



Phylogenetic relationships of the Cobitoidea (Teleostei: Cypriniformes) inferred from mitochondrial and nuclear genes with analyses of gene evolution

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ABSTRACT

The superfamily Cobitoidea of the order Cypriniformes is a diverse group of fishes, inhabiting freshwater ecosystems across Eurasia and North Africa. The phylogenetic relationships of this well-corroborated natural group and diverse clade are critical to not only informing scientific communities of the phylogeny of the order Cypriniformes, the world's largest freshwater fish order, but are key to every area of comparative biology examining the evolution of traits, functional structures, and breeding behaviors to their biogeographic histories, speciation, anagenetic divergence, and divergence time estimates. In the present study, two mitochondrial gene sequences (COI, ND4 + 5) and four single-copy nuclear gene segments (RH1, RAG1, EGR2B, IRBP) were used to infer the phylogenetic relationships of the Cobitoidea as reconstructed from maximum likelihood (ML) and partitioned Bayesian Analysis (BA). Analyses of the combined mitochondrial/nuclear gene datasets revealed five strongly supported monophyletic Cobitoidea families and their sister-group relationships: Botiidae + (Vaillantellidae + (Cobitidae + (Nemacheilidae + Balitoridae))). These recovered relationships are in agreement with previous systematic studies on the order Cypriniformes and/or those focusing on the superfamily Cobitoidea. Using these relationships, our analyses revealed pattern lineage- or ecological-group-specific evolution of these genes for the Cobitoidea. These observations and results corroborate the hypothesis that these group-specific-ancestral ecological characters have contributed in the diversification and/or adaptations within these groups. Positive selections were detected in RH1 of nemacheilids and in RAG1 of nemacheilids and genus *Vaillantella*, which indicated that evolution of RH1 (related to eye's optic sense) and RAG1 (related to immunity) genes appeared to be important for the diversification of these groups. The balitorid lineage (those species inhabiting fast-flowing riverine habitats) had, as compared with other cobitoid lineages, significantly different dN/dS, dN and dS values for ND4 and IRBP genes. These significant differences are usually indicative of weaker selection pressure, and lineage-specific evolution on genes along the balitorid lineage. Furthermore, within Cobitoidea, excluding balitorids, species living in subtropics had significantly higher dN/dS values in RAG1 and IRBP genes than those living in temperate and tropical zones. Among tropical cobitoids, genes COI, ND5, EGR2B, IRBP and RH1, had a significantly higher mean dS value than those species in subtropical and temperate groups. These findings suggest that the evolution of these genes could also be ecological-group-specific and may have played an important role in the adaptive evolution and diversification of these groups. Thus, we hypothesize that the genes included in the present study were actively involved in lineage- and/or ecological-group-specific evolutionary processes of the highly diverse Cobitoidea. These two evolutionary patterns, both subject to further testing, are hypothesized as integral in the diversification with this major clade of the world's most diverse group of freshwater fishes.

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Abbreviations: COI, cytochrome *c* oxidase subunit I; ND4, NADH dehydrogenase subunit 4; ND5, NADH dehydrogenase subunit 5; Cyt *b*, cytochrome *b*; RAG1, recombination activating gene 1; RH1, rhodopsin; EGR2B, early growth response protein 2B; IRBP, interphotoreceptor retinoid binding protein; ML, maximum likelihood; BA, Bayesian approach; LRT, likelihood ratio test; CAI, codon adaptation index; ENC, effective number of codons; dN, nonsynonymous substitution; dS, synonymous substitution.

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1. Introduction

The Cypriniformes represents a fish order noted as the most highly diverse group of freshwater fishes. At present, 20 families within three superfamilies (Paedocyprioidea, Cyprinoidea, Cobitoidea) are recognized in recent research efforts (Mayden and Chen, 2010). The superfamily Paedocyprioidea only constitutes one family, Paedocypridae. The Cyprinoidea includes families Cyprinidae, Psilorhynchidae, Leptobarbidae, Danionidae, Cultridae, Xenocyprinidae, Tincidae, Tanichthyidae, Gobionidae, Achaeognathidae and Leuciscidae (all formerly recognized under the overwhelmingly diverse Cyprinidae). The Cobitoidea includes Gyriinocheilidae, Catostomidae, Cobitidae, Botiidae, Nemacheilidae, Vaillantellidae, Ellopostomatidae, and Balitoridae. While these former subfamilies within Cypriniformes are recognized by Nelson (2006), there is no phylogenetic basis for the previous classification. Depending on different authors, the superfamily Cobitoidea might contain a broad group including Gyriinocheilidae, Catostomidae, Cobitidae and Balitoridae (Nelson, 2006), only loach species including Cobitidae and Balitoridae (Sawada, 1982), or the families listed above, recently derived from substantial molecular genetic data and analyses (Chen et al., 2008; Mayden et al., 2008; Šlechtová et al., 2007). Because of its high species abundance and diversification, the cobitoids (26% species of the Cypriniformes) represent a critical element in resolving the phylogenetic relationships of the Cypriniformes.

The family Cobitidae first proposed by Regan (1911) was supported in pre-phylogenetic observations by Hora (1932). The latter author initially identified two subfamilies in Cobitidae, Cobitinae and Nemacheilinae. Later Berg (1940), also supported by pre-phylogenetic observations, reclassified the family into three subfamilies, Cobitinae, Nemacheilinae, and Botiinae, which were widely accepted by later authors (Chen and Zhu, 1984; Nalbant, 1963; Ramaswami, 1953). Using 52 osteological characters, Sawada (1982) proposed a phylogeny of the Cobitoidea (but only loaches) as (Botiinae + Cobitinae) + (Nemacheilinae + Homalopterinae), and this classification was followed by other authors (Kottelat, 2001; Nelson, 2006; Siebert, 1987). Based on mtDNA control region sequences, Liu et al. (2002) suggested that the Nemacheilinae and Cobitinae were sister clades and clustered with Balitoridae (=Homalopteridae), with the subfamily Botiinae at the most basal position. Tang et al. (2006), using a detailed phylogenetic analysis of mitochondrial cytochrome *b* and control region sequences, corroborated the classification of Liu et al. (2002). These three subfamilies were thus elevated to the family level as to maintain consistency between phylogenetic relationships and a natural classification. Šlechtová et al. (2007) analyzed the phylogenetic relationships of the Cobitoidea using only one nuclear gene (RAG1) and proposed relationships as Botiidae + (Vaillantellidae + (Cobitidae + (Nemacheilidae + Balitoridae))). Interestingly this study could not corroborate the monophyly of the Cobitidae (*sensu* Sawada, 1982) but validated with strong support that the Cobitidae and Botiidae were not closely related. Rather, this and later studies (Liu et al., 2010; Mayden et al., 2008, 2009) demonstrated with strong nodal supports that the cobitines were really sister to a clade of balitorines plus nemacheilines, and the botiines were sister to all other loach-like Cobitoidea. Multiple studies have now confirmed *Vaillantella* as sister to cobitines, balitorines, and nemacheilines, appearing on the phylogeny between botiines and remaining loaches (Mayden et al., 2009; Šlechtová et al., 2007).

Based on four nuclear genes and complete mitochondrial genome, Mayden et al. (2009) analyzed phylogenetic relationships of the Cypriniformes (with 12 samples of the Cobitoidea besides one catostomid), in which the same phylogenetic relationships of the Cobitoidea, proposed by Šlechtová et al. (2007), were recognized. These recent studies have made significant advancements in our previous, only rudimentary, understanding of the systematics and natural classification of the Cypriniformes, especially the Cobitoidea.

The evolutionary relationships of *Vaillantella* were controversial as “phylogenies” or statements of relationships were not based

on synapomorphies. Nalbant and Bănărescu (1977) considered Vaillantellinae, containing only *Vaillantella*, in an intermediate evolutionary position between Nemacheilinae and Botiinae. However, their study lacked supporting synapomorphic data and should not be considered equivalent to those supplying supporting evidence. Many authors (Kottelat, 1994; Roberts, 1989; Sawada, 1982) disagreed with this hypothesis, supporting the traditional morphological hypothesis that *Vaillantella* was a genus of the subfamily Nemacheilinae (from the pre-phylogenetic paper by Weber and de Beaufort, 1916). However, these studies were also not based on outgroup comparisons for derived characters.

Whole mitogenome sequence data and phylogenetic analyses by Saitoh et al. (2006) and sequence data from multiple nuclear and mitochondrial gene loci by Mayden et al. (2009) strongly supported *Vaillantella* as sister to Cobitinae + (Balitorinae + Nemacheilinae). Nalbant (2002) proposed the sister-group relationship between Vaillantellinae and Botiinae under the family Botiidae, a relationship that has been refuted in multiple studies. Recently, studies by Šlechtová et al. (2007) and Mayden et al. (2009) argued for Vaillantellinae to be elevated to a separate family Vaillantellidae to be consistent with phylogenetic relationships. This family forms a lineage sister to and independent of Cobitidae + (Nemacheilidae + Balitoridae) based on molecular data. Mayden et al. (2009), using nuclear and mitochondrial genes, recovered a sister group relationship identical to that of Saitoh et al. (2006, see above). At about the same time, the phylogenetic position of *Ellopostoma* was examined by Chen et al. (2009) and this enigmatic genus was strongly supported as sister to the Nemacheilidae, like *Vaillantella*, that necessitated the formation of the new family Ellopostomatidae, to maintain a natural classification. These studies and others (Chen et al., 2008; Mayden and Chen, 2010; Mayden et al., 2008) provide critical, stable, and well supported evidence as to large-scale relationships between and within the Paedocypridoidea, Cyprinoidea and Cobitoidea. As such, we strongly recommend that the above referenced phylogenetic hypotheses, based on molecular and/or morphological data, should be tested with increased character/taxon sampling as these studies and others are clearly subject to sampling error. Thus, hypotheses put forth as to the sister-group relationships regarding groupings from species to families in the Cobitoidea require additional investigation with additional genes or more taxa or additional taxa for the same genes to evaluate pre-existing hypotheses and offer greater insight into this amazingly highly diverse and extremely popular group of fishes. These fishes have highly divergent life histories and biologies of interest to not only the hobbyist and aquarium trade but are of great interest in aquaculture, scientific studies that may be useful in aquaculture for human food sources, as well as systematic and evolutionary studies.

Aside from the above referenced and logically sound reasons for deeper investigation into the evolutionary relationships of the Cobitoidea, it has been suggested that biodiversity is eventually attributed to gene evolution (Seehausen et al., 2008). As such, a detailed examination of gene evolution should thus provide insight into fundamental questions regarding organismal evolution and diversification as seen in the Cobitoidea. One such question is how gene evolution can contribute to diversification within lineages (Bromham, 2009). Variation of evolutionary rates within or between lineages might be one of the most common phenomena in gene evolution. With the accumulation of abundant molecular data and requisite phylogenies for the identification of lineages for appropriate and meaningful comparisons or evaluations, only with these essential data can the community better understand causes and/or influences of variation, variation in evolutionary rates via anagenesis along lineages, or other types of genetic modifications within a phylogenetic context.

The evolutionary rate of change of a gene could result from at least three potential intrinsic factors that have already been identified. These include 1) efficiency of DNA repair, 2) generation-time effect and/or 3) metabolic rate (Britten, 1986; Laird et al., 1969; Martin

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