

## **Article**



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## Monophyly of the Agoniatinae (Characiformes: Characidae)

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## **Abstract**

The Characidae is the most diverse family of Neotropical fishes, currently encompassing more than one thousand valid species. Some subgroups within this family still lack phylogenetic definitions, being diagnosed on the basis of combination of characters, a common procedure in pre-cladistic studies. Agoniatinae, currently composed by two valid species, *Agoniates anchovia* and *A. halecinus*, is one of them. In the present study the Agoniatinae is redefined using a phylogenetically oriented comparative survey that included the two *Agoniates* species plus 114 species representing all the major clades of the Characidae and their closest relatives. Six derived morphological characters are identified as synapomorphies for the Agoniatinae: deep notch on the posterior region of the maxilla joining the ventral margin of the infraorbital 2; dentigerous portion of premaxilla shorter than the ascending process of this bone; dentary canine preceded by tricuspid teeth; ventral margin of the urohyal markedly convex; base of the uppermost ray of the ventral lobe of the caudal fin much expanded, being as deep as the distal margin of hypural 2; and *levator arcus palatini* muscle with a posterodorsal bundle of fibers attaching to the dorsal face of the sphenotic spine.

Key words: Agoniates, morphology, osteology, myology, systematics

## Introduction

The Characidae includes 1027 valid species (Eschmeyer and Fong 2012) distributed throughout inland waters of large portions of the Americas. The family contains several subunits whose phylogenetic relationships have been differently interpreted recently (Reis *et al.* 2003; Mirande 2010; Oliveira *et al.* 2011). Noteworthy is the conflicting results of the two most recent comprehensive studies dealing with phylogenetic relationships of the Characidae (Mirande 2010; Oliveira *et al.* 2011) producing remarkably divergent classifications.

The subfamily Agoniatinae is represented by the single genus *Agoniates* Müller and Troschel, originally erected to allocate *A. halecinus* Müller and Troschel from Guiana. A second species, *A. anchovia* Eigenmann, was described by Eigenmann (1914) based on specimens from Río Beni, upper Amazon River basin, Bolivia, collected by J. D. Haseman. A third species was described by Géry (1963) as *A. ladigesi*, but Zarske and Géry (1997) synonymized this species with *A. anchovia*. *Agoniates halecinus* is widespread in the Amazon basin, while *A. anchovia* apparently occurs primarily in the upper Amazon (Lima and Zanata 2003). The genus *Agoniates* was allocated into the group Tetragonopterina by Günther (1864) and partially based on the conclusions of Géry (1963), Uj (1990) raised Agoniatinae to family rank. Lima and Zanata (2003) defined *Agoniates* as being the sole member of the Agoniatinae, a similar arrangement proposed by Mirande (2010) and Oliveira *et al.* (2011). In the present study, we follow these recent classifications in assigning a subfamilial rank for the genus.

The first authors to make evolutionary inferences about the genus were Cuvier and Valenciennes (1849) who commented that *Agoniates* was intermediate between "Hydrocyns" and "Tétragonoptères". Regan (1911) suggested the possible close relationship between *Agoniates* and *Salminus* Agassiz. Eigenmann (1912) commented about the similarity between *Agoniates* and *Hydrolycus* Müller and Troschel and Howes (1976) admitted that some features shared by agoniatines and cynodontines might represent derived specializations. Géry (1963), in a pre-cladistic context