



Research paper

The potential colonization histories of *Opsariichthys bidens* (Cyprinidae) in China using Bayesian binary MCMC analysis



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ABSTRACT

Vicariance and/or long-distance dispersal shape the distribution patterns of many extant taxa, and orogenesis and/or climate fluctuations are key factors that drive the events of vicariance and/or dispersal. In this study, we yielded biogeographical inferences from Bayesian binary MCMC (BBM) analysis to explore the potential colonization histories of *Opsariichthys bidens* in China and to identify potential factors responsible for the colonization histories. Many vicariance and dispersal events were identified. The results suggested that *O. bidens* seemed to have originated from the Yangtze River and/or the Pearl River and experienced a Yangtze River–Pearl River split at 7.04 million years ago (Ma). BBM analysis revealed that the Pearl River populations had undergone expansions to the Hainan drainages, the Lancangjiang River (upper Mekong) and the Nanpanjiang River (upper branch of the Pearl River) at 0.74 Ma. Meanwhile, the Yangtze River populations expanded to the northeastern drainages during the Early Pleistocene. Subsequently, the northeastern drainages dispersed to the Yellow River during the Middle Pleistocene. More recently, the northeastern drainage populations also dispersed to the Huaihe River and back to the Yangtze River. A portion of the Pearl River populations originated from the Yangtze River dispersed to the Jiulongjiang River during the Middle Pleistocene. These time scales fit well with the uplift of the Qinghai-Tibet Plateau and Pleistocene glacial cycles, indicating the two factors played vital roles in shaping the colonization histories of *O. bidens*.

1. Introduction

Reconstructing the ancestral ranges of a monophyletic clade or a species, called the ancestral area, is an important goal of historical biogeography (Brown and Lomolino, 1998). Phylogenetically based historical biogeographical reconstructions have been used to probe the evolutionary history of organisms in space and time during last two decades. To date, improvements in many model- and event-based approaches, e.g., the dispersal-extinction cladogenesis (DEC) model (Ree et al., 2005; Ree and Smith, 2008), the Bayesian island biogeography (BIB) method (Sanmartin et al., 2008; Sanmartin et al., 2010) and the event-based method dispersal vicariance analysis (DIVA; Ronquist, 1997), facilitate the biogeographical inferences of particular taxa. Bayesian binary MCMC (BBM) can obtain ancestral ranges at each node and calculate probabilities of each ancestral range at nodes, which has

been widely used in biogeographical reconstructions (Ali et al., 2012; Parada et al., 2013; Bourguignon et al., 2017).

Cyprinids are a major component of the primary freshwater ichthyofauna in East Asia (Bănărescu and Coad, 1991). In China, cyprinids occur in almost all freshwater habitats, which makes them of particular interest for biogeographical inferences. *Opsariichthys bidens*, one of the most widespread cyprinid species in East Asia, has a wide distribution in the rivers in China, the Korean Peninsula and Vietnam (Chen, 1998). Several DNA-based analyses have been employed to examine the genetic diversity and phylogeographic structure of *O. bidens* populations in China's rivers (Perdices et al., 2005; Berrebi et al., 2006; Li et al., 2009), and the results consistently suggested that *O. bidens* populations had likely undergone deep genetic split and might harbor more than one species. However, we know little about where *O. bidens* originated and how they migrated into their current distributions. The factors

Abbreviations: BBM, Bayesian binary MCMC; QTP, Qinghai-Tibet Plateau; cytb, mitochondrial cytochrome *b* gene; HD, Hainan drainages; PR, Pearl River; LR, Lancangjiang River; JL, Jiulongjiang River; YTR, Yangtze River; YR, Yellow River; HR, Huaihe River; ND, Northeastern drainage system includes Heilongjiang River, Haihe River, Liaohe River, Tumen River and Yalujiang River; HH, Haihe River; LH, Liaohe River; YLJ, Yalujiang River; TM, Tumen River; HLJ, Heilongjiang River; RASP, Reconstruct Ancestral State in Phylogenies

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driving these colonization events also remain unclear.

Orogenesis and/or climate fluctuations have exert remarkable influences on the genetic patterns of many fish species in East Asia (Xiao et al., 2001; Li et al., 2012; Yu et al., 2014; Ma et al., 2015; Yang et al., 2016). The most famous orogenic event is the periodic uplift of the Qinghai-Tibet Plateau (QTP). The uplift of the QTP created novel drainages and altered drainage structure patterns in East Asia (Clark et al., 2004), which may have facilitated divergence and colonization patterns of fish populations. Cyclic climate changes during the Quaternary Period also influenced species distributions and their genetic patterns (Hewitt, 2000; Hewitt, 2004) and often occurred in China (Huang, 1982). The distributions of fish populations would be contracted during the glacial periods and be expansion after the glaciation retreat.

Herein, we used samples from the majority of drainage systems in China to infer the colonization histories of *O. bidens* populations via Bayesian binary MCMC (BBM) analysis. The aims of this study are to explore the colonization histories of *O. bidens* populations and to explain what factors are responsible for the colonization histories.

2. Materials and methods

2.1. Data collection

The materials in this study include the mitochondrial cytochrome *b* gene (cytb) sequences of *O. bidens* from previous papers (Perdices et al., 2005; Li et al., 2009) and associated sampling locality information from the Genbank database. Two hundred and forty-five sequences (243 ingroups and 2 outgroups) (Table S1) were analyzed. The ingroup sequences covered almost all major rivers of China. Outgroups of *Candidia*

barbatus (AY958200) and *Parazacco spilurus fasciatus* (AY958195) used in Li et al. (2009) were chosen as outgroups in our study.

2.2. Dating the tree

MUSCLE (Edgar, 2004) was used for DNA sequence alignment with default settings. The best-fit nucleotide substitution models (GTR + I + G) were selected using the Akaike information criterion in MRMODELTEST 2.3 (Nylander, 2004). To estimate the divergence time of *O. bidens* lineages, we used a coalescent time estimation method in BEAST 1.6.1 (Drummond and Rambaut, 2007). The divergence times were estimated using a Yule speciation tree prior under the strict-clock model due to the lack of a fossil record. The molecular clock of cyprinids of 1.52% per site per million years for cytb was used to calculate the divergence times (Doadrio et al., 2002). One hundred million generations of the MCMC chains were run, with sampling every 1000 generations. The effective sample sizes (ESSs > 200) were used for determining the Bayesian statistical significance of each parameter in TRACER 1.5 (Rambaut and Drummond, 2007). The sampled trees were annotated in TreeAnnotator 1.6.1 (BEAST software) and the first 50% of sampled trees were treated as burn-in with the posterior probability limit set to 0.5. Finally, the posterior probability and divergence times were visualized in Figtree 1.3.1 (<http://tree.bio.ed.ac.uk/software/figtree>).

2.3. Ancestral distribution analysis

The distribution range of *O. bidens* populations was divided into the following eight drainage groups: Hainan drainages (HD), Pearl River (PR), Lancangjiang River (LR), Jiulongjiang River in Fujian Province

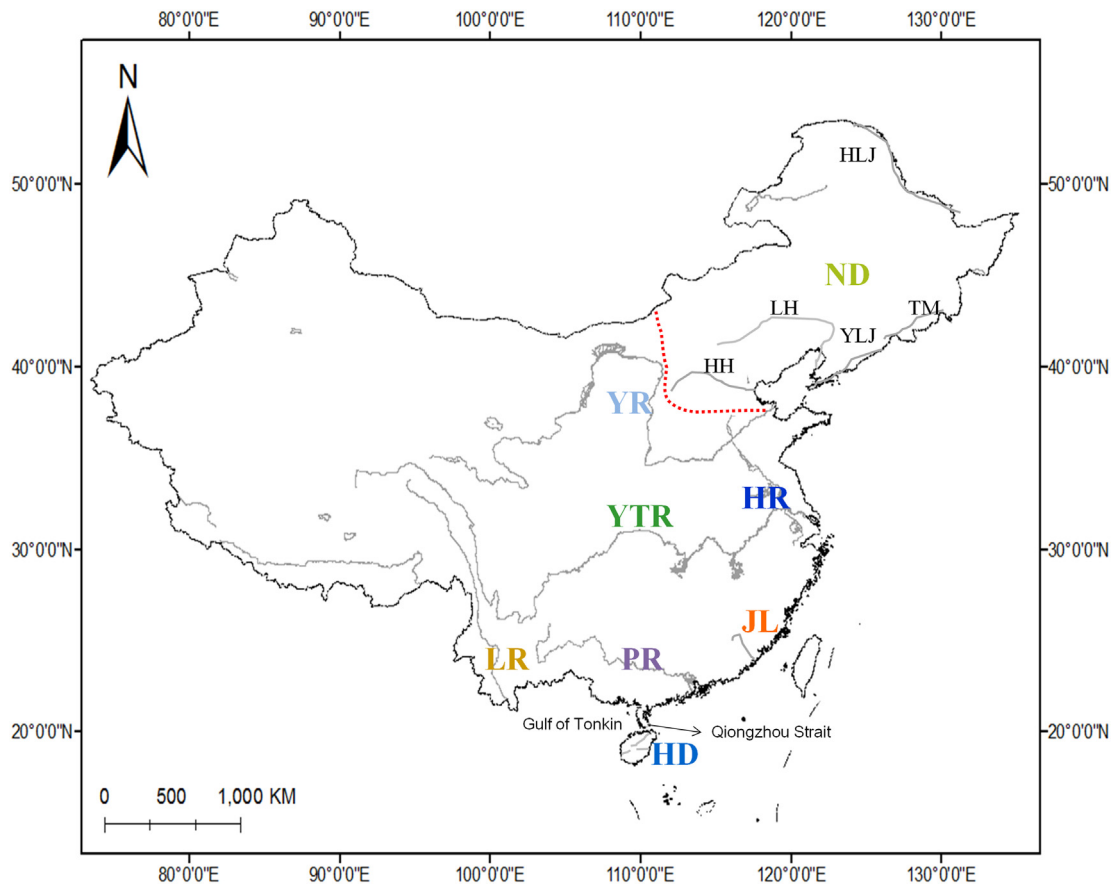


Fig. 1. Biogeographical regions of *Opsariichthys bidens* populations in our study: HD, Hainan drainages; PR, Pearl River; LR, Lancangjiang River; JL, Jiulongjiang River; YTR, Yangtze River; YR, Yellow River; HR, Huaihe River; ND, Northeastern drainages; HH, Haihe River; LH, Liaohe River; YLJ, Yalujiang River; TM, Tumen River; HLJ, Heilongjiang River.

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