

Vicariance, colonisation, and fast local speciation in Asia Minor and the Balkans as revealed from the phylogeny of spined loaches (Osteichthyes; Cobitidae)

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Abstract

We reconstruct the phylogeny of the morphologically diagnosable subgenera *Bicanestrinia*, *Beysehiria*, and *Cobitis* sensu stricto of the genus *Cobitis* from Asia Minor and the Balkans. We used the complete cytochrome *b* gene of 65 specimens in order to infer their evolutionary history in this zoogeographically interesting area. Our phylogeographic analysis did not evidence the previously suggested monophyly of the *Bicanestrinia* subgenus but revealed five monophyletic lineages in the area: the lineages *Bicanestrinia* I–IV including all species of *Bicanestrinia* plus the lineage *Cobitis* s. str. The monotypic subgenus *Beysehiria* from Lake Beyşehir in Anatolia was closely related to the syntopic population of *C. turcica* and nested inside the lineage *Bicanestrinia* III. The strictly allopatric distribution of the four lineages of *Bicanestrinia* suggests that vicariance has played a major role in the diversification of *Bicanestrinia*. All analysed species of *Cobitis* s. str. from Asia Minor and Balkans were closely related to *Cobitis* s. str. from Central Europe, the Danube basin and the Caucasus, indicating at least two colonisation events into Asia Minor and the Balkans. A third, recent colonisation event led to the presence of *C. strumicae*, generally restricted to the Aegean Sea drainage, in the Danube basin. Besides the evidences of vicariance and colonisation events in the phylogenetic history of the genus *Cobitis* in Asia Minor and the Balkans, our analysis suggested also a rapid morphological evolution of *C. bilseli* in a lacustrine environment. Application of *Cobitis* mitochondrial cytochrome *b* clocks of 0.68% sequence divergence per million years (MY) suggest that the split between the five major lineages happened approximately 12.4–17.6 MYA, and according to the lack of basal resolution of this monophyletic group probably the split of all lineages happened within a narrow time window.

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1. Introduction

Freshwater organisms are bound to hydrogeographic systems and their distribution is linked to the hydrogeographic history of the inhabited area. Therefore, the geological events might have differently affected the evolutionary history of freshwater organisms and terrestrial animals and

plants. One of the most important areas for the colonisation of Europe by terrestrial animals and plants are Asia Minor and the Balkans, having served first as a bridge for African mammals during Early Miocene, and second as refuges and source areas for its recolonisation after Pleistocene glaciations (Hewitt, 1999; Rögl, 1998; Rokas et al., 2003). However, their impact on the colonisation history in strictly freshwater fauna is poorly studied.

The geological history of Asia Minor and the Balkans during Cenozoic was greatly influenced by the collision of the African and Arabian plates with the Eurasian plate,

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promoting the closure of Tethys Sea and the upfolding of the Alpidic mountain chain along the southern margin of Eurasia (Neveeskaja et al., 1987; Rögl, 1998, 1999). The most important consequences for Asia Minor and the Balkans were the fusion of the seven Anatolian subplates, the upfolding of the Balkan, Caucasus, Pindus, and Taurus mountains and the uplift of the Central Anatolian highlands (Hrbek and Meyer, 2003; Kosswig, 1964). The complex geological history has also caused multiple connections, redirections, and truncations of water systems and their faunas in the whole area and led to multiple events of vicariance and local isolations (Economidis and Bănărescu, 1991; Hrbek et al., 2002). These geological processes have promoted speciation of freshwater fishes favouring the presence of local endemics (Hrbek et al., 2002; Kosswig, 1964). However, most of the endemic taxa are restricted to small local areas and only very few have a wide distribution. One of the few exceptions is provided by spined loaches of the subgenus *Bicanestrinia* (genus *Cobitis*; Cobitidae), which are endemic to Asia Minor and the Balkans, occurring in the whole area from western Iran to western Greece.

According to recent phylogenetic studies, the genus *Cobitis* is represented in Europe by five major mitochondrial lineages (six if the Iberian *C. calderoni* is counted as major lineage): the most distinct is the ‘Siberian lineage’ that represents the sister lineage to a group formed by the ‘Adriatic lineage’ and the subgenera *Iberocobitis*, *Bicanestrinia*, and *Cobitis* s. str. without resolved phylogenetic relationships (Ludwig et al., 2001; Perdices and Doadrio, 2001). In previous phylogenetic studies, the *Bicanestrinia* lineage appeared as a monophyletic group (Ludwig et al., 2001; Perdices and Doadrio, 2001) that occurs with some species of *Cobitis* s. str. in Asia Minor and the Balkans. *Cobitis* s. str. is the most widespread subgenus of *Cobitis* ranging from western France to the Volga in Europe and from Mongolia to Japan in Asia (Bănărescu, 1990). Within Asia Minor and the Balkans, *Cobitis* s. str. inhabits Central Greece and the Turkish Aegean basin. Besides these five mitochondrial lineages, the monotypic subgenus *Beysehiria* was recently described as an endemic lineage from the endorheic Lake Beyşehir in Anatolia (Erkakan et al., 1999), but not yet studied genetically. Therefore, the spined loaches of the genus *Cobitis* include a local endemic (= *Beysehiria*), a whole-range endemic (= *Bicanestrinia*) and a Eurasian group (= *Cobitis* s. str.) in Asia Minor and the Balkans offering a great model to study the impact of vicariance, colonisation, and local isolation in freshwater fish speciation in the whole of the area. It further enables to show the phylogenetic connections of the faunas of Asia Minor and the Balkans with those of surrounding areas. Moreover, the geological complexity of Asia Minor and the Balkans made the phylogenetic relationships of these freshwater fishes an important database for the biogeographical reconstruction of the area. We use the complete mitochondrial cytochrome *b* gene to reconstruct the phylogeny of the subgenera *Beysehiria*, *Bicanestrinia*, and *Cobitis* s. str. from

Asia Minor, the Balkans and surrounding areas with special emphasis on the geographic structure. This reconstruction should enable us to draw conclusions on the origin of the subgenera of the spined loaches and the major evolutionary mechanisms shaping their biogeographical patterns.

2. Materials and methods

2.1. Taxon sampling and laboratory protocols

An overview about the geographic origin of the samples and GenBank accession numbers can be found in Table 1 and Fig. 1. A total of 65 specimens of spined loaches were analysed. The material for this study includes 10 species of *Bicanestrinia*: *C. arachthosensis*, *C. elazigensis*, *C. hellenica*, *C. levantina*, *C. linea*, *C. meridionalis*, *C. punctilineata*, *C. strumicae*, *C. trichonica*, and *C. turcica*; the only species of *Beysehiria* (*C. bilseli*) and three species of *Cobitis* s. str. from the Aegean region: *C. fahirae*, *C. stephanidisi*, and *C. vardarensis*. From neighbouring areas, we included three species and one undescribed species of *Cobitis* s. str.: *C. elongatoides*, *C. taenia*, *C. tanaitica*, and *C. sp.*; four species of the ‘Adriatic lineage’ (*C. bilineata*, *C. elongata*, *C. ohridana*, and *C. zandarea*) and one species, *C. melanoleuca*, of the ‘Siberian lineage’. Some more distantly related European loach fishes served as outgroup taxa (*Sabanejewia balcanica*, *S. larvata*, and *Misgurnus fossilis*).

DNA was extracted from fin or muscle tissue with chloroform-phenol standard methods (Palumbi et al., 1991; Sambrook et al., 1989). Amplification protocols were performed as previously described (Perdices and Doadrio, 2001). The entire cytochrome *b* gene (1140 bp) was PCR amplified using the primers GluDG.L (5′ TGA CT TGA AACC A YCG TTG 3′; Palumbi, 1996) and H16460 (5′ CGAYC TTCGG ATTAA CAAGA CCG 3′; <http://nmg.si.edu/bermlab.htm>). The purified PCR band was used as template in a cycle sequencing reaction using the dRhodamine terminator cycle sequencing kit (PE Applied Biosystems). In some cases, the internal primer Cb3H (5′ GGCAA ATAGG AARTA TCATT C 3′; Palumbi, 1996) was also used for sequencing.

2.2. Phylogenetic analysis

Sequences were aligned and revised with Sequencer ver. 4.0 (Gene Codes). No length variation was found in any of the mtDNA genes analysed. Nucleotide composition was examined for variable sites, and the χ^2 homogeneity test of base frequencies was done in PAUP* v. 4.0b10 (Swofford, 2002) for all positions. Nucleotide saturation was analysed by plotting uncorrected p distances at 1st, 2nd, and 3rd codon position against absolute distance values. Relations between genotypes were resolved by distance methods with Sequencer 6.1 (<http://nmg.si.edu>).

Phylogenetic trees were reconstructed using maximum parsimony (MP) and Bayesian criteria. In MP analysis,

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