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Phylogenetic relationships of the species and biogeography of the characid genus *Oligosarcus* Günther, 1864 (Ostariophysi, Characiformes, Characidae)

ALEXANDRE CUNHA RIBEIRO¹ & NAÉRCIO AQUINO MENEZES²

¹Departamento de Biologia e Zoologia, Instituto de Biociências, Universidade Federal de Mato Grosso. Av. Fernando Corrêa da Costa, s/n, 78060-900, Cuiabá, MT, Brazil. E-mail: alexandrecunharibeiro@gmail.com

²Museu de Zoologia da Universidade de São Paulo. P.O. Box 42594, 04299-970, São Paulo, Brazil. E-mail: naercio@usp.br

Abstract

The characid genus *Oligosarcus* consists of 20 described species distributed throughout most of South American river basins below 14° south latitude. This study focus on the phylogenetic relationships of the species of *Oligosarcus* based on the analysis of osteological characters to provide data to discuss the biogeographic history of the genus. The analysis resulted in a single most parsimonious tree with 152 steps (CI= 0.355 and RI= 0.600). The 18 included *Oligosarcus* species were hierarchically organized into 17 clades. A minimal age of 15 Ma for the genus is suggested based on the putatively cladogenetic event represented by the continued shortening of the Eastern Cordillera that established the eastern boundary of the modern central Andean plateau and was responsible for cladogenesis between the common ancestor of *O. schindleri* + *O. bolivianus* versus the remaining congeners. There is a pronounced disjunction in the upland species distribution by the lowland areas of the Chaco-Pantanal basin. This indicates that upland habitats (headwater streams) are preferential habitats for a set of species including *O. argenteus*, *O. bolivianus*, *O. brevioris*, *O. paranensis*, *O. perdido*, *O. pinto*, *O. planaltinae*, *O. brevioris*, and *O. schindleri*. Fragmentation of populations of *O. pinto* and *O. perdido* are at least 2.5 Ma old, since the origin of the upper Paraguay depression clearly promoted the present-day observed disjunction in the distribution of these species. The lowland *Oligosarcus* species are all included in a single clade but the obtained results suggest that fragmentation of upland versus lowland components of the genus was not causally related to a single vicariant event. The available fossil record of *Oligosarcus* indicates that the genus already occurred in the coastal plain at about 2.3 to 1.25 Ma. The sister-group relationship between *O. hepsetus* and *O. longirostris* provided additional evidences of the so-called historical affinities between the SE Brazilian coastal plain and the Rio Iguaçú drainage basin.

Key word: Characidae, Historical Geology, Neotropical Region

Introduction

The characid genus *Oligosarcus* consists of 20 described species (Menezes 1987; Miquelarena & Protogino 1996; Ribeiro *et al.* 2007; Menezes & Ribeiro 2010; Mirande *et al.* 2011) (Figure 1) distributed throughout most of the South American river basins below 14° south latitude (Menezes 1988). This wide distributional range includes the Bolivian and Argentinean Andean highlands, the Brazilian crystalline shield, and lowland areas of the Paraná-Paraguay and coastal rivers of southern and southeastern South America, from the Brazilian state of Bahia in the north to Uruguay, in the south. The alpha taxonomy of *Oligosarcus* was previously deeply studied (Menezes 1969a; Menezes 1987; Menezes & Géry 1983) and the current valid species are relatively well-delimited and diagnosed. *Oligosarcus itau* Mirande, Aguilera & Azpelicueta 2011, *O. amome* Almirón, Casciotta, Piálek, Doubnerová & Rican 2015 and *O. platensis* (Messner 1962) are not included in the present study because their placement in *Oligosarcus* is controversial. They lack some of the morphological synapomorphies herein described for purported congeners and the phylogenetic analysis undertaken by Mirande *et al.* (2011) to support their inclusion in the genus is based only on five species. Additionally two features (presence of two rows of premaxillary teeth and of pentacuspitate teeth on dentary) used to diagnose *O. itau* (Mirande *et al.* 2011), *O. amome* (Almirón *et al.* 2015) and *O. platensis* (Messner 1962) are absent in all of the species herein analysed

The northern limit of the distribution of *Oligosarcus* along the coastal plain is indicative of a high degree of distributional range expansion along the Atlantic slope coastal plain. This limit coincides with the abrupt reduction of the Brazilian northeastern continental platform in the shore area of southern Bahia State. This coincides with the northern limit of distribution of several freshwater fishes widespread along the coastal drainages, such as *Mimagoniates microlepis*, *Rachoviscus* spp, *Parauchenipterus strialulus*, *Pseudachenipterus affinis*, *Aspidoras virgulatus*, *Scleromystax prionotus* and *Otothyris travassosi* (Menezes *et al.* 2007). However, such expansions of distributional ranges were possible only during periods of significant lowering of sea level, when the South American continental platform became exposed. This kind of intense sea level fluctuation is well known from the late Quaternary, when the sea level was about 100 m lower than present (Weitzman *et al.* 1988; Menezes & Weitzman 1990). However, the fossil record of *Oligosarcus*, represented by some fragments and from a complete dentary from Argentina (Bogan 2009) undoubtedly belonging to clade 8, demonstrate that the genus already occurred in the coast plain much earlier, in a time interval of about 2.3 to 1.25 Ma (Bogan 2009). There is evidence that the South American platform was completely exposed between 2 to 1.8 Ma (Justus 1990) and available for the development of lowland fluvial systems including floodplains and marginal lagoons (Abreu & Calliari 2005).

The sympatry among the lowland components is observed mostly in the southern Brazilian coast. *Oligosarcus hepsetus* and *O. acutirostris*, for example, do not overlap distributionally (Menezes 1988). It is important to point out that the species of *Oligosarcus* in clade 10 are relatively large fish predators. This suggests that, competitive exclusion and habitat partitioning represented an important process in determining present-day distributions in the genus. Recent systematic collecting efforts in the upper Paraná basin (Castro *et al.* 2003; 2004; 2005) failed to find any specimen of *O. pintoi* and *O. paranensis* in the same sampling location. Thus they are not syntopic despite their sympatry and abundance in the upper Paraná basin. Competitive exclusion can over a large time interval, lead to the observed distribution of *O. pintoi* and *O. paranensis* in the upper Paraná basin, with the latter having a peripheral distribution related to *O. pintoi* in that system. The role of this ecological process cannot be neglected as a putative important mechanism in shaping distributions in the lowland components of the genus over time.

Finally, one of the interesting results from the analysis of the area cladogram is the indication that the coastal plain of southeastern Brazil and the upland Rio Iguaçu are closely related. The historical affinities between the Iguaçu river basin and the coastal drainages is a recurrent pattern, demonstrated and discussed in detail by several authors (Ribeiro 2006; Torres *et al.* 2008; Torres & Ribeiro 2008; Menezes *et al.* 2008; Menezes & Weitzman 2009) and will not be reiterated herein.

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