



Historical biogeography of a new antitropical clade of temperate freshwater fishes

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ABSTRACT

Aim Any discovery of new biogeographical pattern in landlocked animals may challenge hypotheses that account for the evolution of intercontinental faunas. In this study, we examined the evolutionary origin and historical biogeography of temperate, freshwater perch-like fishes within a molecular phylogenetic framework.

Location Temperate Eastern Eurasia, the Americas and Australia.

Methods Data from five nuclear markers obtained from 15 targeted species and a broad sampling of percomorphs were assembled to investigate their phylogeny and historical biogeography. We (1) applied a fossil-calibrated Bayesian reconstruction to provide a phylogenetic time-scale for the diversification of the taxa, (2) inferred the evolution of habitat preference through a tree-based character reconstruction method, and (3) reconstructed the evolution of range distributions using a dispersal–extinction–cladogenesis model.

Results We recovered a new antitropical freshwater clade, Percichthyoidea, composed of Sinipercidae, Percichthyidae (including *Percilia* but excluding *Macquaria colonorum*), Ellassomatidae and Centrarchidae. Our time-scale analysis indicates that the Percichthyoidea originated around the Cretaceous–Palaeogene transition. Ancestral habitat reconstructions revealed only one marine-to-freshwater transition that preceded the origin of the percichthyoids; the warm-to-temperate transition occurred earlier. Ancestral-area inference indicates a wide-ranging pan-American and Eastern Eurasian distribution of the most recent common ancestor of Percichthyoidea. The initial diversification event occurred between the southern (Percichthyidae) and northern (remaining percichthyoids) clades. A second divergence occurred between Eastern Eurasia (Sinipercidae) and North America (Centrarchidae plus Ellassomatidae). The trans-Pacific distribution of the Percichthyidae may have preceded the final breakup of south Gondwana.

Main conclusions The present-day distribution of the Percichthyoidea is unique within extant fishes, comprising four trans-Pacific continental blocks across the two hemispheres. Current geological and palaeoenvironmental reconstructions may well explain the longitudinal but not the latitudinal pattern of this freshwater fish clade, as it requires a transequatorial freshwater system connecting temperate regions of South and North America during the Late Cretaceous/Palaeogene. An alternative hypothesis is discussed, in which the ancestor of the Percichthyoidea was not completely adapted to freshwater.

Keywords

Antitropical distribution, Centrarchidae, dispersal–extinction–cladogenesis, freshwater fish biogeography, historical biogeography, nuclear markers, Percichthyidae, Percomorpha, vicariance.

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INTRODUCTION

Groups of freshwater fishes distributed across oceans are of particular interest to biogeographers because of their limited tolerance to salinity and the assumption of low dispersal capabilities across marine environments (Briggs, 1979). Disjunct intercontinental distributions of related freshwater fishes have been explained both by vicariance (e.g. land fragmentations through tectonics) and dispersal (e.g. land bridges emerging through eustatic sea-level variations). For example, the distributions of several groups of freshwater fishes in South America and Africa are hypothesized to be the direct consequence of the separation of these two continents during the Cretaceous Period (Lundberg, 1993; but see Chen *et al.*, 2013), whereas the distributions of shared freshwater fishes between North America and Eastern Eurasia are better explained by dispersal through the periodically emerged Beringia land bridge during the Mesozoic/Cenozoic (Choudhury & Dick, 1998; Oaks, 2011).

Most transoceanic distributions of freshwater fishes are longitudinal and well documented (Berra, 2007). They mostly occur between South America and Africa [e.g. Cichlidae, Characiformes and Siluriformes; mostly tropical (Murray, 2001; Chen *et al.*, 2013)], North America and Eurasia [paddlefishes (Grande & Bemis, 1991), sturgeons (Choudhury & Dick, 1998) and Catostomidae (Smith, 1992); temperate] or Australia, South America and South Africa [Galaxiidae (Waters & Burrige, 1999); temperate]. Any discovery of a new distribution pattern in groups of freshwater fishes may therefore challenge hypotheses that account for the evolution of intercontinental faunas (Lundberg *et al.*, 2007).

Here, we address the phylogenetic positions and biogeographical patterns of temperate freshwater fishes of the largest extant group of teleost fishes, Percomorpha. It includes about 245 families (Eschmeyer & Fong, 2011; Eschmeyer, 2013) and is deeply nested within the phylogeny of Teleostei (Chen & Mayden, 2010). Most percomorph families live predominantly in tropical marine environments. Only about 23 families include exclusively or predominantly freshwater species, and only nine of them include exclusively or predominantly temperate freshwater species (Nelson, 2006; Berra, 2007).

These include the Abyssocottidae (six genera, 22 species) and Comephoridae (one genus, two species), both of Lake Baikal, the freshwater (and catadromous) notothenioid Pseudaphritidae (one species; south-eastern Australia), the Cheimarrichthyidae (one species; New Zealand), the Ellassomatidae (pygmy sunfishes; one genus; six species; North America), and the four percid families Percidae (perches; 10 genera; 187 species in North America and 14 in Western Eurasia), Centrarchidae (sunfishes and basses; eight genera; 31 species; North America), Siniperidae (two genera; about 14 species; Eastern Eurasia) and Percichthyidae (southern temperate perches; 10 genera; about 15 species; Australia and South America) (Johnson, 1984; Roberts, 1993; Nelson, 2006) (Fig. 1).

The elucidation of phylogenetic relationships of Percomorpha is complicated by their formidable diversity and rapid diversification. The phylogenetic positions of most temperate freshwater perch-like families have been left unresolved within large polyphyletic groups (e.g. Perciformes, Percoidei) (Rosen, 1982; Johnson & Patterson, 1993; Nelson, 2006). A resolved phylogenetic tree is, however, a prerequisite to examining hypotheses regarding the evolution of habitat associations and historical biogeography (Chen & Mayden, 2010). Using multilocus data (Chen *et al.*, 2003, 2007; Miya *et al.*, 2003; Dettai & Lecointre, 2005; Smith & Craig, 2007; Azuma *et al.*, 2008; Li *et al.*, 2009; Wainwright *et al.*, 2012), a phylogenetic framework begins to emerge, with the recurrent detection of several distinct lineages (summarized in Chen & Mayden, 2010). The taxonomic coverage in these studies has, however, remained insufficient to discuss the evolution and biogeography of the temperate freshwater perch-like fishes.

As part of a larger project aimed at providing a comprehensive phylogenetic hypothesis for the Percomorpha, we report here on the finding of a new clade of temperate freshwater perch-like fishes comprising the Percichthyidae (including *Percilia* but excluding *Macquaria colonorum*), Siniperidae, Centrarchidae and Ellassomatidae and examine the evolutionary origin and historical biogeography of this group. Our study provides evidence for a new pattern of distribution of lineages, the first antitropical clade of temperate freshwater fishes (Fig. 1). This pattern defies the current geological and palaeoenvironmental context and opens up

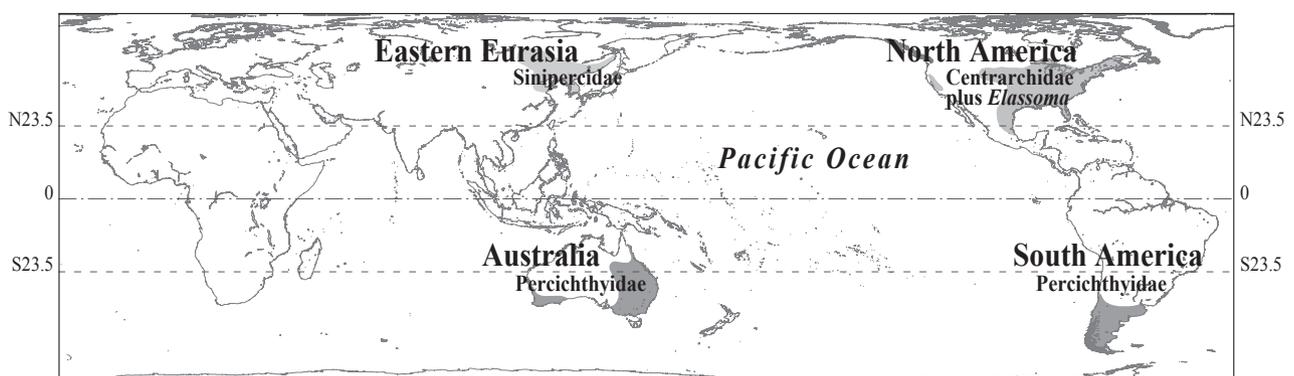


Figure 1 Present-day geographical distribution of the four families of temperate perch-like fishes (Percichthyoidea) examined: Siniperidae, Centrarchidae, Percichthyidae and Ellassomatidae. Distributions follow Berra (2007).

new avenues for discussion and research about the biogeographical history of the Percomorpha.

MATERIALS AND METHODS

Taxonomic sampling

We examine five Australian percichthyid species from five different genera, two South American percichthyid species from the genera *Percichthys* and *Percilia*, two species of Sini-percidae from the genera *Siniperca* and *Coreoperca*, four species of Centrarchidae and two species of Elasmomatidae (*Elassoma*), as well as a broad sampling of 55 taxa representing the main lineages of the Percomorpha recently identified in molecular analyses (Chen *et al.*, 2003, 2007; Miya *et al.*, 2003; Dettai & Lecointre, 2005; Smith & Craig, 2007; Li *et al.*, 2009; Wainwright *et al.*, 2012). This sampling strategy allows us to: (1) test the monophyly of the four studied families; (2) search for their close relatives; and (3) provide calibration points for fossil-based dating reconstruction. We select two non-percomorph beryciform species, *Beryx splendens* and *Myripristis murdjan*, to root the tree. The list of taxa examined in this study is given in supporting information (see Appendix S1 in the Supporting Information).

DNA data

DNA sequences were generated from five nuclear genes located on different chromosomes [recombination activation gene 1 (*RAG1*), rhodopsin (*RH*), and early growth response protein genes 1, 2B and 3 (*EGR1*, *EGR2B* and *EGR3*); Chen *et al.*, 2008]. Some sequences used in this study were retrieved from GenBank or previously determined in Chen *et al.* (2013). Protocols for collecting new DNA sequences follow those outlined in Chen *et al.* (2008). The complete list of primers used in this study is given in Appendix S1. The newly obtained sequences have been deposited in the NCBI GenBank database (see Appendix S1 for accession numbers).

Phylogenetic analysis and divergence time estimation

DNA sequences were edited using CODONCODE ALIGNER 4.0.4 (CodonCode Corporation, Centerville, MA, USA) and SE-AL 2.0a11 (available at <http://tree.bio.ed.ac.uk/software/seal/>). They were initially aligned with the automatic multiple alignment program MUSCLE (Edgar, 2004) using the online server at <http://www.ebi.ac.uk/Tools/msa/muscle/index.html>. These were then adjusted manually based on the inferred amino-acid translations. Regions containing large insertion/deletion segments (e.g. tandem repeats in *EGR* genes), showing high dissimilarity in sequence length, which may result in invalid assertions of homology, were discarded from phylogenetic analyses. The total data matrix included 72 taxa and 5001 nucleotide positions. Maximum-likelihood phylogenetic analyses were conducted on two data matrices

and two different partitioning schemes. The first matrix, named '123', includes all first, second and third codon positions (5001 bp). The second matrix, named '123 no indel', excluded all insertion and deletion positions (indels) to minimize the impact of missing or 'gap' data (4386 bp), because missing data may mislead phylogenetic reconstruction (Lemmon *et al.*, 2009; Wiens & Morrill, 2011). The two different partitioning schemes were: (1) each codon position (across all genes) was assigned to a partition (three partitions in total); (2) for each of the five individual genes, each codon position was assigned to a partition (15 partitions).

Phylogenetic analyses were performed using the partitioned maximum-likelihood (ML) method as implemented in RAXML-HPC (Stamatakis, 2006), through its graphical interface RAXMLGUI 0.93 (Silvestro & Michalak, 2012). Heuristic searches were conducted under mixed models of sequence evolution, which allows individual model parameters of nucleotide substitutions to be estimated independently for each partition in an analysis. As recommended in the manual of RAXML-HPC (Stamatakis, 2006), a GTR+ Γ model (with four discrete rate categories) for each partition was used without incorporating invariant sites. A thorough ML tree search was conducted across 100 distinct runs. The optimal tree was determined by comparison of the likelihood scores among the suboptimal trees obtained per run. To evaluate the robustness of the internal branches of the ML tree, 1000 bootstrap replications (MLBS) were calculated for each data set under the GTR+ Γ model.

The partitioned Bayesian method, as implemented in BEAST 1.7.4, incorporating a relaxed molecular clock calibrated with a set of fossils, was used to simultaneously infer phylogenetic relationships and divergence times (Drummond *et al.*, 2012). Given the highly similar ML phylogenetic trees when using previous datasets and data partitioning schemes, we analysed only the smallest dataset ('123 no indel'), partitioned according to codon positions (three partitions) to save computation time. We chose a GTR+ Γ model of sequence evolution for each partition, and unlinked the substitution model, rate-heterogeneity model and base frequencies across partitions.

The fossil record is essential for calibrating molecular-based time estimation, because it offers direct evidence for the presence of a taxon at a defined time in the past – its strict minimum age. Its maximum age needs to be estimated, and this estimation depends on the observer's perception of the quality of the fossil record: the better the quality of the fossil record, the more precise the estimate of its maximum age is. Our phylogenetic tree was time-calibrated with a series of seven percomorph fossils that provide hard minimum ages and soft maximum age limits through an exponential distribution in which the 95% upper credibility limit was equal to the maximum age of the stratum where the fossil was excavated. †*Eolates gracilis* is the first fossil assigned to the family Latidae of Lower Eocene age (Ypresian, 48.6–55.8 Ma); we use this fossil to constrain the time to the most recent common ancestor (TMRCA) of the clade *Centropomus* + *Lates* (Otero, 2004). †*Proluvarus necopinatus*, is the first fossil assigned to the family

Luvaridae, from the Lower Eocene (Ypresian, 48.6–55.8 Ma); we use this fossil to constrain the TMRCA of the clade *Prionurus* + *Luvarus* (Bannikov & Tyler, 1995; Klanten *et al.*, 2004). †*Eophryne barbutii* is the first articulated fossil of the family Antennariidae, from the early Eocene or late Ypresian (47.8–53.0 Ma); it is used to calibrate the TMRCA of the clade *Lophius* + *Antennarius* (Carnevale & Pietsch, 2009). †*Archaeotetraodon winterbottomi* is the first tetraodontid fossil known from the Oligocene and its age has been estimated at 32–34 Ma; this fossil is used to calibrate the TMRCA of the clade *Takifugu* + *Tetraodon* (Carnevale & Tyler, 2010). †*Moclaybalistes danekrus* is a stem balistoid from the Palaeocene (at 59 Ma); we use this fossil to calibrate the TMRCA of the clade *Triacanthodes* + *Balistes* (Santini & Tyler, 2003). The oldest *Micropterus* fossil is represented by a damaged articular bone from the Toledo Bend site in Texas, dated to the early Miocene of approximately 23.0 Ma; we use this species to calibrate the TMRCA of the clade *Micropterus* + *Lepomis* (Albright, 1994). The first fossils of Sparidae are known as early as the Palaeocene (i.e. as early as 65.5 Ma) in Europe and North Africa (Orrell *et al.*, 2002); the first fossils of Moronidae are dated to about 50 Ma (Williams *et al.*, 2012). We therefore used a minimum age of 65.5 Ma to calibrate the TMRCA of the clade ((*Morone*, *Dicentrarchus*), *Sparus*).

Following Santini *et al.* (2009), we constrained the minimum age of the crown group Beryciformes (*Beryx* and *Myripristis*) to 99 Ma (Late Cretaceous) by using the oldest crown group beryciform fossils (such as *Hoplopteryx* and *Trachichthyoides*) from the Cenomanian. The maximum age of the root of the tree was constrained to the age of the first acanthomorph otolith fossils (about 125 Ma; i.e. the age of the clade Beryciformes + Acanthomorpha).

Habitat evolution reconstruction

We independently reconstructed the evolution (ancestral condition at each node) of the salinity [i.e. marine, euryhaline (including brackish species) and freshwater] and water temperature preference [i.e. tropical (> 25 °C) and temperate (< 25 °C)] on the BEAST time-calibrated maximum clade credibility tree using the 'Mk1' model, as implemented in MESQUITE 2.72 (Maddison & Maddison, 2009). Salinity and water temperature preferences, along with the distributions of families closely related to the temperate freshwater perches, were compiled from Nelson (2006) and Berra (2007).

Ancestral-range reconstruction

The model-based dispersal–extinction–cladogenesis (DEC) likelihood method of LAGRANGE (Ree *et al.*, 2005; Ree & Smith, 2008) was used to reconstruct ancestral geographical ranges at tree nodes. The effects of different dispersal rates and area combinations in LAGRANGE were explored – all rates of dispersal among areas equal to 1, or marine dispersal among areas impossible (rates of 0), and all area combinations included (i.e. 15 combinations possible), or excluding biologi-

cally irrelevant combinations, such as Australia plus North America (i.e. 10 combinations possible). We selected the default options of the other parameters; in particular, the total number of ancestral areas was not constrained (up to four).

RESULTS

Phylogenetics

Our first data matrix includes a total of 5001 aligned positions for the exon regions of the five nuclear genes in 72 taxa. The second matrix, in which all indel positions were deleted, includes a total of 4386 positions. These two matrices contained 2485 and 2178 variable sites, respectively, and 1996 and 1790 of those sites, respectively, were parsimony informative. Regardless of the matrix and the partition schemes considered, all analyses yielded mostly identical and strongly supported topologies for recovering the previously resolved main percomorph lineages (i.e. clades F, L and Q, etc.) (Fig. 2; see also Appendix S2). The monophyly of a group composed of the Percichthyidae (minus *Macquaria colonorum*), Siniperidae, Ellassomatidae and Centrarchidae is strongly supported (MLBS > 89%). Within this clade (named Percichthyoidea), the last three families form a well-supported monophyletic group (MLBS > 92%); Eurasian Siniperidae are sister to the North American clade of Ellassomatidae + Centrarchidae. The marine *Howella* and *Lateolabrax* (Asian sea-perches), both sometimes recognized as members of the Percichthyidae (Nelson, 2006), were not found to be closely related to the freshwater Australian and South American percichthyids. Instead, *Howella* and *Lateolabrax* form a clade related to other marine perches such as Acropomatidae and Symphysanodontidae (Fig. 2). The phylogenetic position of the brackish Australian percichthyid *Macquaria colonorum* is unexpected, as it is not closely related to the freshwater percichthyids. The South American percichthyid genus *Percilia* is the sister group of a second South American percichthyid genus, *Percichthys*, and both are nested within the Australian percichthyids.

The Percichthyoidea and the Cirrithoidea (Perciformes: Percicoidei) form a monophyletic group (MLBS > 96%) that is then the sister group of a clade including the families Kyphosidae, Oplegnathidae, Teraponidae and Kuhliidae (MLBS > 83%) (Fig. 2).

Divergence times

Our Bayesian molecular time-tree calibrated with a set of seven fossils (Fig. 3) provides an age for the origin of the Percichthyoidea of 61.1 Ma [95% credible interval (CI): 47.0–75.9 Ma]. The age of the split leading to the separation of percichthyoid taxa from their extant sister-group, Cirrithoidea, was estimated at 65.9 Ma (CI: 51.2–81.2 Ma). Within the percichthyoid clade, the respective ages of the crown groups are: Percichthyidae, 45.5 Ma (CI: 30.0–61.5 Ma); Siniperidae, 30.8 Ma (CI: 11.5–50.4 Ma); North American Ellassomatidae + Centrarchidae clade, 42.8 Ma (CI: 31.4–55.7 Ma).

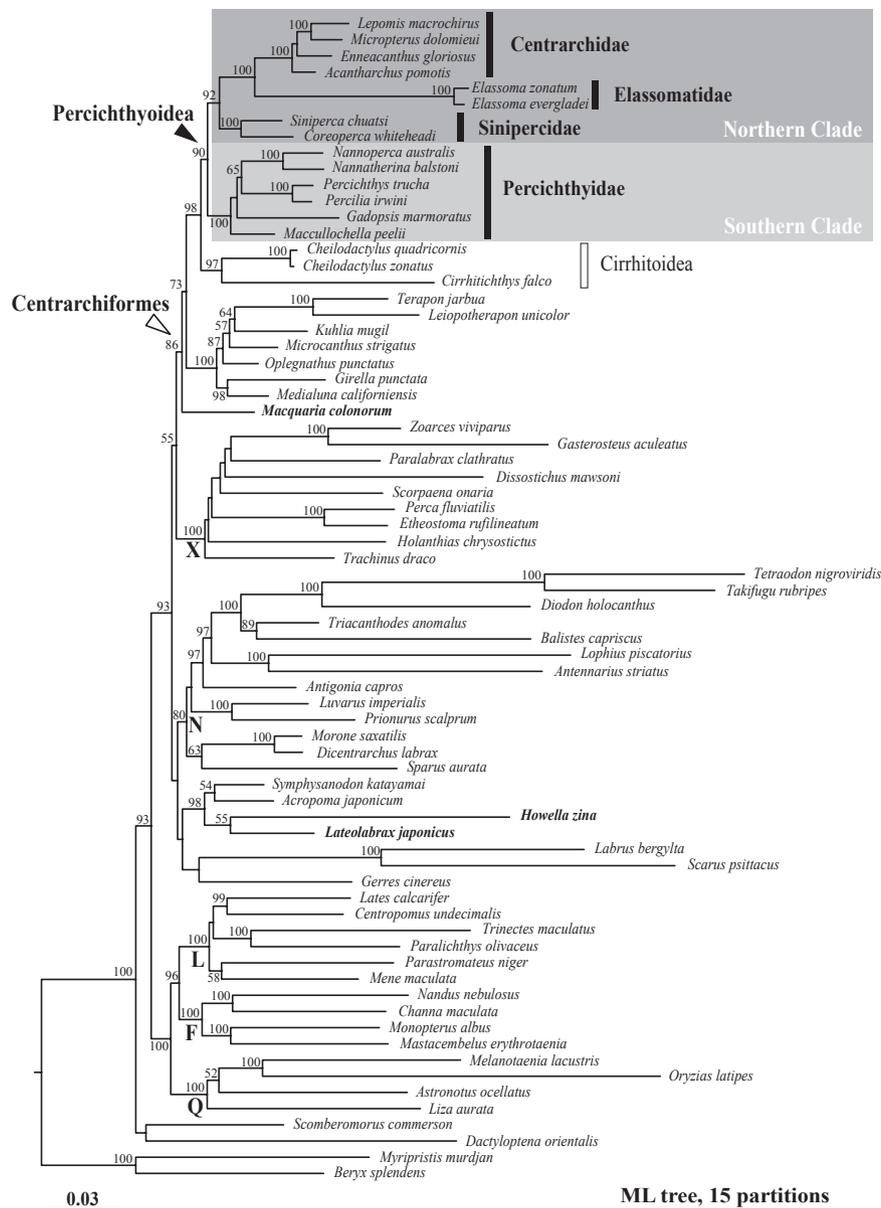


Figure 2 Maximum-likelihood (ML) tree of percomorphs obtained from the partitioned RAxML analysis of the five nuclear gene dataset, matrix '123', which included an assignment of 15 partitions with respect to individual genes and codon positions. Branch lengths are proportional to the number of inferred substitutions. Numbers at nodes are bootstrap proportions (values < 50%, not shown). The tree is rooted with two beryciform taxa. Estuarine and marine 'percichthyids' are highlighted in bold. The main percomorph clades (F, L, N, Q and X) as resolved in previous molecular studies, e.g. Chen *et al.* (2003, 2007) and Dettai & Lecointre (2005), are indicated.

Evolution of salinity and temperature preference

Our reconstructions of habitat and character evolution (Fig. 4a,b) show that the transition from marine to freshwater environments and the transition from tropical to temperate environments were not synchronized within the 'centrarchiform' clade. The marine/freshwater transition probably occurred between the stem origin (divergence with the Cirrhitidae) and crown origin (most recent common ancestor) of the percichthyoid clade, whereas the tropical/temperate transition predated the initial diversification of the 'centrarchiform' clade.

Ancestral areas

Our two ancestral-area reconstruction analyses (differing from each other in the constraints applied to the relative dispersal rates and range possibilities) provide similar hypotheses for the distribution of the most recent ancestor of each of the three clades (Centrarchidae, Elasmomatidae), ((Centrarchidae, Elasmomatidae), Sinipercidae), and ((*Percichthys*, *Percilia*), (*Nannatherina*, *Nannoperca*)) (Fig. 5). However, the results of the analyses suggest two different hypotheses for the ancestral area of the most recent common ancestor of the percichthyoid

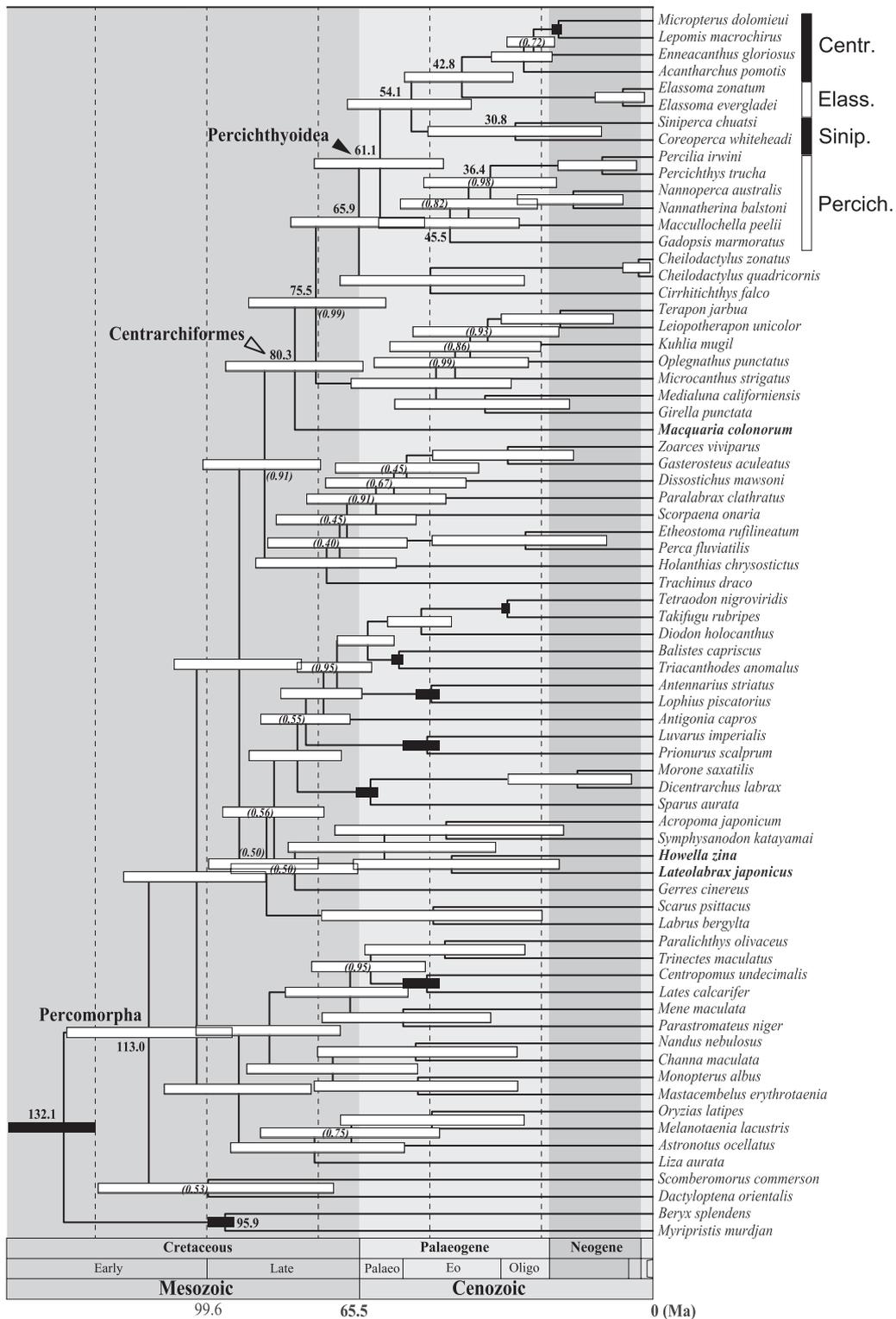


Figure 3 Phylogenetic chronogram of the Teleostei based on a Bayesian relaxed clock approach (using BEAST 1.7.4), using the matrix ‘123 no indel’ partitioned in three, and calibrated with seven fossil-based constraints following exponential distributions (see text for details). The maximum age for the root is constrained to 125 Ma and the minimum age of the crown group (*Beryx splendens* and *Myripristis murdjan*) is constrained to 99 Ma. Horizontal time-scale is in million years before present (Ma). Black horizontal bars indicate calibration constraints on the corresponding nodes; grey horizontal bars at nodes are 95% age credibility intervals. Numbers given in parentheses at nodes are the Bayesian posterior probabilities if below 1. Arrowheads indicate the origins of the ‘Centrarchiformes’ and the origin of the Percichthyoidea. Estuarine and marine ‘percichthyids’ are highlighted in bold. Centr., Centrarchidae; Class., Elasmomatidae; Sinip., Sinipercidae; Perci., Percichthyidae.

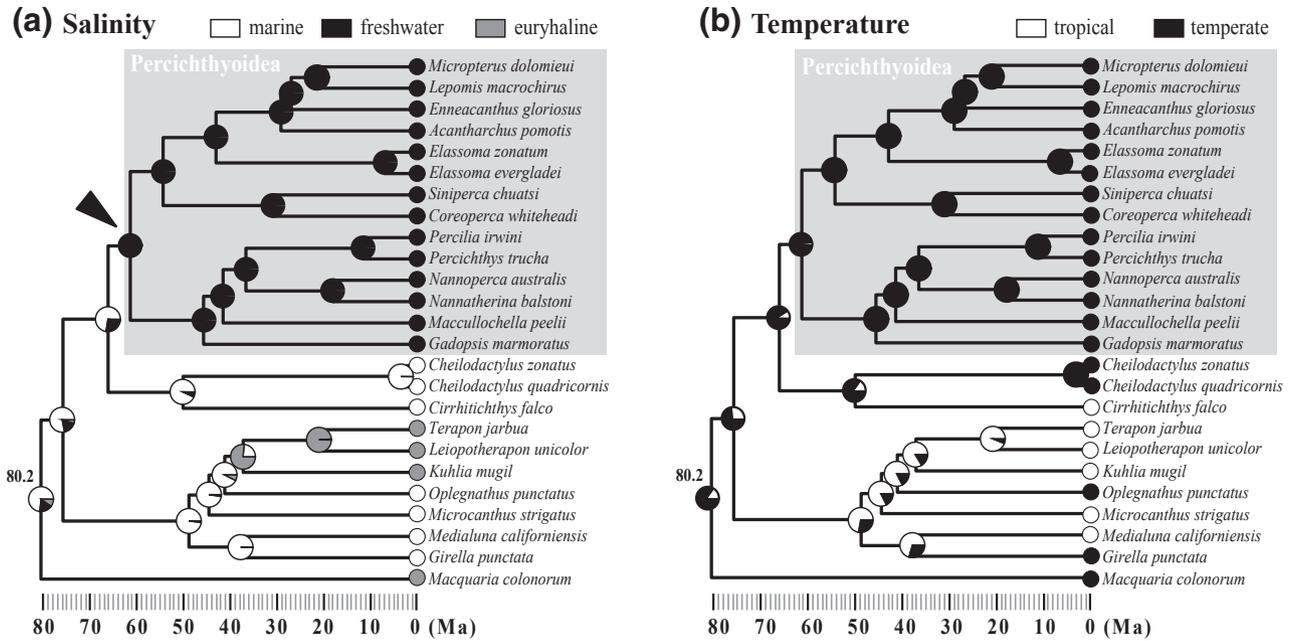


Figure 4 Reconstructions of the evolution of salinity preference (a) and temperature preference (b) within the ‘centrarchiform’ clade, using likelihood optimization on the Bayesian time-tree topology (Fig. 3). In both reconstructions (a, b), the relative probabilities of each state (sum = 1) are drawn using pie charts at each node. Salinity preference: black, freshwater; grey, euryhaline; white, marine. Temperature preference: black, temperate; white, tropical.

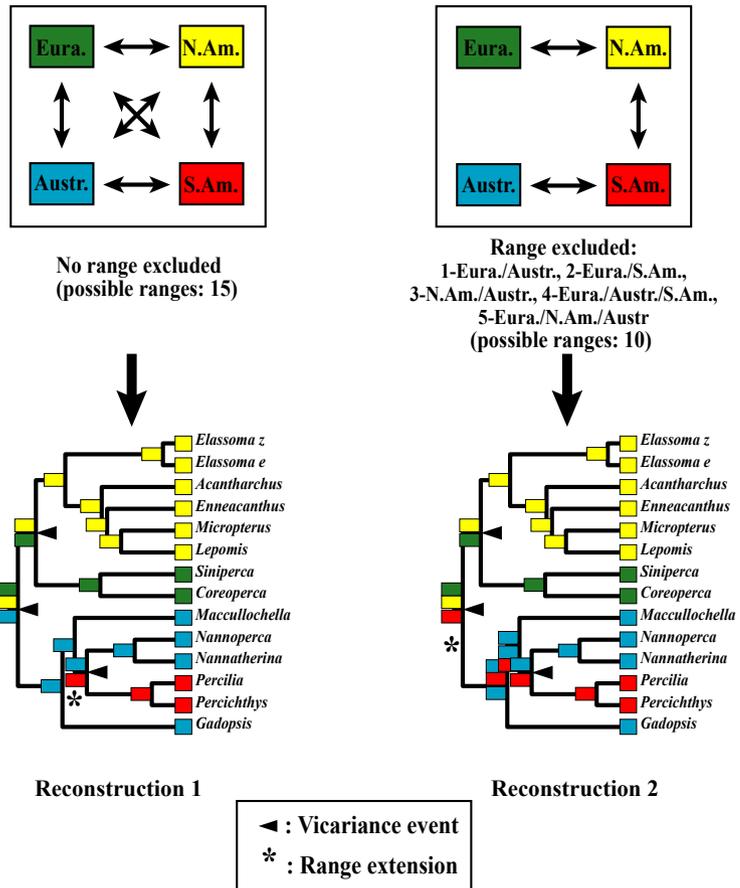


Figure 5 Two ancestral area reconstructions within the temperate freshwater perch-like clade (Percichthyoidea) onto the Bayesian time-tree displayed in Fig. 3, in which all non-percichthyoids have been deleted, using the dispersal–extinction–cladogenesis method as implemented in the software LAGRANGE (Ree *et al.*, 2005). The most likelihood ancestral areas are drawn at each node. Each ancestral-area combination is made up of the ranges of its two descendant (daughter) lineages. For example, in the first reconstruction, the inferred ancestral area of the most recent common ancestor of the Percichthyoidea is made up of Eurasia, North America plus Australia. The four area units are: North America (N.Am., code colour: yellow); Eastern Eurasia (Eura., green); Australia (Austr., blue); South America (S.Am., red). Vicariance events are indicated with black arrowheads; dispersal events are indicated with stars.

group and of the most recent common ancestor of the Percichthyidae. Notwithstanding the inferred salinity preference evolution (see above), we first consider all intercontinental dispersals to be equiprobable, including transoceanic dispersals (reconstruction 1, Fig. 5). In this reconstruction, the inferred ancestral range of the most recent common ancestor of Percichthyoidea covers North America, Eurasia and Australia. This biogeographical area seems unlikely, because no extant or extinct group of freshwater fishes has such a distribution. When some biogeographically implausible ranges (including the previous range) were excluded and we further imposed limits on dispersals, excluding long-distance transoceanic dispersals following our inferences of the evolution of ecological preference (Fig. 4a), the most recent common ancestor of the Percichthyoidea was distributed in South America, North America and Eastern Eurasia (reconstruction 2, Fig. 5). Each of the two reconstructions (1 and 2, Fig. 5) necessitates one dispersal event between South America and Australia to explain the distribution of the Percichthyidae, but with different timings.

DISCUSSION

A new clade of temperate freshwater fishes

An exclusive relationship gathering the Siniperacidae, Elasmomatidae, Centrarchidae and Percichthyidae *sensu* Johnson (1984), minus *Macquaria colonorum*, has never previously been proposed. This clade, named Percichthyoidea, contains only temperate freshwater species and exhibits a unique pattern of distribution among living fishes (Fig. 1). The Percichthyoidea is not closely related to the temperate freshwater perch family Percidae, which belongs to clade X (Fig. 2). Our phylogenetic analyses also corroborate Percichthyoidea as part of the larger clade including Cirrhitidae, Oplegnathidae, Teraponidae, Kuhliidae and Kyphosidae. The content of this clade is similar to the 'centrarchiform' clade hypothesized by Near *et al.* (2012, 2013) (but see Betancur-R. *et al.*, 2013), comprising also the family Enoplosidae, not examined here; the relationships within Percichthyoidea are, however, notably different between these studies.

Using partly overlapping datasets of several nuclear genes, neither Near *et al.* (2012, 2013) nor Betancur-R. *et al.* (2013) recovered a monophyletic Percichthyoidea relative to Cirrhitidae, Cheilodactylidae and Enoplosidae. To assess the reasons for such phylogenetic discordance between our study and these previous studies, we first employed the hypothesis tests for alternative topologies using the likelihood-based approximately unbiased (AU) test (Shimodaira, 2002) based on the most recent and the most complete dataset of Near *et al.* (2013) and on our own dataset. We found that the constrained tree topology in which the monophyly of the Percichthyoidea is enforced is not statistically rejected (AU test, $P = 0.184$) based on the dataset of Near *et al.* (2013), whereas the constrained tree topology of the non-monophyletic Percichthyoidea, *sensu* Near *et al.* (2013), is rejected using our own dataset (AU test, $P = 0.032$). Furthermore, simultaneous

analyses combining our five nuclear genes with 14 nuclear genes of Near *et al.* (2012, 2013) and Betancur-R. *et al.* (2013) for individual gene sequences of the common taxa among the studies produced ML trees in which the Percichthyoidea is monophyletic (see Appendix S3). These results together suggest that the nuclear genes used herein provide sufficient phylogenetic signal to resolve the positions of Percichthyidae and the clade (Siniperacidae, Centrarchidae and Elasmomatidae) relative to Cirrhitidae, Cheilodactylidae and Enoplosidae, and more signal than the markers used by Near *et al.* (2012, 2013) and Betancur-R. *et al.* (2013).

The monophyletic status of each of the families Centrarchidae, Elasmomatidae and Siniperacidae is well documented (Roberts, 1993; Near *et al.*, 2012), whereas the content of the Percichthyidae remains controversial (Johnson, 1984; Arratia, 2003; Eschmeyer, 2013). Johnson (1984) restricted Percichthyidae to only the South American and Australian temperate freshwater/euryhaline perch-like fishes, based on morphological evidence, thereby excluding all other marine and freshwater taxa that were previously added to this family by Gosline (1966). Our molecular study and other studies (Smith & Craig, 2007; Near *et al.*, 2012, 2013; Betancur-R. *et al.*, 2013) confirm that none of the marine and freshwater taxa excluded by Johnson (1984) is closely related to any freshwater/euryhaline percichthyids.

None of Smith & Craig (2007), Near *et al.* (2012, 2013) and Betancur-R. *et al.* (2013), however, found the remaining freshwater/euryhaline Percichthyidae to be monophyletic. Smith & Craig (2007) found *Bostockia porosa* and the brackish-water-adapted *Macquaria novemaculeata* to be only distantly related to the two other Australian percichthyids examined, while Near *et al.* (2012, 2013) and Betancur-R. *et al.* (2013) found *Macquaria novemaculeata* and its sister species *Macquaria colonorum* (both classified in *Percalates* in Johnson, 1984) to be distantly related to other South American and Australian freshwater percichthyids. We also found *Macquaria colonorum* as a separate and distant lineage from the freshwater percichthyids (Fig. 2). The phylogenetic position of the freshwater *Bostockia porosa* warrants further investigation, although Jerry *et al.* (2001) found this species to be related to the genera *Nannoperca* and *Nannatherina*.

Percichthyoidea exhibits a unique pattern of distribution

The geographical distribution of the extant percichthyoid clade is unique among freshwater fishes as it encompasses the four main temperate regions surrounding the Pacific Ocean (excluding New Zealand): south-western and south-eastern Australia, southern South America, eastern Eurasia and North America (Fig. 1). The distribution of this group of fishes combines two general biogeographical patterns: the longitudinal trans-Pacific and latitudinal antitropical patterns. An antitropical distribution is a common pattern in temperate marine (e.g. Cheilodactylidae) (Burrige, 2002) and anadromous fishes (e.g. lampreys, Osmeridae) (Ilves & Taylor, 2009;

Renaud, 2011), but this pattern has not previously been reported for any strictly freshwater fish lineage.

The noteworthy pattern of the percichthyoid clade relates also to its longitudinal distribution across four continents. Unlike antitropicality, such a distribution pattern is rather common in temperate freshwater fishes (Donoghue & Smith, 2004). For example, sturgeons (Acipenseridae), perches (Percidae), salmonids and relatives (Salmonidae), and pikes (Esocidae) all have distributions covering most of North America and Eurasia (Berra, 2007). Paddlefishes (Polyodontidae) and suckers (Catostomidae) are known from North America and only Eastern Eurasia, both from fossils and extant species (Smith, 1992; Choudhury & Dick, 1998). The Galaxiidae (mostly freshwater) occurs in South Africa, South America, Australia and New Zealand (Waters *et al.*, 2000; Nelson, 2006).

Origin of Percichthyoidea: freshwater or marine?

The first proposed biogeographical scenario for the origin of the Percichthyoidea ('freshwater origin') derives from our analyses based on phylogenetics, time estimation, and ancestral habitat and area reconstructions. The phylogenetic analyses support the monophyly of the Percichthyoidea. Our time-estimation analysis provides a relatively robust time-scale for the origin and diversification of the Percichthyoidea at 61.1 Ma (CI: 47.0–75.9 Ma) (Fig. 3). The inferred origin for the percichthyoid fishes considerably post-dates the complete separation of Gondwana and Laurasia (dated to about 140 Ma), the separation of Gondwana into West (Africa and India–Madagascar block) and East (South America, Antarctica–New Zealand and Australia–New Guinea) (dated to around 100 Ma), and the final separation of New Zealand from Antarctica (dated to around 85 Ma) (Smith *et al.*, 1994). The ancestral-habitat reconstruction supports the hypothesis that the most recent common ancestor of the Percichthyoidea was adapted to temperate freshwater environments. The ancestral-range reconstruction (Fig. 5: reconstruction 2) establishes that the area occupied by the most recent common ancestor of percichthyoids included North America, South America and Eurasia.

Based on these analytical findings, the most recent common ancestor of the Percichthyoidea appears to have been a temperate and freshwater taxon, and was distributed in North America, South America and Eastern Eurasia around the Cretaceous–Palaeogene (K/Pg) transition. This is a challenging scenario, because both current geological and palaeoclimatic reconstructions reject the possibility of a pan-American temperate freshwater habitat crossing the equator at that time. Near the K/Pg transition, geological reconstructions show the presence of a proto-Antillean island chain surrounded by shallow seas separating South and North America (reviewed in Hedges, 2006). No primary freshwater fishes – those intolerant to saltwater – are known to have occurred in these islands, and crossing even short marine distances may have proven impossible for restricted freshwater fishes (Sparks & Smith, 2005) (but see below). Interestingly, however, some primary freshwater fishes (e.g. Characiformes and Siluriformes) and some ter-

restrial vertebrates (e.g. lizards, mammals and dinosaurs) crossed this region around that period and expanded their ranges across the two continents (Cifelli & Eaton, 1987; Nydam, 2002; Hedges, 2006; Newbrey *et al.*, 2009; Chen *et al.*, 2013). The proto-Antillean island arc was not a permanent connection, as shown by the marine faunal similarity between the East Pacific and the West Atlantic (Iturralde-Vinent & MacPhee, 1999), but unidentified episodic island chains between South and North America may explain these biotic exchanges. Such island chain connections have not yet been documented from geological data (White, 1986; Newbrey *et al.*, 2009).

The second difficulty we face in this explanation for the distribution of the ancestor of the Percichthyoidea is that around the K/Pg transition, the global climate, although cooler than during most of the preceding Cretaceous period, may still have been too warm to support a temperate corridor connecting both hemispheres (Scotese *et al.*, 1999). Palaeoclimatology also shows, however, that climatic conditions were unstable during that period, with some episodes of climate change (Jenkyns, 2003). Biogeography echoes these climatic data, as it shows that, despite an overall warm climate around the K/Pg transition, transequatorial (marine) dispersals of temperate organisms were possible (White, 1986; Burrige, 2002; Waters *et al.*, 2002).

The second scenario for the origin of the Percichthyoidea is more in line with the prevailing geological context at the end of the Cretaceous, but is less compatible with our analytical results. In this marine-origin scenario, the ancestor of the Percichthyoidea was not completely adapted to the freshwater environment. According to this hypothesis, there is no need for a strictly freshwater route between South and North America, and the distribution of the ancestor of the Percichthyoidea would have encompassed the coastal marine areas of South and North America and the region in between. This scenario requires two late complete transitions from marine to freshwater environments in South and North America, along with the extinction of related marine lineages. It is tempting to link these transition events with the late restrictions of epicontinental seas in North and South America (Haq *et al.*, 1987; Harries, 2009) and the extinction events with the increase of sea temperature observed during the Palaeocene and culminating during the Eocene (Zachos *et al.*, 2003; Friedman, 2010). Alternatively, a putative diadromous ancestor may have founded the antitropical groups, followed by the loss of the marine phase of its life history. The loss of marine phases in diadromous taxa is commonly observed across short time-scales [e.g. galaxiid fishes becoming non-diadromous in lakes with histories of < 1 Myr old (Waters & Wallis, 2001); see also salmonids (Taylor *et al.*, 1996), stickleback (Ortí *et al.*, 1994), etc.]. Thus, such a process could have occurred many times over the several million years of history of the Percichthyoidea.

Biogeography of the northern clade

Regardless of the ecological requirements of the ancestral Percichthyoidea, the most recent common ancestor of the

clade (Sinipercidae, (Centrarchidae, Elasmomatidae)) was probably temperate and freshwater, and occurred in Eurasia and North America during the Palaeocene (54.1 Ma; Fig. 5). At that time, a vicariance event separated the Eurasian Sinipercidae lineage from the North American Centrarchidae + Elasmomatidae lineage. The distribution pattern of the clade (Sinipercidae, (Centrarchidae, Elasmomatidae)), covering Eastern Eurasia and North America, has been frequently observed in other groups of freshwater organisms [e.g. paddlefish, catostomids, cyprinid genera *Phoxinus* (Eurasia) and *Chrosomus* (North America)]. During most of the Palaeocene, eastern Asia and western North America formed a continuous landmass called Beringia, and considerable evidence exists for biotic interchanges across this landmass from the end of the Cretaceous to the Palaeogene (Sanmartín *et al.*, 2001; Lundberg *et al.*, 2007; Krassilov *et al.*, 2010; Oaks, 2011). Our results indicate that the submergence of the Beringia Bridge at the end of the Palaeocene period may have promoted the allopatric differentiation of the Sinipercidae and the clade Elasmomatidae + Centrarchidae.

Biogeography of the southern clade

Regarding the southern clade, the Percichthyidae appears to have first experienced a range expansion from South America to Australia between 61 and 45 Ma, at a time where South America and Australia were probably widely connected via Antarctica (Smith *et al.*, 1994). Diversification events in Australia during the Eocene preceded a vicariance event separating the South American percichthyids (*Percichthys* and *Percilia*) from their Australian sister clade (*Nannoperca* and *Nannatherina*), near the end of Eocene, at about 36 Ma (CI: 21.6–51.4 Ma) (Fig. 3). We cannot reject the hypothesis that the later event was mediated by the complete split of the austral landmass, isolating Antarctica from other continents, that occurred 55–34 Ma (Smith *et al.*, 1994; Lawver & Gahagan, 2003).

The fossil record of Percichthyidae supports the hypothesis that some members of the family were present in South America as early as the Palaeocene. The two oldest percichthyid fossils include †*Percichthys lonquimayi* and †*Percichthys sandovali* from the Upper Palaeocene (Thanetian, 55.8–58.7 Ma) (Arratia, 1982), but the classification of these two Palaeocene fossils in the genus *Percichthys* is incongruent with our more recent molecular-based age estimate of extant *Percichthys*. Their phylogenetic positions in relation to the extant percichthyids warrant further investigation and the result should provide significant evidence for the early evolution of the Percichthyidae. The Australian percichthyid fossils are much younger, known from the mid-Eocene, with †*Macquaria antiquus*, which may be closely related to catadromous *Macquaria* spp., and from the early Miocene, with †*Maccullochella 'macquariensis'* (see review in Unmack, 2001). Of potential interest is the discovery of two fossil scales in New Zealand fresh waters (Central Otago) of Miocene age (about 20 Ma), assigned to the family Percichthyidae (McDowall & Lee, 2005). Because New Zealand separated from Gondwana more than

80 Ma and the freshwater Percichthyidae is younger than 61 Myr, the presence of these two scales may be indicative of marine dispersal capacity in Percichthyidae and this would therefore challenge a strictly freshwater scenario. The evolutionary affinity of these New Zealand fossil taxa is, however, rather elusive (McDowall & Lee, 2005), and they may be related to the catadromous *Macquaria* spp. lineage. McDowall (2010, p. 334) concluded his chapter on the biogeography of New Zealand freshwater fishes by stating that '... the place of this putative New Zealand percichthyid is unlikely to ever be resolved with any clarity unless much more and better fossil material is discovered'.

CONCLUSIONS

We report a new clade of temperate freshwater perch-like fishes, comprising Percichthyidae, Sinipercidae, Centrarchidae and Elasmomatidae. This clade, Percichthyoidea, has a unique geographical distribution, combining most of the temperate areas surrounding the Pacific Ocean. To explain its antitropical distribution, it is necessary to postulate either the existence of a past pan-American equatorial freshwater and temperate environment never before hypothesized or, alternatively, the existence of a 'marine' temperate ancestor and two independent late marine-to-freshwater transitions, in North America and South America.

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REFERENCES

- Albright, L.B. (1994) Lower vertebrates from an Arikarean (earliest Miocene) fauna near the Toledo Bend Dam, Newton County, Texas. *Journal of Paleontology*, **68**, 1131–1145.
- Arratia, G. (1982) A review of the freshwater percoids from South America (Pisces, Osteichthyes, Perciformes, Percichthyidae and Perciliidae). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **540**, 1–52.

- Arratia, G. (2003) Family Percichthyidae (temperate basses). *Check list of the freshwater fishes of South and Central America* (ed. by R.E. Reis, S.O. Kullander and C.J. Ferraris), pp. 596–597. EdiPUCRS, Porto Alegre.
- Azuma, Y., Kumazawa, Y., Miya, M., Mabuchi, K. & Nishida, M. (2008) Mitogenomic evaluation of the historical biogeography of cichlids toward reliable dating of teleostean divergences. *BMC Evolutionary Biology*, **8**, 215.
- Bannikov, A.F. & Tyler, J.C. (1995) Phylogenetic revision of the fish families Luvaridae and Kushlukiidae (Acanthuroidei), with a new genus and two new species of Eocene luvarids. *Smithsonian Contributions to Paleobiology*, **81**, 1–45.
- Berra, T.M. (2007) *Freshwater fish distribution*. Academic Press, San Diego, CA.
- Betancur-R., R., Broughton, R.E., Wiley, E.O. *et al.* (2013) The tree of life and a new classification of bony fishes. *PLoS Currents: Tree of Life* (18 April 2013, edn 1). doi:10.1371/currents.tol.53ba26640df0ccea75bb165c8c26288.
- Briggs, J.C. (1979) Ostariophysan zoogeography: an alternative hypothesis. *Copeia*, **1979**, 111–118.
- Burridge, C.P. (2002) Antitropicality of Pacific fishes: molecular insights. *Environmental Biology of Fishes*, **65**, 151–164.
- Carnevale, G. & Pietsch, T.W. (2009) An Eocene frogfish from Monte Bolca, Italy: the earliest known skeletal record for the family. *Palaeontology*, **52**, 745–752.
- Carnevale, G. & Tyler, J.C. (2010) Review of the fossil pufferfish genus *Archaeotetraodon* (Teleostei, Tetraodontidae), with description of three new taxa from the Miocene of Italy. *Geobios*, **43**, 283–304.
- Chen, W.-J. & Mayden, R.L. (2010) A phylogenomic perspective on the new era of ichthyology. *BioScience*, **60**, 421–432.
- Chen, W.-J., Bonillo, C. & Lecointre, G. (2003) Repeatability of clades as criterion of reliability: a case study for molecular phylogeny of Acanthomorpha (Teleostei) with larger number of taxa. *Molecular Phylogenetics and Evolution*, **26**, 262–288.
- Chen, W.-J., Ruiz-Carus, R. & Ortí, G. (2007) Relationships among four genera of mojarras (Teleostei: Perciformes: Gerreidae) from the western Atlantic and their tentative placement among percomorph fishes. *Journal of Fish Biology*, **70** (Supplement sb), 202–218.
- Chen, W.-J., Miya, M., Saitoh, K. & Mayden, R.L. (2008) Phylogenetic utility of two existing and four novel nuclear gene loci in reconstructing Tree of Life of ray-finned fishes: the order Cypriniformes (Ostariophysi) as a case study. *Gene*, **423**, 125–134.
- Chen, W.-J., Lavoué, S. & Mayden, R.L. (2013) Evolutionary origin and early biogeography of otophysan fishes (Ostariophysi: Teleostei). *Evolution*, **67**, 2218–2239.
- Choudhury, A. & Dick, T.A. (1998) The historical biogeography of sturgeons (Osteichthyes: Acipenseridae): a synthesis of phylogenetics, palaeontology and palaeogeography. *Journal of Biogeography*, **25**, 623–640.
- Cifelli, R.L. & Eaton, J.G. (1987) Marsupial from the earliest Late Cretaceous of Western US. *Nature*, **325**, 520–522.
- Detta, A. & Lecointre, G. (2005) Further support for the clades obtained by multiple molecular phylogenies in the acanthomorph bush. *Comptes Rendus Biologies*, **328**, 674–689.
- Donoghue, M.J. & Smith, S.A. (2004) Patterns in the assembly of temperate forests around the Northern Hemisphere. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 1633–1644.
- Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, **29**, 1969–1973.
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, **32**, 1792–1797.
- Eschmeyer, W.N. (2013) *Catalog of fishes*. California Academy of Sciences, San Francisco, CA. Available at: <http://research.calacademy.org/ichthyology/catalog/fishcatmain.asp> (accessed 15 October 2013).
- Eschmeyer, W.N. & Fong, J.D. (2011) Pisces. *Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness* (ed. by Z.-Q. Zhang), pp. 26–38. Zootaxa 3148. Magnolia Press, Auckland, New Zealand.
- Friedman, M. (2010) Explosive morphological diversification of spiny-finned teleosts in the aftermath of the end-Cretaceous extinction. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1675–1683.
- Gosline, W.A. (1966) The limits of the fish family Serranidae, with notes on other lower percoids. *Proceedings of the California Academy of Sciences*, **33**, 91–111.
- Grande, L. & Bemis, W.E. (1991) Osteology and phylogenetic relationships of fossil and recent paddlefishes (Polyodontidae), with comments on the interrelationships of Acipenseriformes. *Journal of Vertebrate Paleontology*, **11**, 1–121.
- Haq, B.U., Hardenbol, J. & Vail, P.R. (1987) Chronology of fluctuating sea levels since the Triassic. *Science*, **235**, 1156–1167.
- Harries, P.J. (2009) Epeiric seas: a continental extension of shelf biotas. *Earth system: history and natural variability*, Vol. IV (ed. by V. Cilek and R.H. Smith), pp. 138–155. EOLSS Publishers, Oxford, UK.
- Hedges, S.B. (2006) Paleogeography of the Antilles and origin of West Indian terrestrial vertebrates. *Annals of the Missouri Botanical Garden*, **93**, 231–244.
- Ilves, K.L. & Taylor, E.B. (2009) Molecular resolution of the systematics of a problematic group of fishes (Teleostei: Osmeridae) and evidence for morphological homoplasy. *Molecular Phylogenetics and Evolution*, **50**, 163–178.
- Iturralde-Vinent, M.A. & MacPhee, R.D.E. (1999) Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, **238**, 1–95.
- Jenkyns, H.C. (2003) Evidence for rapid climate change in the Mesozoic–Palaeogene greenhouse world. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **361**, 1885–1916.
- Jerry, D.R., Elphinstone, M.S. & Baverstock, P.R. (2001) Phylogenetic relationships of Australian members of the family Percichthyidae inferred from mitochondrial 12S rRNA

- sequence data. *Molecular Phylogenetics and Evolution*, **18**, 335–347.
- Johnson, G.D. (1984) Percoidei: development and relationships. *Ontogeny and systematics of fishes* (ed. by H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall and S.L. Richardson), pp. 464–498. American Society of Ichthyologists and Herpetologists, Gainesville, FL.
- Johnson, G.D. & Patterson, C. (1993) Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bulletin of Marine Science*, **52**, 554–626.
- Klanten, S.O., van Herwerden, L., Choat, J.H. & Blair, D. (2004) Patterns of lineage diversification in the genus *Naso* (Acanthuridae). *Molecular Phylogenetics and Evolution*, **32**, 221–235.
- Krassilov, V.A., Kodrul, T.M. & Maslova, N.P. (2010) Plant systematics and differentiation of species over trans-Berian land connections including a newly recognized cupressaceous conifer *Ditaxocladus* Guo & Sun. *Bulletin of Geosciences*, **85**, 95–110.
- Lawver, L.A. & Gahagan, L.M. (2003) Evolution of Cenozoic seaways in the circum-Antarctic region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **198**, 11–37.
- Lemmon, A.R., Brown, J.M., Stanger-Hall, K. & Lemmon, E.M. (2009) The effect of ambiguous data on phylogenetic estimates obtained by maximum likelihood and Bayesian inference. *Systematic Biology*, **58**, 130–145.
- Li, B., Dettai, A., Cruaud, C., Couloux, A., Desoutter-Meniger, M. & Lecointre, G. (2009) Rnf213, a new nuclear marker for acanthomorph phylogeny. *Molecular Phylogenetics and Evolution*, **50**, 345–363.
- Lundberg, J.G. (1993) African–South American freshwater fish clades and continental drift: problems with a paradigm. *Biological relationships between Africa and South America* (ed. by P. Goldblatt), pp. 156–199. Yale University Press, New Haven, CT.
- Lundberg, J.G., Sullivan, J.P., Rodiles-Hernández, R. & Hendrickson, D.A. (2007) Discovery of African roots for the Mesamerican Chiapas catfish, *Lacantunia enigmatica*, requires an ancient intercontinental passage. *Proceedings of The Academy of Natural Sciences of Philadelphia*, **156**, 39–53.
- Maddison, W.P. & Maddison, D.R. (2009) *Mesquite: a modular system for evolutionary analysis*. Version 2.72. Available at: <http://mesquiteproject.org/>.
- McDowall, R.M. (2010) A biogeographical synthesis: 1. The big picture. *New Zealand freshwater fishes: an historical and ecological biogeography*, pp. 329–337. Springer, Dordrecht.
- McDowall, R.M. & Lee, D.E. (2005) Probable perciform scales from a Miocene freshwater lake deposit, Central Otago, New Zealand. *Journal of the Royal Society of New Zealand*, **34**, 338–344.
- Miya, M., Takeshima, H., Endo, H., Ishiguro, N.B., Inoue, J.G., Mukai, T., Satoh, T.P., Yamaguchi, M., Kawaguchi, A., Mabuchi, K., Shirai, S.M. & Nishida, M. (2003) Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **26**, 121–138.
- Murray, A.M. (2001) The fossil record and biogeography of the Cichlidae (Actinopterygii: Labroidei). *Biological Journal of the Linnean Society*, **74**, 517–532.
- Near, T.J., Sandel, M., Kuhn, K.L., Unmack, P.J., Wainwright, P.C. & Smith, W.L. (2012) Nuclear gene-inferred phylogenies resolve the relationships of the enigmatic Pygmy Sunfishes, *Elassoma* (Teleostei: Percomorpha). *Molecular Phylogenetics and Evolution*, **63**, 388–395.
- Near, T.J., Dornburg, A., Eytan, R.I., Keck, B.P., Smith, W.L., Kuhn, K.L., Moore, J.A., Price, S.A., Burbrink, F.T., Friedman, M. & Wainwright, P.C. (2013) Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. *Proceedings of National Academy of Sciences USA*, **110**, 12738–12743.
- Nelson, J.S. (2006) *Fishes of the world*, 4th edn. John Wiley & Sons, Hoboken, NJ.
- Newbrey, M.G., Murray, A.M., Wilson, M.V.H., Brinkman, D.B. & Neuman, A.G. (2009) Seventy-five-million-year-old tropical tetra-like fish from Canada tracks Cretaceous global warming. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3829–3833.
- Nydam, R.L. (2002) Lizards of the Mussentuchit local fauna (Albian–Cenomanian boundary) and comments on the evolution of the Cretaceous lizard fauna of North America. *Journal of Vertebrate Paleontology*, **22**, 645–660.
- Oaks, J.R. (2011) A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles. *Evolution*, **65**, 3285–3297.
- Orrell, T.M., Carpenter, K.E., Musick, J.A. & Graves, J.E. (2002) Phylogenetic and biogeographic analysis of the Sparidae (Perciformes: Percoidei) from cytochrome *b* sequences. *Copeia*, **2002**, 618–631.
- Ortí, G., Bell, M.A., Reimchen, T.E. & Meyer, A. (1994) Global survey of mitochondrial DNA sequences in the three-spine stickleback: evidence for recent migrations. *Evolution*, **48**, 608–622.
- Otero, O. (2004) Anatomy, systematics and phylogeny of both Recent and fossil latid fishes (Teleostei, Perciformes, Latidae). *Zoological Journal of the Linnean Society*, **141**, 81–133.
- Ree, R.H. & Smith, S.A. (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, **57**, 4–14.
- Ree, R.H., Moore, B.R., Webb, C.O. & Donoghue, M.J. (2005) A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution*, **59**, 2299–2311.
- Renaud, C.B. (2011) *Lampreys of the world: an annotated and illustrated catalogue of lamprey species known to date*. FAO Species Catalogue for Fishery Purposes 5. Food and Agriculture Organization, Rome, Italy.
- Roberts, C.D. (1993) Comparative morphology of spined scales and their phylogenetic significance in the Teleostei. *Bulletin of Marine Science*, **52**, 60–113.
- Rosen, D.E. (1982) Teleostean interrelationships, morphological function and evolutionary inference. *American Zoologist*, **22**, 261–273.

- Sanmartín, I., Enghoff, H. & Ronquist, F. (2001) Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society*, **73**, 345–390.
- Santini, F. & Tyler, J.C. (2003) A phylogeny of the families of fossil and extant tetraodontiform fishes (Acanthomorpha, Tetraodontiformes), Upper Cretaceous to Recent. *Zoological Journal of the Linnean Society*, **139**, 565–617.
- Santini, F., Harmon, L.J., Carnevale, G. & Alfaro, M.E. (2009) Did genome duplication drive the origin of teleosts? A comparative study of diversification in ray-finned fishes. *BMC Evolutionary Biology*, **9**, e194.
- Scotese, C.R., Boucot, A.J. & McKerrow, W.S. (1999) Gondwanan palaeogeography and palaeoclimatology. *Journal of African Earth Sciences*, **28**, 99–114.
- Shimodaira, H. (2002) An approximately unbiased test of phylogenetic tree selection. *Systematic Biology*, **51**, 492–508.
- Silvestro, D. & Michalak, I. (2012) raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity and Evolution*, **12**, 335–337.
- Smith, G.R. (1992) Phylogeny and biogeography of the Catostomidae, freshwater fishes of North America and Asia. *Systematics, historical ecology and North American freshwater fishes* (ed. by R.L. Mayden), pp. 778–813. Stanford University Press, Stanford, CA.
- Smith, W.L. & Craig, T. (2007) Casting the percomorph net widely: the importance of broad taxonomic sampling in the search for the placement of serranid and percid fishes. *Copeia*, **2007**, 35–55.
- Smith, A.G., Smith, D.G. & Funnell, M. (1994) *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge University Press, Cambridge, UK.
- Sparks, J.S. & Smith, W.L. (2005) Freshwater fishes, dispersal ability, and nonevidence: “Gondwana life rafts” to the rescue. *Systematic Biology*, **54**, 158–165.
- Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**, 2688–2690.
- Taylor, E.B., Foote, C.J. & Wood, C.C. (1996) Molecular genetic evidence for parallel life-history evolution within a Pacific salmon (sockeye salmon and kokanee, *Oncorhynchus nerka*). *Evolution*, **50**, 401–416.
- Unmack, P.J. (2001) Biogeography of Australian freshwater fishes. *Journal of Biogeography*, **28**, 1053–1089.
- Wainwright, P.C., Smith, W.L., Price, S.A., Tang, K.L., Sparks, J.S., Ferry, L.A., Kuhn, K.L., Eytan, R.I. & Near, T.J. (2012) The evolution of pharyngognath: a phylogenetic and functional appraisal of the pharyngeal jaw key innovation in labroid fishes and beyond. *Systematic Biology*, **61**, 1001–1027.
- Waters, J.M. & Burrige, C.P. (1999) Extreme intraspecific mitochondrial DNA sequence divergence in *Galaxias maculatus* (Osteichthys: Galaxiidae), one of the world’s most widespread freshwater fish. *Molecular Phylogenetics and Evolution*, **11**, 1–12.
- Waters, J.M. & Wallis, G.P. (2001) Cladogenesis and loss of the marine life-history phase in freshwater galaxiid fishes (Osmeriformes: Galaxiidae). *Evolution*, **55**, 587–597.
- Waters, J.M., Dijkstra, L.H. & Wallis, G.P. (2000) Biogeography of a southern hemisphere freshwater fishes: how important is marine dispersal? *Molecular Ecology*, **9**, 1816–1821.
- Waters, J.M., Saruwatari, T., Kobayashi, T., Oohara, I., McDowall, R.M. & Wallis, G.P. (2002) Phylogenetic placement of retropinnid fishes: data set incongruence can be reduced by using asymmetric character state transformation costs. *Systematic Biology*, **51**, 432–449.
- White, B.N. (1986) The isthmian link, antitropicality and American biogeography: distributional history of the Atherinopsinae (Pisces: Atherinidae). *Systematic Zoology*, **35**, 176–194.
- Wiens, J.J. & Morrill, M.C. (2011) Missing data in phylogenetic analysis: reconciling results from simulations and empirical data. *Systematic Biology*, **60**, 719–731.
- Williams, E.P., Peer, A.C., Miller, T.J., Secor, D.H. & Place, A.R. (2012) A phylogeny of the temperate seabasses (Moronidae) characterized by a translocation of the mt-*nd6* gene. *Journal of Fish Biology*, **80**, 110–130.
- Zachos, J.C., Wara, M.W., Bohaty, S., Delaney, M.L., Petrizzo, M.R., Brill, A., Bralower, T.J. & Premoli-Silva, I. (2003) A transient rise in tropical sea surface temperature during the Paleocene-Eocene Thermal Maximum. *Science*, **302**, 1551–1554.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Taxa, genes and GenBank accession numbers for nuclear gene sequences of representative species, and a list of primers used in the study.

Appendix S2 Highlights from maximum likelihood trees of percomorphs obtained from the alternative analyses (see Materials and Methods) depicting the evolutionary relationships of ‘centrarchiform’ fishes.

Appendix S3 Simultaneous analysis in combining 19 nuclear genes; 15,060 characters and 22 taxa resulting in maximum-likelihood trees, well matched with the monophyly of the Percichthyoidea.

BIOSKETCH

Wei-Jen Chen is an associate professor at the Institute of Oceanography, National Taiwan University, and is interested in marine biology and evolutionary biology. The focus of the research team is on biodiversity, biogeography, integrated genomics, natural history, and mechanisms of evolution of ray-finned fishes.

Author contributions: W.-J.C. led the project and conducted the sample and data collection; W.-J.C. and S.L. conceived the ideas, analysed the data, and wrote the paper; L.B.B. and R.L.M. provided samples and contributed to the writing.

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