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Gill arch and hyoid arch diversity and cypriniform phylogeny: Distributed integration of morphology and web-based tools

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Abstract

Using the multiple tools available to support an online collaborative environment, we surveyed 62 morphological features from the hyoid arch and gill arches of 53 species of cypriniform fishes that matched those sampled in recent molecular

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analyses and two sets of outgroup species (‘Saitoh outgroups’ and ‘Basal outgroups’). This is a skeletal region whose variation is considered historically significant within fishes and Cypriniformes in particular, and we review previous work in light of our own. The clarity of description of characters was enhanced by the use of a community reference ontology, the Teleost Anatomy Ontology. Terms, synonyms, and definitions for skeletal features from this region were contributed to this ontology, and links to these terms and relationships are included in our character descriptions. One thousand two hundred sixty-three images of features from this region were linked to ontology terms and deposited in a community image repository, Morphbank; these are linked to the characters described herein. Character data were analyzed using parsimony and Bayesian methods for two sets of outgroups, one of which matched that used in previous molecular analyses. The parsimony results, using either outgroup set, indicated similar higher-level relationships, including a sister group relationship between cyprinids and loaches. A basal trichotomy among *Gyrinocheilus*, catostomids and cyprinids + loaches was the result of Saitoh outgroup analysis in contrast to a sister group relationship between *Gyrinocheilus* and catostomids discovered in the Basal outgroup analysis. Interestingly, analyses including basal outgroups recovered a monophyletic Cyprinidae, consistent with all previous studies. Character evolution that supports higher-level nodes of interest in the consensus tree is described. In some respects, it might be a surprise that 62 morphological characters from a small skeletal region for only 53 cypriniform species (out of over 3,200 total species) could provide as much resolution as it does. We expect, however, further phylogenetic resolution as morphological data from across skeleton regions are combined, species sampling is increased, and molecular data are added.

Key words: Branchial arches, Hyoid arch, Pharyngeal arches, Ostariophysi, Cypriniformes, Skeleton, Ontology

Introduction

The Cypriniformes comprise one of the most diverse groups of freshwater fishes in the world, with over 3,200 species (J. S. Nelson, 2006). These fishes have a worldwide distribution, absent in only South America, Australia, and Antarctica (Berra, 2007). They include many economically important species, as well as the zebrafish, *Danio rerio* (Hamilton), a member of the Cyprinidae and an important model for vertebrate embryogenesis.

The higher-level relationships of Cypriniformes have been incompletely resolved by previous morphological studies that have been focused on smaller taxonomic subsets (Cavender & Coburn, 1992; Howes, 1981; Sawada, 1982; Wu *et al.*, 1981) or particular morphological regions (Conway & Mayden, 2007; G. J. Nelson, 1969; Sawada, 1982; Siebert, 1987; Wu *et al.*, 1981) (Fig. 1). Recent molecular studies focused on variation in whole mitochondrial genome sequences and nuclear genes, however, have added resolution (Chen *et al.*, 2008; Chen & Mayden, 2009; Mayden *et al.*, 2009; Mayden & Chen, 2010; Mayden *et al.*, 2008; Saitoh *et al.*, 2006; Tang *et al.*, 2010), though basal inconsistencies remain (Fig. 2). In the first of these higher-level molecular studies (Saitoh *et al.*, 2006), which was based on the mitochondrial genome of 53 cypriniform and six outgroup species, a monophyletic Cyprinidae was recovered as the sister group to all other cypriniforms (Fig. 2A). Among these, catostomids + gyrinocheilids are the most basal lineage, and the sister group to *Parabotia* + *Botia* (former cobitids, now elevated as Botiidae (Nalbant, 2002)), *Vaillantella,* and cobitids + balitorids (Fig. 2A). Recent nuclear gene data (Chen *et al.*, 2008; Mayden *et al.*, 2008) however, favor Catostomidae as sister to other cypriniforms (Fig. 2B) and recover Cyprinidae as the sister group to the lineage that includes gyrinocheilids and loaches (botiids, *Vaillantella*, and cobitids + balitorids).

The level and nature of phylogenetic congruence between molecular and morphological data is of importance in developing a more comprehensive understanding of the evolution within any taxon. We began such an assessment by surveying the morphology of the hyoid and gill arches, a region whose variation is considered phylogenetically significant within fishes (G. J. Nelson, 1969), and Cypriniformes in particular (Siebert, 1987). Our specific initial goal, and the work we report here, was to duplicate the species coverage used in the molecular phylogenetic study of Saitoh *et al.* (2006), and to comprehensively document the variation in gill arch morphology within these 59 species. We examine our resultant phylogenetic analyses of morphological data against two different higher-level molecular topologies (Fig. 2), and we discuss the evolution of gill arch morphology in relation to these and to previous morphological hypotheses. Future work will involve increased taxon sampling and combined molecular and morphological analyses.