North American tetras: Such abundant fishes, such a complex evolutionary history

Tetras of Central and North America are fishes that belong in genus *Astyanax*, family Characidae. They are among the most abundant and frequent freshwater fishes in tropical America. Although some authors consider all *Astyanax* in the region to be only one, extremely variable species, usually called "*A. fasciatus*", or at most acknowledge the existence of two widespread species, *A. mexicanus* (northern Mexico and Texas) and *A. aeneus* (southern Mexico and Central America), other opinions recognize up to 18 species or more.

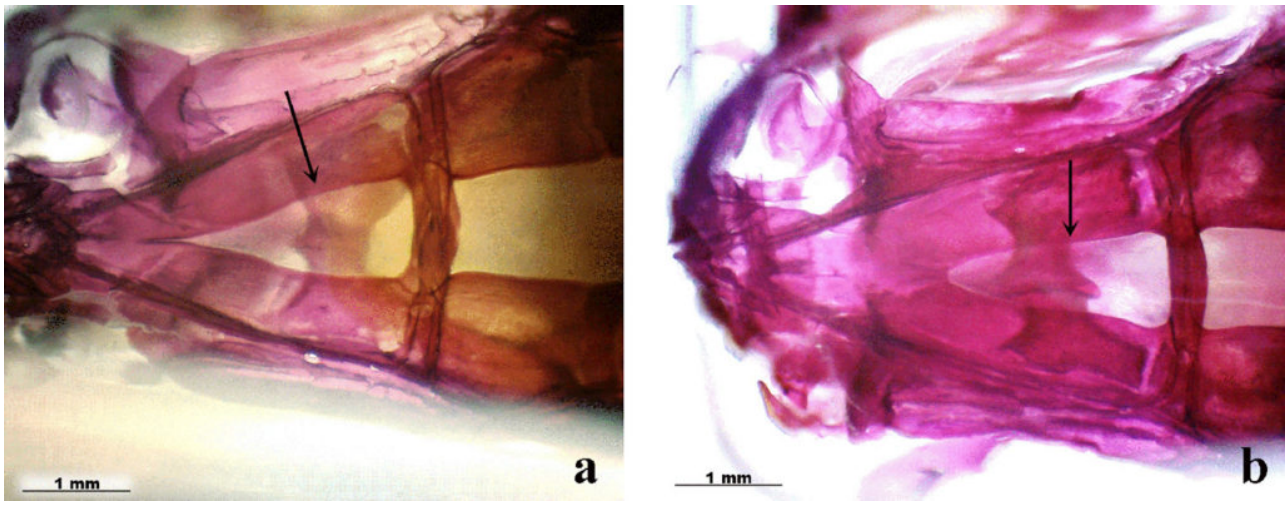

Fig. 1. An example of a character based on bone shape, used to build a phylogeny for Astyanax. The fontanel on the top of the skull is (a) longer, with sides convex at mid-length (arrow), sharp-tipped, for the species present in northern Mexico and Texas, (b) shorter, with sides straight at mid-length (arrow), blunt-tipped, for the species present in the central-southern Gulf of Mexico versant.

The article *A phylogeny of Astyanax (Characiformes: Characidae) in Central and North America* (published in the journal *Zootaxa* in 2016) presented a hypothesis (i.e. a phylogeny) for the pattern of interrelationships of 34 species of *Astyanax*, 27 of them once considered part of *A. fasciatus* in Central America and Mexico. The cladistic analysis (a method for determining which anatomical or genetic traits are evolutionarily derived and shared between species or lineages, hence supporting descent from a recent common ancestor) was based on 52 morphological characters, mostly the shape of bones in the skull and axial skeleton, but also pigmentation and meristics, with three outgroups (other characids, for comparison). The bones were made observable by means of a chemical process termed "clearing and staining", applied to museum specimens (Fig. 1).

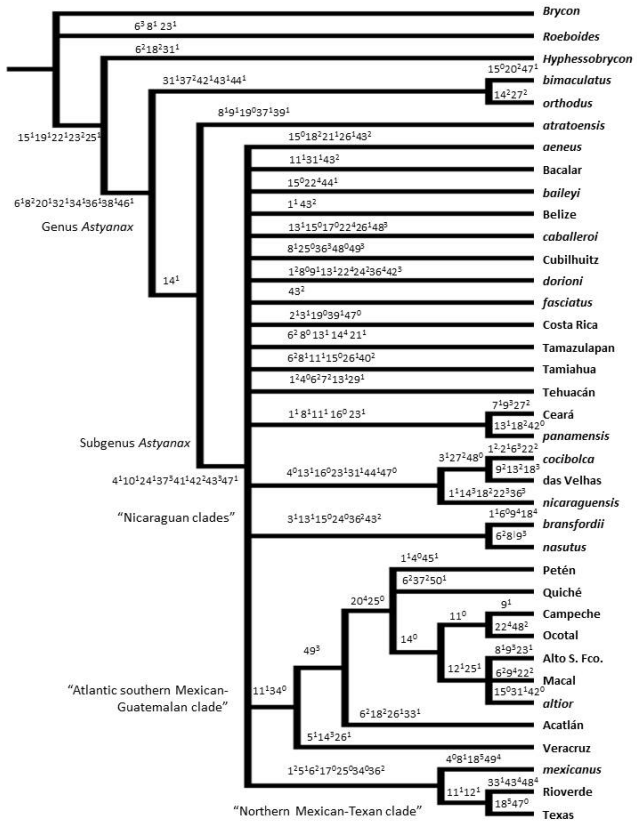

Fig. 2. The cladogram for species of Astyanax in North and Central America. Undescribed species are designated by their region or locality. Numbers above lines are apomorphies (shared derived characters), with the superindex indicating the character state (e.g., 0 for “fontanel sharp-tipped”, 1 for “fontanel blunt-tipped”).

The analysis showed that such broadly used names as *A. aeneus* turned out to be non-natural, that is, they were wrongly applied before to a mixture of several lineages, so the use of the name should be restricted to the populations that form a natural group, that is, that share a most recent common ancestor to the exclusion of other populations (in the case of *A. aeneus*, the populations in the Pacific versant from southern Mexico to Honduras). The presence of exclusive characters support recognition of several new species, not just one (*fasciatus*) or two (*aeneus* and *mexicanus*). There were only five resolved clades (i.e., natural species groups ¾ see Fig. 2), three of them including both Brazilian and Central American species, one purely Nicaraguan, and one for central-northern Mexico and Texas, the latter being the most derived (i.e., recently evolved) group. The genus *Bramocharax*, a name traditionally applied to long-snouted characins, was not recovered as a natural group, and thus it was confirmed to be a synonym of *Astyanax*; the snout and other traits turned out to be homoplasies, i.e., characters that evolved independently in parallel. Coincidence with previous cladistic hypotheses based on molecules rather than bones

was not complete to every detail, but the main picture holds as here described. The findings point at a more complex biogeographic history of the region than usually recognized: the traditional view claims that Neotropical fishes, among them the Characidae, invaded North America from South America in the last few million years. However, the occurrence of Brazilian species within Central American clades bespeaks a secondary “back to South America” pattern, which has been observed also in evolutionary hypotheses for other freshwater fishes in the tropical New World. These results change the estimation of species biodiversity and hence the conservation strategies; the conservation of seemingly arcane little fishes may seem removed from more urgent needs, but one should remember that biotically healthy freshwaters, with all their native species present, are the hallmark of an environment that is able to provide all ecosystem services to the human population living in those basins.

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