



Mitochondrial diversity of *Opsariichthys bidens* (Teleostei, Cyprinidae) in three Chinese drainages

A. Perdices^{a,b,*}, D. Sayanda^a, M.M. Coelho^a

^a Universidade de Lisboa, Faculdade de Ciências, Departamento de Biologia Animal, Centro de Biologia Ambiental, Bloco C-2, 3º Piso, Campo Grande, 1749-016 Lisbon, Portugal

^b Museo Nacional de Ciencias Naturales, CSIC, C/José Gutiérrez Abascal, 2, 28006 Madrid, Spain

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Abstract

We describe the phylogeographic structure of 28 Chinese populations of the cyprinid *Opsariichthys bidens* across three main Chinese river drainages. Our study is based on the phylogenetic analysis of the complete mitochondrial cytochrome *b* gene (1140 bp). We combined this analysis with population processes inferred from nested clade analysis (NCA) and mismatch distributions. Both analyses showed that Chinese *O. bidens* consists of five mtDNA lineages (*Opsariichthys* 1–5) with high genetic divergence among them. Molecular divergences (TrN + G) higher than 20% among the *Opsariichthys* 1–5 mtDNA lineages suggest a taxonomic underestimation at the species level. About 92% of the genetic variance among samples was explained by differences among *Opsariichthys* mtDNA lineages. Drainage-restricted haplotypes with high frequencies and moderate nucleotide diversity show that *Opsariichthys* populations have evolved independently. NCA results were congruent with the phylogeny, and unimodal mismatch distributions with negative Tajima's *D* values suggest population expansions in some *Opsariichthys* lineages. The phylogeographic structure of the *Opsariichthys* 1–5 mtDNA lineages appears to be related to their long-term interruption of gene flow ($\theta_{ST} > 0.97$). Our results suggested that fragmentation of ancestral ranges might have caused *Opsariichthys* diversification in Chinese waters. However, current distribution of common haplotypes across the Yangtze and Pearl drainages suggests a recent river connection that could have favoured gene flow across drainages. Overall, the results indicated that the richness of current Asian widespread species might have been underestimated, and that the cyprinid populations of *O. bidens* in the Yangtze, Pearl and Hai He drainages may correspond to five species.

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1. Introduction

Cyprinids represent one of the most diverse freshwater fish groups and are a major component of the primary freshwater fish fauna of Eurasia (Banareescu and Coad, 1991). The wide distribution of the family Cyprinidae and the genus or species high diversity (Howes, 1991) turn this family of particular interest for evolutionary studies.

Moreover, their morphological and genetic diversity coupled with their broad ecological preferences (Howes, 1991) make the cyprinids one of the most suitable groups to rear in captivity for aquaculture purposes (Winfield and Nelson, 1991). However, this high variation and adaptability is often associated with an absence of consensus in their basic knowledge, i.e., alpha taxonomy. Recent phylogenetic studies have revealed certain systematic inaccuracies of the European cyprinids (Kotlík et al., 2004), and in some taxa, a species underestimation (Doadrio and Carmona, 2003). Although much

* Corresponding author. Fax: +35121750028.
E-mail address: aperdices@fc.ul.pt (A. Perdices).

effort has been paid on the molecular systematics of European, African (Gilles et al., 1998, 2001; Machordom and Doadrio, 2001a,b; Zardoya and Doadrio, 1999), and North American cyprinids (Dowling et al., 2002), Asian cyprinids are still poorly studied. Cyprinids achieved their maximal diversity in Asiatic waters and represent more than 50% of the freshwater fish diversity in the main Asian rivers, e.g., Yangtze drainage (=Chang Jiang) (Fu et al., 2003). Unfortunately, there is a lack of molecular studies on Asian cyprinids, which has resulted in untested or unsolved phylogenetic relationships of cyprinids (Cunha et al., 2002; Gilles et al., 2001).

Detailed studies across populations of some Chinese cyprinid species have shown that broad distributed species might not represent single taxa (Su et al., 2001). Intraspecific phylogeographic studies have revealed multiple mitochondrial lineages inside different cyprinid taxa distributed throughout the Yangtze drainage (Perdices et al., 2004; Xiao et al., 2001). Taking into account that only a minority of Asian cyprinids have been analysed at the population level, description of new taxa should increase in the incoming years. Species with broad ranges are potential candidates to show population structure and to reveal different evolutionary histories. This was the case of the cyprinid *Zacco platypus* recently studied under a phylogeographic perspective (Perdices et al., 2004). Four genetic distinct *Zacco* mtDNA lineages (A–D) have been observed in the Yangtze drainage with enough genetic distinctiveness (mean 8.9%, TrN+I distances) to be considered different species. These four *Zacco* mtDNA lineages are geographically related to upper and middle courses of the Yangtze drainage (Perdices et al., 2004). The species *Opsariichthys bidens* (fam. Cyprinidae) lives in sympatry with *Z. platypus* in many localities. The geographical distribution of the cyprinid genus *Opsariichthys* extends throughout main drainages across Central and South East China. Although more than four species of *Opsariichthys* have been described for Chinese continental waters, all are synonymised with *O. bidens* (<http://www.FishBase.org>). Therefore, a single species is recognised for the Yangtze, Pearl (=Zhu Jiang), and Hai He (Beijing area) drainages. Even though the genus *Opsariichthys* is considered a primitive cyprinid (Howes, 1980; Regan, 1911), and potentially useful to solve basal cyprinid relationships, little has been done to address its phylogenetic relationships (Okazaki et al., 2002).

The wide distribution of *O. bidens* across China's main drainages (i.e., Yangtze and Pearl) also poses an interesting biogeographical question about its origin and evolution. Given the intolerance of the Cyprinidae to waters with some salt content, members of this primary freshwater fish division cannot disperse other than through continental river connections (Myers, 1949). Therefore, we would expect vicariance to play a strong role shaping *O. bidens* populations. Phylogenetic and

population analysis of *O. bidens* across China's main drainages could potentially reveal the historical connections of main Asiatic rivers, and identify evolutionary mechanisms that have shaped current spatial genetic variation.

The main goals of this study based on the complete cytochrome *b* (cyt *b*) gene are: (1) to determine the phylogenetic relationships of the *O. bidens* populations throughout three of China's main drainages (Yangtze, Pearl, and Hai He), and to reconstruct their most likely phylogeographical pattern across the Yangtze and Pearl drainages; and (2) to infer historical population processes (e.g., population fragmentation, range expansion, or long distance colonisation), or present-day processes (e.g., restricted gene flow) that might have affected current distributions of *O. bidens* in China.

2. Materials and methods

One hundred and thirty-eight specimens of *O. bidens* were sequenced from 14 rivers of three drainages in China (Fig. 1, Supplementary Appendix 1). From 1 up to 16 individuals from the same population were sequenced for the complete mitochondrial gene cyt *b* (1140 bp). We have included populations with only one or two specimens to cover the broadest range of *O. bidens* in China. Voucher specimens and their associated lots have been deposited at the NRMT (Supplementary Appendix 1). Sequences have been deposited in the GenBank library under the Accession Nos. AY646512–AY646649. The cypriniforms *Raiamas guttatus* (AF051875, Xiao and Zhang, unpublished) and *Aphyocypris chinensis* (AF307452, He et al., unpublished) were selected as phylogenetic outgroups.

2.1. DNA extraction and sequencing of the cytochrome *b*

DNA extraction follows a salt/chloroform protocol (Miller et al., 1988) with an extra step of 24:1 chloroform–isoamyl alcohol. Mitochondrial PCR amplification protocols were performed as previously described (Perdices et al., 2004). Purified PCR products were used as template in cycle sequencing reactions and sequenced on an Applied Biosystems 3700 DNA sequencer following manufacturer's instructions. Chromatograms and alignments were verified with Sequencher ver. 4.0 (Gene Codes).

2.2. Analysis of haplotypes

Patterns of phylogeographical variation of *O. bidens* were analysed combining phylogenetic and population methods. A phylogenetic analysis of the cyt *b* sequences was performed using maximum parsimony (MP), minimum evolution (ME), and Bayesian inference (BI). We used Modeltest 3.06 (Posada and Crandall, 1998) to find

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