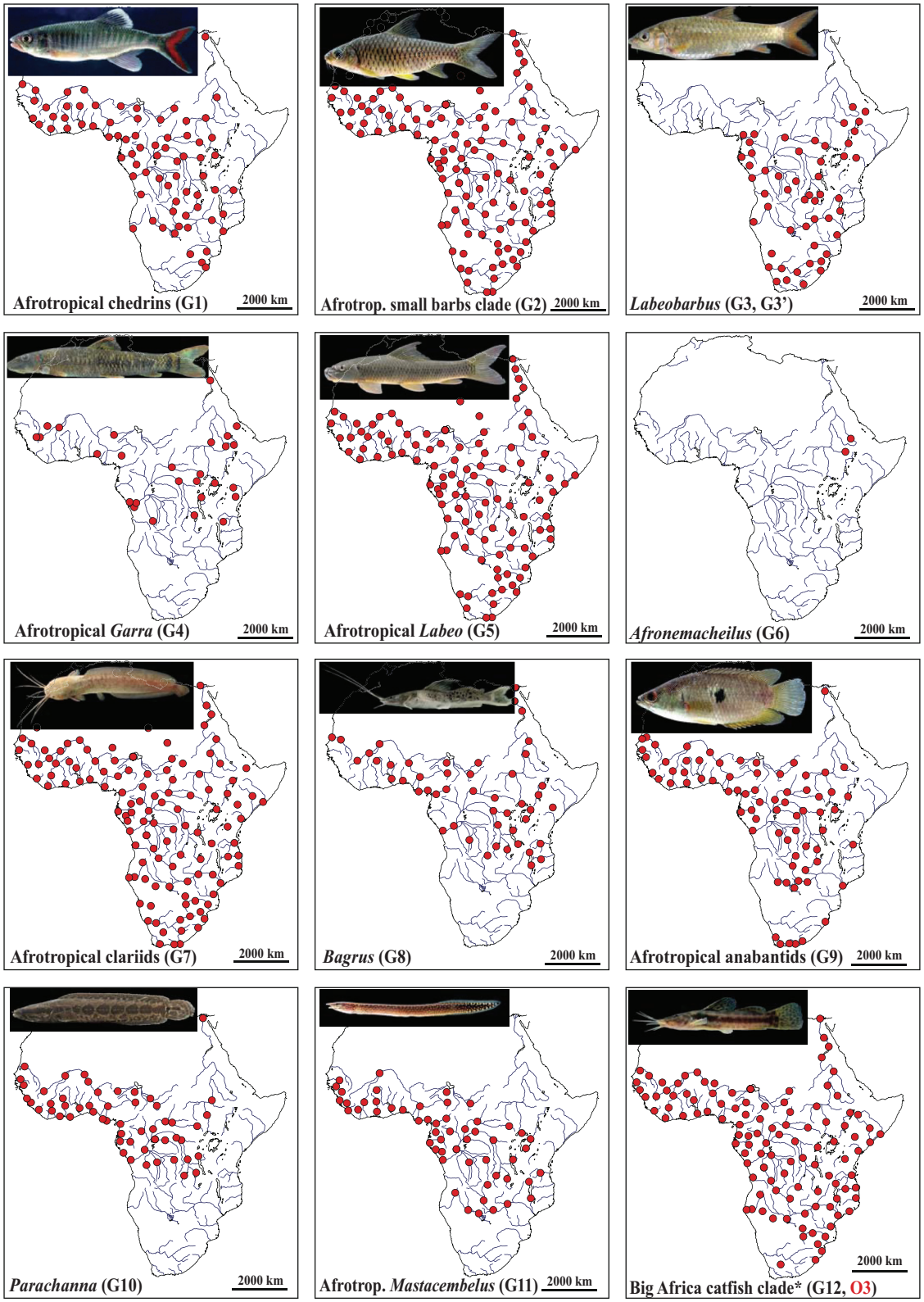

Figure 4. Schematic maps of African main freshwater systems, on which are indicated separately the distributions (with red-filled circles) of 12 lineages of Afrotropical freshwater fishes (* indicates a subsequent range extension out of Africa of one sublineage). Distributional data are from *Faunafri* (Paugy *et al.*, 2008).

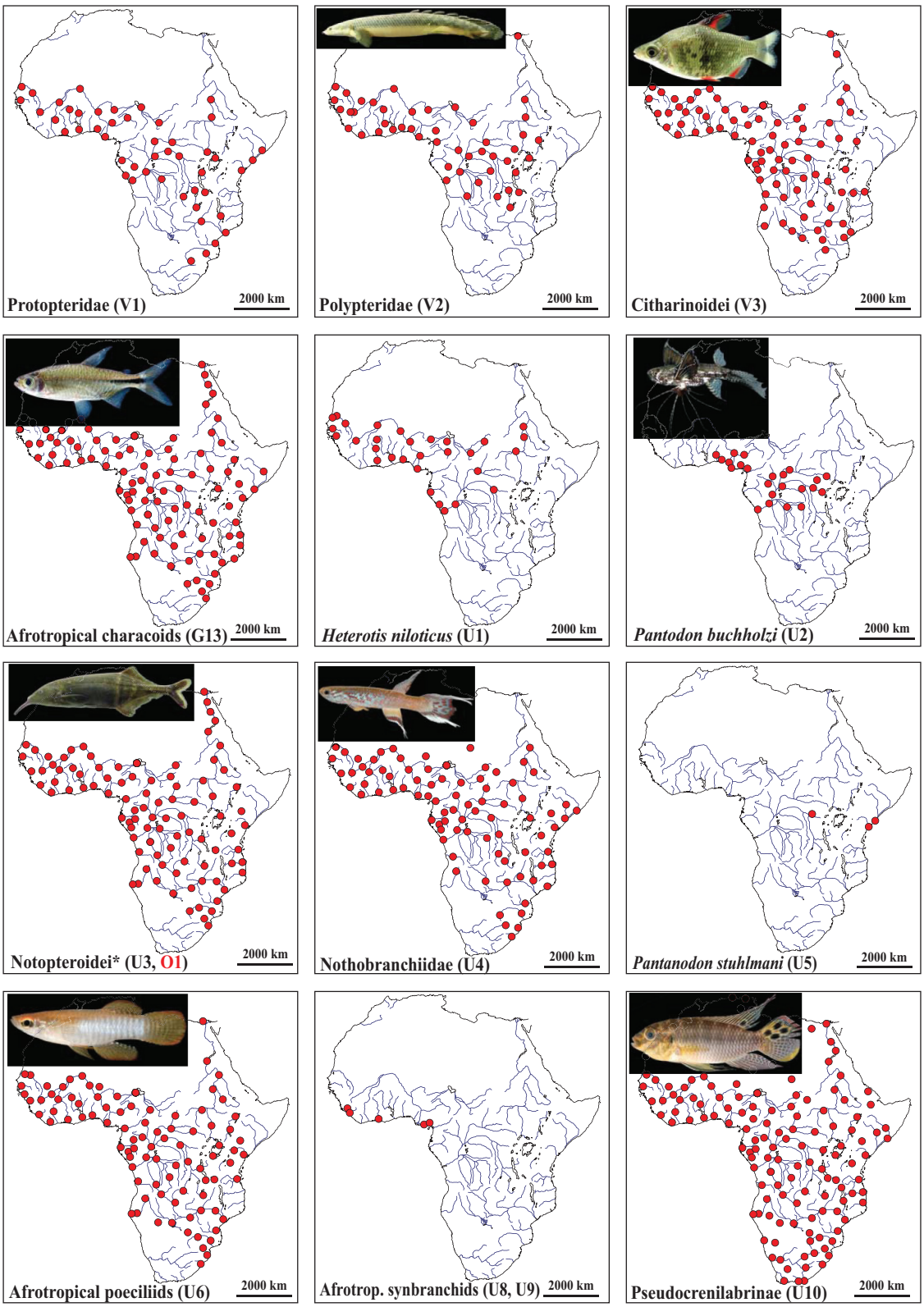

Figure 5. Schematic maps of African main freshwater systems, on which are indicated individually the distributions (with red-filled circles) of 12 lineages of Afrotropical freshwater fishes (* indicates a subsequent range extension out of Africa of one sublineage). Distributional data are from *Faunafri* (Paugy *et al.*, 2008).

in December 2018) provides the number of species for each lineage. For each lineage, I reported its phylogenetic position and, specifically, I reported its non-Afrotropical sister group when known (which is either marine or freshwater). As already mentioned, some of these Afrotropical lineages encompass more than one family (e.g. Notopteroidei, the Big Africa catfish clade), some contain only one family (e.g. Nothobranchiidae and Polypteridae) and others comprise only a part of a family (e.g. the Afrotropical chedrines, the Afrotropical freshwater tetraodontids).

Biogeographical hypotheses for the origins of Afrotropical fish lineages

Based on palaeogeological and palaeoclimatic information, as briefly reviewed in the Introduction and Figure 2, and the inferred ecological preference of the AFF ancestors relative to salinity, I considered seven biogeographical hypotheses that have previously been suggested to explain the origins of the AFF lineages. For each of the hypotheses, I made time-calibrated phylogenetically based predictions on the evolution of ancestral habitat and ancestral range of the AFF lineages (Fig. 6).

*Hypothesis 1: marine origin (*Fig. 6*)*

According to this hypothesis, the most recent non-Afrotropical ancestor of an AFF lineage colonized the Afrotropics after a marine-to-freshwater habitat transition. In this case, the AFF lineage should be nested in a marine fish group, and the ancestral character reconstruction analysis would highlight the marine-to-freshwater habitat transition at the origin of the AFF lineage. Although there is no time restriction for this hypothesis (because marine-to-freshwater shifts might have occurred at any geological time), I looked for possible correlation between the large marine transgressions at the end of the Cretaceous and such habitat transitions.

The divergence between the AFF lineage and its marine sister group provides the strict maximal age for its initial presence in the Afrotropics. The age of the AFF crown group corresponds to the strict minimal age of its initial presence in Afrotropics. Therefore, the marine-to-freshwater habitat transition (at the origin of the AFF lineage) occurred at any time within this maximal–minimal age interval.

This hypothesis is rejected if the phylogenetically based ancestral habitat reconstruction shows that the most recent common ancestor of an AFF lineage and its non-Afrotropical sister group is freshwater adapted.

*Hypotheses 2 and 3: continentaldrift-mediatedvicariance [either with Madagascar+India (hypothesis 2) or with South America (hypothesis 3)] (*Fig. 6*)*

According to each of these two hypotheses, the presence of an AFF lineage in the Afrotropics was caused by the Gondwanan fragmentation, i.e. either by the separation of Africa and Madagascar+India (between 130 and 120 Mya; hypothesis 2) or by the separation of Africa and South America (between 120 and 105 Mya; hypothesis 3).

For each of these two hypotheses, a sister-group relationship is postulated between the AFF lineage and either a Madagascan or an Oriental freshwater fish lineage (hypothesis 2) or a South American freshwater fish lineage (hypothesis 3). Importantly, for each of these two hypotheses, a strict time restriction is needed; the time divergence between the AFF lineage and its sister group must overlap the time of separation either between Africa and Madagascar+India (130–120 Mya; hypothesis 2) or between Africa and South America (120–105 Mya; hypothesis 3).

These two vicariant hypotheses are rejected if at least one of these predictions is not met.

*Hypothesis 4: pre-Gondwanan fragmentation origin (*Fig. 6*)*

Under this hypothesis, the presence of an AFF lineage in the Afrotropics pre-dated the fragmentation of Gondwana, which started at ~130 Mya. Therefore, the time divergence between the AFF lineage and its freshwater non-Afrotropical sister group must strictly pre-date 130 Mya. The distribution of the freshwater non-Afrotropical sister group is not elucidated, because I do not explore the pre-Gondwanan fragmentation biogeography further.

Hypothesis 4 is rejected if the divergence between the AFF lineage with its sister group strictly post-dated 130 Mya.

*Hypotheses 5 and 6: South America–Africa post-separation (< 100 Mya) dispersal either through the Northern Hemisphere (dispersal; hypothesis 5) or through the Atlantic Ocean (direct marine dispersal; hypothesis 6) (*Fig. 6*)*

According to these hypotheses, the ancestors of an AFF lineage colonized the Afrotropics from South America through dispersal across the eastern Nearctic and western Palaearctic during late Mesozoic–early Cenozoic extreme greenhouse periods (hypothesis 5) or directly through the Atlantic Ocean (hypothesis 6). At first glance, both hypotheses seem unlikely, because they need several steps. Hypothesis 5 requires crossing short intercontinental marine regions, temperature-driven continental range extension and selective extinction in the Northern Hemisphere. Hypothesis 6 requires habitat transitions, long-distance marine dispersal and selective extinction of marine forms.

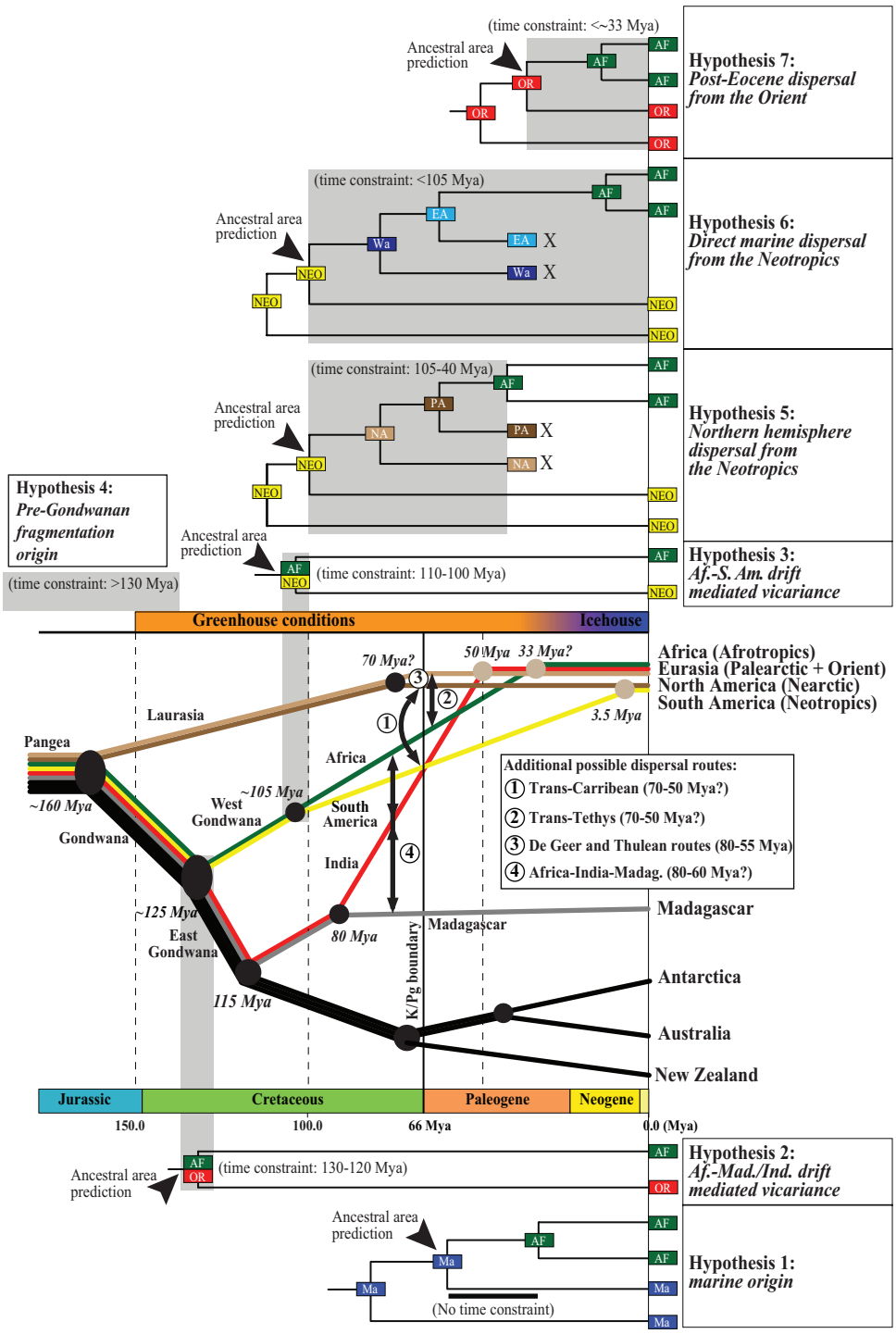

Figure 6. Geological area diagram and seven biogeographical hypotheses explaining the origins of Afrotropical freshwater fish lineages with, for each hypothesis, their time and phylogenetic predictions. The geological area diagram shows the relationships among the main continental landmasses (black ovals and dots indicate continental fragmentations, whereas grey dots indicate continental collisions). Modified from Sanmartín & Ronquist (2004) and Cracraft (1974). Double-headed black arrows indicated four possible dispersal routes. Hypothesis 1, marine origin after a marine-to-freshwater transition; hypothesis 2, India/Madagascar–Africa drift vicariance; hypothesis 3, South America–Africa drift vicariance; hypothesis 4, pre-Gondwanan fragmentation origin; hypothesis 5, Northern Hemisphere dispersal from Neotropics; hypothesis 6, direct trans-Atlantic marine dispersal from Neotropics; and hypothesis 7, post-Eocene dispersal from the Orient. The Afrotropical

Under these two hypotheses, predictions are the same: an AFF lineage should have at least two successive South American freshwater outgroups. The split between the AFF lineage and its South American sister group must post-date the time of the final separation between Africa and South America (< 100 Mya). This divergence provides the maximal age for its initial presence in the Afrotropics. The age of the Afrotropical freshwater fish crown group provides the minimal age for its initial presence in the Afrotropics.

*Hypothesis 7: post-Eocene (< 34 Mya) dispersal from the Orient through a trans-Tethyan land bridge (*Fig. 6*).*

Under this hypothesis, the ancestors of an AFF lineage colonized the Afrotropics from the Orient (or Palaearctic) after Africa collided with Eurasia (< 34 Mya). In this case, an AFF lineage should have at least two successive Oriental (or Palaearctic) freshwater outgroup taxa. Moreover, the time divergence between the AFF lineage and its Oriental (or Palaearctic) sister group should be < 34 Mya. In this context, the maximal age for the initial presence of an AFF lineage in the Afrotropics is equal to the split between this AFF lineage and its outgroup. The age of the AFF crown group provides the minimal age for its initial presence in the Afrotropics. Therefore, the dispersal event from the Orient (or the Palaearctic) occurred in this interval.

Divergence time estimation and the age of crown group Teleostei

Divergence time estimations based on time-calibrated molecular phylogenies are now central in evolutionary biology, and historical biogeography in particular. However, for a given taxonomic group, divergence time inferences sometimes differ among studies owing to the choice of different parameters, including molecular markers and taxonomic sampling quality, the model of sequence evolution and time-calibration constraints. Although recent methods of molecular dating tend to correct some problems and improve practices, some inconsistencies persist between molecular-based divergence time estimation and the time scale suggested by the fossil record. This is the case for the age of the crown group Teleostei and its early diversification timing. The earliest crown group teleost fossils are from the Late Jurassic (Tithonian; Arratia, 1987, 2000; also see Schwarzhans, 2018, who examined the Jurassic/Cretaceous teleost otolith record) and, consequently, they provide a strict minimal age of 152 Mya for the crown group Teleostei. In contrast, molecular studies (in which the age of the Teleostei is not constrained a priori), repeatedly estimated the age of the crown group Teleostei between 330 (Carboniferous) and 250 Mya (limit Permian/Triassic) (e.g. Near *et al.*, 2012; Azuma *et al.*, 2008). This 100–180 Myr gap between molecular clocks and fossil estimation has important consequences for the biogeography of freshwater fish, impacting inference on transcontinental processes (tectonic vicariance vs. post-drifting dispersal) in explaining their distribution.

The Triassic and Jurassic fish fossil record is considered to be of good quality and informative, with the occurrence of several primitive forms along with stem group Teleostei (from ~270 Mya, Permian), but there are no crown group teleost fossils known from before the Jurassic (Arratia, 1987, 2000). Therefore, it appears unlikely that crown group teleosts could have been unnoticed in the fossil record for > 100 Myr. Given this and the fact that Teleostei are necessarily older than 152 Mya (i.e. the age of its earliest fossils), I minimize the gap (i.e. the ghost lineage of the crown group Teleostei) to ~100 Myr in postulating that the age of the crown group Teleostei is not older than 250 Mya (limit Permian-Triassic) and is likely to be younger (see Cavin, 2017; Chen *et al.*, 2013; Lavoué, 2016; Fig. 7).

Phylogenetic tree mining, digitalization and preparation

Source trees used in this work were first selected based on a literature survey. Time-calibrated phylogenies from published figures were digitized to Newick or Nexus formats using GraphClick v.3.0 (http://www.arizona-software.ch/graphclick/) and a text editor. I modified some of these trees as follows: (1) only one specimen per species was sampled, and other conspecific specimens were pruned; (2) only one species per group of closely related species sharing the same geographical distribution was sampled, and others were pruned; (3) distant and biogeographically non-informative outgroups have been deleted; and (4) when more closely related and biogeographically informative outgroups were needed, they were added manually.

Habitat evolution reconstruction and ancestral range estimation

The ancestral habitat preference relative to salinity was reconstructed onto the time-calibrated trees (in

(AF) distributed taxa and Afrotropical inferred ancestral regions are highlighted in green; Oriental (OR), Neotropical (NEO), Nearctic (NA), Palaearctic (PA) and marine (Ea, marine East Atlantic; Ma, marine; Wa, marine West Atlantic) taxa and ancestral regions are indicated in red, yellow, light brown, medium brown and blue, respectively. Background light grey rectangles indicate the time frame of each hypothesis.

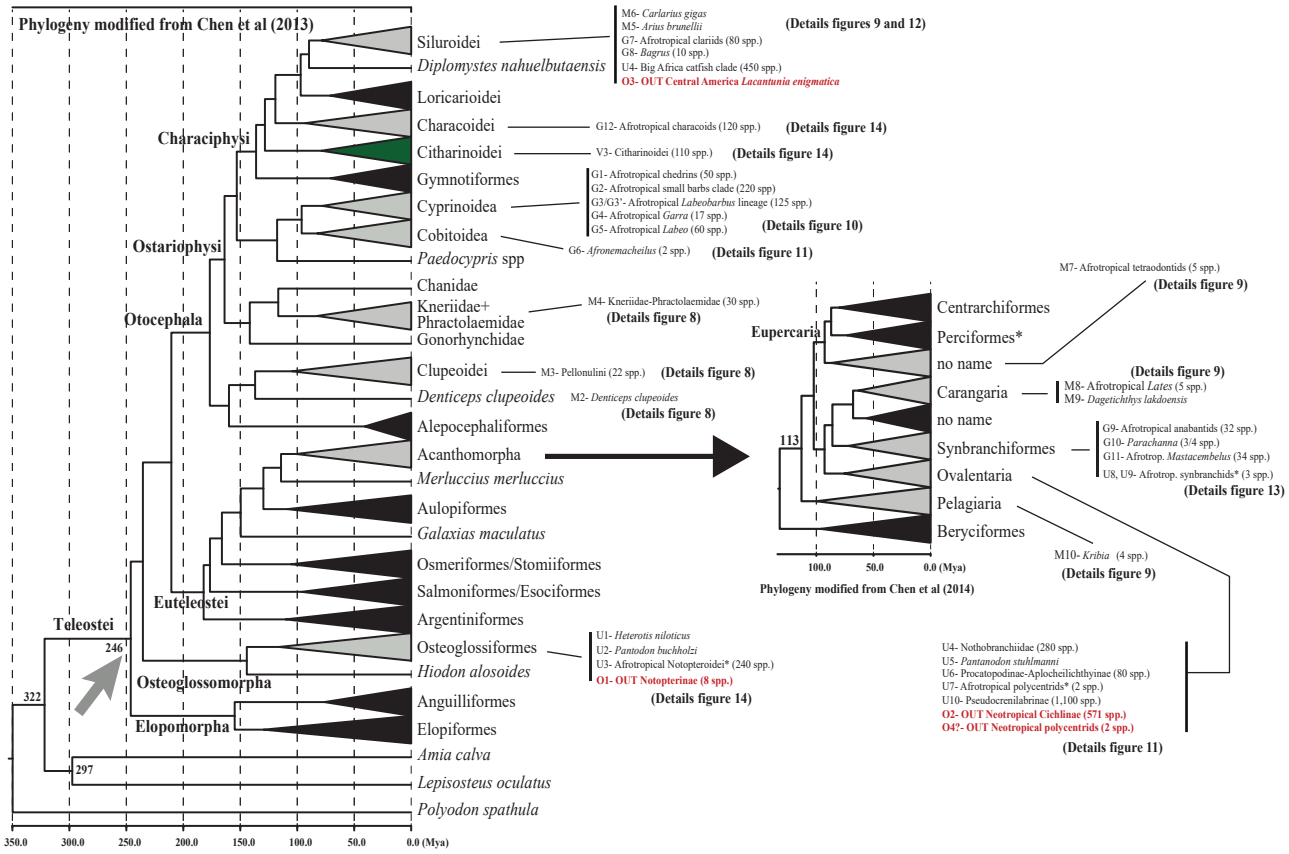

Figure 7. Schematic time-calibrated phylogenetic trees of the main lineages of Teleostei (left tree) and Acanthomorpha (right tree), on which are indicated the phylogenetic positions of the lineages of Afrotropical freshwater teleost fishes identified in the present study (plus the four non-Afrotropical lineages that dispersed from the Afrotropics; indicated in red and numbered O1–O4). The time-calibrated phylogenies of non-teleost Polypteridae and Protopteridae are shown in Figure 14. Simplified chronograms are modified from Chen et al. (2013, 2014b); the black-filled clades do not comprise Afrotropical freshwater representatives. The grey arrow indicates the age of the crown group Teleostei, which was constrained a priori to ~250 Mya. Numbers at selected nodes are ages (in million years ago) of the corresponding clades.

Nexus format) sourced from the literature (for three lineages, I did not find time information and used only cladograms). I used a symmetric one-rate model (Mk1) of character evolution, as implemented in Mesquite v.3.3 (Maddison & Maddison, 2017). The Mk1 model assumes that transitions between each of the habitat states occur at the same rate. Three character states were assigned for salinity preference: fresh water, marine and euryhaline (if necessary). Salinity preference estimations for each species were collected from *Fishbase* (Froese & Pauly, 2018), the *Catalog of Fishes* (Eschmeyer *et al.*, 2018) and additional sources (see References section).

Time-calibrated trees (in Newick format) were then used to model geographical range evolution. For two lineages, I did not find time information and used only cladograms. The program R and the package BioGeoBEARS v.1.1.1 (Matzke, 2018) were used to estimate the ancestral range evolution of each lineage. Each terminal taxon was assigned to a set of seven predefined regions: Afrotropics (AF), Neotropics (NEO), Nearctic (NA), Palaearctic (PA), Orient (OR), Australia (AUS) and Madagascar (MA). I set the maximal number of areas at a given node to two [except for the analyses involving Osteoglossomorpha because one osteoglossomorph taxon, the phareodontins, occurs in five areas and Otophysi because one otophysan taxon, the Siluroidei, occurs in five areas; in these two cases, the maximal number of areas was set to five]. Ancestral geographical range evolution was inferred under two different likelihood models, which were implemented in BioGeoBEARS (Matzke, 2018): a dispersal–extinction–cladogenesis (DEC) model (Ree & Smith, 2008) and a BAYAREALIKE model (which is a likelihood interpretation of the Bayesian

BayArea model of Landis *et al.*, 2013). These two models estimate dispersal and extinction in a similar way, but DEC favours cladogenetic events that lead to underestimation of anagenetic range evolution (Ree & Sanmartín, 2018), whereas BAYAREALIKE assumes that ancestral ranges are inherited identically, because it excludes the vicariant process (Landis *et al.*, 2013). Therefore, in using both reconstruction models, I explore the role of these two different mechanisms under the assumption that vicariance (cladogenesis) would have been the predominant mechanism before 100 Mya (i.e. before the Cretaceous isolation of Africa), whereas dispersal (anagenesis) might have predominated thereafter. Finally, I did not include any founder effect (J) in the DEC model (known as the DEC+J model), because Ree & Sanmartín (2018) provided information about theoretical issues when using it. The DEC+J model leads to unexpected results, in which the rate of anagenetic range evolution is, unexpectedly, very low (Ree & Sanmartín, 2018).

Palaeontological information

The importance of the fossil record for study of the historical biogeography of organisms is widely recognized (e.g. Grande, 1985b). For each of the 37 AFF groups identified, I reviewed its fossil record to extract the following information: (1) its oldest fossil in the Afrotropics, which provides a strict minimal age for the presence of the group in the Afrotropics (this age is then compared with the molecular-based minimal age estimations and, when older, it refines the time interval of origin); and (2) evidence for the past presence of a taxon, currently endemic to the Afrotropics, outside this region, because a possible range extension may be informative regarding the biogeographical process.

Information from the fossil record (including fossil taxa, localities and age) was compiled mainly from original descriptions and completed with recent reviews.

RESULTS

Below is a brief review of the most recent knowledge on the phylogenetic systematics of each Afrotropical freshwater lineage, with the aim of testing several biogeographical hypotheses regarding their origins. For each lineage, I usually present a time-calibrated phylogenetic tree, on which either the ancestral habitat preference or the area evolution is reconstructed (Figs 8–14). All results are summarized in Table 1 and Figure 15. Afrotropical freshwater lineages are classified into categories and listed, depending on their hypothesized origins (Fig. 6).

Biogeographical hypothesis 1 is not rejected: lineages with direct marine origin

Lineage M1: Afrotropical freshwater Fontitrygon (Table 1; Fig. 3)

The worldwide-distributed stingray family Dasyatidae comprises 97 species (Fricke *et al.*, 2018). Most dasyatid species live in marine environments, with a few being able to enter brackish and freshwater environments and a few strictly confined to fresh water (Last *et al.*, 2016). Of all stingrays occurring along the coasts of Africa, current evidence indicates that only two species are strictly adapted to fresh water: *Fontitrygon garouaensis* (Stauch & Blanc, 1962) and the rare *Fontitrygon ukpam* (Smith, 1863) (both species belonging to subfamily Urogymninae with 39 species in total; Compagno & Roberts, 1984). Both species are endemic to West African river basins. Besides these two freshwater species, the genus *Fontitrygon* contains two western Atlantic species and two eastern Atlantic species. *Fontitrygon* is sister to the rest of Urogymninae (Last *et al.*, 2016). According to Last *et al.* (2016), the four African (marine and freshwater) species of *Fontitrygon* form a monophyletic group based on tail-fold morphology, but their relative positions are not resolved. In particular, it is not known whether *Fontitrygon garouaensis* and *Fontitrygon ukpam* form a clade. There are no fossils of *Fontitrygon* known and no published genetic data for the two freshwater species.

Kirchhoff *et al.* (2017) estimated the maximal age of the crown group subfamily Urogymninae to ~98 Mya [95% confidence interval (CI): ~117–80 Mya]. I hypothesized that the ancestors of *Fontitrygon garouaensis* and *Fontitrygon ukpam* adapted to Afrotropical freshwaters after a marine-to-freshwater shift that I estimated to have occurred broadly between a maximum of 98 Mya and a minimum of 5 Mya.

Lineage M2: Denticeps clupeoides (Table 1; Figs 3, 8A)

Denticeps clupeoides Clausen, 1959 (Denticipitidae) is the only extant species of the suborder Denticipitoidei. The only excavated fossil of the suborder Denticipitoidei is the middle Eocene (46–45 Mya) freshwater †*Palaeodenticeps tanganikae* from East Africa (Greenwood, 1960). This fossil provides a strict minimal age for the presence of this lineage in African fresh waters. The maximal age estimation of the presence of denticipitoids in the Afrotropics is based on time-calibrated molecular phylogenies. The sister group of Denticipitoidei is the predominantly marine suborder Clupeoidei, both forming the order Clupeiformes (Greenwood, 1968; Near *et al.*, 2012; Lavoué *et al.*, 2013). The evolutionary reconstruction of the salinity preference showed that the most recent

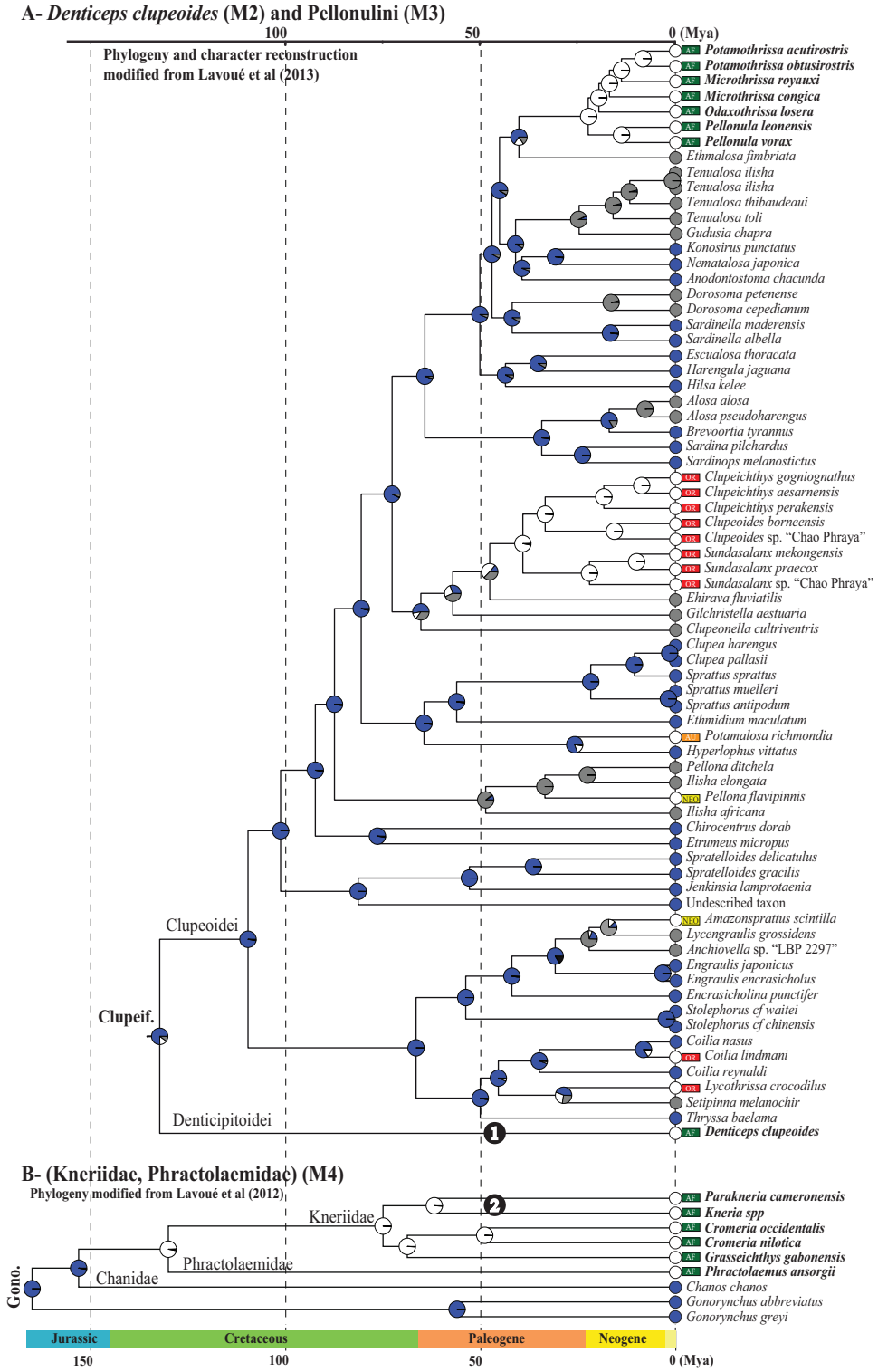

Figure 8. Maximum-likelihood reconstructions of the evolution of salinity preference onto time-calibrated phylogenetic trees. A, Clupeiformes, showing the origins of *Denticeps clupeoides* and Pellonulini (tree and character reconstruction modified from Lavoué *et al.*, 2013). B, Gonorynchiformes, showing the origin of the clade (Kneriidae, Phractolaemidae) (tree modified from Lavoué *et al.*, 2012). Salinity preference is classified into three states: 'marine' indicated in blue, 'euryhaline' in grey and 'fresh water' in white. At each node, the relative probabilities of each state (sum = 1) are drawn using pie charts.

common ancestor of the Clupeiformes was marine, making a marine origin for the Denticipitoidei the most likely hypothesis (Lavoué *et al.*, 2013) (Fig. 8A). The precise dating of the marine-to-freshwater transition along the long branch supporting *Denticeps clupeoides* cannot be determined. Near *et al.* (2012) estimated the divergence between *Denticeps clupeoides* and Clupeoidei to 175 Mya (95% CI: 220–140 Mya). More congruent with the early fossil record of Teleostei and Clupeomorpha, Lavoué *et al.* (2013) revised this divergence to 135 Mya (95% CI: 145–125 Mya) using a different time-calibration scheme.

Therefore, I hypothesized that the ancestor of the *Denticeps clupeoides* lineage invaded the Afrotropical fresh waters after a marine-to-freshwater transition that occurred broadly between a soft maximal age of 145 Mya and a strict minimal age of 45 Mya.

Lineage M3: tribe Pellonulini (Table 1; Figs 3, 8A)

The Afrotropical tribe Pellonulini (Clupeidae) comprises ~22 species of freshwater sardines classified into 11 genera (Whitehead, 1985). The monophyly of this lineage has not yet been confirmed because of the difficulty in classifying some diminutive species, such as *Congothrissa* and *Thrattidion*. Based on morphological evidence, Grande (1985a) found the Pellonulini to be monophyletic, whereas Poll (1964), Taverne (1977) and Gourène & Teugels (1994) classified *Congothrissa* in a distinct family (Congothrissidae) of unresolved position in the suborder Clupeoidei. There are no molecular data available for *Congothrissa* and *Thrattidion*, and no pellonulin fossils are known. Here, I followed the phylogenetic hypothesis of Grande (1985a: 279), who considered this group to be monophyletic based on the following synapomorphy: 'articulation of postcleithrum with supra cleithrum well behind cleithrum'.

The tribe Pellonulini is nested in subfamily Dorosomatinae *sensu* Lavoué *et al.* (2014), a mostly marine tropical clade of sardines. The sister group of Pellonulini might be *Ethmalosa fimbriata* (Bowdich, 1825), a tropical marine species native to the west coast of Africa, although this relationship received only weak statistical support, and the taxonomic sampling of Dorosomatinae needs to be expanded (Wilson *et al.*, 2008; Lavoué *et al.*, 2013). Given that *Ethmalosa fimbriata* and most dorosomatins are marine, Lavoué *et al.* (2013) inferred that the ancestor of Pellonulini was marine and that Pellonulini subsequently evolved after a marine-to-freshwater transition (Fig. 8A).

Wilson *et al.* (2008) estimated the divergence between Pellonulini and *Ethmalosa fimbriata* to 37.3 Mya (95% CI: 52–25 Mya) and the age of the crown group Pellonulini to ~33 Mya (no CI provided), whereas Lavoué *et al.* (2013) provided the following information: the divergence between Pellonulini and *Ethmalosa fimbriata* was estimated to 48 Mya (95% CI: 60–35 Mya), and the early diversification of Pellonulini was estimated to ~25 Mya (95% CI: 35–17 Mya). Lavoué *et al.* (2013) did not examine the genus *Sierrathrissa*, which was found to be sister to the rest of Pellonulini by Wilson *et al.* (2008); therefore, the minimal age of this clade is necessarily > 17 Mya (within the 95% CI).

To summarize, I hypothesized that the Pellonulini invaded Afrotropical fresh waters after a marine-to-freshwater transition that I estimated to have occurred broadly between a maximum of 60 Mya and a minimum of 17 Mya (it is likely that the minimal age of the crown group Pellonulini is, in fact, > 17 Mya for the reason given above).

Lineage M4: families Kneriidae and Phractolaemidae (Table 1; Figs 3, 8B)

The Afrotropical gonorynchiform families Kneriidae and Phractolaemidae form a clade. The sister group of this clade is the family Chanidae, which includes the living Indo-West Pacific marine milkfish *Chanos chanos* (Forsskål, 1775), along with several fossils of marine origin (e.g. †*Rubiesichthys*, †*Parachanos*). The marine family Gonorynchidae is the sister group of this clade (Lavoué *et al.*, 2005, 2012; Near *et al.*, 2014a; but for an alternative phylogenetic hypothesis, see Ribeiro *et al.*, 2018). The evolutionary reconstruction of the salinity preference unequivocally indicates that the clade (Kneriidae, Phractolaemidae) evolved after a marine-to-freshwater transition (Fig. 8B).

The oldest fossil known in this freshwater lineage is †*Mahengichthys singidaensis*, from the Middle Eocene (46–45 Mya) Mahenge deposits in East Africa (Davis *et al.*, 2013). This crown group fossil is either sister to the kneriid genus *Kneria* (Davis *et al.*, 2013) or sister to the whole family Kneriidae (including *Kneria*, *Parakneria*, *Cromeria* and *Grasseichthys*; Near *et al.*, 2014a).

Davis *et al.* (2013) reanalysed the mitogenomic dataset of Lavoué *et al.* (2012), which they combined with their morphological dataset (including †*Mahengichthys singidaensis*). These authors estimated the ages of the stem and crown groups of

The Afrotropical (AF) freshwater species are indicated in bold. The distribution of each other freshwater species is also indicated after its salinity preference as follows: Australia (AUS), Neotropics (NEO) and Orient (OR). Numbers in black-filled circles indicate the strict minimal age for the corresponding lineage, as obtained from the fossil record (for details, see main text and Fig. 15).

(Kneriidae, Phractolaemidae) to 152.3 Mya (95% CI: 171–141 Mya) and 129.3 Mya (95% CI: 152–107 Mya), respectively. The age of crown group Gonorynchiformes was estimated as 164.2 Mya (95% CI: 185–147 Mya). Near *et al.* (2014a), using a nuclear dataset along with an expanded morphological dataset of Davis *et al.* (2013) (including †*Mahengichthys singidaensis* and several other fossils), overestimated the stem age to 182.9 Mya and the crown age of (Kneriidae, Phractolaemidae) to 121.7 Mya. Moreover, the age of the Gonorynchiformes was estimated to 219.8 Mya, Late Triassic, which is unlikely.

To summarize, the clade (Kneriidae, Phractolaemidae) evolved after a marine-to-freshwater transition that occurred broadly between 171 and 107 Mya (Davis *et al.*, 2013). Although †*Mahengichthys singidaensis* provides a strict minimal age for the presence of this lineage in Africa, the marine-to-freshwater transition might have pre-dated this fossil substantially.

Lineages M5 and M6: Arius brunellii and Carlarius gigas (Table 1; Figs 3, 9A)

The ariid catfish species *Arius brunellii* Zolezzi, 1939 (Juba River, East Africa) and *Carlarius gigas* (Boulenger, 1911) (formerly in *Arius*; Volta and Niger Rivers, West Africa) are considered to be the only two freshwater-restricted species of Ariidae in the Afrotropics. All others are marine, sometimes entering estuaries and lower river courses because of their physiological tolerance to low salinity (Marceniuk & Menezes, 2007; Marceniuk *et al.*, 2012). The evolution of the salinity preference in subfamily Ariinae shows that *Arius brunellii* and *Carlarius gigas* probably adapted to fresh water after two independent habitat transitions (Fig. 9A).

The genus *Carlarius* is monophyletic and includes species living along the west coast of Africa (Betancur-R *et al.*, 2009; Marceniuk *et al.*, 2012). The maximal age of the marine-to-freshwater transition leading to *Carlarius gigas* is inferred to 19 Mya (within 95% CI; see supporting information in Betancur-R *et al.*, 2012). Given that *Carlarius gigas* was not sampled by Betancur-R *et al.* (2012), this broad estimation corresponds to the age of the crown group of the genus *Carlarius*. Likewise, I consider a minimal age of the marine-to-freshwater transition to be 5 Mya in the absence of phylogenetic evidence regarding the position of *Carlarius gigas* relative to the other species of *Carlarius*.

The age of the marine-to-freshwater shift leading to *Arius brunellii* is even more difficult to estimate, because the genus *Arius* is not monophyletic, and *Arius brunellii* was not included in recent studies. Using the time-calibrated phylogeny of Betancur-R *et al.* (2012), I estimated the maximal age of this lineage broadly to 19 Mya, which corresponds to the age of the paraphyletic genus *Arius*, and I set up a soft minimal age of only 5 Myr.

Given that the family Ariidae is mostly a marine group of fishes, the fossil record offers little help in estimation of the minimal age for these two transitions precisely. Longbottom (2010) discussed the African catfish fossil record and suggested that the oldest African ariid in Africa is †*Arius fraasi* Peyer, 1928 from the middle Eocene and †*Eopeyeria aegyptiaca* (Peyer, 1928) from the late Eocene. Recently, a new marine ariid, †*Qarmoutus hitanensis* El-Sayed *et al.*, 2017, was described from the late Eocene. None of these fossils seems related to freshwater species (El-Sayed *et al.*, 2017).

In summary, *Arius brunellii* and *Carlarius gigas* evolved after two distinct marine-to-freshwater transitions that might have occurred between 19 and 5 Mya.

Lineage M7: Afrotropical freshwater Tetraodon (Table 1; Figs 3, 9B)

The Afrotropical freshwater *Tetraodon* comprise five species that form a monophyletic group (Igarashi *et al.*, 2013; Santini *et al.*, 2013). Yamanoue *et al.* (2011) inferred the phylogenetic position of two species of Afrotropical freshwater tetraodontids, *Tetraodon mbu* Boulenger, 1899 and *Tetraodon miurus* Boulenger, 1902, and they found the sister group to be the Indo-West Pacific genus *Chelonodon*. This group is nested in other Indo-West Pacific marine species. The evolutionary reconstruction of the salinity preference of Tetraodontidae shows that Afrotropical freshwater tetraodontids adapted to fresh water after a single marine-to-freshwater transition (Fig. 9B).

Yamanoue *et al.* (2011) estimated the divergence between the Afrotropical freshwater species of *Tetraodon* and the genus *Chelonodon* to ~38 Mya and the divergence between *Tetraodon mbu* and *Tetraodon miurus* was estimated to 17 Mya (no 95% CI provided). Santini *et al.* (2013) re-examined the molecular phylogeny and the time diversification of the African freshwater pufferfishes, including the five Afrotropical freshwater species. These authors found younger age estimates than Yamanoue *et al.* (2011). Santini *et al.* (2013) estimated the stem age of the Afrotropical freshwater lineage to ~13 Mya (95% CI: 17–9 Mya) and the crown age to ~5 Mya (95% CI: 7.5–5.0 Mya). Although using different taxonomic sampling of Tetraodontiformes, the age estimation of Santini *et al.* (2013) is more in agreement with the age estimation of Near *et al.* (2013). For example, the estimations of the divergence between *Tetraodon miurus* and *Arothron nigropunctatus* (Bloch & Schneider, 1801) were similar in the two studies: 19 Mya by Santini *et al.* (2013) and 20 Mya by Near *et al.* (2013). Therefore, I conclude that

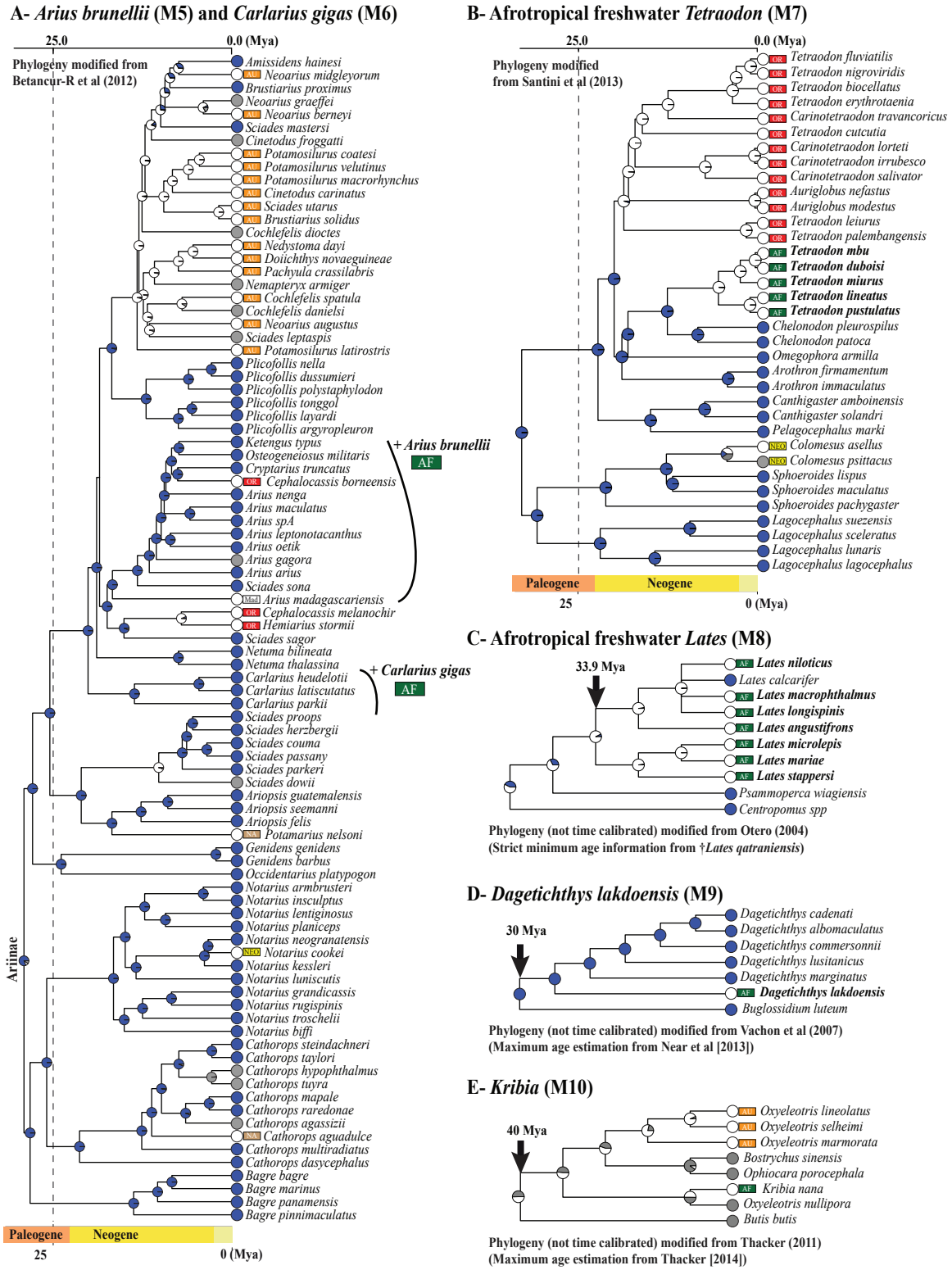

Figure 9. Maximum-likelihood reconstructions of the evolution of salinity preference onto phylogenetic trees. A, Ariidae, showing the possible phylogenetic positions and origins of *Carlarius gigas* and *Arius brunellii* (time-calibrated tree modified from Betancur-R *et al.*, 2012). B, part of Tetraodontidae, showing the origin of Afrotropical freshwater

the ancestors of Afrotropical freshwater pufferfishes invaded Afrotropical freshwaters after a marine-to-freshwater transition that occurred between 17 and 5 Mya. There are no fossils known.

Lineage M8: Afrotropical freshwater Lates (Table 1; Figs 3, 9C)

I followed the classification of Otero (2004), in which the family Latidae includes three genera, with *Lates* being the sister to the marine Indo-West Pacific genus *Psammoperca* (Li *et al.*, 2011). *Hypopterus macropterus* (Günther, 1859) (Australia, marine) is closely related to *Psammoperca* (Greenwood, 1976; Iwatsuki *et al.*, 2018; Pethiyagoda & Gill, 2013). Latidae is sister to the marine family Centropomidae (*Centropomus*).

The genus *Lates* is monophyletic and comprises two subgenera: *Luciolates* {with four endemic freshwater species in Lake Tanganyika: *Lates angustifrons* Boulenger, 1906, *Lates mariae* Steindachner, 1909, *Lates microlepis* Boulenger, 1898 and *Lates stappersii* (Boulenger, 1914)} and *Lates* [including three African freshwater species, *Lates longispinis* Worthington, 1932, *Lates macrophthalmus* Worthington, 1929 and *Lates niloticus* (Linnaeus, 1758) (the first two are endemic to Lake Rudolf) and four Indo-West Pacific marine species, such as *Lates calcarifer* (Bloch, 1790)]. As a consequence of this classification, the African freshwater species form a paraphyletic group, because the freshwater species of the subgenus *Lates* are more closely related to marine species. However, more data are needed to resolve their relationships fully. Using a modified version of the phylogeny of Otero (2004), in which *Centropomus* is added as an outgroup (Li *et al.*, 2011), I reconstructed the evolution of the salinity preference in Latidae and found that the whole family might have a freshwater origin, with three subsequent freshwater-to-marine transitions (Fig. 9C). This ML reconstruction is in conflict with the most parsimonious solution, which requires only two transitions. There are two possible reasons that could mislead the ML reconstruction: the low taxonomic coverage of marine species (with only two marine species sampled) and the absence of branch length proportional to time (species of *Lates*might have diverged substantially more recently than marine species; Li *et al.*, 2011). When Latidae is studied further phylogenetically, it is likely that the results will show that the Afrotropical freshwater species of *Lates* evolved after a marine-to-freshwater transition.

Several African freshwater fossils from Miocene and Pliocene sites are assigned to the genus *Lates*, with the oldest fossil (†*Lates qatraniensis*) described from the late Eocene/early Oligocene of Egypt (33.9 Mya; Murray, 2004; Murray & Attia, 2004). According to Murray & Attia (2004), †*Lates qatraniensis* is closely related to *Lates niloticus*. Molecular estimation provides a maximal age for the divergence between the clade (Centropomidae, Latidae) and its sister group of ~62.5 Mya (Near *et al.*, 2013).

To summarize, I favour the hypothesis in which the Afrotropical freshwater *Lates* invaded Africa after a single marine-to-freshwater transition that occurred broadly between a soft maximum of 62.5 Mya and a strict minimum of 33.9 Mya.

Lineage M9: Dagetichthys lakdoensis (Table 1; Figs 3, 9D)

Dagetichthys lakdoensis Stauch & Blanc, 1964 is the only species of flatfish (Pleuronectiformes; Soleidae) that is believed to be restricted completely to Afrotropical fresh water. There are no genetic data available for this species, but two morphological studies have examined its systematics (Chapleau & Desoutter, 1996; Vachon *et al.*, 2007). *Dagetichthys lakdoensis* is considered to be sister to the five other species of *Dagetichthys*, all marine and distributed in the Indo-West Pacific and Atlantic regions (Chapleau & Desoutter, 1996; Vachon *et al.*, 2007). The reconstruction of the salinity preference of the genus *Dagetichthys* shows that the most recent ancestor of *Dagetichthys* was marine, and *Dagetichthys lakdoensis* evolved after a marine-to-freshwater transition (Fig. 9D). There is no age estimation for *Dagetichthys lakdoensis*, but the crown group Soleidae is dated to only ~30 Mya (95% CI: 35–25 Mya) by Near *et al.* (2013). There is no calibrating information to constrain the minimal age of *Dagetichthys lakdoensis* that I set up softly to 5 Mya. Therefore, *Dagetichthys lakdoensis* is

Tetraodon (time-calibrated tree modified from Santini *et al.*, 2013). C, Latidae, showing the phylogenetic positions and origins of Afrotropical freshwater species of *Lates* (not time-calibrated tree modified from Otero, 2004; the first Afrotropical freshwater fossil provides a strict minimal age for the crown group *Lates*). D, part of Soleidae, showing the phylogenic position of *Dagetichthys lakdoensis* (not time-calibrated tree modified from Vachon *et al.*, 2007; maximal age estimation of *Dagetichthys* from Near *et al.*, 2013). E, part of Eleotridae, showing the possible phylogenetic position and origin of *Kribia* (not time-calibrated tree from Thacker & Hardman, 2005; maximal age estimation of Eleotridae from Thacker, 2014). Salinity preference is classified into three states: 'marine' indicated in blue, 'euryhaline' in grey and 'fresh water' in white. At each node, the relative probabilities of each state (sum = 1) are drawn using pie charts. The Afrotropical (AF) freshwater species are indicated in bold. The distribution of each other freshwater species is also indicated after its salinity preference as follows: Australia (AUS), Neartic (NA), Neotropics (NEO) and Orient (OR).

likely to have invaded Africa after a single marine-to-freshwater transition that occurred broadly between 30 and 5 Mya. No related fossils are known.

Lineage M10: Genus Kribia (Table 1; Figs 3, 9E)

The family Butidae comprises eight genera and 44 species (Fricke *et al.*, 2018). Most of the African butid species (genera *Butis* and *Bostrychus*) are found in marine environments, estuaries and mangroves and are tolerant of a large range of salinity, and the genus *Kribia* is the only strictly Afrotropical freshwater butid genus. The phylogeny of the Butidae is known poorly, because fewer than ten species have been examined so far. Thacker & Hardman (2005) and Agorreta & Rüber (2012) found *Kribia nana* (Boulenger, 1901) is to be sister to *Oxyeleotris nullipora* Roberts, 1978, an Australian–New Guinean, predominantly brackish water species. Although the taxonomic sampling of Butidae is incomplete, I used the phylogeny of Butidae from Thacker (2014) to reconstruct the evolution of salinity (Fig. 9E). Results are equivocal, because the most recent common ancestor of *Kribia nana* and *Oxyeleotris nullipora* could have been either brackish or freshwater. I favour slightly the hypothesis that *Kribia* evolved after a brackish-to-freshwater transition, because most of the unsampled species of Butidae are from marine or brackish water.

Thacker (2014) estimated the age of the crown group Butidae [i.e. the divergence *Butis butis* (Hamilton, 1822) and the rest of the butid species] to ~45 Mya (95% CI: 59–34 Mya), and Near *et al.* (2013) estimated the age of Butidae between ~50 and 25 Mya. There are no minimal age estimates and no related fossils known.

Consequently, the age of the brackish-to-freshwater transition leading to the Afrotropical genus *Kribia* must strictly be younger than 59 Mya and probably younger than 34 Mya. I set the minimal age for the presence of *Kribia* in Africa to only 5 Mya in the absence of a more precise estimate.

Lineages that originated from late Cenozoic dispersal events from the Oriental region (hypothesis 7)

Lineage G1: Afrotropical chedrines (Table 1; Figs 4, 10A; Supporting Information, Fig. S1)

The Afrotropical chedrines comprise ~50 species classified into eight genera: *Chelaethiops* (five species), *Engraulicypris* (one species), *Leptocypris* (nine species), *Mesobola* (four species), *Neobola* (four species), *Opsaridium* (12 species), *Raiamas* (14 African species) and *Rastrineobola* (one species). The Afrotropical chedrines were found to be monophyletic in a molecular study, and the group is supported by a derived pharyngeal dentition (Liao *et al.*, 2012). The Afrotropical chedrin clade is nested within the subfamily Chedrinae of the cyprinoid family Danionidae (Tan & Armbruster, 2018), and it is the sister group of the Oriental species of *Raiamas* (Liao *et al.*, 2012; Sungani *et al.*, 2017). The ancestral range reconstruction onto the time-calibrated phylogenetic tree of Sungani *et al.* (2017) shows that Afrotropical chedrines dispersed from the Orient (Fig. 10A). Using a dense taxonomic sampling, Sungani *et al.* (2017) estimated the maximal age of the Afrotropical chedrin lineage to ~22 Mya (95% CI: 31–17 Mya), with the clade starting to diversify soon after that, at ~20 Mya (95% CI: 26.2–14.5 Mya). These estimations of age by Sungani *et al.* (2017) are in conflict with the estimations of Hirt *et al.* (2017), who inferred a maximal age of the Afrotropical chedrin lineage to < 10 Mya. However, the sparse taxonomic sampling of Chedrinae used by Hirt *et al.* (2017) could explain the difference in the dating inference between the two studies. Given that the study of Sungani *et al.* (2017) was designed specifically to investigate the evolution of Afrotropical chedrines, I follow its conclusions. Therefore, the Afrotropical chedrines dispersed from the Oriental region between a maximum of 31 Mya and a minimum of 14.5 Mya.

Lineage G2: Afrotropical small barbs clade (Table 1; Figs 4, 10B; Supporting Information, Fig. S1)

The Afrotropical small barbs (Smiliogastrinae, Cyprinidae), also known as diploid barbs, form a monophyletic group that contains ~220 species classified into six genera: the species-rich *Enteromius* (previously classified into '*Barbus*'), *Barboides*, *Barbopsis*, *Clypeobarbus*, *Caecobarbus* and *Pseudobarbus* (including '*Pseudobarbus*') (Yang *et al.*, 2015; Ren & Mayden, 2016; Hayes & Armbruster, 2017). However, Tan & Armbruster (2018) treated *Barbopsis* and *Caecobarbus* as *incertae sedis* in Cyprinidae, because of the lack of recent comparative study on these genera. To the above-listed genera of Afrotropical small barbs, I add *Coptostomabarbus* and *Prolabeops* tentatively, based on some external morphological similarities, as noted by Farm (2000) and Daget (1984), respectively.

The Afrotropical small barbs clade is the sister group of the Oriental genus *Systomus* (Ren & Mayden, 2016). Both lineages are nested among Oriental representatives, making the hypothesis of a dispersal from the Orient most likely, as confirmed by the ancestral range reconstruction onto the tree published by Ren & Mayden (2016) (Fig. 10B). Ren & Mayden (2016) estimated the maximal age of this dispersal event (which corresponds to the time divergence between *Systomus* and the Afrotropical small barbs) as 26.4 Mya (95% CI: 30.5–22.1 Mya) and its minimal age (which corresponds to the age of the Afrotropical small barbs clade) as 24.5 Mya (95% CI: 28.4–20.5 Mya). Otero

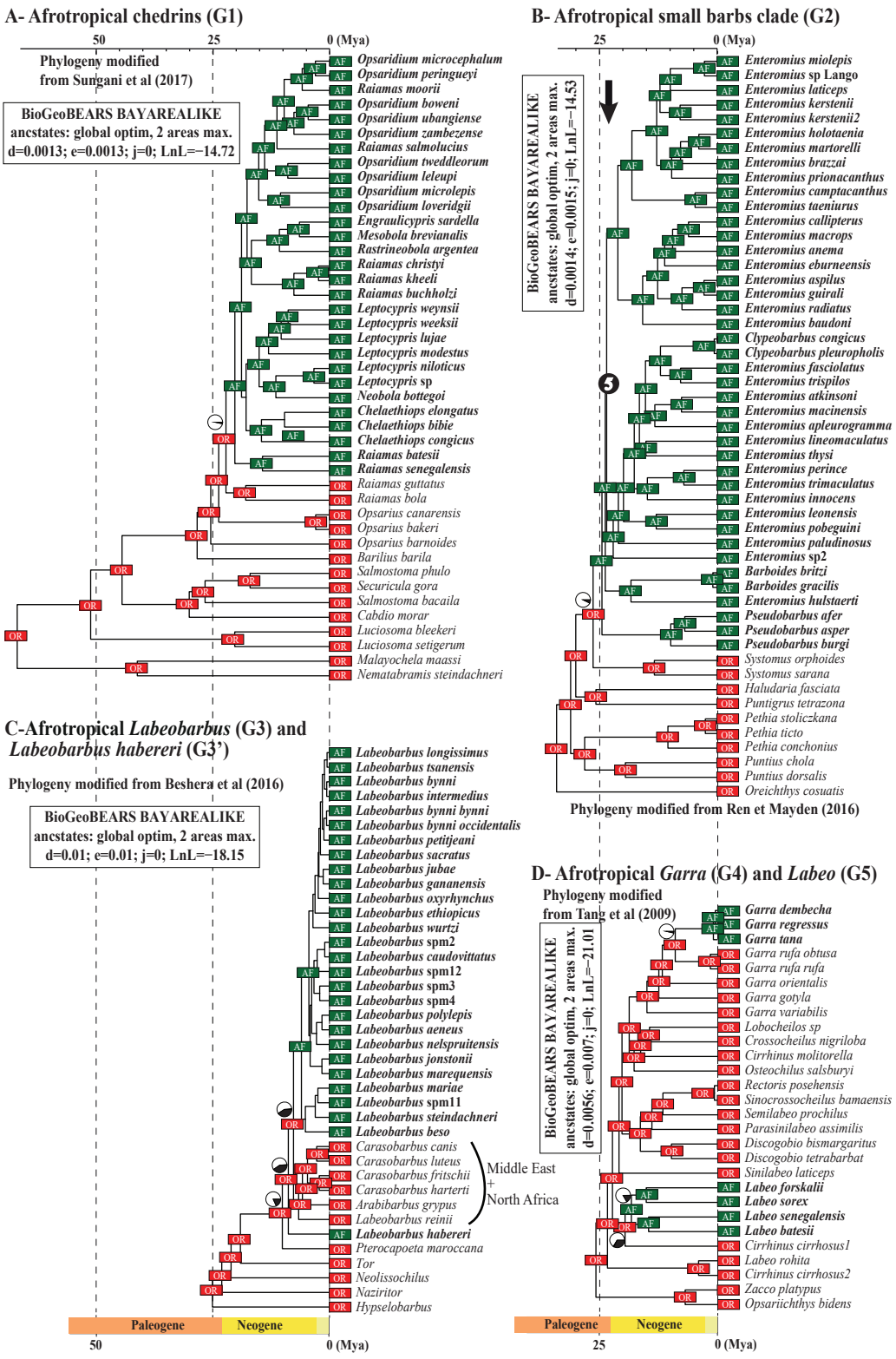

Figure 10. Four time-calibrated phylogenetic trees of distinct cyprinoid lineages, on which are estimated geographical range evolution using the BAYAREALIKE model (Landis *et al.*, 2013) as implemented in BioGeoBEARS (Matzke, 2018). A, Chedrini (Chedrinae, Danionidae), showing the origin of the Afrotropical chedrines (tree modified from Sungani *et al.*,

(2001) assigned to this clade a early Miocene (~23 Mya) cyprinid fossil from the Afro-Arabian continental plate. The age of this fossil provides a strict minimal age for the early presence of this lineage in the Afrotropics.

In summary, the ancestors of the Afrotropical small barbs dispersed to the Afrotropics from the Orient between 30.5 and 23 Mya.

Lineages G3 and G3′: Afrotropical Labeobarbus and Labeobarbus habereri (Table 1; Figs 4, 10C; Supporting Information, Fig. S1)

The Afrotropical *Labeobarbus* lineage comprises ~125 species and three genera, *Acapoeta*, *Labeobarbus* (*Varicorhinus* is a junior synonym) and *Sanagia* (Vreven *et al.*, 2016), and it is currently classified in subfamily Torinae of Cyprinidae (Tan & Armbruster, 2018). I also add *Xenobarbus* (known only from its type series) and *Prolabeo* to this lineage, although current evidence supporting their placement is tenuous in absence of a taxonomic revision. These two genera might be related to other Afrotropical cyprinid lineages (such as *Labeo*). Tan & Armbruster, (2018) left them *incertae sedis* in Cyprinidae.

Available genetic data show that the Afrotropical *Labeobarbus* lineage forms a monophyletic group to the exclusion of *Labeobarbus habereri* (Steindachner, 1912), which is more closely related to some Middle Eastern and North African species (Beshera *et al.*, 2016). The Afrotropical *Labeobarbus* lineage and *Labeobarbus habereri* are related to the genera *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys* and *Pterocapoeta*, which are distributed in the Middle East and North Africa, in the transition zone between the Afrotropics and the Orient (Fig. 1) (Yang *et al.*, 2015; Beshera *et al.*, 2016; Borkenhagen, 2017). Altogether, these fishes are nested in the otherwise Oriental subfamily Torinae (Tan & Armbruster, 2018). The ancestral range reconstruction indicated that *Labeobarbus* originated from the Orient after one or two dispersal events depending on how the distributions of Middle Eastern and North African genera are coded (Fig. 10C). The time divergence between *Labeobarbus* and its non-Afrotropical sister group is estimated to ~7.6 Mya (95% CI: 9.5–6 Mya) and the age of the crown group *Labeobarbus* to ~5.9 Mya (95% CI: 7.5–4.6 Mya) (Beshera *et al.*, 2016). These age estimations are comparable in the studies of Beshera *et al.* (2016) and Hirt *et al.* (2017). There are no fossils related to this lineage.

In summary, the *Labeobarbus* lineage reached the Afrotropics after a dispersal event from the Orient, which occurred between 9.5 and 4.6 Mya. *Labeobarbus habereri* can be considered as the result of either the same dispersal event or an independent dispersal.

Lineage G4: Afrotropical Garra (Table 1; Figs 4, 10D; Supporting Information, Fig. S1)

The genus *Garra* comprises ~150 Oriental species and 18 Afrotropical species. This genus is currently classified in tribe Garrini of subfamily Labeoninae in Cyprinidae (Stiassny & Getahun, 2007; Tang *et al.*, 2009; Yang *et al.*, 2012; Tan & Armbruster, 2018). *Garra* is not monophyletic (Yang *et al.*, 2012), but at least its Afrotropical species that have been examined form a monophyletic group deeply nested in Oriental *Garra* (Tang *et al.*, 2009; Yang *et al.*, 2012). According to Yang *et al.* (2012), the sister group of Afrotropical *Garra* may be a clade including *Garra barreimiae* Fowler & Steinitz, 1956 and *Garra rufa* (Heckel, 1843), two species from the most western part of the Oriental region. The ancestral range reconstruction supported an Oriental origin for Afrotropical *Garra* (Fig. 10D).

Tang *et al.* (2009) estimated the age of the stem group of Afrotropical species (i.e. the divergence between the Afrotropical *Garra* and its Oriental sister group) to ~9 Mya (no CI provided). The age of the crown group of Afrotropical species is not known because Tang *et al.* (2009) examined only three closely related African species from Lake Tana in Ethiopia, whereas 18 Afrotropical species are known. Therefore, in the absence of more comprehensive information, I constrain the minimal age softly to 5 Mya.

In summary, the Afrotropical *Garra* is the result of a freshwater dispersal event from the Oriental region, which occurred between 9 and 5 Mya.

Lineage G5: Afrotropical Labeo (Table 1; Figs 4, 10D; Supporting Information Fig. S1)

The genus *Labeo* comprises ~40 species distributed in the Orient and 60 species endemic to the Afrotropics (Lowenstein *et al.*, 2011). The genus *Labeo* belongs to the tribe Labeonini of Labeoninae of Cyprinidae

2017). B, part of the tribe Cyprinini (Cyprininae, Cyprinidae), showing the origin of the Afrotropical small barbs clade (tree modified from Ren & Mayden, 2016). C, part of the tribe Cyprinini, showing the origin of *Labeobarbus* (tree modified from Beshera *et al.*, 2016). D, Labeonini (Cyprinidae), showing the origins of Afrotropical *Labeo* and *Garra* (tree modified from Tang *et al.*, 2009). The Afrotropical (AF) distributed taxa and Afrotropical inferred ancestral regions are highlighted in green; Oriental (OR) taxa and ancestral regions are highlighted in red. Black and white pie charts at specific ancestral area reconstruction show the probability (white) of the corresponding reconstruction. Number in black-filled circle indicates strict minimal age for the corresponding lineage, as obtained from the fossil record (for details, see main text and Fig. 15).

(Tan & Armbruster, 2018). The Afrotropical *Labeo* forms a monophyletic group that is nested among Oriental species of *Labeo* (Yang *et al.*, 2012). Tang *et al.* (2009), using a smaller taxonomic sampling than Yang *et al.* (2012), reconstructed the time-calibrated phylogenetic relationships of four species of African *Labeo* in tribe Labeonini. Using this time-calibrated tree, I inferred that Afrotropical *Labeo* originated after a dispersal event from the Orient (Fig. 10D). In the absence of Oriental species of *Labeo* sampled, Tang *et al.* (2009) found the Oriental species *Cirrhinus cirrhosus* (Bloch, 1795) to be the sister of Afrotropical *Labeo*. These authors estimated the time divergence between these two lineages to ~19 Mya and the age of the crown group Afrotropical *Labeo* to ~17 Mya (no CI provided). Therefore, the ancestors of Afrotropical *Labeo* reached Afrotropical freshwaters after a dispersal event from the Orient, which occurred between 19 and 17 Mya.

Lineage G6: Afronemacheilus (Table 1; Figs 4, 11A; Supporting Information Fig. S2)

The two species of the genus *Afronemacheilus* are the only Afrotropical representatives of the diverse Oriental freshwater family Nemacheilidae, which comprises almost 700 species (Fricke *et al.*, 2018). According to Prokofiev (2009), who examined the morphology of *Afronemacheilus* along with a selection of Oriental nemacheilids, *Afronemacheilus* is the sister group of the genus *Nun*, and these two genera together are sister to the genus *Seminemacheilus* (Fig. 11A; but see discussion by Prokofiev & Golubtsov, 2013). Using the phylogeny of Prokofiev (2009), I reconstructed the ancestral range evolution and confirmed that *Afronemacheilus* originated from the Orient (Fig. 11A).

There is still no comprehensive time tree for the family Nemacheilidae and no age estimation for the divergence between *Nun* and *Afronemacheilus*. Šlechtová *et al.* (2008) estimated the time divergence only between the genera *Schistura* and *Nemacheilus* (i.e. the age of the crown group Nemacheilidae) to ~48 Mya. Hirt *et al.* (2017) reconstructed the time tree of the higher taxonomic level of Cypriniformes, and they found a younger age for the crown group Nemacheilidae, i.e. 35 Mya. There are no African nemacheilid fossils and no molecular estimation of the age of *Afronemacheilus*. Therefore, I set it to a soft minimum of 5 Mya.

The presence of *Afronemacheilus* in Africa is the result of a dispersal event from the Orient, which occurred broadly between 35 and 5 Mya.

Lineage G7: Afrotropical clariids (Table 1; Figs 4, 12; Supporting Information Fig. S3)

The Afrotropical part of the freshwater family Clariidae comprises ~80 species classified into ~13 genera (e.g. *Channallabes*, *Clariallabes*, *Clarias*, *Dinotopterus*, *Gymnallabes*, *Heterobranchus*, *Tanganikallabes*; Devaere *et al.*, 2007). They form a monophyletic group that is the sister group of the Oriental clariids (~40 species and three genera). The whole family Clariidae is then the sister group of the Oriental family Heteropneustidae, indicating that the Afrotropical clariids originated in the Orient and reached Africa after a dispersal event (Fig. 12).

Lundberg *et al.* (2007) estimated the stem age of the Afrotropical clariids (i.e. the divergence time between Afrotropical and Oriental clariids) to ~35 Mya and the crown group age of the Afrotropical clariids (i.e. the divergence between *Clarias gabonensis* Günther, 1867 and *Heterobranchus longifilis* Valenciennes, 1840 in that study) to 26 Mya (no CI provided for both estimates). In conflict with the fossil record, Agnèse & Teugels (2005) inferred an age for the stem Afrotropical clariids of only 13 Mya, whereas Jansen *et al.* (2006) overestimated the age of the Afrotropical clariid crown group to 56 Mya (and the age of the Siluriformes to 400 Mya, Devonian).

The oldest known clariid remains are from the early or middle Eocene of Pakistan (Oriental region) (Gayet, 1987), whereas the oldest clariid fossils from the African continental plate are from the early Oligocene (30 Mya) of Oman (Otero & Gayet, 2001). Gayet & Meunier (2003) noted that some very fragmentary fossils from the Eocene of Egypt could also belong to Clariidae.

Therefore, the Afrotropical freshwater clariids form a monophyletic group that dispersed from the Orient between 35 and 30 Mya.

Lineage G8: Bagrus (Table 1; Figs 4, 12; Supporting Information, Fig. S3)

The ten species of the Afrotropical genus *Bagrus* belong to the large freshwater family Bagridae (~220 species and 20 genera), which is otherwise distributed in the Orient and nested in the Big Asia catfish clade (Sullivan *et al.*, 2006). The sister group of *Bagrus* is *Hemibagrus* (Sullivan *et al.*, 2006; Lundberg *et al.*, 2007). The ancestral range reconstruction unambiguously supported the Oriental origin of *Bagrus* (Fig. 12). Lundberg *et al.* (2007), using a molecular clock, tentatively estimated the divergence time between *Bagrus* and *Hemibagrus* to ~40 Mya (no CI provided). There is no molecular-based estimation for the age of the crown group *Bagrus*. Recently, Longbottom (2010) reviewed the African fossil record of bagrids and suggested that it is not as old as it was previously thought, because of the previous lack of resolution and definition of the family Bagridae. Until recently, the family Bagridae was a polyphyletic group that consisted of three distantly related families, Austroglanididae, Bagridae *s.s.* and Claroteidae. The

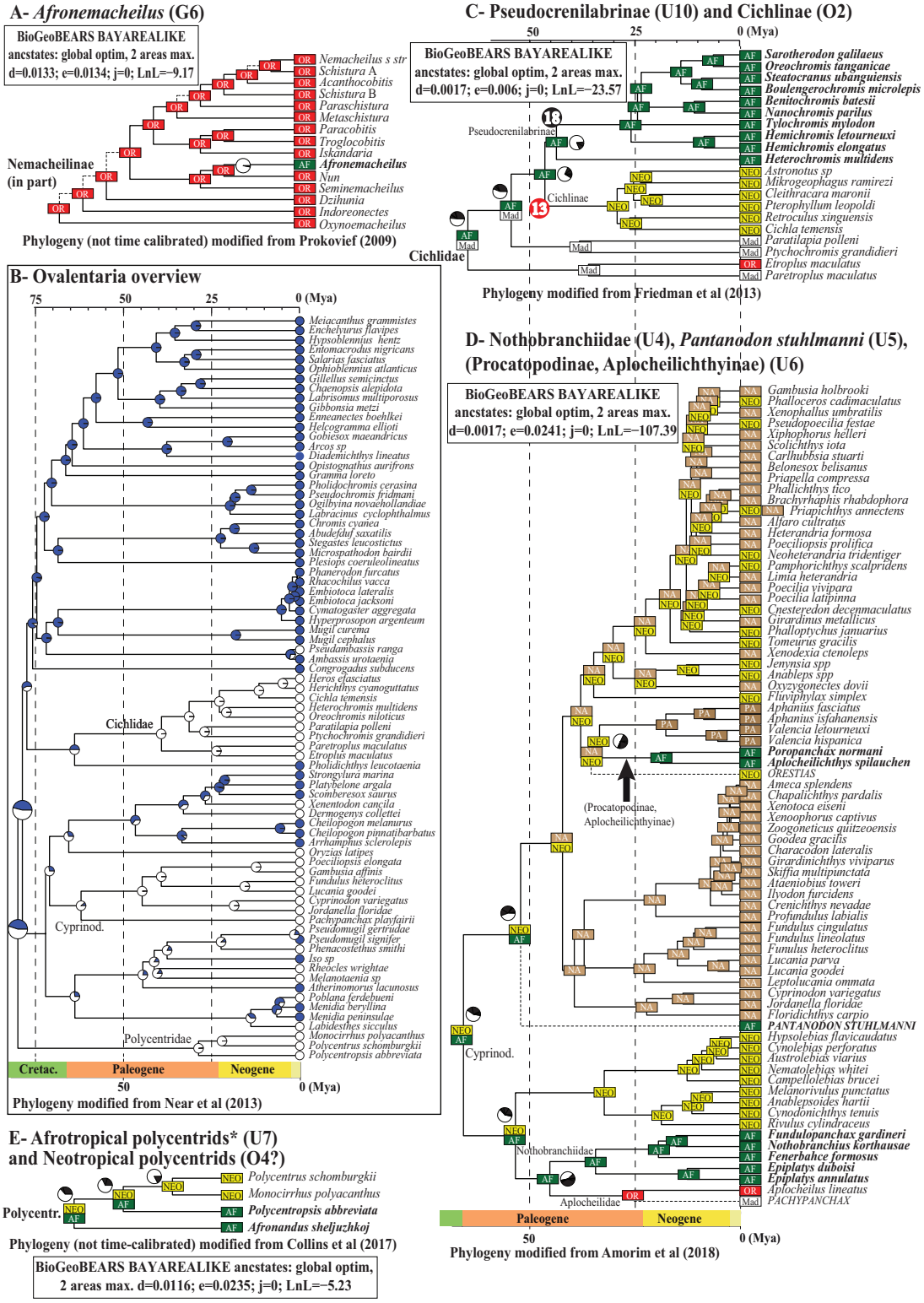

Figure 11. Phylogenetic trees of lineages of Nemacheilinae (Cypriniformes) and Ovalentaria (Acanthomorpha), on which are estimated geographical range evolution using the BAYAREALIKE model (Landis *et al.*, 2013) as implemented in BioGeoBEARS (Matzke, 2018). A, part of Nemacheilinae (Cobitoidea, Cypriniformes), showing the origin of *Afronemacheilus* (not time-calibrated tree modified from Prokofiev, 2009). B, overview of the time-calibrated phylogeny of Ovalentaria, on

oldest fossil assigned to *Bagrus* is from the Oligocene of Oman (~30 Mya; Otero & Gayet, 2001; Longbottom, 2010). Therefore, I use the divergence time between *Bagrus* and *Hemibagrus*, estimated as 40 Mya, as the maximal age for the dispersal of *Bagrus* in Afrotropics and the oldest fossil of *Bagrus* in Africa as its strict minimal age (30 Mya).

Lineage G9: Afrotropical anabantids (Table 1; Figs 4, 13A, B; Supporting Information, Fig. S4)

The Afrotropical anabantids comprise three genera and 32 species and they form a monophyletic group that is nested in the freshwater clade (Anabantiformes, Synbranchiformes), which is predominantly distributed in the Orient (Fig. 13A; Rüber *et al.*, 2006; Near *et al.* 2013). Using DNA, Rüber *et al.* (2006) postulated that *Anabas testudineus* (Bloch, 1792) is the sister group of Afrotropical anabantids; the morphology-based hypothesis of Wu *et al.* (2017) is congruent with this hypothesis. Using the phylogenetic tree of Rüber *et al.* (2006) (Fig. 13B), I showed that Afrotropical anabantids originated from the Orient. The time estimations provided by Rüber *et al.* (2006: fig. 7) indicate that the divergence between Afrotropical anabantids and *Anabas testudineus* occurred 35 Mya (95% CI: 43–28 Mya), and the early divergence of the Afrotropical anabantids started 30 Mya (95% CI: 37–23 Mya) (see also Wu *et al.*, 2019). There are no Afrotropical anabantid fossils that provide a strict minimal age for the presence of anabantids in Africa. Therefore, the time-calibrated phylogenetic evidence supports the hypothesis that Afrotropical anabantids originated from a single event of dispersal from the Oriental region, which is dated between 43 and 23 Mya.

Lineage G10: Parachanna (Table 1; Figs 4, 13A, D; Supporting Information Fig. S4)

The Afrotropical snakehead genus *Parachanna* includes three species and is the sister group of the Oriental and more species-rich genus *Channa* (Adamson, Hurwood & Mather, 2010), together with the Oriental genus *Aenigmachanna* (Britz *et al.*, 2019), they form the family Channidae. The Channidae belongs to a larger freshwater clade, the Anabantiformes, mostly distributed in the Orient (Near *et al.*, 2013). The ancestral range reconstruction confirmed that *Parachanna* has Oriental roots (Fig. 13D).

Using molecules, Adamson *et al.* (2010) estimated the age of the split between *Channa* and *Parachanna* to ~43 Mya (95% CI: 48–40 Mya). Brown *et al.* (2010) inferred the age of this split to 34 Mya (95% CI: 35–33 Mya) and the age of the crown group *Parachanna* (i.e. the divergence between *Parachanna insignis* (Sauvage, 1884) and *Parachanna obscura* (Günther, 1861) in the study by Brown *et al.*, 2010) to ~14 Mya (95% CI: 21–8 Mya) (see also Wu *et al.*, 2019). Murray (2006) found a channid fossil in Africa (Egypt), †*Parachanna fayumensis*, from the late Eocene (~36 Mya); this taxon is more closely related to *Parachanna* than to *Channa*. In addition, Murray *et al.* (2010) described a new *Parachanna* fossil also from Egypt (†*Parachanna* sp.), which is a little bit older at 38 Mya.

Therefore, the current evidence indicates that *Parachanna* dispersed once from the Orient to Africa between 48 Mya and a strict minimum of 38 Mya. The biogeography of the Afrotropical channids is discussed by Murray (2012).

Lineage G11: Afrotropical Mastacembelus (Table 1; Figs 4, 13A, C; Supporting Information, Fig. S4)

The 41 Afrotropical species of the spiny-eel genus *Mastacembelus* form a monophyletic group that is nested within the family Mastacembelidae, which occurs otherwise in the Orient (44 Oriental species) (Brown *et al.*, 2010; Day *et al.*, 2017). The Mastacembelidae belongs to the freshwater order Synbranchiformes (Near *et al.*, 2013). The Oriental species *Mastacembelus mastacembelus* (Banks & Solander, 1794) is the sister group of the Afrotropical species. The ancestral BAYAREALIKE range reconstruction showed that the most recent common ancestor of the Afrotropical lineage

which is reconstructed the evolution of salinity preference (tree modified from Near *et al.*, 2013). Salinity preference is classified in two states: 'marine' indicated in blue and 'fresh water' in white. At each node, the relative probabilities of each state (sum = 1) are drawn using pie charts. C, Cichlidae, showing the origin of Pseudocrenilabrinae (tree modified from Friedman *et al.*, 2013). D, Cyprinodontiformes, showing the origins of Nothobranchiidae, *Pantanodon stuhlmanni* and the clade (Procatopodinae, Aplocheilichthyinae) (tree modified from Amorim *et al.*, 2018, with addition of taxa from Pohl *et al.*, 2015 and Reznick *et al.*, 2017). E, Polycentridae, showing the origin of Afrotropical polycentrids (not time-calibrated tree modified from Collins *et al.*, 2015). In reconstructions A and C–E, the Afrotropical (AF) distributed taxa and Afrotropical inferred ancestral regions are highlighted in green; Oriental (OR, red), Neotropical (NEO, yellow), Nearctic (NA, light brown), Palaearctic (PA, medium brown), Madagascan (Mad, white) and Australian (AUS, orange) taxa and ancestral regions are indicated. Black and white pie charts at specific ancestral area reconstruction show the probability (white) of the corresponding reconstruction. Number in black-filled circle indicates strict minimal age for the corresponding lineage, as obtained from the fossil record (for details, see main text and Fig. 15).

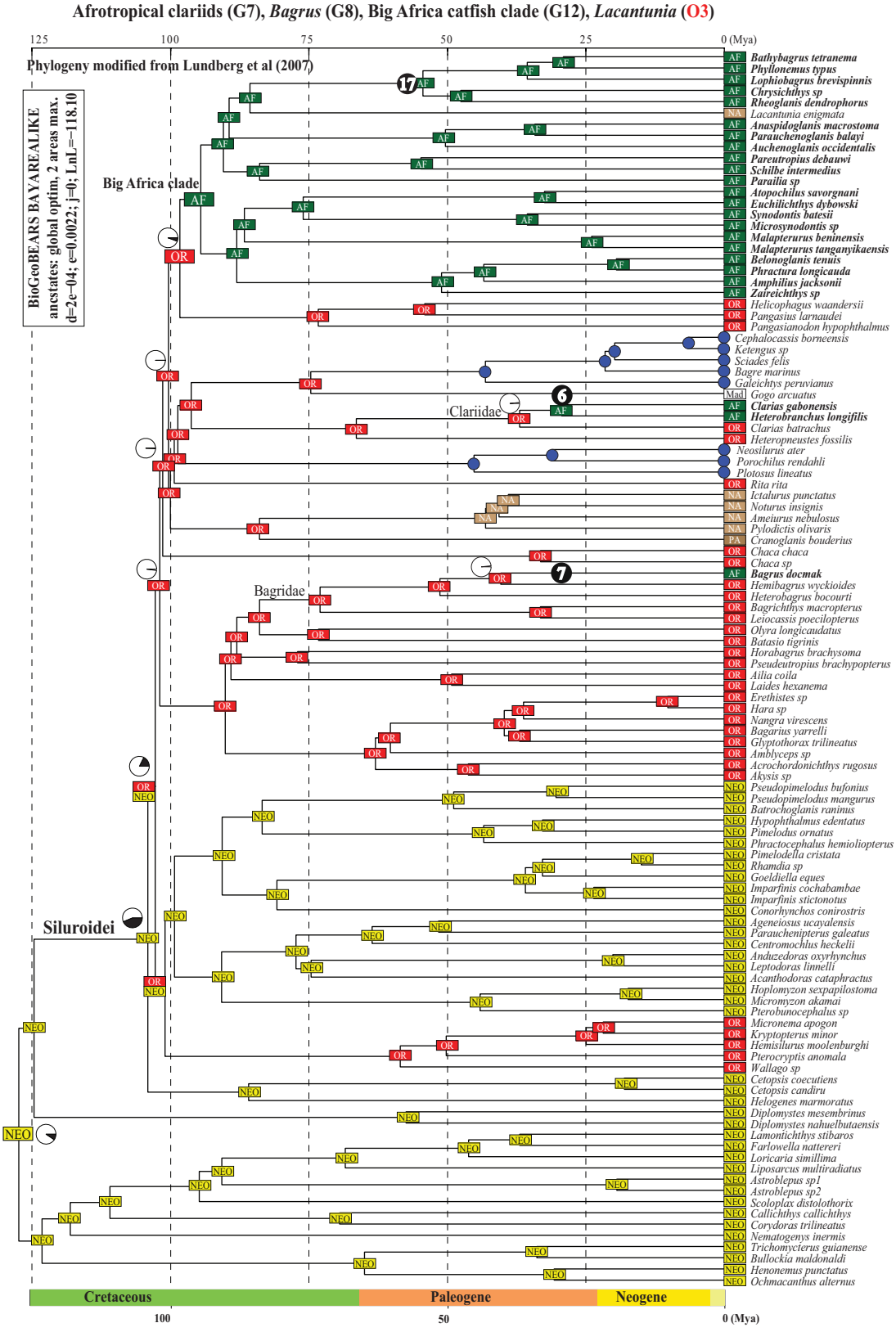

Figure 12. Time-calibrated phylogenetic tree of Siluriformes, on which are estimated geographical range evolution using the BAYAREALIKE model (Landis *et al.*, 2013) as implemented in BioGeoBEARS (Matzke, 2018). This analysis shows the

and *Mastacembelus mastacembelus* was distributed in the Orient and the Afrotropics, with the presence of *Mastacembelus* in Africa being the result of a dispersal event followed by a range reduction through extinction in the Orient (Fig. 13C). This scenario conflicts with that of Day *et al.* (2017), who found that the whole family Mastacembelidae originally diversified in the Orient and the Afrotropics, using the DEC model (see also Supporting Information, Fig. S4). According to Brown *et al.* (2010), the divergence between Afrotropical *Mastacembelus* and *Mastacembelus mastacembelus* occurred 18 Mya (95% CI: 27.5–14 Mya), and the early diversification of the Afrotropical *Mastacembelus* started 16 Mya (95% CI: 21–12 Mya). Day *et al.* (2017) dated this diversification somewhat more recently, to 15.4 Mya (95% CI: 23.9–8.8 Mya). There are no known spiny-eel fossils related to the Afrotropical *Mastacembelus*. Therefore, the ancestral range estimation indicated that the Afrotropical *Mastacembelus* lineage has an Oriental origin, and it reached Africa shortly before its divergence from *Mastacembelus mastacembelus*, between 27.5 and 12 Mya.

Lineages that originated from Late Cretaceous or early Cenozoic dispersal events from the Oriental region

Lineage G12: Big Africa catfish clade (Table 1; Figs 4, 12; Supporting Information, Fig. S3)

The biogeography of the globally distributed catfish suborder Siluroidei was considered to be puzzling, in part because of the early and rapid diversification of this group, making it difficult to infer interfamilial relationships. Sullivan *et al.* (2006) and Lundberg *et al.* (2007) provided a landmark in the phylogenetic resolution of Siluroidei in identifying 13 main lineages, three from the Neotropics, six from the Orient, one from the Afrotropics, one from the Palaearctic and Nearctic, and two secondarily adapted to a marine environment. The large Afrotropical siluroid lineage identified by Sullivan *et al.* (2006) and Lundberg *et al.* (2007) comprises five Afrotropical catfish families, Amphiliidae (100 species; species count from Fricke *et al.*, 2018), Claroteidae (90 species), Malapteruridae (20 species), Mochokidae (~210 species), the Afrotropical part of Schilbeidae (30 species), along with the southern Nearctic monospecific family Lacantuniidae and, possibly, the Afrotropical family Austroglanidae (not examined in any molecular study). This clade has been named informally the Big Africa catfish clade (Sullivan *et al.*, 2006: 645). Its monophyly needs to be evaluated further, because there is no morphological synapomorphy known to support it, and a few studies showed its lack of monophyly (e.g. Chen *et al.*, 2013).

The phylogenetic position of the Big Africa catfish clade among the main siluroid lineages is poorly resolved. However, of the several lineages that have been proposed to be the sister group of the Big Africa catfish clade, none of them is from the Neotropics (Sullivan *et al.*, 2006; Lundberg *et al.*, 2007; Nakatani *et al.*, 2011; Kappas *et al.*, 2016; Arcila *et al.*, 2017). Sullivan *et al.* (2006), Lundberg *et al.* (2007) and Arcila *et al.* (2017) discerned a weak signal for a monophyletic group composed of the majority of non-Neotropical lineages (excluding Siluridae). Using the phylogenetic tree of Lundberg *et al.* (2007: fig. 2), to estimate the ancestral range evolution in Siluriformes (Fig. 12), surprisingly, I found a well-supported reconstruction evidencing only two early dispersal events from the Neotropics to the Orient, followed by three dispersal events from the Orient to the Afrotropics, which occurred at different periods. The oldest of these events resulted in the Big Africa catfish clade.

Lundberg *et al.* (2007) estimated the age of the crown group Siluroidei to ~102 Mya (95% CI: 109–95 Mya) (Fig. 12) and Kappas *et al.* (2016) to 97 Mya (95% CI: 110–85 Mya), whereas Chen *et al.* (2013) found a younger estimate of ~90 Mya (95% CI: 100–80 Mya). In these three studies, the age of Siluriformes was estimated to ~128, ~133 and ~100 Mya, respectively. Lundberg *et al.* (2007: fig. 2) found that the Big Africa catfish clade diverged from its sister group ~90 Mya, and it started to diversify ~80 Mya.

According to Longbottom (2010), five Afrotropical freshwater catfish families have fossil records from the Cenozoic: Bagridae, Clariidae, Claroteidae, Mochokidae and Schilbeidae. The last three families belong to the Big Africa catfish clade. Longbottom (2010) did not confirm any previous Cretaceous (from Cenomanian and Maastrichtian) records presented by Gayet & Meunier (2003). The earliest occurrence of the Big Africa catfish clade in Africa is from the Palaeocene (Thanetian, 59.2–56 Mya) with the genus

origins of Afrotropical clariids, *Bagrus* and the Big Africa clade (tree modified from Lundberg *et al.*, 2007). The Afrotropical (AF) distributed taxa and Afrotropical inferred ancestral regions are highlighted in green; Oriental (OR, red), Neotropical (NEO, yellow), Nearctic (NA, light brown), Palaearctic (PA, medium brown), Madagascan (Mad, white) and Australian (AUS, orange) taxa and ancestral regions are indicated. Black and white pie charts at specific ancestral area reconstruction show the probability (white) of the corresponding reconstruction. Numbers in black-filled circles indicate strict minimal age for the corresponding lineage, as obtained from the fossil record (for details, see main text and Fig. 15).

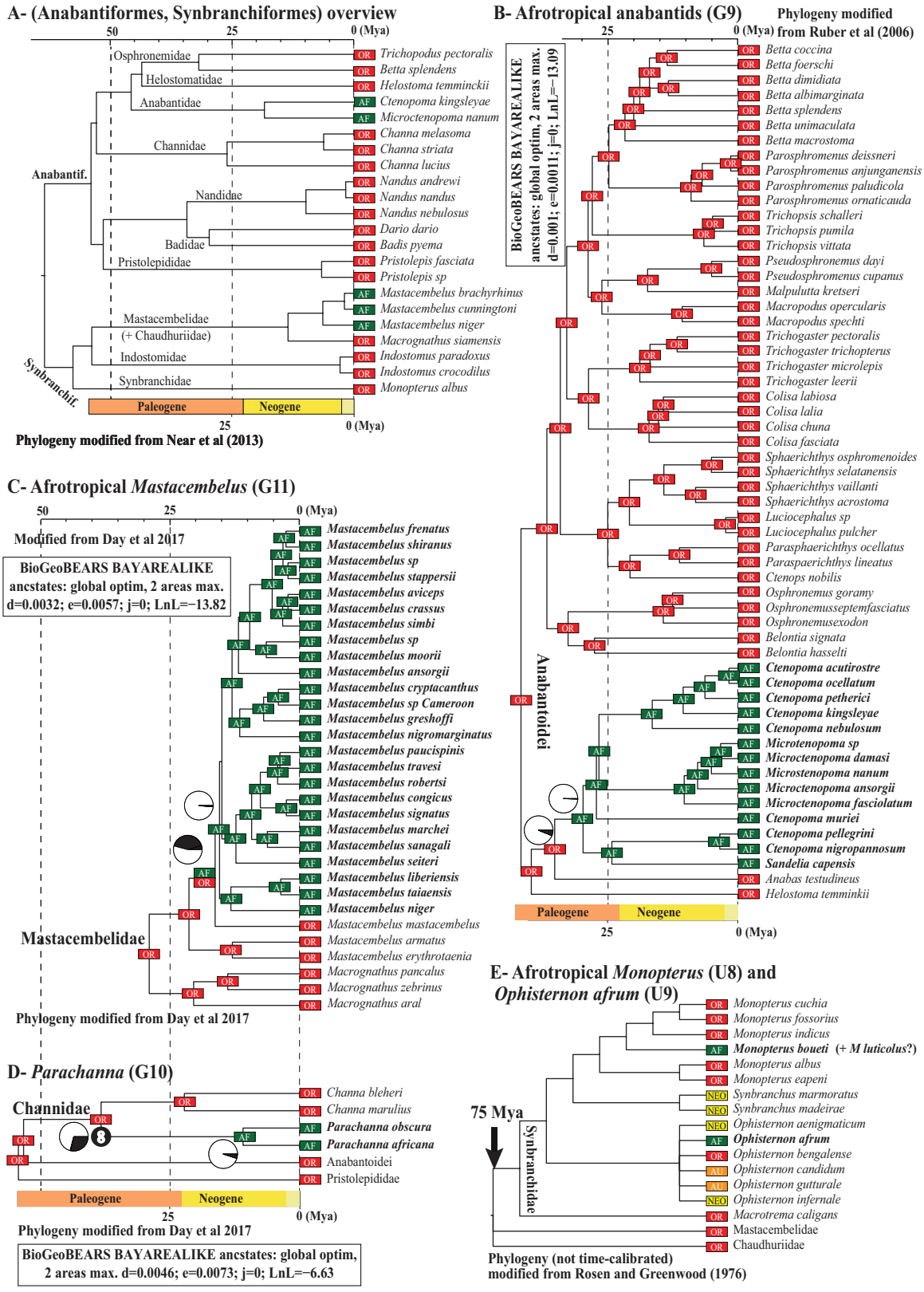

Figure 13. Phylogenetic trees of distinct lineages of the clade (Anabantiformes, Synbranchiformes), on three of which are estimated geographical range evolution using the BAYAREALIKE model (Landis *et al.*, 2013) as implemented in BioGeoBEARS

†*Nigerium* (family Claroteidae), followed by a middle Eocene (46–45 Mya) species of the same family, †*Chrysichthys mahengeensis* (Murray & Budney, 2003; Longbottom, 2010). These are the earliest occurrences of Afrotropical catfish fossils definitely identified (Longbottom, 2010). There are two other families of the Big Africa catfish clade with a more recent fossil record: the Mochokidae, which are represented by fossil *Synodontis* from the Oligocene (Otero & Gayet, 2001), and the Schilbeidae, which are represented by fossil *Schilbe* from the late Miocene of Kenya (Stewart, 2001).

Taking all evidence together, the Big Africa catfish clade reached Africa after a dispersal event from the Orient that pre-dated the Eocene. I set the initial presence of the Big Africa catfish clade in the Afrotropics to a maximum of 90 Mya and a minimum of 80 Mya. The genus †*Nigerium* provides a strict minimal age of 56 Mya.

Gondwanan break-up-mediated vicariant freshwater lineages (> 105 Mya) (hypothesis 3)

Lineage V1: Protopteridae (Table 1; Figs 5, 14A; Supporting Information, Fig. S5)

The four extant species of the Afrotropical lungfish genus *Protopterus* (Protopteridae) are the sister of the Neotropical freshwater species *Lepidosiren paradoxa* Fitzinger, 1837 (Lepidosirenidae) (Criswell, 2015; Kemp *et al.*, 2017). Kemp *et al.* (2017) built a comprehensive morphological phylogeny of lungfish, and the African fossil record of lungfish was reviewed by Otero (2011). Using DNA, the divergence between *Protopterus* and *Lepidosiren paradoxa* was estimated to 120 Mya (95% CI: 165–94 Mya) by Heinicke *et al.* (2009) and Tokita *et al.* (2005) (Fig. 14A). This is congruent with the chronology of the fossil record (Kemp *et al.*, 2017). The presence of lungfishes in Africa is as old as the Permian (277 Mya) or even older, although the oldest lungfish remains belong to some stem groups. The first Afrotropical fossils closely related to the genus *Protopterus* are from the Cenomanian (100.5–94 Mya; Werner, 1994; Claeson *et al.*, 2014).

In summary, the Afrotropical genus *Protopterus* is sister to the Neotropical genus *Lepidorisen*, and their divergence is dated between 165 and 94 Mya. The vicariant hypothesis postulating that the divergence between *Protopterus* and *Lepidosiren* was caused by the separation of Africa and South America is not rejected (Fig. 14A) (Lundberg, 1993; Cavin *et al.*, 2008).

Lineage V2: Polypteridae (Table 1; Figs 5, 14B; Supporting Information Fig. S5)

The Polypteridae is a freshwater family of primitive-looking fishes that comprises only 20 Afrotropical species classified in two genera, *Polypterus* and the monotypic *Calamoichthys* [= *Erpetoichthys*; see Rizzato & Bockmann (2017) for nomenclatural discussion]. The Polypteridae is considered to be the sister group of all other actinopterygians (Inoue *et al.*, 2003; Suzuki *et al.*, 2010); the two lineages diverged from each other ~370 Mya (Devonian; no CI provided) (Gardiner *et al.*, 2005; Friedman, 2015; Lu *et al.*, 2016).

Extant polypterids comprise ~20 species; all species are endemic to Africa, where they diversified only recently (the crown group age is estimated to the Miocene; see Near *et al.*, 2014b). The fossil record of this group indicates that: (1) all fossil species are from fresh water; (2) the Polypteridae was already present (and well diversified) in North Africa during the Cenomanian period (100.5–93.9 Mya), with at least nine genera known (Dutheil, 1999; Grandstaff *et al.*, 2012); and (3) late Cretaceous (Maastrichtian, 72.1–66.0 Mya) and Palaeocene polypterid fossils [†*Dagetella sudamericana* (Gayet & Meunier, 1991) and †*Latinopollia suarezi* (Meunier & Gayet, 1996)] have been excavated from South America (Gayet *et al.*, 2002; Brito *et al.*, 2007). All Cretaceous and Palaeocene fossils are stem polypterid fossils, and their relative phylogenetic positions (especially between Afrotropical and Neotropical fossils) are not yet resolved.

To summarize, the polypterids are an ancient group of Afrotropical freshwater fish (even if extant

(Matzke, 2018). A, overview of the time-calibrated phylogeny of the clade (Anabantiformes, Synbranchiformes) (modified from Near *et al.*, 2013). B, Anabantoidei, showing the origin of the Afrotropical anabantids (time-calibrated tree modified from Rüber *et al.*, 2006). C, Mastacembelidae, showing the origin of the Afrotropical mastacembelids (time-calibrated tree modified from Day *et al.*, 2017). D, Channidae, showing the origin of *Parachanna* (tree modified from Day *et al.*, 2017). E, Synbranchidae, showing the phylogenetic positions of Afrotropical species of *Ophisternon* and *Monopterus*; no ancestral range estimation was possible with BioGeoBEARS because this tree contains one polytomy (not time-calibrated tree modified from Rosen & Greenwood, 1976; maximal age estimation from Near *et al.*, 2013). The Afrotropical (AF) distributed taxa and Afrotropical inferred ancestral regions are highlighted in green; Oriental (OR), Neotropical (NEO) and Australian (AUS) taxa and ancestral regions are indicated in red, yellow and orange, respectively. Black and white pie charts at specific ancestral area reconstruction show the probability (white) of the corresponding reconstruction. Number in black-filled circle indicates strict minimal age for the corresponding lineage, as obtained from the fossil record (for details, see main text and Fig. 15).

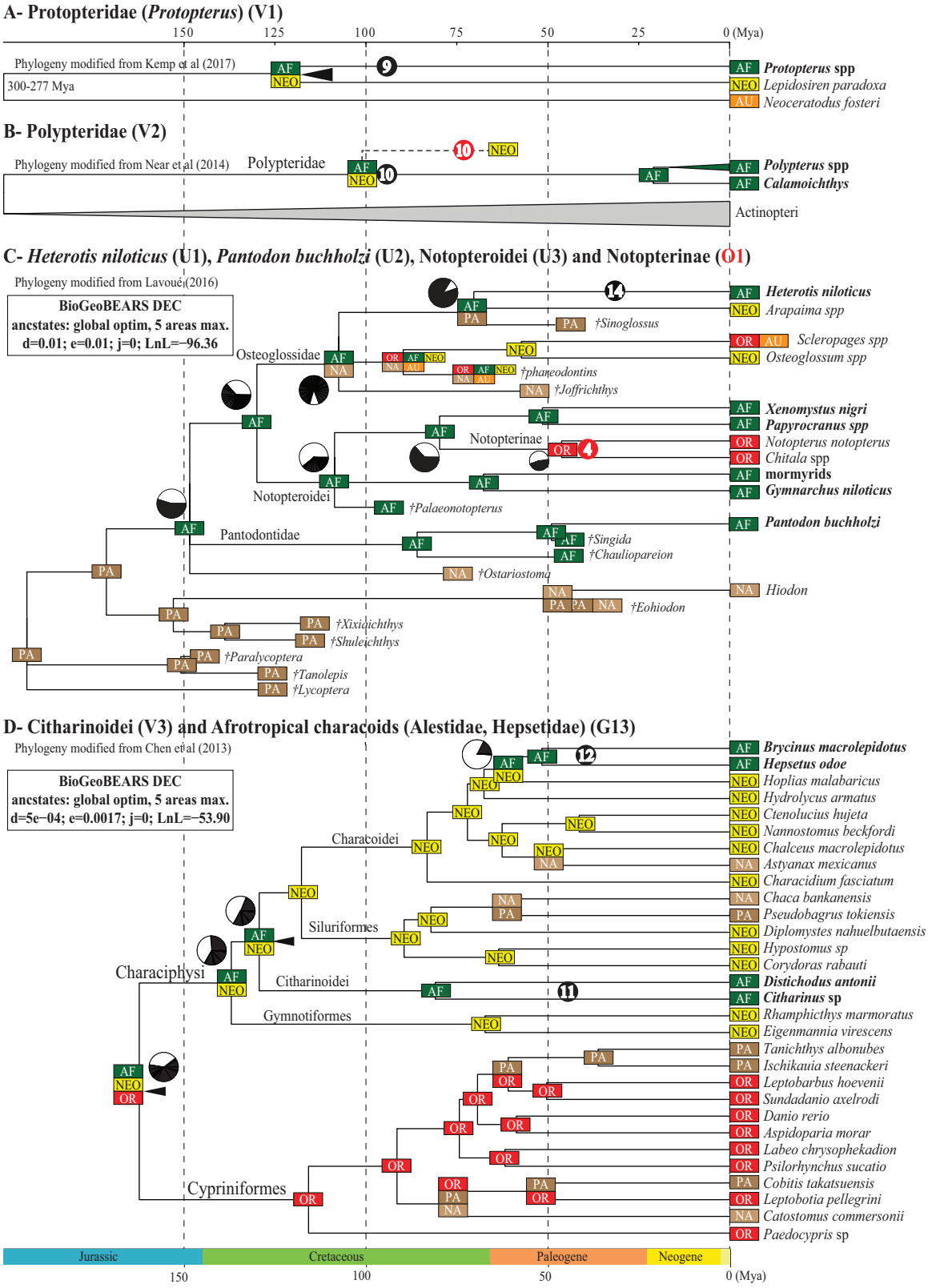

Figure 14. Four time-calibrated phylogenetic trees of early Mesozoic Afrotropical freshwater lineages; on two of them are estimated geographical range evolution using a dispersal–extinction–cladogenesis (DEC) model (Ree & Smith, 2008) as

species diversified only recently), maybe as old as the Jurassic–Cretaceous limit (145 Mya), and the strict minimal age of their presence in Africa is 93.9 Mya (but likely to be earlier). The vicariant hypothesis postulating that the divergence between Afrotropical polypterids and Neotropical polypterid fossils was caused by the separation between Africa and South America is not rejected (Fig. 14B) (Lundberg, 1993; Cavin *et al.*, 2008).

Lineage V3: Citharinoidei (Table 1; Figs 5, 14D; Supporting Information, Fig. S5)

Citharinoidei comprises ~110 species classified into two families: Citharinidae and Distichodontidae (Vari, 1979). According to Nakatani *et al.* (2011), Chen *et al.* (2013) and Chakrabarty *et al.* (2017), the Citharinoidei is the sister group of Siluriformes+Characoidei, whereas Arcila *et al.* (2017), based on a large taxonomic and genomic dataset, placed the Citharinoidei as the sister of Characoidei, making Characiformes monophyletic, in congruence with morphological evidence (Fink & Fink, 1996, 1981). Although the phylogenetic position of Citharinoidei is still debated, it is important to indicate that, whatever the correct phylogenetic hypothesis: (1) the sister group of Citharinoidei is of Neotropical origin (either Characoidei or Siluriformes+Characoidei); and (2) the divergence time between the Citharinoidei and its sister group is comparable.

Chen *et al.* (2013) estimated the divergence time between the Citharinoidei and its Neotropical sister group to be 128.4 Mya (95% CI: 145–115 Mya), whereas Near *et al.* (2012) estimated it to ~100 Mya (95% CI: 120–80 Mya). Chen *et al.* (2013) inferred the age of crown Citharinoidei (i.e. the divergence between Distichodontidae and Citharinidae) as 78.8 Mya (95% CI: 110–38 Mya), and Arroyave *et al.* (2013) estimated it as 91 Mya (95% CI: 110–73 Mya). I note that on the tree displayed in figure 8 of Arroyave *et al.* (2013), the Eocene (45 Mya) fossil †*Eocitharinus macrognathus* (Murray, 2003) calibrates the divergence between Citharinidae and Distichodontidae, whereas this fossil is a stem member of the Citharinoidei and, therefore, it should have calibrated one node below (i.e. the divergence between the Citharinoidei and its sister group). Murray (2003b) stated that the phylogenetic position of this fossil in Citharinoidei is uncertain because it does not share any derived character with any of the two extant families, Citharinidae and Distichodontidae. †*Eocitharinus macrognathus* is by far the oldest fossil known of Citharinoidei (Murray, 2003b; Argyriou *et al.*, 2015; Otero *et al.*, 2017).

When I reconstructed the ancestral range evolution in Otophysi using the DEC model (Fig. 14D; Chen *et al.*, 2013), I found that Citharinoidei evolved in the Afrotropics after a vicariant event caused by the final separation of Africa and South America.

In summary, molecular-based dating suggests that the divergence between Citharinoidei and its Neotropics-originated sister group occurred between 145 and 115 Mya. The fossil record provides a strict (but probably too young) minimal age for the presence of Citharinoidei in the Afrotropics of 45 Mya. The vicariant hypothesis, assuming that the divergence between Afrotropical citharinoids and their Neotropical sister group was caused by the separation between Africa and South America, is not rejected (Fig. 14D) (Malabarba & Malabarba, 2010; Chen *et al.*, 2013).

Freshwater lineages that reached the Afrotropics by dispersal from the Neotropics, after Gondwanan break-up (hypothesis 5 or 6)

Lineage G13: Afrotropical characoids (Table 1; Figs 5, 14D; Supporting Information, Fig. S5)

The Afrotropical characoids comprise two families, Alestidae and Hepsetidae, with ~114 species. The phylogeny of the suborder Characoidei is still in flux, with several different hypotheses proposed, especially regarding the relationships among the Afrotropical taxa relative to the Neotropical ones (e.g. Calcagnotto *et al.*, 2005; Zanata & Vari, 2005; Arroyave & Stiassny, 2011; Oliveira *et al.*, 2011; Arcila *et al.*, 2017). All studies

implemented in BioGeoBEARS (Matzke, 2018). A, extant lungfishes, showing the origin of *Protopterus* (tree modified from Kemp *et al.*, 2017; the ancestral range was manually estimated). B, early evolution of Actinopterygii, showing the origin of Polypteridae (tree modified from Near *et al.*, 2014b; the ancestral range was estimated manually). C, Osteoglossomorpha, including extant and extinct taxa, showing the origins of *Heterotis niloticus*, Notopteroidei and *Pantodon buccholzi* (tree modified from Lavoué, 2016). D, Otophysi, showing the origins of Citharinoidei and the clade (Alestidae, Hepsetidae) (tree modified from Chen *et al.*, 2013). The Afrotropical (AF) distributed taxa and Afrotropical inferred ancestral regions are highlighted in green; Oriental (OR), Neotropical (NEO), Nearctic (NA), Palaearctic (PA) and Australian (AUS) taxa and ancestral regions are indicated in red, yellow, light brown, medium brown and orange, respectively. Black and white pie charts at specific ancestral area reconstruction show the probability (white) of the corresponding reconstruction. Numbers in black-filled and red-filled circles indicate strict minimal age for the corresponding lineage, as obtained from the fossil record (for details, see main text and Fig. 15).

agree that Alestidae (minus the miniature genera *Arnoldichthys* and *Lepidarchus*) form a monophyletic group. However, studies conflict on the phylogenetic position of Alestidae relative to *Arnoldichthys* and *Lepidarchus*, the genus *Hepsetus* (Hepsetidae) and some Neotropical families. For example, Oliveira *et al.* (2011) and Arcila *et al.* (2017) found *Hepsetus* sister to Alestidae, making the Afrotropical characoids monophyletic (but neither *Arnoldichthys* nor *Lepidarchus* was sampled in these two studies), whereas Calcagnotto *et al.* (2005) and Arroyave *et al.* (2011) found *Hepsetus* to be only distantly related to the alestids. Additionally, *Arnoldichthys* was found to be the sister group of Alestidae by Calcagnotto *et al.* (2005), but not closely related to Alestidae by Arroyave *et al.* (2011). In the morphological work of Zanata & Vari (2005), the Afrotropical alestids are hypothesized to be the closest relative of the Neotropical genus *Chalceus* (forming a trans-Atlantic family Alestidae). Herein, I consider the Afrotropical characoids (i.e. Alestidae+Hepsetidae) monophyletic and nested in Neotropical counterparts (Oliveira *et al.*, 2011; Arcila *et al.*, 2017). Although Chen *et al.* (2013) examined a limited taxonomic sampling, their ancestral range reconstruction within Otophysi showed that Afrotropical characoids originated from the Neotropics after a dispersal event. I inferred the same scenario (Fig. 14D).

Chen *et al.* (2013) estimated the divergence time between Afrotropical characoids and their Neotropical sister group to 72 Mya (95% CI: 76–66 Mya) and the age of the Afrotropical characoid crown group [i.e. the divergence between *Phenacogrammus* (Alestidae) and *Hepsetus* (Hepsetidae)] to 63 Mya (95% CI: 73–55 Mya).

The Palaearctic (western Europe) †*Alestoides eocaenicus* Monod & Gaudant, 1998 and the North African †*Hydrocynus* sp. (Hammouda *et al.*, 2016) are the two oldest fossils unambiguously assignable to the Afrotropical characoids (Otero *et al.*, 2008; Malabarba & Malabarba, 2010); both fossils are of Eocene age (56–41 Mya), with †*Hydrocynus* sp. representing the first fossil of Alestidae in Africa. According to Monod & Gaudant, 1998, the early Eocene (56–48 Mya) Palaearctic fossil genus †*Alestoides*, known only from teeth, might be related closely to extant *Alestes*, but more evidence is needed to confirm this hypothesis. †*Mahengecharax carrolli* from the middle Eocene (46–45 Mya) might belong to an extinct (stem?) characoid lineage (Murray, 2003a; Zanata & Vari, 2005).

Therefore, the divergence between Afrotropical characoids and their Neotropical sister group strictly post-dated the final separation of South America and Africa, rejecting the vicariant hypothesis and indicating that they dispersed from South America to Africa. Afrotropical characoid ancestors reached the Afrotropics between 76 and 56 Mya.

Afrotropical lineages of unresolved origins

Lineage U1: Heterotis niloticus (Table 1; Figs 5, 14C; Supporting Information, Fig. S5)

Within the family Osteoglossidae, Afrotropical *Heterotis niloticus* (Cuvier, 1829) is the sister of the Neotropical genus *Arapaima* (Li & Wilson, 1996a; Hilton, 2003; Forey & Hilton, 2010; Lavoué, 2016). Noticeably, an Oriental freshwater Eocene fossil, †*Sinoglossus lushanensis* Su, 1986, is closely related to this clade either as its sister group (Li & Wilson, 1996a; Forey & Hilton, 2010) or as the sister group only to *Heterotis niloticus* (Li & Wilson, 1996b) or in an unresolved position relative to *Heterotis niloticus* and *Arapaima* (Wilson & Murray, 2008; Lavoué, 2016). The uncertainty in the phylogenetic position of †*Sinoglossus lushanensis* adds difficulties to resolution of the biogeography of *Heterotis niloticus* and *Arapaima*. The ancestral range estimation using the DEC model inferred Afrotropics+Palaearctic as the region of origin of the clade (*Heterotis niloticus*, *Arapaima*, †*Sinoglossus lushanensis*) and Afrotropics+Nearctic as the region of origin of the whole Osteoglossidae (Fig. 14C). However, no firm conclusion can be drawn because the analysis provides other possibilities that are only slightly less likely for the ancestral region of each of these two nodes. The biogeography of the Osteoglossidae is certainly complex, as shown by the discovery of many osteoglossid fossils from different continental regions (Hilton & Lavoué, 2018). Resolution of the biogeography of the Osteoglossidae and the origin of *Heterotis niloticus* will require a phylogenetic study that includes a larger selection of fossils.

Lavoué (2016) the estimated divergence time between *Heterotis niloticus*, *Arapaima* and †*Sinoglossus lushanensis* to be 69 Mya (95% CI: 80–58 Mya), strictly post-dating the separation of South America with Africa. Otero *et al.* (2017) assigned fragmentary palaeontological remains from the Oligocene (28 Mya) to *Heterotis*, making them the earliest record of this lineage in Africa.

In summary, the trans-Atlantic distribution of *Heterotis niloticus* and *Arapaima* is the result of a dispersal event, but the current phylogenetic data are insufficient to determine its direction. The earliest presence of the *Heterotis niloticus* lineage in the Afrotropics is estimated between 80 Mya and a strict minimum of 28 Mya.

Lineage U2: Pantodon buchholzi (Table 1; Figs 5, 14C; Supporting Information, Fig. S5)

The family Pantodontidae comprises one extant species, *Pantodon buchholzi* Peters, 1876. The Pantodontidae is the sister group of the rest of the Osteoglossiformes

(Lavoué & Sullivan, 2004; Lavoué *et al.*, 2011; Lavoué, 2016; for the alternative phylogenetic hypothesis, see Hilton, 2003; Wilson & Murray, 2008; Bian *et al.*, 2016; for a review of the two hypotheses, see Hilton & Lavoué, 2018). The ancestral range reconstruction indicates that the origin of the *Pantodon* lineage in the Afrotropics corresponds to its divergence with the rest of the Osteoglossiformes (Fig. 14C).

Lavoué (2016) estimated the divergence time between the Pantodontidae and the rest of Osteoglossiformes (its sister group) as 148 Mya (95% CI: 181–120 Mya). The oldest fossils related to *Pantodon* are the Afrotropical †*Chauliopareion mahengeense* and †*Singida jacksonoides* from the middle Eocene (Murray & Wilson, 2005; Lavoué, 2016). Taverne & Capasso (2012) described a fossil marine species (†*Prognathoglossum kalassyi* Taverne & Capasso, 2012) from the Cenomanian of Lebanon (100.5–93.9 Mya) that they assigned to the family Pantodontidae. Although potentially of interest, the phylogenetic position of this fossil needs to be confirmed before its implications for the origin of Pantodontidae can be considered. Lavoué (2016) estimated the divergence time between †*Chauliopareion mahengeense* and the clade (†*Singida jacksonoides*, *Pantodon buchholzi*) to 80 Mya (95% CI: 120–55 Mya), providing a strict minimal age of 55 Myr for the presence of this lineage in Africa.

In summary, with the present data, the earliest presence of the *Pantodon buchholzi* lineage in the Afrotropics can be estimated broadly between 181 and 55 Mya.

Lineage U3: African Notopteroidei (Table 1; Figs 5, 14C; Supporting Information Fig. S5)

The freshwater suborder Notopteroidei comprises 220 Afrotropical and eight Oriental species classified into three families, the Afrotropical weakly electric families Gymnarchidae and Mormyridae and the Afrotropical–Oriental family Notopteridae. Notopteroidei is sister to the family Osteoglossidae, which is distributed worldwide (Lavoué, 2016). The ancestral range estimation slightly favoured the hypothesis in which the whole order Osteoglossiformes originated and diversified early in the Afrotropics, with Notopteroidei as one of its Afrotropical lineages (Fig. 14C).

Considering that crown Teleostei is not older than 200 Mya, Lavoué (2016) estimated the divergence time between Notopteroidei and Osteoglossidae to be 130 Mya (95% CI: 150–108 Mya) and the age of the crown group Notopteroidei to 110 Mya (95% CI: 130–95 Mya). The oldest notopteroid fossil known is †*Palaeonotopterus greenwoodi* from the Cenomanian of Morocco (Forey, 1997). This fossil provides a strict minimal age of 94 Mya for the earliest presence of Notopteroidei in Africa.

In summary, the Afrotropical notopteroids form a paraphyletic group relative to the Oriental notopteroids. Their origin is still unclear, because the biogeography of Osteoglossiformes is not yet fully resolved, with many non-Afrotropical osteoglossiform fossils awaiting phylogenetic placement (see Hilton & Lavoué, 2018). At present, the early occurrence of Notopteroidei in the Afrotropics can be estimated between a soft maximum of 150 and a strict minimum of 94 Mya.

Lineage U4: Nothobranchiidae (Table 1; Figs 5, 11B, D; Supporting Information, Fig. S2)

The order Cyprinodontiformes is a large, monophyletic group comprising mostly freshwater species (Parenti, 1981). It is divided into two suborders, Aplocheiloidei and Cyprinodontoidei, with 11 or 12 families. Afrotropical cyprinodontiforms belong to three separate families, Nothobranchiidae (lineage U4), Pantanodontidae (see lineage U5, below) and Poeciliidae (see lineage U6, below) (Parenti, 1981; Pollux *et al.*, 2014; Pohl *et al.*, 2015; Reznick *et al.*, 2017; Bragança *et al.*, 2018).

The Afrotropical family Nothobranchiidae includes 275 species classified into 14 genera (Eschmeyer *et al.*, 2018). In suborder Aplocheiloidei, Nothobranchiidae is sister to Aplocheilidae, which includes the Oriental genus *Aplocheilus* and the Madagascan genus *Pachypanchax*. The Neotropical family Rivulidae (= Cynolebiidae) is, in turn, sister to these two families (Parenti, 1981; Pollux *et al.*, 2014; Pohl *et al.*, 2015; Reznick *et al.*, 2017; Bragança *et al.*, 2018). Using a modified version of the time-calibrated phylogenetic tree of Amorim & Costa (2018) (Fig. 11D), I estimate the ancestral ranges at nodes in Cyprinodontiformes. The most likely estimation favours a scenario in which the most recent common ancestors of Cyprinodontiformes and Aplocheiloidei were distributed in the Afrotropics+Neotropics. The split between the Neotropical Rivulidae and the clade (Nothobranchiidae, Aplocheilidae) was followed by regional extinctions (as inferred by the BAYAREALIKE model), followed by a dispersal event from the Afrotropics to the Orient in Aplocheilidae (Fig. 11D). Although this biogeographical scenario has the highest likelihood, there are other reconstructions that are only slightly less likely.

The timing of the diversification in Aplocheiloidei is insufficiently investigated. Reznick *et al.* (2017) estimated the age of the crown Aplocheiloidei to ~71 Mya (no 95% CI provided), the divergence between Aplocheilidae and Nothobranchiidae to ~63 Mya and the age of the crown group Nothobranchiidae to 52 Mya. Amorim & Costa (2018) revised these ages to 52 Mya (95% CI: ~65–40 Mya), 45 Mya (95% CI: ~55–35 Mya), 34 Mya (95% CI: ~45–25 Mya), respectively.

In comparison to the fossil record of Cyprinodontoidei, there are only few aplocheiloid fossils. The oldest one is †*Kenyaichthys kipkechi* Altner & Reichenbacher, 2015 from the late Miocene (6 Mya) of the Central Rift Valley in Kenya, which is placed in the extinct family †Kenyaichthyidae (Altner & Reichenbacher, 2015), which provides only limited information on the relationships of this group. Altner & Reichenbacher (2015) suggested that this family might be more closely related to Neotropical Rivulidae (= Cynolebiidae) than to the Afrotropical Nothobranchiidae, but these authors concluded that more studies are needed.

In summary, the Afrotropical Nothobranchiidae, Oriental–Madagascan Aplocheilidae and Neotropical Rivulidae diverged from each other strictly after the separation of Africa with India, Madagascar and South America. However, the ancestral range estimation analysis weakly supports that the Cyprinodontiformes evolved early in the Afrotropics+Neotropics, and the most recent common ancestor of Aplocheiloidei lived also in this region, a scenario that rejects all seven predefined hypotheses (Fig. 6). The origin of Nothobranchiidae is therefore unresolved.

Lineage U5: Pantanodon stuhlmanni (Table 1; Figs 5, 11D; Supporting Information Fig. S2)

The genus *Pantanodon* (Cyprinodontiformes) includes two valid species, the Afrotropical *Pantanodon stuhlmanni* (Ahl, 1924) and the Madagascan *Pantanodon madagascariensis* (Arnoult, 1963) (Rosen, 1965); the latter is listed as extinct in the IUCN Red List of Threatened Species (Sparks, 2016). Although *Pantanodon stuhlmanni* is sometimes considered a brackish water species (Froese & Pauly, 2018), Matthes (1975) listed *Pantanodon stuhlmanni* as a freshwater species, and populations of *Pantanodon stuhlmanni* are known to occur in the Central Congo basin (Decru *et al.*, 2017). *Pantanodon madagascariensis* was a freshwater species.

Owing to its morphological distinctiveness, *Pantanodon* was difficult to classify, with several alternative hypotheses published (Parenti, 1981). Recently, molecular phylogenetic studies show that *Pantanodon stuhlmanni* represents one of the main lineages of Cyprinodontiformes (Pohl *et al.*, 2015; Bragança *et al.*, 2018). *Pantanodon madagascariensis* was not examined. Using the tree of Amorim & Costa (2018), I investigated the geographical origin of *Pantanodon* and found that the most recent common ancestor of *Pantanodon* and Cyprinodontoidei lived in the Neotropics+Afrotropics (Fig. 11D). As for the origin of Nothobranchiidae, there are other possible reconstructions that are only slightly less likely.

There is no time-calibrated phylogeny that includes *Pantonodon*. However, in combining the dating information from Amorim & Costa (2018) and the phylogenetic information of Pohl *et al.* (2015), I estimate the divergence time of the *Pantanodon* lineage roughly. Its maximal divergence time is equal to the age of the crown group Cyprinodontiformes, 65 Mya (95% CI ~79–53 Mya), whereas its minimal divergence time is equal to the age of the crown group Cyprinodontoidei, 42 Mya (95% CI ~47–33 Mya). Three fossil species of *Pantanodon* [†*Pantanodon cephalotes* (Agassiz, 1839), †*Pantanodon egeranus* (Laube, 1901) and †*Pantanodon malzi* (Reichenbacher & Gaudant, 2003)] are known (Costa, 2012), all described from the western Palaearctic, with the oldest of late Oligocene age (~23 Mya). According to Costa (2012), at least †*Pantanodon cephalotes* and †*Pantanodon egeranus* are stem *Pantanodon*. Current evidence is largely inconclusive regarding the geographical origin of *Pantanodon*. Its presence in the Afrotropics can be estimated roughly between 79 and 33 Mya.

Lineage U6: Aplocheilichthyinae and Procatopodinae (Table 1; Figs 5, 11D; Supporting Information, Fig. S2)

Within Cyprinodontoidei, the Afrotropical poeciliids form a monophyletic group that includes 74 species currently classified into two subfamilies, Aplocheilichthyinae and Procatopodinae. These subfamilies were merged in the single family Procatopodidae by Fricke *et al.*, 2018). The family Poeciliidae of Parenti (1981) is not monophyletic (Pollux *et al.*, 2014; Reznick *et al.*, 2017), and the Afrotropical poeciliids are more closely related to the Palaearctic (western European) genera *Aphanius* (also occurring in North Africa and the Middle East; Aphaniidae) and *Valencia* (Valenciidae) than to the remaining poeciliids (Pohl *et al.*, 2015; Amorim & Costa, 2018). The Afrotropical poeciliid clade plus its Palaearctic sister group are nested among several Neotropical and Nearctic (including Central American) taxa (Pohl *et al.*, 2015; Reznick *et al.*, 2017; Amorim & Costa, 2018). The ancestral range inference indicates that the most recent common ancestor of the clade [(Aphaniidae, Valenciidae), (Procatopodinae, Aplocheilichthyinae)] lived in Neotropics (Fig. 11D), but there are other reconstructions that are only slightly less likely. Under the most likely scenario, the ancestors of the clade (Aphaniidae, Valenciidae) and the clade (Procatopodinae, Aplocheilichthyinae) would have dispersed independently from the Neotropics to the Palaearctic and Afrotropics, respectively.

The divergence time between the Afrotropical group and its Palaearctic sister group is estimated to ~60 Mya by Reznick *et al.* (2017) and 33 Mya by Amorim & Costa (2018), which in the latter case corresponds to the minimal age of the oldest crown group fossil,

†*Prolebias stenoura* Sauvage, 1874 (early Oligocene). This clade is nested in the Neotropical and Nearctic representatives, and it diverged from them ~ 65 Mya (Reznick *et al.*, 2017) or 37 Mya (95% CI: ~40–35 Mya) (Amorim & Costa, 2018). The crown group age of Afrotropical poeciliids is estimated to 33 Myr by Reznick *et al.* (2017) and 19 Mya (95% CI: ~25–10 Mya) by Amorim & Costa (2018). Costa (2012) reviewed the European fossil record of Cyprinodontoidei: the Early Oligocene extinct genera †*Francolebias* and †*Prolebias* represent the earliest stem records of the extant clade (*Aphanius*, *Valencia*) in the Palaearctic.

Altogether, molecular-dated phylogenetic evidence rejects the vicariant hypothesis (Parenti, 1981; Ghedotti, 2000), and the ancestral range estimation analysis (Fig. 11D) somewhat supports the hypothesis that Afrotropical poeciliids dispersed from the Neotropics after the final separation of Africa and South America, but independently from its sister group, the Palaearctic clade (*Aphanius*, *Valencia*). The occurrence of this dispersal event is dated broadly between 65 and 33 Mya.

Lineage U7: family Polycentridae (Table 1; Figs 3, 11B, E; Supporting Information, Fig. S2)

The Afrotropical polycentrid genera *Afronandus* and *Polycentropsis* form a paraphyletic group relative to the Neotropical polycentrid genera *Monocirrhus* and *Polycentrus* (Collins *et al.*, 2015). The Polycentridae belongs to a large clade, the Ovalentaria, containing both marine and freshwater lineages. Within Ovalentaria, the phylogenetic position of Polycentridae is unresolved. Eytan *et al.* (2015) found different sister-group possibilities for Polycentridae. Collins *et al.* (2015) suggested that Polycentridae is sister to Pseudochromidae (one genus *Congrogadus*; marine), whereas Near *et al.* (2013) and Friedman *et al.* (2013) found Polycentridae sister to the rest of Ovalentaria. Using the phylogenetic tree of Near *et al.* (2013), I reconstructed the evolution of the salinity preference in Ovalentaria (Fig. 11B) and found that the habitat of origin and early diversification of Ovalentaria are ambiguous, because the origin could have been in either marine or fresh water with similar probabilities. Consequently, whether the Polycentridae evolved after a marine-to-freshwater transition is not resolved. Next, I used the cladogram of Polycentridae, derived from the phylogram published by Collins *et al.* (2015), to estimate the evolution of the ancestral ranges. The results indicated that the most recent common ancestor of the Polycentridae lived in a region consisting of the Neotropics+Afrotropics (Fig. 11E). It is somewhat unexpected that this reconstruction is more likely than the reconstruction in which the Polycentridae originated in the Afrotropics (the latter is also the more parsimonious). The absence of age calibration and the small size of this taxonomic group make it difficult to reconstruct geographical range evolution reliably.

According to Near *et al.* (2013), who examined the phylogenetic positions of three polycentrid genera, *Polycentropsis*, *Monocirrhus* and *Polycentrus* (but not *Afronandus*), the age of stem group Polycentridae is ~90 Mya (95% CI: 95–85 Mya), whereas its crown age is ~30 Mya (95% CI: 40–25 Mya). There is no age estimation provided by Collins *et al.* (2015) or by Eytan *et al.* (2015), but Matschiner *et al.* (2017), who examined only one species, estimated the stem age of Polycentridae to ~100 Mya.

Altogether, the current evidence does not allow me to resolve the origin of Polycentridae confidently, with regard to both its ancestral habitat preference and its early region of diversification. The earliest presence of Polycentridae in the Afrotropics is estimated broadly between 95 and 25 Mya. There are no polycentrid fossils.

Lineages U8 and U9: Afrotropical Monopterus and Ophisternon (Table 1; Figs 5, 13A, E; Supporting Information, Fig. S4)

There are currently 24 species in the family Synbranchidae, which are classified into four genera and two subfamilies. Subfamily Synbranchinae includes three genera: *Monopterus* with two species in the western Afrotropics (*Monopterus boueti* (Pellegrin, 1922) and *Monopterus luticolus* Britz *et al.*, 2016), and 14 Oriental and eastern Palaearctic species (some populations of *Monopterus albus* (Zuiew, 1793) in Australia may have been introduced recently, see discussion by Rosen & Greenwood, 1976), *Ophisternon* with six species and *Synbranchus* with three species. The six species of *Ophisternon* are distributed in the western Afrotropics [*Ophisternon afrum* (Boulenger, 1909)], the Orient (*Ophisternon bengalense* McClelland, 1844), Australia and New Guinea [*Ophisternon candidum* (Mees, 1962) (the blind cave eel), some populations of *Ophisternon bengalense* and *Ophisternon gutturale* (Richardson, 1845)] and the Neotropics/southern Nearctic [*Ophisternon infernale* (Hubbs, 1938) and *Ophisternon aegnigmaticum* Rosen & Greenwood, 1976. The three species of *Synbranchus* occur in the Neotropics and southern Nearctic. Subfamily Macrotreminae is monospecific, comprising only *Macrotrema caligans* (Cantor, 1849), which occurs in the Oriental region. Most species are capable of some aerial respiration, and some have developed cave adaptation (Graham, 1997; Proudlove, 2010).

Synbranchidae belongs to the order Synbranchiformes (Near *et al.*, 2013), a clade including the majority of Oriental freshwater species. In this order, Synbranchidae is sister to the clade [Indostomidae (Mastacembelidae, Chaudhuriidae)] (Near *et al.*, 2013). Some authors

consider some synbranchid species as secondarily adapted to fresh water (for example, see Perdices *et al.*, 2005). However, there is no phylogenetic evidence to support this assertion, because the relationships between strictly freshwater species and species able to support some degree of salinity are not known.

The most recent taxonomic revision was carried out by Rosen & Greenwood (1976), who wrote (p. 6): 'Few groups of teleostean fishes have had so long and obscure a taxonomic history as the swamp eels.' These authors suggested the following phylogenetic arrangement among genera: (((*Monopterus*, *Synbranchus*) *Ophisternon*) *Macrotema*)}. Britz *et al.* (2016) showed that Afrotropical species of *Monopterus* and some Indian species of *Monopterus* are closely related. If correct, it means that Afrotropical species of *Monopterus* and *Ophisternon* evolved from at least two independent biogeographical events. I did not attempt to reconstruct the ancestral range evolution, because the phylogeny of Synbranchidae, especially that of the genus *Synbranchus*, is partly unresolved (Fig. 13E). According to Near *et al.* (2013), the maximal (stem) age of Synbranchidae is 75 Mya (95% CI: 80–65 Mya). There is no minimal age for the presence of either *Monopterus* or *Ophisternon* in the Afrotropics, which I set softly to 5 Mya. In the absence of a comprehensive time-calibrated phylogeny, the biogeography of Afrotropical species of synbranchid is unresolved, and several hypotheses might account for their distribution. Only the hypothesis of continental drift-mediated vicariance can be rejected currently.

Lineage U10: Pseudocrenilabrinae (Table 1; Figs 5, 11B, C; Supporting Information, Fig. S2)

Subfamily Pseudocrenilabrinae, with > 1100 species (Fricke *et al.*, 2018), is the most diversified Afrotropical freshwater fish lineage, encompassing more than one-third of the total diversity of Afrotropical freshwater fishes. The early biogeography of Cichlidae and the origin of Pseudocrenilabrinae are still debated, notwithstanding recent progress made on their time-calibrated phylogeny (Fig. 11C). The family Cichlidae is subdivided into four monophyletic subfamilies, each occupying a different continental region: Pseudocrenilabrinae in the Afrotropics (with two species of the genus *Iranocichla* in Iran; Coad, 1982; Esmaeili *et al.*, 2016), Cichlinae in the Neotropics (including Central America), Etroplinae in Madagascar and the Orient (restricted to South India), and Ptychochrominae in Madagascar (Fricke *et al.*, 2018). Pseudocrenilabrinae is sister to the Neotropical Cichlinae. The Madagascan Ptychochrominae is sister to the Afrotropical plus Neotropical cichlids, and Etroplinae is sister to the rest of the Cichlidae. The phylogenetic relationships among these four subfamilies are well supported (Fig. 11C).

The biogeography of the Cichlidae has been discussed intensively, because the phylogenetic branching among the subfamilies coincides with successive steps of fragmentation of Gondwana. However, direct evidence from the fossil record and indirect evidence from molecular dating (using fossils for calibrations) strongly support a Late Cretaceous–early Cenozoic age for the family Cichlidae, therefore rejecting the hypothesis that the distribution of the Cichlidae is the result of the fragmentation of Gondwana (e.g. Vences *et al.*, 2001; Friedman *et al.*, 2013; Near *et al.*, 2013).

In addition to their possible Cenozoic age, recent molecular-based studies showed: (1) that Cichlidae belongs to a large clade of Acanthomorpha, the Ovalentaria, in which Cichlidae is identified as the sister group of the Indo-West Pacific marine family Pholidichthyidae (one genus, *Pholidichthys*) (Eytan *et al.*, 2015; Near *et al.*, 2013); and (2) the paraphyly of the Oriental–Madagascan cichlids, at the base of the Cichlidae tree. Using the tree of Ovalentaria from Near *et al.* (2013), the habitat preference reconstruction shows that the salinity preference of the most recent ancestor of the clade (Cichlidae, Pholidichthyidae) is unresolved (either marine or freshwater; Fig. 11B). In addition, the ancestral range estimation shows that the region of origin of the whole Cichlidae could have been the Afrotropics+Madagascar. The restricted distribution in the Afrotropics of the most recent common ancestor of the clade (Pseudocrenilabrinae, Cichlinae) would have been the result of one extinction event in Madagascar (given that the BAYAREALIKE model does not consider vicariant events), and Cichlinae reached the Neotropics after one dispersal event.

Cichlid fossils are found in Africa, Europe and South America (including the Caribbean region) (Chakrabarty, 2004). All are freshwater fish, and the oldest cichlid fossils, from the Eocene (46–45 Mya), are found in Africa (Murray, 2000a,b; Murray, 2001a,b) including the extinct genus †*Mahengechromis* (five species; Murray, 2000a, 2001b). These fossils provide a strict minimal age for the presence of Cichlidae in Africa, but not necessarily for subfamily Pseudocrenilabrinae, because Murray (2001b) was uncertain about the phylogenetic position of these fossils owing to their puzzling morphology.

Friedman *et al.* (2013) estimated the age of the crown group Cichlidae to 64.9 Mya (95% CI: 76.0–57.3 Mya), the divergence between Ptychochrominae and the clade (Cichlinae, Pseudocrenilabrinae) to 55 Mya (95% CI: 64–48 Mya) (corresponding to the soft maximal age for the presence of cichlids in Africa), and the age of the crown group Pseudocrenilabrinae to 46.4 Mya (95% CI: 54.9–40.9 Mya) (corresponding to the minimal age for the presence of Cichlidae in Africa). I note that McMahan *et al.* (2013) estimated the age of crown group Cichlidae to 75 Mya (95% CI: ~80–62 Mya) and Matschiner *et al.* (2017) to 85.7 Mya (95% CI: 93.8–77.8 Mya).

In summary, the combined analysis (habitat preference reconstruction and ancestral range estimation) is rather inconclusive to determine confidently whether Cichlidae evolved after a marine-to-freshwater transition and the location of their area of early diversification. The early presence of Pseudocrenilabrinae in the Afrotropics is not resolved. Evidence from molecular clock dating rejects the vicariant hypotheses (hypotheses 2 and 3), and I estimate the early presence of Pseudocrenilabrinae in the Afrotropics broadly between 64 (or earlier) and 48 Mya.

Dispersal events out of Africa

Lineage O1: Notopterinae (Orient) (Table 1; Fig. 14C; Supporting Information, Fig. S5)

The monophyletic Oriental subfamily Notopterinae comprises two genera, *Chitala* and *Notopterus*, and about eight species (Roberts, 1992; Kottelat, 2013). It is sister to the Afrotropical subfamily Xenomystinae that comprises two genera, *Papyrocranus* and *Xenomystus* (Lavoué & Sullivan, 2004; Inoue *et al.*, 2009). The family Notopteridae is then the sister group of the Afrotropics-endemic Mormyroidei (Gymnarchidae+Mormyridae), indicating that Notopterinae originated from Afrotropical fresh waters, as confirmed by the ancestral range reconstruction (Fig. 14C).

Lavoué (2016) estimated the time divergence between Notopterinae and Xenomystinae to a maximum of 83.2 Mya (95% CI: 105–60 Mya) and a minimum of 47 Mya (95% CI: 55–43 Mya). Notopterid otoliths ('genus Notopteridarum' *nolfi* Rana, 1988; Nolf *et al.*, 2008) from the Deccan Intertrappean Beds (India) dated to the Late Cretaceous mark the earliest presence of Notopteridae in the Orient. However, these otoliths do not share the modification present in recent species, leading Nolf *et al.* (2008) to suggest that they belong to some stem notopterid species. Another Oriental fossil of Notopteridae is described from the Eocene of Sumatra (56.0–33.9 Mya) (Sanders, 1934). Although a taxonomic revision of this fossil is needed (Hilton & Lavoué, 2018), it seems to be closely related to extant *Notopterus notopterus* (Pallas, 1769), and it provides a strict minimal age for the presence of Notopterinae in the Orient.

In summary, Notopterinae originated in the Afrotropics and reached the Orient between 105 and 43 Mya; after the separation of Africa and Madagascar–India but before the collision of Africa and Eurasia.

Lineage O2: Cichlinae (Neotropical) (Table 1; Fig. 11C; Supporting Information Fig. S2)

The Neotropical cichlids (including some Central American species) form the monophyletic subfamily Cichlinae, which comprises about 570 freshwater species. Cichlinae is sister to the Afrotropical Pseudocrenilabrinae (Fig. 11C).

Friedman *et al.* (2013), McMahan *et al.* (2013) and Matschiner *et al.* (2017) concluded that the trans-Atlantic distribution of Cichlidae is the result of a dispersal event, because the divergence between Cichlinae and Pseudocrenilabrinae strictly post-dated the separation of Africa and South America. The ancestral range estimation favours the hypothesis in which the most recent common ancestor of the clade (Pseudocrenilabrinae, Cichlinae) lived in Afrotropics, and the ancestors of Cichlinae dispersed from Africa to South America (Fig. 11C).

Friedman *et al.* (2013) estimated the age of the divergence between Cichlinae and Pseudocrenilabrinae to 46.4 Mya (95% CI: 54.9–40.9 Mya) and the age of the crown group Cichlinae to 29.2 Mya (95% CI: 34.8–25.5 Mya), whereas McMahan *et al.* (2013) estimated the age of the crown group Cichlinae+Pseudocrenilabrinae to ~71 Mya (95% CI: 80–60 Mya) and the age of the crown group Cichlinae to 63 Mya (95% CI: 74–54 Mya).

The early presence of cichlines in the Neotropics is documented by two middle Eocene (49 Mya) fossils (Malabarba *et al.*, 2010; Perez *et al.*, 2010): the geophagine †*Gymnogeophagus eocenicus* Malabarba, Malabarba & del Papa, 2010 and the possible heroine †*Plesioheros chauliodus* Perez, Malabarba & del Papa, 2010. These two fossils provide a strict minimal age for the crown group Cichlinae and its presence in Neotropics. In short, Cichlinae might have dispersed from the Afrotropics to the Neotropics between 55 (or earlier) and 49 Mya.

Lineage O3: Lacantunia enigmatica (Nearctic) (Table 1; Fig. 12; Supporting Information, Fig. S3)

Lacantunia enigmatica Rodiles-Hernández, Hendrickson & Lundberg, 2005 was only described recently from the most southern part of the Nearctic (Rodiles-Hernández *et al.*, 2005). Lundberg *et al.* (2007) found unexpected but strong support for the inclusion of this species in the Big Africa clade of Sullivan *et al.* (2006). In this clade, *Lacantunia enigmatica* is the sister of Claroteidae. The ancestral range estimation strongly supported an Afrotropical origin for *Lacantunia enigmatica* (Fig. 12).

Lundberg *et al.* (2007) estimated the divergence time between *Lacantunia enigmatica* and its sister group to ~85 Mya (95% CI: 95–75 Mya), whereas it was estimated to 71 Mya (95% CI: 77–66 Mya) and 49.6 Mya (95% CI: 57.9–45.2 Mya) by Chen *et al.* (2013) and Matschiner *et al.* (2017), respectively. The minimal age for the presence of the *Lacantunia* lineage in Central America is difficult to estimate because this lineage is monospecific and there is no fossil known. Therefore, I apply a very soft minimum of 5 Mya.

In summary, *Lacantunia enigmatica* is the result of a dispersal event from the Afrotropics that occurred

between 77 and 5 Mya, well after the final separation between Africa and South America.

Lineage O4?: Neotropical polycentrids (Table 1; Fig. 11E; Supporting Information, Fig. S2)

The Neotropical genera *Monocirrhus* (two species) and *Polycentrus* (one species) form a monophyletic group that is sister to the Afrotropical *Polycentropsis abbreviata* Boulenger, 1901 (Collins *et al.*, 2015) (Fig. 11E). The Afrotropical *Afronandus sheljuzhkoi* (Meinken, 1954) is then the sister to these three genera. The ancestral range estimation analysis using the BAYAREALIKE model showed the divergence between Neotropical polycentrids and *Polycentropsis abbreviata* is inferred to be the result of a range contraction (with extinction in the Afrotropics). However, this result is questionable, because of the use of a small phylogeny (four terminal taxa) that is not time calibrated. There are no polycentrid fossils, and the timing of diversification is, so far, tentative. Near *et al.* (2013) estimated the divergence between *Polycentropsis abbreviata* and the Neotropical clade roughly to 35 Mya (95% CI: 45–25 Mya) and the age of the Neotropical crown group to only 25 Mya (95% CI: 35–20 Mya).

Altogether, the present evidence is inconclusive to reveal the biogeography of Polycentridae and, in particular, the origin of Neotropical polycentrids. The divergence time between Neotropical polycentrids and *Polycentropsis abbreviata* is estimated imprecisely between 45 and 20 Mya, which rejects the continental drift-mediated vicariant hypothesis (hypothesis 3).

Origins of Afrotropical euryhaline fishes

The eel family Anguillidae includes only catadromous or facultative catadromous species that are flexible in their use of freshwater habitats (Daverat *et al.*, 2006). Spawning areas of species of *Anguilla* are located offshore, in the open ocean. Seventeen species are valid (Fricke *et al.*, 2018), and four of them frequent estuarine and freshwater environments of the east coast of Africa (Whitfield, 2005). None of these four species is endemic to the Afrotropics: *Anguilla bengalensis* (Gray, 1831) is known from East Africa to West Malaysia, *Anguilla bicolor* McClelland, 1844 and *Anguilla marmorata* Quoy & Gaimard, 1824 occur from East Africa to Australia, and the distribution of *Anguilla mossambica* (Peters, 1852) is restricted to east African watersheds along with oceanic waters off Madagascar and the western Mascarenes. These four species do not form a monophyletic group, with each species having a distinct phylogenetic position in the genus *Anguilla* (Mohindra *et al.*, 2017). Inoue *et al.* (2010) showed that the genus *Anguilla* has a marine (deep-sea) origin. Recent phylogeographical studies indicate low geographical structures among populations of species of *Anguilla bicolor* and *Anguilla marmorata* in the Indian Ocean, possibly owing to the marine reproductive migrations of adults (Ishikawa *et al.*, 2004; Minegishi *et al.*, 2012).

The worm eel family Ophichthidae comprises 339 valid species classified into two subfamilies, the Myrophinae (69 species) and Ophichthinae (270 species). A large proportion of ophichthid species are strictly marine, with only a few coastal species entering estuaries. Whitfield (2005) listed *Myrophis plumbeus* (Cope, 1871) as an estuarine migrant occurring in the eastern Atlantic, from Senegal to Angola. This species is otherwise known from the western Atlantic. Like *Myrophis punctatus* Lütken, 1852, which occurs in the western Atlantic (Able *et al.*, 2011), *Myrophis plumbeus* spends most of its life in estuarine environments but enters marine environments to spawn. Other species of *Myrophis* are marine. The phylogenetic position and divergence time of *Myrophis plumbeus* relative to other species of *Myrophis* are not known, but current evidence supports a recent and marine origin of this species.

Whitfield (2005) listed *Gilchristella aestuaria* (Gilchrist, 1913) (Ehiravinae, Clupeidae), endemic to the east coast of Africa, under the guild estuarine residents, and *Ethmalosa fimbriata* (Dorosomatinae, Clupeidae), endemic to the Gulf of Guinea, under the guild estuarine migrants. These two species are separate lineages. *Gilchristella aestuaria* is sister to the Oriental tribe Ehiravini, and *Ethmalosa fimbriata* is sister to the Afrotropical tribe Pellonulini (Fig. 8) (Lavoué *et al.*, 2013, 2014). The ancestral habitat preference reconstruction indicates that *Ethmalosa fimbriata* evolved from a marine ancestor, and its physiological tolerance to lower salinity appeared < 40 Mya, whereas *Gilchristella aestuaria* might have a brackish origin, and the presence of this lineage in the Afrotropics may be as old as the early Cenozoic (Fig. 8).

The glassperch family Ambassidae (Ovalentaria) comprises marine, euryhaline and freshwater species (54 species in total) and is widely distributed in the Indo-West Pacific region. As for many marine families having a similar pattern of distribution, the centre of diversity (in terms of numbers of species and genera) of Ambassidae lies in the Southeast Asia region. According to Whitfield (2005), three species of Ambassidae are listed as estuarine migrants on the east coast of Africa, none of them endemic to the Afrotropics: *Ambassis ambassis* (Lacepède, 1802) is distributed in the western Indian Ocean from East Africa to Madagascar and the western Mascarenes, *Ambassis dussumieri* Cuvier, 1828 is known from East Africa to Southeast Asia, and *Ambassis natalensis* Gilchrist & Thompson, 1908 is distributed from East

Africa to Southeast Asia and Australia (Eschmeyer *et al.*, 2018). There is no published phylogeny for the entire family and, in particular, for the genus *Ambassis* that includes all marine ambassid species. Therefore, it is not known whether these three species form a monophyletic group. Their respective sister group is also not identified. Although largely incomplete, the pattern of distribution of each of the three Afrotropical populations of Ambassidae species favours recent and independent dispersal through marine environments.

Two species of the family Atherinidae (76 species in total, classified into four subfamilies; Fricke *et al.*, 2018) are recorded from estuarine environments of the east coast of Africa (Whitfield, 2005): *Atherina breviceps* Valenciennes, 1835 (Atherininae) occurs in the southeastern Atlantic and southwestern Indian Ocean regions, and *Atherinomorus lacunosus* (Forster, 1801) (Atherinomorinae) is known from East Africa to Australia. Campanella *et al.* (2015) confirmed that *Atherina breviceps* and *Atherinomorus lacunosus* are not sisters and that these species evolved independently from a marine ancestor. Campanella *et al.* (2015) classified these two species as marine, illustrating the ambiguity in assigning these species to a guild regarding their salinity preference. The presence of these two taxa in the Afrotropics is likely to be recent (Neogene?) and the result of marine dispersal (Campanella *et al.*, 2015).

Only one species from the halfbeak family Hemiramphidae, *Hyporhamphus capensis* (Thominot, 1886), is listed as an estuarine resident by Whitfield (2005). This species is distributed in the western Indian Ocean, from South Africa to Mozambique. Hemiramphidae includes 61 species, 37 placed in the genus *Hyporhamphus* that are mostly marine. Although the phylogenetic position of *Hyporhamphus capensis* has not been studied, a likely hypothesis is that *Hyporhamphus capensis* in the Afrotropics evolved from a marine ancestor. No age estimation is known.

The seahorse and pipefish family Syngnathidae is divided into two subfamilies, Nerophinae and Syngnathinae (Hamilton *et al.*, 2017). Whitfield (2005) listed a total of four species of Syngnathinae and five species of Nerophinae as estuarine migrants. From the subfamily Syngnathinae, Whitfield (2005) listed *Hippichthys cyanospilos* (Bleeker, 1854), *Hippichthys heptagonus* Bleeker, 1849 and *Hippichthys spicifer* (Rüppell, 1838), which are otherwise widely distributed across the Indo-West Pacific region, from East Africa to Japan and Australia. *Syngnathus temminckii* Kaup, 1856 and *Enneacampus kaupi* (Bleeker, 1863) are the only endemic species of Syngnathinae in this region. *Syngnathus temminckii* is known from Namibia to South Africa, and *Enneacampus kaupi* occurs in the eastern Atlantic from Senegal to Angola. From subfamily Nerophinae, three species of *Microphis* (stream pipefishes) are listed by Whitfield (2005): *Microphis aculeatus* (Kaup, 1856) occurs in the eastern Atlantic from Senegal to Angola, *Microphis brachyurus* (Bleeker, 1854) is widely distributed from East Africa to Japan and Australia, and *Microphis fluviatilis* (Peters, 1852) occurs from East Africa to Madagascar. Adults of this genus reside in mainly fresh and brackish waters and breed in coastal rivers.

Current evidence shows that: (1) none of the syngnathid species listed in Whitfield (2005) is restricted fully to fresh water, and the salinity preference of each species is different; (2) they belong to the Syngnathidae, which originated and mainly evolved in marine environments; and (3) the phylogeny of these Afrotropical syngnathid species is poorly studied. Based on these points, it can be assumed that these species might have evolved after a recent and incomplete transition from a marine environment.

Whitfield (2005) listed one species of the marine family Apogonidae (339 species) from the east coast of Africa as an estuarine migrant, *Fibramia lateralis* (Valenciennes, 1832) (subfamily Apogoninae). *Fibramia lateralis* is otherwise widely distributed in the Indo-West Pacific region, from East Africa to Japan and Australia. There is no population genetic study for this species, and I consider that the population of *Fibramia lateralis* frequenting the Afrotropical estuaries has a recent marine origin.

Species of the sleeper families Eleotridae and Butidae (*sensu* Thacker, 2011; see also Chakrabarty *et al.*, 2012) are typical residents of tropical brackish habitats and can also enter freshwater habitats for long periods. Only species of the genus *Kribia* (see lineage M10) can be considered to be fully adapted to fresh water (Thacker, 2011). Whitfield (2005) reported the presence of four species of Eleotridae from western and central Afrotropical estuaries. All estuarine migrants are endemic to this region (from Senegal to Angola): *Dormitator lebretonis* (Steindachner, 1870), *Eleotris daganensis* Steindachner, 1870, *Eleotris senegalensis* Steindachner, 1870 and *Eleotris vittata* Duméril, 1861. Two additional species of Eleotrinae, listed as estuarine migrants (Whitfield, 2005), occur on the east coast of the Afrotropics: *Eleotris fusca* (Forster, 1801) is distributed from East Africa to Japan and New Caledonia, and *Eleotris mauritianus* Bennett, 1832 is distributed in the western Indian Ocean, from East Africa to Madagascar. One additional species of Eleotridae, *Hypseleotris cyprinoides* (Valenciennes, 1837), is listed as freshwater stragglers by Whitfield (2005). However, according to Thacker & Unmack (2005), who reviewed the systematics of the genus *Hypseleotris* (about 12 species), *Hypseleotris*

cyprinoides should be considered as an euryhaline species widely distributed from East Africa to Japan and Australia (Eschmeyer *et al.*, 2018). In the phylogenetic tree published of the genus *Hypseleotris* by Thacker & Unmack (2005), *Hypseleotris cyprinoides* is sister to the rest of *Hypseleotris* (all others are freshwater fish and endemic to Australia). The individual of *Hypseleotris cyprinoides* of South Africa sampled by these authors was genetically similar to other individuals of the same species sampled in Madagascar, Southeast Asia and Japan. Furthermore, Whitfield (2005) reported the presence of three species of euryhaline Butidae in the Afrotropics: *Butis butis* and *Butis koilomatodon* (Bleeker, 1849) are distributed from East Africa to Japan and Australia, whereas *Bostrychus africanus* (Steindachner, 1879) is endemic to western and central African tropical estuaries (from Senegal to Angola). The phylogenies of Eleotridae and Butidae are still incomplete, and the phylogenetic positions of most Afrotropical brackish and euryhaline species of these two families have not been studied. However, considering the current evidence, marine dispersal might explain the presence of these species in the Afrotropics.

The goby family Gobiidae is the largest fish family, with 1894 valid species (Fricke *et al.*, 2018) classified into five subfamilies, Gobiinae (1238 species), Gobionellinae (466 species), Oxudercinae (44 species), Sicydiinae (111 species) and Amblyopinae (35 species). Whitfield (2005) listed 32 species of gobies that regularly frequent Afrotropical estuaries (either as migrants or residents). The overall pattern of distribution of African euryhaline gobies is similar to the distribution of other euryhaline groups: most of the goby species frequenting the eastern Afrotropical estuaries have widespread distributions in the Indo-West Pacific region, with only few exceptions [e.g. *Pandaka silvana* (Barnard, 1943) is endemic to southern African brackish environments]. Most of the euryhaline species of gobies in the West Africa–eastern Atlantic region are endemic, with their relatives distributed either in the Indo-West Pacific region or in the eastern Atlantic (Schliewen, 2011). The phylogeny of the Gobiidae is still incomplete, and in absence of more comprehensive evidence, I favour a recent marine origin for the Afrotropical species of Gobiidae.

DISCUSSION

Africa is a macroevolutionary sink in the Cenozoic for freshwater fish

The AFF fauna comprises > 3000 species that belong to ≥ 37 different lineages. Timing information extracted from time-calibrated phylogenetic trees shows that most of the AFF lineages (and the most successful ones in terms of the number of species) reached Africa after the final fragmentation of Africa and South America (< 105 Mya) and, in particular, during the Cenozoic (i.e. the last 66 Myr). This is in agreement with the fossil record, which shows a faunal turnover between the Late Cretaceous (with fauna dominated by non-teleost taxa) and the middle Eocene (with fauna dominated by modern teleost taxa) (Cavin *et al.*, 2010).

There is direct or indirect evidence to support the presence of only five extant AFF lineages in African freshwaters before the Cenozoic (Table 1; Fig. 14): (1) the (Kneriidae, Phractolaemidae) lineage (its earliest presence in the Afrotropics is estimated to have occurred between > 150 and 107 Mya); (2) the Protopteridae (its earliest presence at between > 150 and 94 Mya); (3) the Polypteridae (its earliest presence at between > 150 and 94 Mya); (4) the Citharinoidei (its earliest presence at between 145 and 105 Mya); and (5) the Notopteroidei (its earliest presence at between > 150 and 94 Mya). Despite their long-term presence in Africa, these five lineages together contribute only ~13% to total fish diversity (i.e. ~400 species).

The hypothesis of a Late Cretaceous origin cannot be rejected for eight additional AFF lineages, because even though their upper age estimation limits fall during the Cretaceous, their lower age estimation limits are in the Cenozoic: (1) the Big Africa catfish clade (as old as 90 Mya, but as young as 58 Mya); (2) *Heterotis niloticus* (80–28 Mya); (3) Denticipitidae (as old as 145 Mya, but as young as 45 Mya); (4) Afrotropical characoids (76–56 Mya); (5) Polycentridae (95–25 Mya); (6) Pantodontidae (> 150–57 Mya); and the two Afrotropical synbranchids (7) *Monopterus* and (8) *Ophisternon* (both as old as 75 Mya, but very probably younger). *Pantodon* (Pantodontidae) is a good example of these uncertainties in timing. Although the divergence between *Pantodon* and its living sister group might be as old as the Late Jurassic-Early Cretaceous (Lavoué, 2016) (Fig. 8B), the absence of any freshwater pantodontid fossil (in Africa or elsewhere) of Mesozoic or early Cenozoic age combined with the recent description of a possible marine Cenomanian fossil assigned to this family, †*Prognathoglossum kalassyi* (Taverne & Capasso, 2012), makes it difficult to delineate the early presence of the lineage of *Pantodon* in Afrotropical fresh waters precisely (Fig. 14).

The remaining AFF lineages (26 of 37) colonized Africa after the K/Pg boundary, either after direct marine-to-freshwater transitions or after dispersal from the Neotropics (in the early Cenozoic) or from the Orient (in the early to late Cenozoic). Although the Afrotropical freshwater ichthyofauna was enriched with ≥ 26 lineages during the Cenozoic, Africa

contributed comparatively little to the freshwater fish diversity of other continental regions during the same period. I identified unambiguously only three out-of-Africa dispersal events (Fig. 15; i.e. Oriental notopterins, southernmost Nearctic *Lacantunia enigmatica* and Neotropical Cichlinae). There are a few other possibilities (e.g. Neotropical polycentrids or Oriental and Madagascan aplocheiliids), but the biogeography of these taxa needs to be resolved better before any firm conclusions can be drawn.

This unbalanced ichthyofaunal exchange between Africa and other continental regions is best illustrated by the situation between Africa and the Orient after the Eocene. At that time, ≥ 11 Oriental lineages successfully invaded the Afrotropics, but no Afrotropical lineage managed to disperse to the Orient [besides the presence of the Afrotropical-originated cichlid genus *Iranocichla*, which is found at the western limit of the Oriental region (Middle East); *Iranocichla* is likely to be of recent origin, maybe late Miocene or Pliocene (Schwarzer *et al.*, 2009), and therefore not discussed herein].

Altogether, Africa (Afrotropics) can be considered a macroevolutionary sink for freshwater fishes in the Cenozoic, with only a few AFF lineages predating the Cenozoic period and fewer AFF lineages successfully escaping the Afrotropics to colonize other continental regions. Furthermore, one part of the AFF fauna originated in western Gondwana while Africa straddled the equator during the greenhouse period of the Late Cretaceous and early Cenozoic.

Lineages originating after a direct marine-to-freshwater transition (hypothesis 1)

Almost one-third of AFF lineages originated from direct marine-to-freshwater transitions (lineages M1–M10 in Table 1; Fig. 15). Altogether, these ten lineages contribute < 2% to the total Afrotropical diversity, with a total of ~70 species. Seven of these transitions occurred during the Cenozoic. The two remaining and likely older transitions produced: (1) the herring-like *Denticeps clupeoides*, which is the only extant representative of suborder Denticipitoidei, the sister group of the suborder Clupeoidei (i.e. the rest of the sardines, anchovies and close relatives) (Fig. 8A); and (2) freshwater gonorhynchiforms (i.e. the families Kneriidae and Phractolaemidae), comprising some of the most developmentally truncated AFF taxa (i.e. *Grasseichthys* and *Cromeria*) (Fig. 8B). I found no correlation between large marine transgressions covering large expanses of West and Central Africa at the end of the Cretaceous (Fig. 2) and the early presence of these marine-derived lineages. In comparison, such correlations between Miocene marine introgressions and marine-to-freshwater transitions were evidence for the presence of most marine-derived fish lineages in Neotropical freshwaters (Lovejoy *et al.*, 1998; Bloom & Lovejoy, 2017). In Africa, only two habitat transitions may have been driven by large Cretaceous marine transgressions, leading to the Denticipitidae and Pellonulini (Fig. 15).

South America–Africa continental drift vicariance (hypothesis 3)

The similarity of the freshwater fish faunas between the Neotropics and Afrotropics was noted early and, subsequently, discussed extensively (Patterson, 1975; Lundberg, 1993; Maisey, 2000; Cavin *et al.*, 2008). In particular, Lundberg (1993) discussed comprehensively the biogeographical relationships between Neotropical and Afrotropical freshwater fishes using phylogenetics and palaeontology. He reported 13 possible sister groups between Neotropical and Afrotropical freshwater fishes (Lundberg, 1993: 165), for which he provided biogeographical hypotheses regarding their divergence. For ten of these groups, Lundberg (1993) did not reject the Africa–South America drift vicariance hypothesis as the cause of their divergence, whereas he suggested a pre-drift intracontinental speciation hypothesis for one group and a post-drift dispersal hypothesis for the last two.

My results differ from those of Lundberg (1993) because, first, recent phylogenetic results challenge several of the clades discussed by Lundberg (1993). For example, the characoid clade (Ctenoluciidae, Hepsetidae) and the siluroid clade ((Doradidae, Auchenipteridae, Ageneiosidae), Mochokidae) discussed by Lundberg (1993) were refuted by recent studies (Sullivan *et al.*, 2006; Arcila *et al.*, 2017). On the contrary, the current phylogenetic framework supports at least eight sister-group relationships between Neotropical and Afrotropical fish taxa, some of which are newly discovered and were not discussed by Lundberg (1993). The second reason explaining the difference between my results and those of Lundberg (1993) is the current possibility of testing time predictions using molecular-based divergence time estimates. Molecular-based dating methods were in their infancy in the early 1990s and uncommonly used in the absence of molecular data for many taxa. Divergence time estimates are now available for several trans-Atlantic sister-group relationships.

My study shows that for only three of these eight trans-Atlantic taxa, the vicariance hypothesis related to fragmentation of west Gondwana cannot be rejected, because their estimated divergence times overlap that of the Africa–South America separation

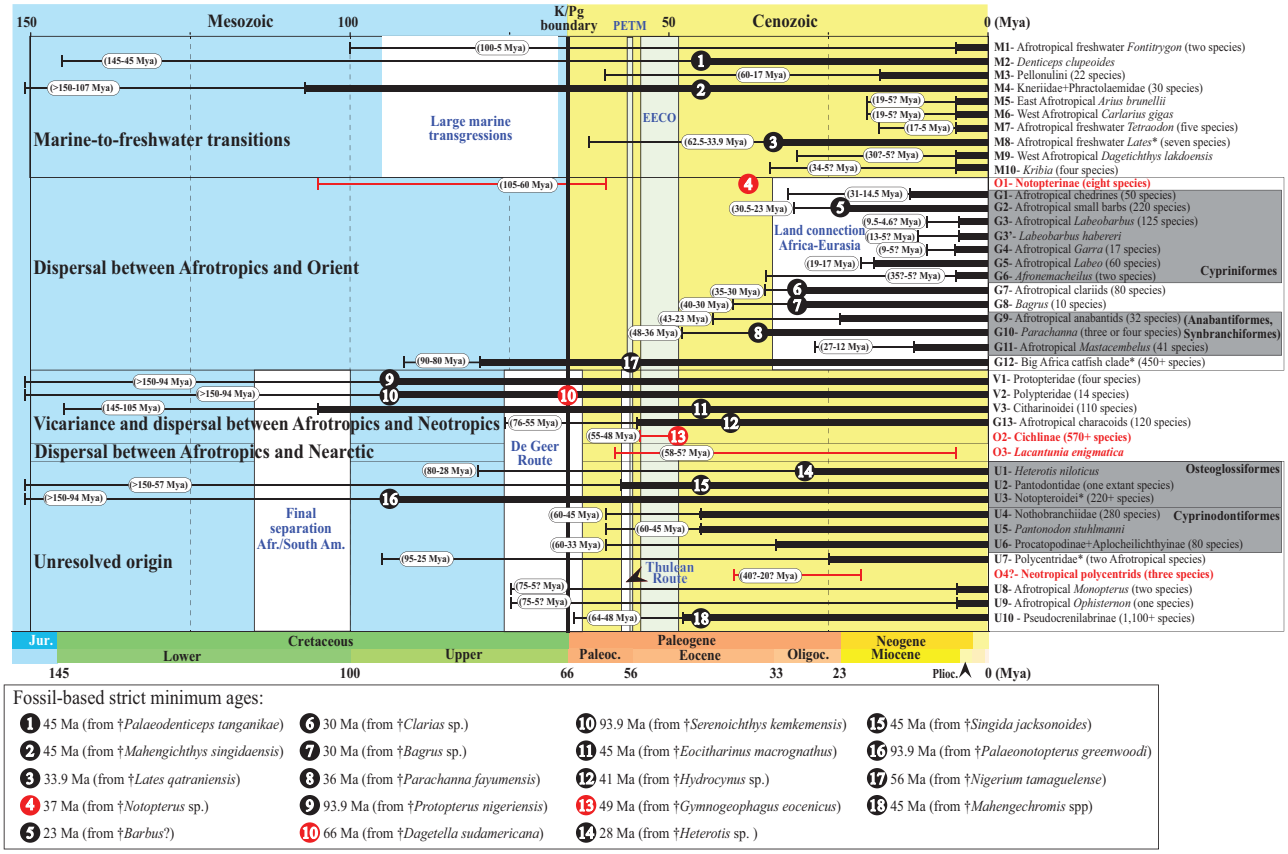

Figure 15. Overview on the origins of the 37 Afrotropical freshwater fish lineages along with the four out-of-Africa dispersal events (listed from O1 to O4). Timespan is from 150 Mya to the present; the boundary between the Cretaceous and Palaeogene (K/Pg, dated to 66 Mya), separating the Mesozoic era (blue background) and the Cenozoic era (yellow background) is indicated, as are the geological periods and epochs preceding the Quaternary (see time scale). For each lineage, the horizontal thick black line indicated its temporal presence in Afrotropics as estimated from time-calibrated molecular phylogenies and the fossil record. Thin black lines represent the maximal and minimal age estimates for the initial presence of the corresponding lineages in Afrotropics. The following three geological events are indicated: (1) the final separation of Africa (Afr.) and South America (South Am.); (2) a land connection between the Orient and Afrotropics after the Afro-Arabic plate collided with the Eurasian plate and closed the Tethys Sea; and (3) the exposure of the De Geer and Thulean routes between the western Palaearctic and eastern Nearctic. The time of two of the most important warm periods (PETM, Palaeocene–Eocene thermal maximum; and EECO, Early Eocene climatic optimum) and the time of large marine transgressions are also indicated. Numbered black dots indicate the strict minimal age for the presence of the corresponding lineage in the Afrotropics as deduced from its earliest African fossil. Numbered red dots indicate the strict minimal age for the out-of-Africa dispersal event of the corresponding non-Afrotropical lineage as deduced from its earliest non-African fossil. The taxonomic identity and the age of each fossil are provided at the bottom.

(Table 1; Fig. 15). These three taxa are as follows: (1) *Protopterus*, which is sister to *Lepidosiren* (Fig. 14A) (Kemp *et al.*, 2017); (2) Afrotropical polypterids, which are sister to extinct Neotropical polypterids (Fig. 14B); and (3) the Citharinoidei, which are sister to either the Characoidei (most likely) or the Characoidei+Siluriformes (Fig. 14D). For the first two taxa, the vicariance hypothesis agrees with the results of Lundberg (1993). The biogeography of Citharinoidei was not discussed by Lundberg (1993).

The estimated maximal divergence times between the four AFF lineages with their respective Neotropical sister groups strictly post-dated separation of Africa and South America. These AFF lineages are as follows: (1) the clade (Alestidae, Hepsetidae); (2) the Pseudocrenilabrinae; (3) *Polycentropsis abbreviata* (Polycentridae); and (4) *Heterotis niloticus* (Table 1; Fig. 15). Therefore, the continental drift vicariance hypothesis related to Africa–South America fragmentation is rejected for these lineages, and

dispersal-based hypotheses must explain their trans-Atlantic distributions.

Northern Hemisphere dispersal (hypothesis 5) as an alternative to direct trans-Atlantic marine dispersal (hypothesis 6) to explain Neotropical–Afrotropical freshwater fish faunal exchanges

Time-calibrated phylogenetic evidence is growing to support trans-Atlantic dispersal for several organisms (including at least four freshwater fish taxa) in the Cenozoic, well after separation of Africa and South America (Zwickl & Hillis, 2002; Lundberg *et al.*, 2007; Friedman *et al.*, 2013; Near *et al.*, 2013; Lavoué, 2016; Matschiner *et al.*, 2017; present study, Fig. 15). However, the mechanisms explaining these dispersal events have rarely been evaluated critically. Often, direct marine dispersal was proposed as an ad hoc hypothesis to explain such post-drifting faunistic exchanges (Briggs, 2003b; Matschiner *et al.*, 2017), but this has been questioned by some authors. For instance, Sparks & Smith (2005) criticized the physiological classification of freshwater fishes of Myers (1938) that is often used to decide whether a freshwater fish group would have been able to survive salinity and disperse through an oceanic environment. This classification is based on the supposed salinity tolerance of freshwater fishes. The classification of Myers (1938) states that the primary freshwater fish division includes fishes that are strictly intolerant of seawater (therefore unable to disperse through marine environments), whereas a secondary freshwater fish division includes fishes that kept ancestral ability to 'survive a short sea journey' (Myers, 1938: 345), therefore implying possible dispersal through marine environments. But there are no factual physiological data to support such a simplification, and irrespective of their classification as primary or secondary, most freshwater fishes do not survive in a marine environment (Sparks & Smith, 2005).

Complementary to the physiological arguments developed by Sparks & Smith (2005) against marine dispersal, I also suggest that marine dispersal between two continental regions is unlikely for freshwater fishes from an evolutionary point of view. This is because it necessitates a combination of four independent evolutionary events (Fig. 16): (1) a freshwater-to-marine transition; (2) long-distance transoceanic dispersal; (3) a marine-to-freshwater transition; and, finally, (4) the selective extinction of marine organisms on each oceanic side. Recent habitat preference reconstructions using phylogenetic trees have shown that marine-to-freshwater transitions are relatively rare events in fishes on a geological scale (Bloom & Lovejoy, 2012; Davis *et al.*, 2012; Lavoué *et al.*, 2013; Conway *et al.*, 2017; Kirchhoff *et al.*, 2017), and freshwater-to-marine events are even rarer. This makes the direct marine dispersal hypothesis unlikely and its recurrence in four different freshwater groups, as observed between Africa and South America during the Cenozoic, even more unlikely.

Furthermore, it also seems highly unlikely that freshwater fishes dispersed over long marine distances using floating rafts (Gayet, 2001; Thiel & Haye, 2006) or by the means of rare, local and untestable phenomena, such as rains of fishes (Gudger, 1929; Bajkov, 1949) or transportation of their eggs by waterbirds (Hirsch *et al.*, 2018 and references cited therein).

After rejecting the possibility of long-distance marine dispersal by freshwater fishes (such as the Cichlidae or Aplocheiloidei), Sparks & Smith (2005) concluded that trans-Atlantic distributions must have been the result of continental drift vicariance. However, the fossil record and molecular dating (present study and others, e.g. Lundberg *et al.*, 2007; Friedman *et al.*, 2013; Lavoué, 2016; Matschiner *et al.*, 2017) consistently reject a Cretaceous age for several trans-Atlantic clades of freshwater fish, including the Cichlidae, Osteoglossidae and Aplocheiloidei.

Given that the vicariance hypothesis is rejected and direct trans-oceanic dispersals seem unlikely, other dispersal processes must be hypothesized to account for trans-Atlantic faunistic exchanges in the Late Cretaceous–early Cenozoic. Ezcurra & Agnolin (2012) observed a trans-Atlantic distribution pattern of archosaurs in the Late Cretaceous, and they proposed a new biogeographical province named Atlantogea, which would have been a chain of islands stretching between Africa and South America. However, the current geological evidence in favour of such a discontinuous land bridge is scarce, and marine environments around these islands would possibly have prevented freshwater fish dispersal.

Therefore, I suggest that dispersal through a northern route, North America–Greenland–Western Europe (hypothesis 5 in Fig. 6; see also Fig. 16), is a more likely hypothesis than direct marine dispersal, raft-mediated dispersal or a hypothetical trans-Atlantic land bridge to explain the intercontinental exchanges of freshwater fishes between Africa and South America from the end of the Cretaceous to the middle Eocene. This Northern Hemisphere dispersal hypothesis is not new (e.g. Lundberg *et al.*, 2007; Friedman *et al.*, 2013), because it was often proposed along with other alternatives, but its mechanism and relative likelihood in the case of freshwater fishes have rarely been discussed.

A short narrative description of this hypothesis (hypothesis 5 in Fig. 6) could be as follows (displayed in Fig. 16). During the late Mesozoic–early Cenozoic

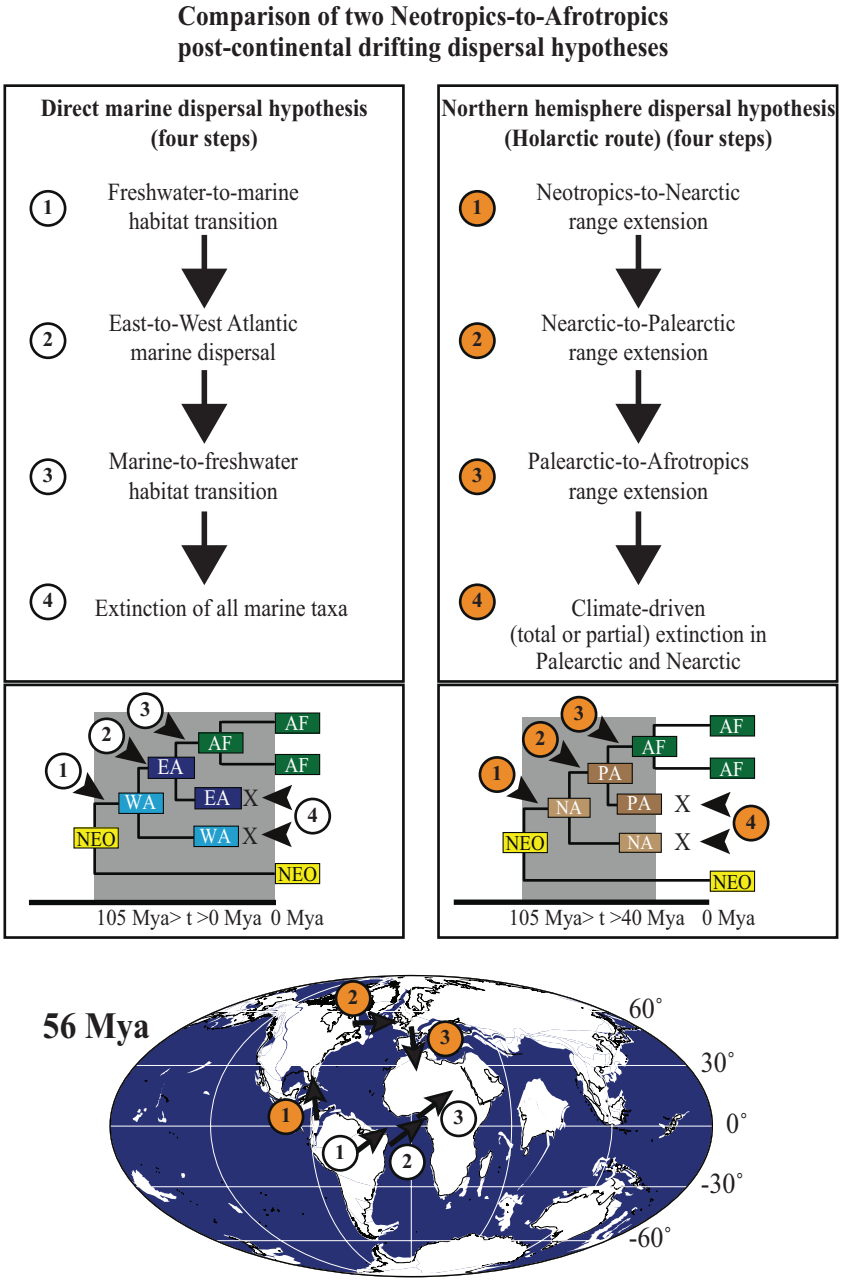

Figure 16. Comparison of the evolutionary events supporting the direct marine dispersal (left) and Northern Hemisphere dispersal (right) hypotheses to explain the post-continental drift dispersal of trans-Atlantic distributed freshwater fish. Each dispersal hypothesis requires four evolutionary events (which are mapped on time-calibrated phylogenetic trees and on a 56 Myr palaeomap reconstruction). The palaeomap was created at www.odsn.de with data from Hay *et al.* (1999). Time scale is in millions of years ago (Mya). For each hypothesis, possible ancestral areas at nodes are shown on phylogenies. Abbreviations: AF, Afrotropics (Africa); EA, eastern Atlantic; NA, Nearctic (North America); NEO, Neotropics (South America); PA, western Palaearctic (Europe); WA, western Atlantic; X, extinction. Background grey rectangles show the time constraint for each hypothesis.

greenhouse period (including the extremely warm PETM and EECO; Fig. 2), when tropical conditions extended to high northern latitudes, Afrotropical and Neotropical freshwater fishes could have extended their distributions northward and colonized continental regions bordering the North Atlantic Ocean as far as Greenland, where the possibility would have existed to travel across, from one continental side to the other

(i.e. from the Nearctic to the Palaearctic, or vice versa). Then, it would have been possible for these lineages to have dispersed to South America or Africa. When the global climate cooled after the middle Eocene, this northern route closed, and most of the tropical lineages in the Northern Hemisphere became extinct; the distributions of those that survived in this region were restricted to the southernmost parts of the Nearctic (i.e. *Lacantunia enigmatica*) and western Palaearctic (i.e. the cyprinodontoid *Valencia* and *Aphanius*).

At first glance, this dispersal hypothesis through a tropical Northern Hemisphere might seem unlikely for tropical freshwater fishes, because it necessitates three continuous intercontinental freshwater routes between: (1) South America (Neotropics) and North America (Nearctic); (2) North America (Nearctic) and Europe (western Palaearctic); and (3) Europe (western Palaearctic) and Africa (Afrotropics) during the Late Cretaceous–middle Eocene interval (Fig. 16).

Below, I briefly review the current palaeobiogeographical and geological evidence to determine whether such a northern dispersal route was possible for tropical freshwater fishes and what predictions can be made.

Interchanges of non-marine organisms between South and North America during the Late Cretaceous to middle Eocene

Fossils of some freshwater fish groups from the Late Cretaceous–Palaeocene interval (75–56 Mya) have been found in South and North America, documenting an expansion of their ranges across the Caribbean region (Gayet, 2001). These freshwater fish groups include Lepisosteidae, Osteoglossidae, Characiformes and Siluriformes (Li & Wilson, 1996a; Cavender, 1998; Newbrey *et al.*, 2009; Grande, 2010; Chen *et al.*, 2014a; White, 1986). Matamoros *et al.* (2015) and Tagliacollo *et al.* (2017) also showed that the earliest colonizations of Central America by cichlids and poeciliids started 58–49 Mya. This pattern of distribution is similar to distributions of some tetrapods (i.e. frogs, lizards, mammals and dinosaurs) and highlights the possibility of regular interchanges between South and North America during this period (Cifelli & Eaton, 1987; Gayet *et al.*, 1992; Gayet, 2001; Nydam, 2002; Graham, 2003; Heinicke *et al.*, 2007).

Geological reconstructions of the proto-Caribbean region show, near the end of the Cretaceous, the presence of an island chain surrounded by shallow seas separating South and North America (reviewed by Hedges, 2006). Low sea-level stands and plate uplift would have been needed to establish any trans-Caribbean land connection (Pindell *et al.*, 1988; Hedges, 2006; Pindell & Kennan, 2009). Although the marine faunal similarity between the eastern Pacific and western Atlantic demonstrates that any trans-Caribbean land connection was not a permanent connection (Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent, 2006), occasional but continuous inter-island links between South and North America might explain the observed trans-Caribbean biotic exchanges.

Interchanges of warm-adapted non-marine organisms between North America and Europe between the Late Cretaceous and middle Eocene

The Late Cretaceous–middle Eocene interval was the most recent greenhouse world (Zachos *et al.*, 2001, 2008; Huber, 2012; Hansen *et al.*, 2013; Scotese, 2015) (Fig. 2), particularly the first 10 Myr of the Eocene (including the PTEM and EECO; Fig. 2) (Markwick, 1998; Huber, 2012). At that time, in northern parts of Europe and North America, the climate was mild, with winter temperatures > 0 °C, summer temperatures > 20 °C and high humidity (Greenwood & Wing, 1995; Huber, 2012). The climatological 'heat piracy' model based on changes in North Atlantic oceanic circulation at the end of the Cretaceous period might have contributed to the warm conditions recorded in this region at the time (MacLeod *et al.*, 2011).

Palaeontological data during this period show that mid-latitude faunas and floras of eastern North America (the eastern Nearctic) and western Europe (the western Palaearctic) comprised many warm-adapted organisms from lineages that are now found only in tropical regions (McKenna, 1975; Tiffney, 2000; Smith *et al.*, 2006; Archibald *et al.*, 2011; Eberle & Greenwood, 2012; Brunke *et al.*, 2017). These data also reveal that these two continental regions shared many taxa as a result of interchanges between Europe and North America and similar warm and humid climatic conditions in these regions (McKenna, 1975; Blondel & Mourer-Chauviré, 1998; Sanmartín *et al.*, 2001; Rose, 2006; Eberle *et al.*, 2009; Mayr, 2009; Eberle & Greenwood, 2012; Stidham & Eberle, 2016).

Geological data support the existence of at least two land bridges through Greenland and across the North Atlantic Ocean (reviewed by Brikiatis, 2014): the De Geer passage (dated 71–63 Mya) and the Thulean passage (dated 57–56 Mya). Besides these two land passages, longitudinal freshwater faunistic exchanges might have been possible through the Arctic Ocean. At that time, the salinity of the Arctic Ocean, which was semi-enclosed, was very low because of the large quantity of rainwater running off the land into it (Brinkhuis *et al.*, 2006; Sluijs *et al.*, 2006).

The fish fossil record in these subarctic regions does not indicate the presence of taxa closely related to living Neotropical or Afrotropical fish taxa, although it shows the presence of warm-adapted taxa. For example, early

Eocene freshwater sediments in the North Polar circle document the presence of the Amiidae and Lepisosteidae (Eberle *et al.*, 2014; Kim *et al.*, 2014; Padilla *et al.*, 2014). Distributions of these taxa are now restricted to the southeastern Nearctic region. I also note the presence of rare characiform and osteoglossid remains of mostly unresolved affinities, both in the Nearctic (Newbrey *et al.*, 2009; Brinkman *et al.*, 2017; Murray *et al.*, 2018) and in the western Palaearctic (Taverne *et al.*, 2007; Otero *et al.*, 2008; Forey & Hilton, 2010).

Interchanges between Europe and Africa: trans-Tethyian relationships of non-marine organisms between the Late Cretaceous and middle Eocene and the Eurogondwana model

During the Late Cretaceous and early Cenozoic, the European fauna (western Palaearctic) had a complex history with multiple origins, including from North America (see previous subsection) and Africa. In particular, distributions of some terrestrial and semi-aquatic vertebrate fossils (e.g. Abelisaurid dinosaurs, crocodiles, snakes, turtles and mammals) reveal several interchanges between Africa and Europe through the western Tethys region (Gheerbrant & Rage, 2006). European freshwater fish fossils of Late Cretaceous age that support trans-Tethyian dispersal include coelacanths (family Mawsoniidae; Cavin *et al.*, 2005), †*Atractosteus africanus* (Arambourg & Joleaud, 1943) (family Lepisosteidae; Cavin *et al.*, 1996), freshwater osteoglossid rests (Taverne *et al.*, 2007; Taverne, 2009; Forey & Hilton, 2010) and Alestidae-like remains (Otero *et al.*, 2008). As a result of these repeated Africa–Europe faunistic exchanges, Le Loeuff (1991) defined this biogeographical region and named it Eurogondwana.

Palaeogeographical reconstructions of southern Europe during the Late Cretaceous and early Cenozoic along with palaeontological data indicate a complex and changing region of islands isolated by shallow marine environments. In some ways, its configuration resembled the proto-Caribbean region. Within this region, terrestrial connections stretching between North Africa and western Europe might have been established through geological and climatic changes.

Post-Eocene dispersal from the Orient (hypothesis 7)

At least 11 Afrotropical lineages originated from dispersal events from the Orient when Africa, in its northwards movement, collided with Eurasia at the end of the Eocene and early Miocene, establishing an overseas route between the two continental regions (Otero & Gayet, 2001; Meulenkamp & Sissingh, 2003). Altogether, these 11 lineages contribute ~20% (i.e. ~630 species) to the total AFF fauna. The fossil record indicates that some of these lineages (i.e. channids, clariids and bagrids) were present in Africa as early as 10 Mya, before the current hypothesized final closure of the Tethys Sea and the establishment of a permanent land bridge (Otero & Gayet, 2001). Otero & Gayet (2001) suggested three different hypotheses to explain this temporal incongruence between the fossil record and the current palaeogeological reconstruction model of this region: (1) early members of these lineages were tolerant of seawater, allowing their dispersal through marine/brackish environments; (2) these lineages were of Gondwanan origin, and their distribution patterns were caused by the fragmentation of Gondwana (i.e. the separation between India/Madagascar and Africa); and (3) an early land connection allowed late Eocene–early Oligocene Afrotropics–Orient exchanges. The first hypothesis is difficult to test in the absence of marine fossil taxa related to these current freshwater lineages, whereas molecular dating inferences support post-Mesozoic origins of these lineages, thereby refuting the second hypothesis. There are some discussions regarding the time of the closure of the Tethys Sea. Based on their own interpretation of the geological evidence, Allen & Armstrong (2008) hypothesized that the closure of the Tethys Sea might have occurred in the late Eocene (~35 Mya). I favour the third hypothesis, and as noted by Otero & Gayet (2001), the intercontinental dispersals of some mammals in the early Oligocene provide independent support for this hypothesis.

Two of the three main Oriental lineages of freshwater fishes invaded Africa several times: the Cypriniformes colonized the Afrotropics six or seven times and the clade (Anabantiformes, Synbranchiformes) four times (Table 1; Fig. 15). Only one lineage (i.e. *Bagrus*) of the Big Asia catfish clade (the third main Oriental lineage) dispersed to Africa.

The only unambiguous dispersal from the Afrotropics to the Orient was that of notopterins. Their dispersal occurred between 105 and 60 Mya. However, this event took place well before the closure of the Tethys Sea (broadly estimated at 34–23 Mya) and well after the separation of Madagascar/India from Africa (estimated at 130–120 Mya). In the next section, I present a dispersal hypothesis between India/Madagascar and Africa, which could explain the distribution of Notopteridae along with those of a few other freshwater fish groups distributed in these two regions (e.g. Big Africa catfish clade/Pangasiidae, Nothobranchiidae/Aplocheilidae).

Unresolved origins and the necessity for a new hypothesis

The current evidence does not allow a confident resolution of the geographical origins of ten Afrotropical lineages (Table 1; Fig. 15). Some of these lineages

are particularly emblematic and successful, such as subfamily Pseudocrenilabrinae (African Cichlidae; > 1100 species), Nothobranchiidae (> 280 species) and suborder Notopteroidei, which includes the charismatic African weakly electric fishes (families Gymnarchidae and Mormyridae; > 220 species). These ten lineages include > 1600 species, and they represent ~50% of the total current species richness. For nine of these lineages, the time-calibrated phylogenetic test rejected the marine-origin hypothesis (hypothesis 1) and the continental drift vicariance hypothesis (either with South America or with India/Madagascar; hypotheses 2 and 3) (The marine-origin hypothesis cannot be rejected entirely for Polycentridae, the tenth lineage). However, the test was not conclusive regarding the other tested hypotheses, because either more than one hypothesis was possible (e.g. *Heterotis niloticus*, synbranchids) or the test rejected all hypotheses (e.g. the Pseudocrenilabrinae). There are reasons that explain the difficulty in offering comprehensive biogeographical hypotheses for these lineages.

Lack of phylogenetics, timing and palaeontological information

The Afrotropical fossorial eels *Monopterus* and *Ophisternon* (family Synbranchidae, lineages U8 and U9 in Table 1; Fig. 15) are groups of AFF for which less phylogenetic and palaeontological information is available (Rosen & Greenwood, 1976). These taxa are only rarely collected and poorly studied, no fossils are known, and the only published phylogenetic tree is not time calibrated (see Fig. 13E, reproduced from Rosen & Greenwood, 1976). The stem age of the family (i.e. the divergence with its sister group) was estimated roughly to be ~75 Mya (Near *et al.*, 2013). Hypothesis 1 (marine origin) along with hypotheses 2, 3 (vicariance) and 4 (pre-drift) are rejected. For the Afrotropical *Monopterus*, the post-Eocene dispersal from the Orient hypothesis (hypothesis 7) is not rejected, but in the absence of timing, an early Cenozoic dispersal from the Orient is also not rejected. The biogeography of *Ophisternon* is even more obscure, because this genus is widely distributed, with species occurring in the Orient, Afrotropics, Neotropics and Australia, and there is no phylogenetic tree of species of *Ophisternon*. Considering that *Ophisternon* originated in the Cenozoic, any post-drift dispersal hypothesis, from either the Orient or the Neotropics, is possible.

Resolved phylogenetic relationships but weakly supported ancestral area inferences

This is the situation for two osteoglossiform lineages, *Pantodon* and Notopteroidei (lineages U2 and U3 in Table 1; Fig. 15). Although the time-calibrated phylogeny of the Osteoglossomorpha, a relictual group of currently freshwater-restricted fishes, is relatively well studied (Hilton, 2003; Lavoué & Sullivan, 2004; Wilson & Murray, 2008; Lavoué, 2016; Hilton & Lavoué, 2018), the regions of origin of *Pantodon* and the Notopteroidei, two ancient lineages (maybe as old as the Early Cretaceous), are uncertain. This is because the ancestral area inference regarding the origins of these two lineages is incomplete. The addition of not yet sampled, non-African fossils to the analysis could modify the reconstruction (Fig. 14C). Current evidence excludes a marine dispersal origin (but see Taverne, 1998; Taverne & Capasso, 2012) and a Cenozoic dispersal for the Notopteroidei. However, the test only provided slight support for the hypothesis in which the most recent common ancestor of Osteoglossiformes lived in Africa, with the consequence that *Pantodon* and Notopteroidei would have the same origin in Afrotropical fresh waters, pre-dating the separation between South America and Africa.

When palaeodistributions challenge conclusions based on current distributions.

The Eocene fossil †*Sinoglossus lushanensis* found in southern China, which is related exclusively to *Heterotis niloticus* and *Arapaima* spp., challenges the biogeographical hypothesis of these extant taxa (Li & Wilson, 1996b; Wilson & Murray, 2008; Forey & Hilton, 2010) (Fig. 14C). *Heterotis niloticus* and the Neotropical genus *Arapaima* diverged from each other after the separation of Africa and South America, strongly suggesting that their distribution is the result of a trans-Atlantic post-drifting dispersal event. However, the addition of the Oriental †*Sinoglossus lushanensis* to the dataset modified the reconstruction to mostly unresolved (Fig. 14C; Supporting Information, Fig. S5). Direct evidence from the fossil record regarding the origin of *Heterotis* in the Afrotropics is inconclusive, because it indicates the presence of *Heterotis* only from the Oligocene (28 Mya) (Otero *et al.*, 2017) (Fig. 15).

The biogeography of the entire Osteoglossidae appears complex, with the discovery of dozens of fossils (some marine) from all continents (except Antarctica). The phylogenetic position of only a few of these fossils has been examined. and they are, in general, unresolved, unstable or unsupported (Hilton, 2003; Forey & Hilton, 2010; Murray *et al.*, 2018). More systematic, palaeontological studies are needed to decipher the biogeography of the Osteoglossidae, in general, and the origin of *Heterotis*, in particular.

Inconclusive test

Although time-calibrated phylogenetic relationships are relatively well resolved for two AFF taxa

(Nothobranchiidae and Pseudocrenilabrinae; lineages U4 and U10 in Table 1; Fig. 15), the seven-hypotheses test is inconclusive. These two AFF taxa share the following four features: (1) they have at least two consecutive freshwater outgroups (this rejects hypothesis 1); (2) their two immediate outgroups live in two different continental tropical regions, the Neotropics and the Orient; and (3) the time divergence between each of these AFF taxa with its respective sister group falls within the interval of the Late Cretaceous to the mid-Cenozoic (roughly between 70 and 40 Mya), after the tectonic isolation of Africa (this rejects hypotheses 2, 3 and 4) and before Africa–Eurasia contact (refutes hypothesis 7); and (4) the regions of origin and early evolution of the Cichlidae and Cyprinodontiformes were made of two distinct continental regions, Afrotropics + Madagascar and Afrotropics + Neotropics, respectively. The phylogenetic sequences of these two AFF lineages differ: the sister group of the Pseudocrenilabrinae is the Neotropical Cichlinae, and a Madagascan cichlid lineage is the sister group of the clade (Pseudocrenilabrinae, Cichlinae), whereas the sister group of the Nothobranchiidae is the Oriental/Madagascan-distributed family Aplocheilidae, and their sister group is the Neotropical family Rivulidae.

The need for a Late Cretaceous–Palaeocene dispersal route between Africa and the Orient (through India?)

Although the origins of some AFF lineages are difficult to infer for the reasons given above, I observed that for two AFF lineages, divergences between the AFFs and their respective Oriental sister groups are roughly similar and conservatively estimated to the Late Cretaceous–early Cenozoic: (1) the Notopterinae/Xenomystinae; and (2) the Big Africa catfish clade/Pangasiidae. To these two groups could be added, in certain circumstances, four groups: (3) the Nothobranchiidae/Aplocheiliidae; (4) the Pseudocrenilabrinae (plus its secondarily distributed Neotropical sister group, Cichlinae)/Ptychochrominae (Madagascar); (5) *Heterotis* (plus *Arapaima*)/†*Sinoglossus lushanensis*; and (6) *Pantanodon stuhlmanni*/*Pantanodon madagascariensis*. Is it possible that a direct freshwater dispersal route between Africa and India (plus Madagascar, Sri Lanka and Seychelles?) has shaped the Afrotropical–Oriental distributions of these lineages during the Late Cretaceous or early Cenozoic? This question has often been addressed, highlighting the difficulty in explaining the intercontinental distribution of freshwater and terrestrial taxa of India based on current palaeogeographical reconstructions (e.g. Briggs, 2003a; Verma *et al.*, 2016).

Recent palaeomaps show that India (and Madagascar) was fully isolated by a marine environment for dozens of millions of years in the Late Cretaceous–middle Cenozoic (Ali & Aitchison, 2008; Gaina *et al.*, 2015; Torvsky *et al.*, 2013), leading Ali & Huber (2010) and Samonds *et al.* (2012) to propose a marine dispersal mechanism based on rafting or swimming and palaeo-oceanic current modelling. However, Briggs (2003a) and others noted that the Indian fossil record at that time documents the presence of a rich and diversified fauna and vegetation with Afrotropical (and Palaearctic) affinities. This contradicts such physical isolation in documenting possible intercontinental exchanges.

The Indian fossil fish fauna of the Maastrichtian (72–66 Mya) comprises, among other taxa (Verma *et al.*, 2016), three freshwater fish taxa with counterparts in Africa at that time: Lepisosteidae (currently extinct in Africa), Notopteridae and the osteoglossid subfamily Heterotinae (Rana, 1988; Nolf *et al.*, 2008). However, owing to the nature of the material (otoliths) of Indian notopterids and heterotins, no better taxonomic precision can be given. Grande (2010) reviewed the osteological morphology of the freshwater India gar, †*Lepisosteus indicus* Woodward, 1908, from the same age or a bit younger (early Cenozoic), and Taverne *et al.* (2009) reviewed the osteological morphology of the freshwater osteoglossid †*Taverneichthys bikanericus* Kumar, Rana & Paliwal, 2005. Their results complement observations made only of otoliths.

The Indian continent, with its northward movement, might have played a role in the intercontinental distribution of some of these groups of fishes (Briggs, 2003a). Recent tectonic studies, such as that of Torsvik *et al.* (2013), have improved the palaeogeological reconstruction of the Indian Ocean region during the Cretaceous–early Cenozoic, because they showed that the geology of this region was different from what was thought previously, because of intense volcanic activities that may have hidden some micro-continental plates. Altogether, these micro-continental plates might have formed a larger one, called Mauritia by Torsvik *et al.* (2013). I cannot predict how much the discovery of the lost continent of Mauritia will modify the palaeogeological reconstruction of the western Indian region, but its study might lead to better understandig of the biogeography of this region.

Conclusions

Recent time-calibrated phylogenetic studies along with palaeontological data allowed me to test for the habitat or geographical origins of 37 monophyletic groups of AFFs. Based on geological and palaeoclimatic evidence, seven a priori hypotheses were built and tested. The test highlighted the origins of 26 AFF lineages: (1) ten lineages are of marine origin; (2) three lineages

originate from Africa–South America drift vicariance; (3) two post-drift dispersals occurred from South America, possibly through the Northern Hemisphere (while two dispersals in the reverse direction occurred during the same period); and (4) 12 lineages dispersed from the Orient after the Eocene (but no dispersal in the reverse direction). An additional hypothesis linking India/Madagascar with Africa in the Late Cretaceous–early Cenozoic is needed to explain the origins of two AFF lineages (the Big Africa catfish clade and Pseudocrenilabrinae) along with the presence of notopterins and Aplocheilidae in the Orient.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Four time-calibrated phylogenetic trees of distinct cyprinid lineages, on which are estimated geographical range evolution using a dispersal–extinction–cladogenesis (DEC) model (Ree & Smith, 2008) as implemented in BioGeoBEARS (Matzke, 2018). A, Chedrini (Cyprinidae), showing the origin of the Afrotropical

chedrins (tree modified from Sungani *et al.*, 2017). B, part of the tribe Cyprinini (Cyprininae, Cyprinidae), showing the origin of the Afrotropical small barbs clade (tree modified from Ren & Mayden, 2016). C, part of the tribe Cyprinini, showing the origin of *Labeobarbus* (tree modified from Beshera *et al.*, 2016). D, Labeonini (Cyprinidae), showing the origins of Afrotropical *Labeo* and *Garra* (tree modified from Tang *et al.*, 2009). The Afrotropical (AF) distributed taxa and Afrotropical inferred ancestral regions are highlighted in green. Oriental (OR) taxa and ancestral regions are indicated in red. Black and white pie charts at specific ancestral area reconstruction show the probability (white) of the corresponding reconstruction. Number in black-filled circle indicates strict minimal age for the corresponding lineage, as obtained from the fossil record (for details, see main text and Fig. 15).

Figure S2. Phylogenetic trees of lineages of Nemacheilinae (Cypriniformes) and Ovalentaria (Acanthomorpha), on which are estimated geographical range evolution using a dispersal–extinction–cladogenesis (DEC) model (Ree & Smith, 2008) as implemented in BioGeoBEARS (Matzke, 2018). A, part of Nemacheilinae (Cobitoidea, Cypriniformes), showing the origin of *Afronemacheilus* (not time-calibrated tree modified from Prokofiev, 2009). B, overview of the time-calibrated phylogeny of Ovalentaria, on which is reconstructed the evolution of salinity preference (tree modified from Near *et al.*, 2013). Salinity preference was classified in two states: 'marine' indicated in blue and 'fresh water' in white. At each node, the relative probabilities of each state (sum = 1) are drawn using pie charts. C, Cichlidae, showing the origin of Pseudocrenilabrinae (tree modified from Friedman *et al.*, 2013). D, Cyprinodontiformes, showing the origins of Nothobranchiidae, *Pantanodon stuhlmanni* and the clade (Procatopodinae, Aplocheilichthyinae) (tree modified from Amorim *et al.*, 2018, with addition of taxa from Pohl *et al.*, 2015; Reznick *et al.*, 2017). E, Polycentridae, showing the origin of Afrotropical polycentrids (not time-calibrated tree modified from Collins *et al.*, 2015). Reconstructions in A and C–E: the Afrotropical (AF) distributed taxa and Afrotropical inferred ancestral regions are highlighted in green, Oriental (OR), Neotropical (NEO), Nearctic (NA), Palaearctic (PA), Madagascan (Mad) and Australian (AUS) taxa and ancestral regions are indicated in red, yellow, light brown, medium brown, white and orange, respectively. Black and white pie charts at specific ancestral area reconstruction show the probability (white) of the corresponding reconstruction. Number in black-filled circle indicates strict minimal age for the corresponding lineage, as obtained from the fossil record (for details, see main text and Fig. 15).

Figure S3. Time-calibrated phylogenetic tree of Siluriformes, on which is estimated geographical range evolution using a dispersal–extinction–cladogenesis (DEC) model (Ree & Smith, 2008) as implemented in BioGeoBEARS (Matzke, 2018). This analysis shows the origins of Afrotropical clariids, *Bagrus* and the Big Africa clade (tree modified from Lundberg *et al.*, 2007). The Afrotropical (AF) distributed taxa and Afrotropical inferred ancestral regions are highlighted in green. Oriental (OR), Neotropical (NEO), Nearctic (NA), Palaearctic (PA), Madagascan (Mad), Australian (AUS) and marine (Ma) taxa and ancestral regions are indicated in red, yellow, light brown, medium brown, white, orange and blue, respectively. Black and white pie charts at specific ancestral area reconstruction show the probability (white) of the corresponding reconstruction. Numbers in black-filled circles indicate strict minimal age for the corresponding lineage, as obtained from the fossil record (for details, see main text and Fig. 15). The three arrowheads indicate inconsistencies in the reconstruction at the corresponding nodes, because these ancestors should have been marine and distributed in a continental freshwater region. Future studies should resolve these inconsistencies.

Figure S4. Phylogenetic trees of distinct lineages of the clade (Anabantiformes, Synbranchiformes), on three of which are estimated geographical range evolution using a dispersal–extinction–cladogenesis (DEC) model (Ree & Smith, 2008) as implemented in BioGeoBEARS (Matzke, 2018). A, overview of the time-calibrated phylogeny of the clade (Anabantiformes, Synbranchiformes) (modified from Near *et al.*, 2013). B, Anabantoidei, showing the origin of the Afrotropical anabantids (time-calibrated tree modified from Rüber *et al.*, 2006). C, Mastacembelidae, showing the origin of the Afrotropical mastacembelids (time-calibrated tree modified from Day *et al.*, 2017). D, Channidae, showing the origin of *Parachanna* (tree modified from Day *et al.*, 2017). E, Synbranchidae, showing the phylogenetic positions of Afrotropical species of *Ophisternon* and *Monopterus*; no ancestral range estimation was possible with BioGeoBEARS because this tree contains one polytomy (not time-calibrated tree modified from Rosen & Greenwood, 1976; maximal age estimation from Near *et al.*, 2013). The Afrotropical (AF) distributed taxa and Afrotropical inferred ancestral regions are highlighted in green. Oriental (OR), Neotropical (NEO) and Australian (AUS) taxa and ancestral regions are indicated in red, yellow and orange, respectively. Black and white pie charts at specific ancestral area reconstruction show the probability (white) of the corresponding reconstruction. Number in black-filled circle indicates strict minimal age for the corresponding lineage, as obtained from the fossil record (for details, see text and Fig. 15).

Figure S5. Four time-calibrated phylogenetic trees of early Mesozoic Afrotropical freshwater lineages; on two of them are estimated geographical range evolution using the BAYAREALIKE model (Landis *et al.*, 2013) as implemented in BioGeoBEARS (Matzke, 2018). A, extant lungfishes, showing the origin of *Protopterus* (tree

modified from Kemp *et al.*, 2017; the ancestral range was manually estimated). B, early evolution of Actinopterygii, showing the origin of Polypteridae (tree modified from Near *et al.*, 2014b; the ancestral range was estimated manually). C, Osteoglossomorpha, including extant and extinct taxa, showing the origins of *Heterotis niloticus*, Notopteroidei and *Pantodon buccholzi* (tree modified from Lavoué, 2016). D, Otophysi, showing the origins of Citharinoidei and the clade (Alestidae, Hepsetidae) (tree modified from Chen *et al.*, 2013). The Afrotropical (AF) distributed taxa and Afrotropical inferred ancestral regions are highlighted in green. Oriental (OR), Neotropical (NEO), Nearctic (NA), Palaearctic (PA) and Australian (AUS) taxa and ancestral regions are indicated in red, yellow, light brown, medium brown and orange, respectively. Black and white pie charts at specific ancestral area reconstruction show the probability (white) of the corresponding reconstruction. Numbers in black-filled and red-filled circles indicate strict minimal age for the corresponding lineage, as obtained from the fossil record (for details, see text and Fig. 15).