Phylogenetic classification of extant genera of fishes of the order Cypriniformes (Teleostei: Ostariophysi)

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Abstract

The order Cypriniformes is the most diverse order of freshwater fishes. Recent phylogenetic studies have approached a consensus on the phylogenetic relationships of Cypriniformes and proposed a new phylogenetic classification of family-level groupings in Cypriniformes. The lack of a reference for the placement of genera amongst families has hampered the adoption of this phylogenetic classification more widely. We herein provide an updated compilation of the membership of genera to suprageneric taxa based on the latest phylogenetic classifications. We propose a new taxon: subfamily Esominae within Danionidae, for the genus Esomus.

Key words: Cyprinidae, Cobitoidei, Cyprinoidei, carps, minnows

Introduction

The order Cypriniformes is the most diverse order of freshwater fishes, numbering over 4400 currently recognized species (Eschmeyer & Fong 2017), and the species are of great interest in biology, economy, and in culture. Occurring throughout North America, Africa, Europe, and Asia, cypriniforms are dominant members of a range of freshwater habitats (Nelson 2006), and some have even adapted to extreme habitats such as caves and acidic peat swamps (Romero & Paulson 2001; Kottelat et al. 2006). Many cypriniforms are important food and recreational fishes, and they are popular in the global ornamental pet trade. The zebrafish, Danio rerio, is a model organism of scientific importance, and has been heavily studied in its development and its genome (Howe et al. 2013). Advancement in sequencing technologies has also allowed the sequencing and publication of whole genome sequences of several cypriniforms (Burns et al. 2015; Wang et al. 2015; Xu et al. 2014; Yang et al. 2016).

Until recently, there was little consensus for the major groupings among families within the Cypriniformes (Conway et al. 2010). Siebert (1987) studied the osteology among all major groups of cypriniforms known at the time, and established the prevailing hypothesis for cypriniform relationships, which recognizes two major subgroupings (Conway et al. 2010). Firstly, the cobitoids have traditionally been classified in multiple families of loaches, alongside the algae eaters (Gyrinocheilidae) and suckers (Catostomidae). In stark contrast, the diverse cyprinoids, which include over 3,000 species and thus constitute the vast majority of cypriniform species, have traditionally been recognized to include two families, Cyprinidae sensu lato and potentially Psilorhynchidae (Conway et al. 2010). Although cyprinoids have long been thought of by many ichthyologists to be morphologically conserved, their morphological diversity rivals that of characiforms (Howes 1991), a clade of fishes currently divided into numerous families. Multiple subgroupings have been recognized within Cyprinidae sensu lato for some time (Howes 1991). More recently, multiple phylogenetic studies have consistently reconstructed major groupings within the cypriniforms, which have validated some of these traditional groupings, as well as rejected the monophyly of others, and demonstrated the non-monophyly of Cyprinidae sensu lato relative to Psilorhynchidae (Chen & Mayden 2009; Mayden & Chen 2010). Because of this, a new phylogenetic
classification for the cypriniforms has been proposed, of which one of the largest changes is recognizing a Cyprinoidei that contains multiple families of fishes previously classified in Cyprinidae sensu lato and new limits of the Cyprinidae itself to a more restricted set of taxa (Cyprinidae sensu stricto). Unfortunately, the adoption of a phylogenetic classification for cypriniforms has been hampered by lack of a centralized reference for what genera belong to what particular family-level groups, but these classifications are distributed across numerous phylogenetic studies. Hence, most scientists continue to recognize Cyprinidae sensu lato, which is rendered non-monophyletic by Psilorhynchidae. Recognition of a broad Cyprinidae masks the morphological and phylogenetic diversity within this group and makes the Cyprinidae and the other families of the Cypriniformes (as well as the related Characiformes, Siluriformes, and Gymnotiformes) unequal taxonomic and phylogenetic units. Further, a broad Cyprinidae limits the use of the Linnean classification scheme to express phylogenetic relationships.

Our aim here is to provide a reference that can be used as a summary for the current understanding of cypriniform phylogeny and a working classification. Though this classification scheme may appear novel to those unfamiliar with cypriniform taxonomic literature, we make relatively few taxonomic changes. The family groups defined herein were defined by previous studies (Chen & Mayden 2009; Mayden & Chen 2010; Kottelat 2012), but the generic composition of the cyprinoid families is distributed among various publications. As in other lists extensively cataloguing and changing the classification of fishes (e.g. Kottelat 2012; Betancur-R et al. 2017), our classification represents a snapshot view of evolutionary relationships given recent analyses. We hope this reference will be useful in providing a foundation to understand the previously proposed phylogenetic classification of family-group names within the Cypriniformes.

Methods

Many of the phylogenetic studies on cypriniform relationships from Siebert (1987) onward refer to two major subdivisions of cypriniforms—cobitoids and cyprinoids—and recognize these taxa at the superfamily level (although see Kottelat [2012] for a recent example that recognizes a suborder for cobitoids). On the other hand, the most recent phylogenetic classification of fishes generally used the subordinal rank rather than the superfamilial rank to group families (Betancur-R et al. 2014), so a recent phylogenomic study on cypriniform fishes (Stout et al. 2016) also recognized these taxa at the suborder level (i.e. Cyprinoidei, Cobitoidei). This usage has been continued in the most recent phylogenetic classification of fishes (Betancur-R et al. 2017). We continue following the Fish Tree of Life convention of using the suborder for the main taxonomic level below the order and above the family here. We state this explicitly to clarify why we depart from the prevailing classification of dividing Cypriniformes into superfamilies (e.g. Siebert 1987; Chen & Mayden 2009; Mayden & Chen 2010; Conway 2011).

To compile a list of all cypriniform genera considered available, we downloaded a list of genera from Catalog of Fishes (Eschmeyer et al. 2017). At the time of this writing, the Catalog of Fishes grouped cypriniform genera into the following taxa: Gyrinocheilidae, Catostomidae, Cobitidae, Botiidae (divided into Botiinae and Leptobotiinae), Nemacheilidae, Balitoridae, Gastromyzontidae, Barbuccidae, Serpenticobitidae, Ellopostomatidae, Vaillantellidae, Psilorhynchidae, and Cyprinidae (divided into eleven subfamilies: Acheilognathinae, Barbinae, Cyprininae, Danioninae, Gobioninae, Leptobarbinae, Leuciscinae, Paedocypridinae, Sundadanioninae, Tincinae, and Xenocypridinae). We then assigned genera/subgenera to tribes, families, and suborders based on recent phylogenetic and taxonomic publications that use and revise family-group names within the Cypriniformes. Two recent molecular phylogenetic studies focus on broader cypriniform relationships: a phylogenomic study incorporating 219 loci and 172 cypriniform species (Stout et al. 2016), and a phylogenetic study based on six nuclear loci: EGR1, EGR2B, EGR3, IRBP, RAG1, and Rh (Hirt et al. 2017). The latter expands on earlier phylogenetic studies across Cyprinoidei, Cobitoidei, and Cypriniformes based on these same loci from the Cypriniformes Tree of Life project (e.g. Chen & Mayden 2009; Chen et al. 2009; Mayden & Chen 2010), and also explores the effect of gene choice on phylogenetic reconstruction; therefore, since it is not entirely independent from some of its previous studies, we focus primarily on the Hirt et al. (2017) latest study when discussing support and conflict for deeper cypriniform relationships from this marker set, but cite other relevant papers for specific taxonomic recommendations. Many other phylogenetic studies focus on particular clades of Cypriniformes, and they will be discussed in relevant sections. In general, we have opted to recognize some of the most recent taxonomic suggestions made by authors based on molecular phylogenetic evidence; however, some of these studies
do not identify morphological synapomorphies or diagnostic characters corresponding to these clades. When such information is available, we cite morphological support corresponding to taxa we are recognizing from the literature, with some caveats, and that morphological support may not have been observed in all members of the taxon as listed here, and that morphological characters may not have been determined using phylogenetic inference but are simply autapomorphic and have diagnostic utility. We referenced van der Laan et al. (2014) for family name authorities. Some family-group names have been proposed or used within the Cypriniformes that are not valid under the code (van der Laan et al. 2014), or are unnamed. We list these names for these clades in quotes as placeholder names (e.g. ‘Osteochilini’, ‘Semilabeonini’, ‘Poropuntiinae’). Additionally, the Squalidus—Hemibarbus clade of Tang et al. (2011), for which no name has been proposed, is listed.

A comprehensive evaluation of the validity of cypriniform genera is outside the scope of this list. We furthermore do not examine subgenera and make no comment on their validity. Our goal is to provide a listing of the placement of genera among family group taxa. Many cypriniform genera are not monophyletic and are in need of taxonomic revision, however, members of these genera usually still belong to a single family-group taxon (e.g. all Schistura belong to Nemacheilidae, all Rasbora belong to the Rasborini tribe), and hence their non-monophyly does not affect the placement of members of this genus in the classification. However, this is not always the case, such as with multiple Puntius species falling outside of the Smiliogastrinae where Puntius is assigned (Yang et al. 2015). We do not list species included in each genus, and because of this, species belonging to a different family, subfamily, or tribe than the genus they are currently assigned to are not explicitly noted.

We restrict our list to recent fishes. The morphological placement of fossil fishes among these clades will require further study given the knowledge of cypriniform relationships from molecular data. This reference is not meant to provide a complete review of cypriniform taxonomic history, which has been reviewed previously. See relevant sections for references reviewing the history of each taxon. The author(s) of all genus-level and species names can be found in Eschmeyer et al. (2017), and authors of all family-level names can be found in van der Laan et al. (2014).

Results and discussion

Gyrinocheilidae, Catostomidae, and Cobitoidei. Within the Cypriniformes are multiple families including benthic species, including the algae eaters of the family Gyrinocheilidae (represented by a single genus, Gyrinocheilus), the suckers of the family Catostomidae, and the diverse loaches, divided amongst numerous families now including Balitoridae, Barbucidae, Botiidae, Cobitidae, Ellopostomatidae, Gasterosteidae, Nemacheilidae, Serpenticobitidae, and Vaillantellidae (Kottelat 2012). The term loach has colloquially been used as a name to refer to members of these families, which together are also strongly supported as a clade (Šlechtová et al. 2007; Conway et al. 2010; Conway 2011; Stout et al. 2016). Previous publications refer to Cobitoidea or Cobitoidei (not always interchangeably), and the clade variably includes or excludes Gyrinocheilus and/or Catostomidae; for consistency, we will refer to the Cobitoidei as a clade exclusively uniting loach families.

Conventionally, Gyrinocheilidae, Catostomidae, and Cobitoidei have been thought to form a single clade, primarily deriving from Siebert’s (1987) work (Conway et al. 2010). Support for the relationships between these taxa, however, has been weak, and various interrelationships have been supported between them (Sawada 1982; Harris et al. 2014). Conway (2011) performed the most comprehensive morphological phylogenetic study on Cypriniformes to date, and was not able to reconstruct strong support for the relationships between Gyrinocheilidae, Catostomidae, Cobitoidei, and Cyprinoidae. Reanalyses of these data have borne the same result (Britz et al. 2014; Liu et al. 2015; Stout et al. 2016), including a modified version of this dataset including the extinct fossil taxon Jianghanichthys, which has shared character states of both cyprinoids and catostomids. The unresolved relationships of Jianghanichthys among cypriniform fishes was used to support the recognition of the only family of Cypriniformes known only from fossils, Jianghanichthyidae (Liu et al. 2015). Furthermore, molecular phylogenetic support for the monophyly of these groups together also remains elusive (Chen et al. 2009), with phylogenetic analyses recovering results such as monophyly (Šlechtová et al. 2007; He et al. 2008; Stout et al. 2016; Hirt et al. 2017), poorly supported relationships or a polytomy between these three clades and Cyprinoidae (He et al. 2008; Hirt et al. 2017; Mayden & Chen 2010; Saitoh et al. 2006), or with cyprinoids as the closest relative to one of these clades (He et al. 2008; Chen et al. 2009; Hirt et al. 2017; Stout et al. 2016). Given the uncertainty of the monophyly of a clade formed by these three taxa, we treat Gyrinocheilidae and Catostomidae
within their own suborders respectively, Gyrinocheiloidei and Catostomoidei, separate from the Cobitoidei and Cyprinoidei, as previously proposed (Stout et al. 2016).

While the interrelationships of Gyrinocheilidae, Catostomidae, and Cobitoidei are uncertain, the membership of taxa to these groups have been stable. Gyrinocheilidae contains a single genus, Gyrinocheilus, including three species distributed in Southeast Asia. The distinctive nature of Gyrinocheilus has long been recognized. Species of Gyrinocheilus have a number of specializations for clinging to rocks in rapidly-flowing water, including lips modified into an oral sucker and the unique presence of spiracles above the gills through which water is inhaled (Roberts & Kottelat 1993). See Conway et al. (2010) and clade K in Conway (2011) for morphological synapomorphies for the family Gyrinocheilidae. The suckers of the family Catostomidae are primarily benthic fishes distributed mostly in North America, with a few Asian species (Smith 1992). Catostomid phylogenetics and classification have been reviewed by Harris et al. (2014), and their classification is reproduced here. The systematics of fossil and extant catostomids was first broadly studied by Smith (1992) incorporating both morphological and biomolecular data. See Smith (1992), Conway et al. (2010), and clade L in Conway (2011) for morphological synapomorphies for Catostomidae. The molecular phylogenetics within Catostomidae have also been explored in numerous studies, as reviewed by Harris et al. (2014). Within Catostomidae, the subfamilies Ictiobiinae, Cycleptinae, Myxocyprininae, Catostominae are recognized, and the Catostominae including the tribes Catostomini, Erimyzonini, Moxostomatini, and Thoburniini are recognized, based largely on Smith’s (1992) phylogenetic results, with subsequent modifications from molecular studies. See Smith (1992) for synapomorphies diagnosing most of these groups, however the classification of Harris et al. (2014) recognizes Myxocyprinus as a separate subfamily (vs. sister to Cycleptus in Cycleptinae) and recognizes Erimyzonini and Thoburniini as distinct from other Moxostomatini (vs. all in a single tribe). Although apomorphies for clades corresponding to Myxocyprininae, Cycleptinae, Erimyzonini, and Thoburniini sensu Harris et al. (2014) are presented by Smith (1992), Smith (1992) does not reconstruct a monophyletic Moxostoma with respect to Thoburniini. The validity of the unique catostomin genera Chasmistes, Deltistes, and Xyrauchen have previously been questioned, as they are repeatedly reconstructed as nested within Catostomus (Chen & Mayden 2012); we tentatively follow Harris et al. (2014) in recognizing these genera as valid. Erimyzonini is occasionally spelled Erimyzon (Harris et al. 2014), however Erimyzont — is the correct stem (van der Laan 2014).

Loaches, fishes of the suborder Cobitoidei, are benthic fishes distributed primarily in Europe and Asia, with a few species in Africa (Kottelat 2012). The monophyly of the loach clade Cobitoidei is consistently recovered in recent morphological and molecular phylogenetic studies. See clade M of Conway (2011) for morphological synapomorphies for the Cobitoidei (note his analysis does not include the more recently-described families Ellopostomatidae, Barbucidae, or Serpenticobitidae). Kottelat (2012) provides the latest phylogenetic classification of Cobitoidei, based on recent molecular phylogenetic studies (Šlechtová et al. 2007; Bohlen & Šlechtová 2009). In general, molecular and morphological studies have converged on four deeply-branching groups of loaches: the Botiidae, the Vaillantellidae, the Cobitidae, and a clade formed by Balitoridae sensu lato (= Barbucidae + Balitoridae + Serpenticobitidae + Gastromyzontidae), Nemacheilidae, and Ellopostomatidae (see further discussion below). See Conway et al. (2010) and clade O of Conway (2011) for morphological synapomorphies for Botiidae, and clade Q for synapomorphies for Cobitidae. See also Sawada (1982) for morphological synapomorphies for Botiidae and Cobitidae. Vaillantella (the sole genus of Vaillantellidae) has a unique morphology among Cypriniformes and is distinguished by an extremely long dorsal fin (Conway et al. 2010); members of this genus have various other characters similar to nemacheilids and botiids. Though morphological classification of this genus has had a tortured taxonomic and phylogenetic history (Saitoh et al. 2006; Šlechtová et al. 2006; 2007; Conway 2011), molecular phylogenetic analyses almost always place Vaillantella as the sister group to a clade formed by all loaches except for Botiidae, and thus it does not belong to any of the traditionally recognized families (Hirt et al. 2017; Šlechtová et al. 2007; Stout et al. 2016). Alternatively, Conway (2011) recovers Vaillantella as sister to Botiidae based on three characters, but two characters are not unique (also found in members of Nemacheilidae) and another character is found in many non-cypriniform otophysans (Conway 2011). See also Nalbant & Bânărescu (1977) and Conway et al. (2010) for description and diagnosis of Vaillantellidae.

With the exclusion of Botiidae, Cobitidae has been consistently recovered as monophyletic by morphological and molecular phylogenetic studies (Šlechtová et al. 2006; 2007; 2008; Chen et al. 2009; Mayden & Chen 2010; Conway 2011; Stout et al. 2016; Hirt et al. 2017). See Conway et al. (2010) and clade Q of Conway (2011) for
morphological synapomorphies of Cobitidae. Cobitids and botiids both have an erectile suborbital spine which has traditionally been used to classify these taxa in a single family, but this character has been either independently gained between these two families and Serpenticobitidae, or independently lost from other cobitoids (Conway 2011). Šlechtová et al. (2008) studied the molecular phylogenetic relationships among members of the family Cobitidae.

Molecular and morphological phylogenetic analyses typically resolve a clade formed by Balitoridae sensu lato (= Barbuccidae + Balitoridae + Serpenticobitidae + Gastromyzontidae), Nemacheilidae, and Ellopustoma. In some older classification schemes, Nemacheilidae and Ellopustoma were considered together with Balitoridae sensu lato (e.g. Siebert 1987), but most recent classification schemes consider the nemacheilids and ellopustomatids as distinct families. Nemacheilidae has not been united by morphological synapomorphies in multiple studies (Sawada 1982; Siebert 1987; Conway 2011), though this family is consistently recovered as monophyletic by molecular phylogenetic studies (e.g. Tang et al. 2006; Šlechtová et al. 2007; Bohlen & Šlechtová 2009; Chen et al. 2009; Mayden & Chen 2010; Liu et al. 2012; Stout et al. 2016; Hirt et al. 2017). Ellopustoma is an unusual small-bodied loach that has been variably placed among Cobitidae, Balitoridae, and Nemacheilidae (Bohlen & Šlechtová 2009; Chen et al. 2009). Although it has not been studied in a morphological phylogenetic framework, multiple molecular phylogenetic studies support its placement in the clade formed by Nemacheilidae and Balitoridae sensu lato (Bohlen & Šlechtová 2009; Chen et al. 2009). Böhlen & Šlechtová (2009) recovered Ellopustoma in a polytomy with Nemacheilidae and Balitoridae sensu lato, while Chen et al. (2009) recover Ellopustoma as sister to Nemacheilidae. Schönhuth et al. (2018) recover Cobitidae as more closely related to Balitoridae, Gastromyzontidae, and Nemacheilidae than Ellopustoma, however this was not strongly supported. For a description and diagnosis for Ellopustomatidae, see Chen et al. (2009).

Prevailing usage of Balitoridae sensu lato (= Barbuccidae + Balitoridae + Serpenticobitidae + Gastromyzontidae) has included a diversity of hillstream loaches and allies, and recent molecular phylogenetic evidence suggests that Barbucca and Serpenticobitis form a clade with these loaches (Šlechtová et al. 2007). Kottelat (2012) had two main arguments for describing and diagnosing two new families for Barbucca and Serpenticobitis respectively. Firstly, including Barbucca and Serpenticobitis in Balitoridae sensu lato would result in a Balitoridae that included “a number of very distinctive groups” (Kottelat 2012). Secondly, Kottelat (2012) argued the distinctive morphologies of Barbucca and Serpenticobitis have resulted in each of these two taxa being classified with multiple different families, and this uncertainty would remain with further research. Balitoridae sensu stricto and Gastromyzontidae correspond to different loach clades of the Balitoridae sensu lato that have been recognized for some time (Hensel 1970; Roberts 1989). Better sampling of balitorids, gastromyzontids, Barbucca, and Serpenticobitis in morphological and molecular systematic studies could clarify the synapomorphies that define these families and resolve relationships within Balitoridae and Gastromyzontidae. Roberts (1989) discusses the validity of previous characters used to diagnose Balitoridae and Gastromyzontidae relevant to Bornean balitorids and gastromyzontids. Balitoridae sensu stricto and Gastromyzontidae are also each supported as monophyletic by multiple molecular phylogenetic studies (Šlechtová et al. 2007; Bohlen & Šlechtová 2009; Randall & Page 2015). Randall & Page (2015), in contrast to Kottelat (2012), recognized the subfamily Gastromyzontinae within a broader Balitoridae (making no comment on Serpenticobitis and Barbucca, but the implication would be that their family-rank names would be considered subfamilies of Balitoridae). We tentatively retain Kottelat’s (2012) classification of recognizing distinct families for these taxa.

Botiidae and Balitoridae are also divided into subfamilies. Based on molecular phylogenetic analysis (Šlechtová et al. 2006), Botiidae is classified into two subfamilies, Leptobotiinae (Leptobotia, Parabotia) and Botiinae (Ambastia, Botia, Chromobotia, Sinibotia, Syncrossus, Yasuhikotakia). In Nalbant’s (2002) original circumscription of these taxa (at the tribe level), Sinibotia was placed among Leptobotiinae instead of Botiinae, therefore his proposed morphological characters defining leptobotines and botiines need to be re-evaluated; the most striking character that does differ between the two subfamilies is that botiines are tetraploid, a derived state among loaches (Šlechtová et al. 2006). For the Balitoridae sensu stricto, which is equivalent to Balitorinae sensu Randall & Page (2015), we also elevated the constituent tribes Balitorini and Homalopteroidini Randall & Page (2015) recognized to subfamily level. In their phylogenetic analysis of molecular data, Randall & Page (2015) were also missing several genera of Balitoridae: Bhavania Hora 1920, Cryptotora Kottelat 1998, Ghatya Randall & Page 2015, Neohomaloptera Herre 1944, and Travancoria Hora 1941. These genera are listed as Balitoridae incertae sedis. Nemacheilidae and Gastromyzontidae have also been classified into subfamilies, but these groupings may
not be natural, so are not followed here. Prokofiev (2010) presented a phylogenetic classification based on morphological characters for four tribes within Nemacheilidae (as Nemacheilinae), but the phylogenetic support for these taxa are poor. Prokofiev (2010) states that his Yunnanilini is not supported by synapomorphies and that a phylogenetic revision is needed. The Prokofiev (2010) tribes are also rejected as monophyletic in molecular phylogenetic studies thus far, despite relatively low taxon sampling across molecular studies for Nemacheilidae; some examples include recovery of *Micronemacheilus*, a member of Yunnanilini, nested within Lefuinini (Liu et al. 2012), *Schistura dabryi*, a member of Nemacheilini, nested within Triplophysini (Liu et al. 2012), and *Tuberoschistura*, a member of Nemacheilini, potentially having a closer relationship to members of Triplophysini than other members of Nemacheilini such as *Acanthocobitis* (Chen et al. 2009). Given this conflict among phylogenetic studies, we tentatively do not recognize subfamilies within the Nemacheilidae. Gastromyzontidae has also been previously classified into subfamilies, however some of these groupings may not be natural, and it may be premature to recognize subfamilies (Kottelat 2012).

**Cyprinoidei.** Cyprinoidei includes all members of the Cyprinidae *sensu lato*, *Psilorhynchus*, and *Paedocypris*. The systematics and classification of Cyprinidae *sensu lato* have previously been reviewed (Hensel 1970; Howes 1991; Conway et al. 2010). We briefly summarize the history here to provide context for the classification presented here. Given the morphological diversity of cyprinoids, major groupings have previously been recognized based on characters such as the presence and innervation of barbels, the number of rows and shape of teeth on the pharyngeal jaws, the presence of a pre-anal keel formed by scales, and the number of rays and presence of spines in the dorsal and anal fins (Hensel 1970; Howes 1991). For convenience, we will refer to the subclades following the families suggested by recent molecular phylogenetic studies, and we tentatively retain the family level classification as proposed by some recent phylogenetic studies (Chen & Mayden 2009; Mayden & Chen 2010). Some of these major groups include the Cyprinidae *sensu stricto* (including carps, barbs, and allies), Leuciscidae (minnows of Europe, Asia, and North America), Danionidae (danios, rasboras, and allies), Acheilognathidae (bitterlings), Gobionidae (gudgeons), and Xenocyprididae (Asian carps, culters, and allies). Some minor groups have also been supported by molecular phylogenetic evidence each represented by one or two genera, including the Leptobarbidae (mad barb, sultan fish), Sundadanionidae, Tanichthyidae, and Tincidae (tench). Some other groups that have traditionally been recognized (e.g. cultrins, schizothoracins, squaliobarbins) are recovered within these major clades and will be commented on further in relevant sections addressing each taxon. Hence, the Cyprinoidei in this current scheme is divided into twelve families: Acheilognathidae, Cyprinidae *sensu stricto*, Danionidae, Gobionidae, Leptobarbidae, Leuciscidae, Paedocyprididae, Psilorhynchidae, Sundadanionidae, Tanichthyidae, Tincidae, and Xenocyprididae.

Possible alternative classification schemes with fewer families have previously been presented. Chen et al. (1984) and Cavender & Coburn (1992) both resolve two major groups of Cyprinidae *sensu lato*, although varied on the placement of *Tinca*. Subsequently, using RAG2 data, Wang et al. (2007b) did not recover the danionins with the Leuciscinae and considered it a separate subfamily, and thus classified Cyprinidae *sensu lato* into three subfamilies. Three major clades corresponding to these groups have continued to generally be recovered by multiple molecular phylogenetic studies with the addition of *Sundadanio, Leptobarbus*, and *Tanichthys* to the clade corresponding to Leuciscinae *sensu Wang et al.* (Saitoh et al. 2006; Chen & Mayden 2009; Mayden & Chen 2010; Stout et al. 2016; Hirt et al. 2017). Conway (2011) recovered relationships consistent with Cavender & Coburn’s two-subfamily scheme in the most comprehensive morphological study of the order to date, but bootstrap support was weak for the monophyly of Leuciscinae *sensu* Cavender & Coburn. Though these studies and others have classified Cyprinidae *s.l.* with two or three subfamilies, the prevailing classification for the last few decades has instead been to recognize many more subfamilies, up to a dozen (e.g. Howes 1991; Nelson 2006; Saitoh et al. 2006; Kottelat & Freyhof 2007; Rüther et al. 2007; Chen & Mayden 2009; Conway et al. 2010; Mayden & Chen 2010; Liao & Kullander 2012; Eschmeyer & Fong 2017; Schönhuth et al. 2018), which as noted are recognized at the family rank here.

The genus *Psilorhynchus*, including fishes referred to as torrent minnows or stone carps, has previously been classified as either a cobitoid or a cyprinoid, and has been recognized as a monogeneric family, Psilorhynchiidae (Conway et al. 2010; Conway 2011). Psilorhynchids bear a coarse similarity to balitorid loaches due to their convergent ecological specialization to a benthic lifestyle in rapidly flowing waters (Conway 2011). While prior morphological studies have either suggested a closer affinity to cobitoids or cyprinoids, the most recent
morphological investigation focusing on Psilorhynchidae and its placement among cypriniforms have demonstrated support for its relationship in a clade as sister to the remaining cyprinoids (Conway 2011). Molecular phylogenetic evidence consistently supports a close relationship of Psilorhynchidae to cyprinoids, with earlier studies either not having sufficient taxon sampling to address relative relationships between Psilorhynchidae to taxa across cyprinoid diversity (Šlechtová et al. 2007), or recovering uncertain relationships for Psilorhynchidae among cyprinoids (He et al. 2008). However, more recent molecular phylogenetic studies with increased taxon sampling have recovered a relationship where Psilorhynchidae is sister to Cyprinidae sensu stricto herein (Mayden & Chen 2010; Chen et al. 2013; Hirt et al. 2017; Schönhuth et al. 2018), which renders Cyprinidae sensu lato paraphyletic. One possible option to resolve this is to recognize Psilorhynchus within Cyprinidae sensu lato at the subfamily level (Chen 1980; He et al. 2008; Liao & Kullander 2012). Most recent classifications, including phylogenetic classifications, have recognized Psilorhynchidae as a distinct family, either co-equal with Cyprinidae sensu lato (Nelson 2006; Conway 2011), or as a member of a Cyprinoidei including multiple families (Chen & Mayden 2009; Mayden & Chen 2010). The clad including all members of the Psilorhynchidae is supported by numerous morphological synapomorphies (Conway 2011).

Paedocypris is a recently-discovered genus of miniature fishes that include some of the smallest vertebrates in the world (Kottelat et al. 2006). Morphological phylogenetic studies have suggested a clade of miniature, paedomorphic fishes including Paedocypris, Sundadanio, and Danionella aligned with cyprinoids (Britz & Conway 2009; Britz et al. 2014), though studying the phylogenetic placement of these taxa using morphology is challenging due to their developmental truncation (Hirt et al. 2017). Molecular phylogenetic studies of the placement of Paedocypris have led to multiple conflicting hypotheses including as members of the Danionidae (Rüber et al. 2007; Tang et al. 2010), as sister to the remainder of Cypriniformes (Mayden & Chen 2010; Hirt et al. 2017), or as sister to the Cyprinoidei (Stout et al. 2016; Hirt et al. 2017). The Cyprinoidei including Paedocypris and Psilorhynchus is diagnosed by the presence of the basioccipital masticatory plate, a keratin-covered process at the anterior end of the basioccipital, upon which the pharyngeal jaws work against to break down food (Britz et al. 2014). Paedocypris, and thus Psycypridae, is unique among cypriniforms and can be easily distinguished by numerous apomorphic characters (Kottelat et al. 2006).

Acheilognathidae, the bitterns, are distinguished from other cyprinids by sexually dimorphic characters such as the presence of an ovipositor in females used to deposit eggs within the gill chambers of mussels, and tubercle-bearing plates in males (Howes 1991; Kottelat & Freyhof 2007). The taxonomic history of Acheilognathidae was reviewed by Chang et al. (2014), and the membership of genera to this family are reproduced here. More recently, a new genus of acheilognathid, Sinorhodeus, was described and is additionally included here (Li et al. 2017). Li et al. (2017) also questioned the diagnoses of Pararhodeus and Paratanakia, but retained them as distinct genera.

The phylogenetic placement of the tench of the genus Tinca has long remained elusive due to its mosaic of characteristics that were used to assign it as either more closely related to leuciscids or to cyprinids, though its recognition as a unique lineage within cyprinoids has long been recognized (Howes 1991; Cavender & Coburn 1992). The genus Tinca has the unique autapomorphy among cyprinoids of possessing a forked pelvic bone with convergent tips (Cavender & Coburn 1992).

Leptobarbus, Sundadanio, and Tanichthys have all previously been considered members of the Danionidae (Kottelat & Witte 1999; Liao & Kullander 2012). These genera all possess a Y-shaped ligament connecting the kinethmoid to the ethmoid, the ancestral state in cyprinoids, but this is absent in all danionids (Liao & Kullander 2012). Molecular phylogenetic studies recover these genera as branches within a clade formed by Tinca, Acheilognathidae, Gobionidae, Leuciscidae, and Xenocyprididae, but these genera were not reconstructed with any of these major groups (Chen & Mayden 2009; Mayden & Chen 2010; Stout et al. 2016; Hirt et al. 2017), leading to the recognition of the separate families Leptobarbidae, Sundadanionidae, and Tanichthyidae. Leptobarbus morphologically appears much like a large bodied Rasbora (Roberts 1989), and Leptobarbus was thought to be related to danionids (Liao & Kullander 2012). Although distinguished from danionids by the Y-shaped ligament, further morphological research is needed for this taxon to study its phylogenetic relationships among cyprinoids and determine other characters that may distinguish it from other cyprinid families. The paedomorphic Sundadanio was also originally assigned to the danionids (Kottelat & Witte 1999). Morphological phylogenetic analysis support a membership of Sundadanio to cyprinoids, but resolution among cyprinoids is poor (Britz et al. 2014). Britz et al. (2011) described a new paedomorphic genus and species Fangfangia spinicleithralis as...
morphologically similar to *Sundadanio*, and we provisionally place it in Sundadanionidae; see Britz et al. (2011) for putative synapomorphies for a clade formed by *Fangfanga* and *Sundadanio*, two of which are based on anal-fin ray characteristics, and also the unique characteristic of the lateral processes of the first centrum being directed ventrally and connected to the pharyngeal process of the basioccipital (vs. directed laterally). See Mayden & Chen (2010) for a morphological diagnosis of the family Tanichthyidae.

The families Cyprinidae, Gobionidae, Leuciscidae, and Xenocyprididae are described in more detail below.

**Cyprinidae sensu stricto.** With the elevation of Cyprinidae *sensu lato* to Cyprinoidei, we recognize a narrower Cyprinidae including carps, barbs, and their allies. This group still includes a large diversity of cyprinid fishes, from Africa and Eurasia (Yang et al. 2015). The cyprinids have previously been recognized as a distinct grouping within the cyprinoids (Cavender & Coburn 1992). See Cavender & Coburn (1992) and clade E of Conway (2011) for morphological synapomorphies diagnosing this group.

Within the Cyprinidae, multiple subgroups such as the cyprinins, barbons, labeonins, garins, oreins, and schizothoracins have previously been recognized, as reviewed by Yang et al. (2015). A phylogenetic classification of the Cyprinidae was recently presented by Yang et al. (2015), including listing genera considered *incertae sedis* within the Cyprinidae. The phylogenomic investigation by Stout et al. (2016) was congruent in the monophyly of clades corresponding to almost all of these taxa, although interrelationships between these clades differed some between studies. While the membership of clades is consistent across studies, we do note that the ancestral hybridization and the polyploidization of multiple clades within the Cyprinidae *s.s.* complicates reconstruction of relationships between clades, and this deserves further research.

We elevate the tribes of Yang et al. (2015) to the subfamily level. Hence, within Cyprinidae we recognize the subfamilies Labeoninae, Probartinae, Torinae, Smiliogastrinae, Cyprininae, Acrossocheilinae, Spinibarbininae, Schizothoracinae, Schizopygopsinae, and Barbinae, as well as ‘Poropuntiinae’. Yang et al.’s (2015) use of the ‘Poropuntiini’ (= ‘Poropuntiinae’) after Poropuntii Rainboth 1991, is a matter of convenience; they stated that the name was not available because no diagnosis was provided, Article 13.1.1 of the ICZN (see also van der Laan et al. 2014). So far, no family-group names exist for any members of this clade. Morphological diagnoses among cyprinid subfamilies previously presented by Yang et al. (2015) were based on characters including varying levels of ploidy, serration on fin rays, scale patterns, and morphology of the lips. See Yang et al. (2015) for morphological diagnoses of their new family group names Probartinae, Acrossocheilinae, and Spinibarbininae. Yang et al. (2015) also discuss morphological diagnoses for the Schizothoracinae, Schizopygopsinae, and ‘Poropuntiinae’. Yang et al. (2015) stated explicitly there is a lack of morphological synapomorphies for the Cyprininae.

Labeoninae is recovered as sister to the remainder of Cyprinidae in multiple phylogenetic studies (Conway 2011; Yang et al. 2015; Stout et al. 2016). Monophyly of this group has been previously supported by both morphological and molecular studies, as reviewed by Yang et al. (2012a). See Cavender & Coburn (1992), Stiassny & Getahun (2007), and Conway (2011) for morphological synapomorphies supporting this group. In recent classifications, there have been multiple schemes by which Labeoninae has been divided. Stiassny & Getahun (2007) split Labeoninae into two subgroups: Labeina and Goinina. Yang et al. (2012a) divide the Labeoninae into four subgroups: Labeina, Garainina, ‘Semilabeonina’, and ‘Osteochilina’. The Labeina and Garainina sensu Stiassny & Getahun (2007), based on morphological data, is significantly rejected by Yang et al.’s (2012a) molecular data, and Stiassny & Getahun’s Labeoina was also not recovered as monophyletic in Stout et al. (2016). We opt to follow Yang et al.’s (2012a) classification, and raise their subtribes to tribe level, resulting in four tribes: Labeonini (using the stem *Labeon-*), given the genitive case of *Labeo is Labeonis*, Goinini (using the stem *Goin-*, pers. comm. van der Laan), ‘Semilabeonini’, and ‘Osteochilini’. ‘Semilabeonini’ and ‘Osteochilini’ are names used here out of convenience in the sense that Yang et al. (2012a) used them, because family-group names for these clades have not been formally described and Yang et al.’s (2012a) names are not valid according to the code (van der Laan et al. 2014). We follow Yang et al. (2012a) in tentatively recognizing *Diplocheilichthys*, *Parapsilorhynchos*, and *Similabeo as incertae sedis* within Labeoninae. Yang et al. (2012a) also comment that the status of *Schismatorhynchos* requires further investigation, and we tentatively recognize *Schismatorhynchos as incertae sedis* within Labeoninae. Kottelat (2013) recognizes *Discolabeo* as a synonym of *Garra*, Zhang et al. (2016) recognize this genus as valid, as indicated by Eschmeyer et al. (2017). We were not able to obtain this text. Given Kottelat’s (2013) recognition of *Discolabeo as Garra*, we recognize *Discolabeo* within Goinini.

Many species often classified as *Garra* are not within Goinini, but rather are placed in the ‘Semilabeonini’. 

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**PHYLOGENETIC CLASSIFICATION OF CYPRINIFORMES**

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Yang et al. (2012a) recovered multiple species of Garra within ‘Semilabeonini’, and recognize Ageneiogarra Garman 1912 for Garra imberba (the type species of Ageneiogarra) and Garra micropulvinus, as well as Placocheilus Wu 1977 given the separation of P. cryptonemus. Wang et al. (2007b) also recovers another species of Garra, G. pingi, as related to members of ‘Semilabeonini’. Lothongkham et al. (2014) consider Placocheilus as a synonym of Garra. Wang et al. (2014) studied the relationships of Garra imberba. Although they included Garra imberba, the type species of Ageneiogarra, and Placocheilus caudofasciatus, the type species of Placocheilus, they recognized both genera within Garra. They recover two major clades of Garra corresponding to species that belong to Garrini and species that belong to ‘Semilabeonini’, the latter including Placocheilus and Ageneiogarra. Wang et al. (2014) also recovered ‘Placocheilus’ dulongensis as clearly more closely related to true Garra than it is to Placocheilus caudofasciatus; hence, some species of Placocheilus should be considered Garra. In summary, multiple studies have demonstrated that Placocheilus and Ageneiogarra are distinct from Garra. Vinagarra has also been recently described based on distinctive mouth characteristics, and includes the species Vinagarra findolabium (Endruweit 2014). Vinagarra has morphological similarities to Placocheilus and Discogobio, Ageneiogarra, and Sinigarra (Endruweit 2014), all previously recovered as part of ‘Semilabeonini’. Molecular data support the placement of Garra findolabium in a clade with Ageneiogarra and Placocheilus, although the interrelationships of the clade are not well resolved (Wang et al. 2014). We tentatively place Vinagarra within ‘Semilabeonini’. Sinigarra napeonis is nested within a clade formed by Ageneiogarra species based on an analysis including three mitochondrial genes and four nuclear genes (Zheng et al. 2016). Therefore, Sinigarra could be a synonym of Ageneiogarra, given that Ageneiogarra has priority over Sinigarra. Zheng et al. (2016) also reconstructed relationships among Chinese karst labeonines, recovering Prolixichelus, Paraqianlabeo, and Cophecheilus as closely-related to other members of ‘Semilabeonini’. Hence, they are listed under ‘Semilabeonini’ here.

The relationships of Chagunius within Cyprinidae have been uncertain. Rainboth (1986; 1989) recognized a similarity between Chagunius, Hypselobarbus, and Discerodontus and hypothesized they formed a clade, but Yang et al. (2012b; 2015) demonstrated that these genera are not each other’s closest relatives. Hypselobarbus is part of Torinae, while Discerodontus is part of the ‘Poropuntiinae’. Yang et al. (2015) classified Chagunius in Smiligostrinae, although they recovered it in variable places including grouped with the Smiligostrinae from mitogenome data (80% bootstrap support), sister to ‘Poropuntiinae’ by RAG1 (although with less than 50% support), and sister to Aaptosyax from multiple mitochondrial genes (although with less than 50% support). In Stout et al. (2016), C. chagunio was placed in different parts of Cyprinidae in concatenation and coalescent-based analysis; concatenation placed it as sister to a group formed by Spinibarbinæ, Acrossocheilinæ, Schizopygopsinæ, Torinae, and Barbinae, while coalescent-based analysis placed it more closely-related to the clade formed by Smiligostrinae + ‘Poropuntiinae’, although with poor support (below 50% bootstrap). Given this conflict and uncertainty for the placement of Chagunius, rather than listing Chagunius as a smiliogastrine, we consider Chagunius as incertae sedis within the Cyprinidae.

Barbus was viewed by Myers (1960) as a “monstrous aggregation”. Through a series of taxonomic works, Barbus was whittled to just some species of Eurasian tetraploids and the diploid ‘Barbus’ of Africa (reviewed by Hayes & Armbruster 2017). Yang et al. (2015) demonstrated that members of Barbus sensu lato were divided among multiple groups (subfamilies here), including the Barbinae, Torinae, and Smiligostrinae. Yang et al. (2015) do not present explicit morphological diagnoses for these barb groups. As part of recognizing a monophyletic Barbus and Smiligostrinae, Yang et al. (2015) recognized a diploid genus of small African barbs, Enteromius, which is now largely recognized as valid, though the genus may require further revision (Skelton 2016; Hayes & Armbruster 2017). Borkenhagen (2017) reconstructed the molecular phylogeny of Torinae, and considered Pterocapoeota, Arabibarbus, Carasobarbus, and Mesopotamichthys as valid. Vreven et al. (2016) review the history of hexaploid members of Torinae, primarily of the genus Labeobarbus, including species formerly classified in Varicorhumus, and the closely-related genera Acapoeota and Sanagia. Ecchathalakenda was described by Menon (1999) for a single species of Hypselobarbus-like fish. Pethiyagoda et al. (2012) tentatively treat this genus as valid. The phylogenetic placement of this taxon has not yet been studied. We tentatively place it as incertae sedis at the level of Cyprinidae. Puntius is here listed as part of Smiligostrinae, but some species currently recognized as Puntius are clearly not members of this group (Yang et al. 2015), hence a revision of this genus is needed.

Within the Schizothoracinae, Yang et al. (2015) recovered the genus Schizothorax as non-monophyletic with
respect to *Aspiorhynchus* and *Schizopyge*, which were nested within this diverse genus. Yang et al. (2015) argue it is premature to revise the genus *Schizothorax*, and retained these genera as valid. They did not comment on Kottelat’s (2013) usage of *Oreinus* for a few species of *Schizothorax*. In Yang et al.’s (2015) analysis, the circumscription of *Oreinus* as defined by Kottelat (2013) is not monophyletic. We thus list *Oreinus* within Schizothoracinae, which is consistent with Yang et al.’s (2015) call that a revision of *Schizothorax* is needed.

We tentatively place *Spinibarbichthys* along with *Spinibarbus* in Spinibarbiniae. This taxon has not been studied in a phylogenetic framework but it is described as similar to *Spinibarbus*, and has previously been considered a subgenus of *Spinibarbus* (Duong et al. 2007).

*Prolabeo* and *Prolabeops* from West Africa are treated as incertae sedis in the Cyprinidae. The genera share a keratinized lower jaw with Labeoninae and some members of Torinae. Authors have suggested an affinity of *Prolabeo* to *Labeo* and *Labeobarbus* (Norman 1932; Daget 1984; Lévêque et al. 1994) and an affinity of *Prolabeops* to *Enteromius* and *Garra* (Thys van den Audenaerde 1965, 1974). Reid (1982) suggested that both genera lack synapomorphies of the Labeoninae, but they were not treated in the recent review of the African Torinae by Vreven et al. (2016). The species additionally share some resemblance to African Smiliogastriniae, making placement of the genera within the Cyprinidae uncertain at this time. Yang et al. (2012a) considered *Prolabeo* and *Prolabeops* as members of Labeoninae incertae sedis, though did not include them in their molecular phylogenetic analysis.

*Caecocypris basini*, a cave species from Iraq, was recognized as incertae sedis within Cyprinidae by Bannister & Bunni (1980) because of the lack of a putative surface ancestor. They also noted similarities to the cave Barb of Somalia, *Barbopsis*, which they suggested was parallelism. Despite the absence of barbels, a maxillary foramen is present; this foramen allows the innervation of the rostral barbel as found in other cyprinoids (Banister & Bunni 1980). In size and form, the species resembles that of the African small barbs (*Enteromius* and related taxa); however, no similar surface species occur in the Middle East and *Caecocypris* has not been analyzed phylogenetically. It seems most likely that *Caecocypris* belongs to Cyprinidae, but we are unsure of which subfamily it would belong to, so we recognize it as incertae sedis in Cyprinidae.

**Gobionidae.** The family Gobionidae, the gudgeons, is one of the most long-recognized subfamilies among the cyprinoids, with most species distributed in East Asia and the remaining in Europe (Tang et al. 2011). The gudgeons are distinctive among cyprinoids and it has been previously suggested that a separate family should be recognized (Kottelat & Freyhof 2007). See Tang et al. (2011) for a review and for the taxonomy reproduced here, with modification as described below. See Bănărescu & Nalbant (1973) for a morphological diagnosis for the Gobionidae.

Molecular phylogenetic studies strongly recover a monophyletic clade of Gobionidae including three or four clades. Tang et al.’s (2011) recent phylogenetic analysis of the Gobionidae recovered three major clades: Gobioninae, Sarcocheilichthyinae, and a *Hemibarbus—*Squalidus clade. Gobioninae includes *Gobiobotia*, the type genus of a group recognized by previous workers called the Gobiobotiinae, but Tang et al. (2011) chose to synonymize the group with Gobioninae. Though Jiang & Zhang (2013) recognized three tribes within the Gobioninae, they use these names for convenience as not all three groups were monophyletic, and thus we do not recognize these tribes here in this phylogenetic classification. The placement of *Coreius* was reconstructed with poor support in a polytomy with Sarcocheilichthyinae and Gobioninae in Tang et al. (2011), thus its placement among those three clades was uncertain. Stout et al. (2016) also recovered three major clades corresponding to the clades identified in Tang et al. (2011), but *Coreius* was not included in their study. Zhao et al. (2016) studied phylogenetic relationships of the Gobionidae using mitogenomes. These authors recovered three clades corresponding to those recovered in Tang et al. (2011), and they recovered strong bootstrap support for *Coreius* forming the sister clade to the clade formed by Sarcocheilichthyinae + Gobioninae; hence, *Coreius* should not be considered part of a monophyletic Sarcocheilichthyini, and we consider it incertae sedis.

Morphological synapomorphies for the subfamilies of Gobionidae were not presented (Tang et al. 2011). Although gudgeons are primarily benthic, the Sarcocheilichthyinae, unlike most gudgeons, include mostly species that have terminal (vs. inferior) mouths (Tang et al. 2011).

The placement of one *Belligobio* species in Tang et al.’s (2011) phylogeny within *Hemibarbus* prompted them to transfer this species to *Hemibarbus*; however, since they did not study the type species, they could not determine the validity of *Belligobio*, and so they retained it as valid. *Placogobio* Nguyen 2001 was described from Vietnam (Kottelat 2013; Eschmeyer et al. 2017). Eschmeyer et al. (2017) provisionally placed this genus within...
Gobionidae. We were unable to obtain the description of Placogobio, and also tentatively recognize Placogobio as Gobionidae incertae sedis. Tang et al. (2011) recovered a clade where the species from the genera Biwia, Microphysogobio, Platymachileus, and Huigobio did not form monophyletic clades, though retained these genera as valid and argued for a need to revise these taxa. Jiang & Zhang (2013) evaluated the validity of species of these genera and maintained these genera as valid, including Huigobio. With additional taxon sampling, Huang et al. (2016) recovered Huigobio nested among species of Microphysogobio, and thus considers Huigobio as a synonym of Microphysogobio. We follow Huang et al. (2016) in recognizing Huigobio as a synonym of Microphysogobio, though a comprehensive taxonomy and phylogeny of Microphysogobio remains unresolved (Jiang & Zhang 2013).

Xenocyprididae. Xenocyprididae is a morphologically diverse clade of fishes including species that have been previously grouped as various subfamilies, such as Cultrinae, Hypophthalmichthyinae, Squaliobarbinae, and others, as reviewed in Tang et al. (2013a). Although morphological definitions have identified many of the subclades of the Xenocyprididae, the Xenocypridinae has not generally been recognized as a single group. These groups were more recently identified as a clade in a molecular phylogenetic study, and given the name Oxygasterinae (Tang et al. 2013a; b); however, Kottelat (2013) determined that this name was unavailable because it was not based on the genus Oxygaster van Hasselt 1823, and that Xenocypridinae is an available name for this group and has precedence. See Tang et al. (2013a) for a review of morphological support for a clade corresponding to the Xenocyprididae.

The opsariichthyines have been recognized for some time to represent a natural group (Chen 1982; Wang et al. 2007a), and several studies have demonstrated that they are sister to the remaining species of xenocypridids (Tang et al. 2013a; Huang et al. 2017). These species have an external morphological similarity to danionids, and were previously considered among them (Tang et al. 2010), but can be morphologically distinguished from danionids by the presence of a Y-shaped ligament connecting the kinethmoid and the ethmoid, which is found in many cyprinoids but not in any danionids (Liao et al. 2011; Liao & Kullander 2012). Opsariichthyinae includes the genera Candidia, Nipponocypris, Opsariichthys, Parazacco, and Zacco (Tang et al. 2013a; Huang et al. 2017; Ito et al. 2017). They are distinguished among cyprinoids by a long anal fin and the separation of the left and right supratemporal canals of the cephalic lateral line system (Ito et al. 2017). A subfamily Xenocypridinae, including all remaining genera of Xenocyprididae exclusive of Opsariichthyinae, is also recognized herein. In non-opsariichthyine xenocypridids, leuciscids, and gobionids, the left and right supratemporal canals are connected, while it is independently separated in the acheilognathids and opsariichthyines (Ito et al. 2017).

Multiple unstudied genera are here placed provisionally within Xenocyprididae as incertae sedis, though we note that given the absence of a long anal fin in these genera, they are likely not members of the Opsariichthyinae as currently diagnosed. We follow Tang et al. (2013a) in provisionally placing Anabarilius, Longiculter, Pogobrama, and Rashorichthys within Xenocyprididae, but these genera have not been studied in a molecular phylogenetic framework. Tang et al. (2013a) mention that the classification of Atrilinea is uncertain, however they mention that Chen’s (1987) phylogenetic analysis suggests Atrilinea may possibly belong to Xenocyprididae. We provisionally place this genus within Xenocyprididae, but echo Tang et al.’s (2013a) call that further study is warranted. Eschmeyer et al. (2017) list Araiocypris and Gymnodanio within Xenocypridinae (= Xenocyprididae) but this appears to be without precedence. We continue this recognition here, but note there is also uncertainty with the respect to their membership here. Araiocypris batodes is a small cyprinoid described from two specimens from northern Vietnam with reduced cephalic sensory system and presence of a soft ventral keel, but no more specific determination of its relationships was possible (Conway & Kottelat 2008). Tang et al. (2010) comment that the placement of Gymnodanio to Danionidae could not be confirmed. The only character suggested for its relationship to other fishes is a similar fin ray count to Barilius (Chen & He 1992), a genus of Chedrinae within Danionidae. Gymnodanio has some unique characters, including a naked body except for lateral line scales, a decurved lateral line, and a soft keel between the pelvic fins and anus. In addition, we recognize Oxygaster as a member of Xenocyprididae and Xenocypridinae. Although multiple studies have been congruent in recognizing Oxygaster within this group (Tang et al. 2013a; b), a recent study has placed this genus as outside of the Xenocyprididae and sister to Leuciscidae (Schönhuth et al. 2018). We tentatively follow Tang et al. (2013a; b), but the phylogenetic relationships of Oxygaster warrant further study.

Danionidae. The classification of Danionidae has been in recent flux with regards to the inclusion of
Paedocypris and Sundadanio, but we exclude them here based on the results of multiple molecular phylogenetic studies (Mayden & Chen 2010; Stout et al. 2016; Hirt et al. 2017). The grouping equivalent to Danionidae has previously been referred to as ‘rasborins’ in much of the phylogenetic literature (e.g. Howes 1991; Cavender & Coburn 1992), though more recently it was shown the family group name Danionidae has priority (Tang et al. 2010). See Cavender & Coburn (1992) for morphological synapomorphies of danionids excluding Opsariichthys and Zacco (which as noted above are xenocypridids). Also, danionids share the absence of the Y-shaped ligament connecting the kinethmoid and the ethmoid, although this absence is also found in some members of other cyprinoid families (Liao & Kullander 2012).

We recognize three major clades in Danionidae that have been previously recovered (Liao et al. 2011; Tang et al. 2010), herein recognized as subfamilies of the same rank: Danioninae, Rasborinae, and Chedrinae. Liao et al. (2011) suggested that the Danioninae and Chedrinae are sister clades and united them under a single taxon of the same rank as Rasborinae. While this conflicted with earlier molecular phylogenetic analyses (Rüber et al. 2007; Mayden & Chen 2010; Tang et al. 2010), a sister-group relationship between Chedrinae and Danioninae was strongly supported by phylogenomic analyses (Stout et al. 2016). See Liao et al. (2011) for morphological synapomorphies supporting each of these three clades.

There has been some conflict on the placement of the genus Esomus among danionid groups. In a phylogenomic analysis, Esomus was recovered as a lineage sister to the remaining subfamilies of Danionidae (Stout et al. 2016). This differs from previous morphological and molecular studies, which have variably suggested Esomus may be a danionine, rasborian, or chedrine (see Stout et al. 2016 for more details). Liao et al. (2011) recovers two non-homoplasious morphological synapomorphies that are exclusive to Chedrinae and Esomus that support their close relationship: a reduced or absent postcleithrum and the orientation of the postcleithrum relative to the ribs (Liao et al. 2011); however, given that Esomus does not possess a postcleithrum, it does not actually share the latter character state with other chedrines. Also, there is homoplasy among cyprinoids for the presence of the postcleithrum (Liao et al. 2011), so the morphological support for a close relationship of Esomus to Chedrinae may be inflated by this absence and the inapplicability of the postcleithrum orientation. Without these postcleithrum characters, Chedrinae and Esominae are not diagnosed by any non-homoplasious synapomorphies in Liao et al.’s (2011) study.

Based on morphological phylogenetic evidence, Bengala elanga (monotypic) is supported as closely related to Luciosoma (Liao et al. 2011; 2012), and we recognize it among the Chedrinae. The placement of Thryssocypris among the cyprinoids is unclear but members of this genus have some potential similarities with danionids (Howes 1991; Tang et al. 2010), so we tentatively place it incertae sedis in Danionidae. We recognize members of Danio, Celestichthys, and Brachydanio as a single genus (Danio) following Kullander (2015). Importantly, this continues recognition (and thus provides taxonomic stability) to the species Danio rerio within Danio, which would be moved to Brachydanio if Danio is split. We feel that recognizing Danio rerio in a different genus would be problematic for what has become an important model organism in biology (McCluskey & Postlethwait 2015), and suggest the use of subgenera within Danio to recognize these clades.

Kottelat (2013) suggested that Opsaridium Peters, 1854 and Sagittabarilius Fowler, 1936 are available names for African Raiamas, which are not closely related to the Asian Raiamas bola and R. guttatus according to molecular analyses (Liao et al. 2012). Since then, a molecular phylogenetic analysis demonstrated that Opsaridium zambezense (the type species of Opsaridium) and Raiamas salmolucius (the type species of Sagittabarilius) are relatively closely related (Sungani et al. 2017). Hence, we recognize Sagittabarilius as a synonym of Opsaridium.

Leuciscidae. The minnows of Leuciscidae are found primarily in Europe, Asia, and North America, and are dominant members of the European and North American cypriniform assemblages (Cavender & Coburn 1992; Kottelat & Freyhof 2007). See “Monophyly of Phoxinins & Leuciscins” in Cavender & Coburn (1992) and Bogutskaya (1992) for morphological synapomorphies for Leuciscidae. The Leuciscidae has previously been divided into two major clades: Leuciscinae and Phoxininae (Cavender & Coburn 1992). The Leuciscinae includes primarily Eurasian genera, and are highly diverse in Europe, and also includes the North American species Notemigonus crysoleucas (Cavender & Coburn 1992; Kottelat & Freyhof 2007; Schönhuth et al. 2018). The Phoxininae sensu Cavender & Coburn includes all North American native cyprinoids (except for N. crysoleucas), and some Eurasian genera (Imoto et al. 2013). See Cavender & Coburn (1992) for morphological synapomorphies supporting each of these clades.

Recently, the Phoxininae sensu Cavender & Coburn were divided into multiple subfamilies corresponding to
major clades that have been supported across multiple phylogenetic studies (Bufalino & Mayden 2010; Schönhuth et al. 2012; Imoto et al. 2013; Schönhuth et al. 2018). These studies identified within the North American Phoxininae a ‘western clade,’ a ‘creek chub-plagopterin clade,’ and an ‘open posterior myodome (OPM) clade’ including the shiners. Though morphological studies are consistent in recovering three major groups (Mayden 1989; Cavender & Coburn 1992), morphological and molecular phylogenies differ in the placement of some genera among these clades (Bufalino & Mayden 2010; Gidmark & Simons 2014). Additionally, these three North American clades group together with a clade of Eurasian phoxinines and Phoxinus (Bufalino & Mayden 2010; Stout et al. 2016; Schönhuth et al. 2018). Most recently, Schönhuth et al. (2018) opted to recognize subfamily-level groupings for species that were previously recognized among Phoxininae, due to their distinctiveness and the fact that Leuciscinae renders Phoxininae sensu lato as paraphyletic (although the relationships between Leuciscinae and some of the other subfamilies were not well-resolved by maximum likelihood). This restricts Phoxininae to only the Eurasian species of Phoxinus, and recognizes the subfamilies Pseudaspininae for the Far East species previously classified among Phoxininae (including Oreoleuciscus, Pseudaspius, Rhynchocephalus, and Tribolodon), the Lavininae for the Western clade, the Plagopterinae for the Creek Chub-Plagopterin clade, and the Pogonichthyinae for the OPM clade. For a review on the history of these groupings and their corresponding genera, see Schönhuth et al. (2018). All three species of the Mexican genus Evarra and the monotypic Stypodon are extinct and have not been studied phylogenetically (Gidmark & Simons 2014). Coburn & Cavender (1992) comment that Evarra is likely to be a western clade member; we tentatively place that genus within the Lavininae. Stypodon signifer, the only member of the genus Stypodon, had molariform pharyngeal teeth and likely ate snails (Miller 2006). The species appears similar to OPM members in external morphology. Its pharyngeal tooth count is unusual 0,3-3,0, however several members of the OPM group lack teeth in the outer row as well (Boschung & Mayden 2004). Although Notemigonus (the only member of the Leuciscinae in North America) also lacks teeth in the outer row, the overall morphology of Stypodon is much more similar to the Pogonichthyinae. We tentatively place it as Pogonichthyinae.

There have been many recent changes in the recognition of genera within the Leuciscidae. For a recent classification of North American genera, which we follow here, refer to Gidmark & Simons (2014). Among their decisions was recognizing the splitting of the genus Notropis based on mitochondrial phylogenetic data, with the following additional genera recognized as valid: Alburnops, Aztecola, Erycyma, Grazodius, Hudsonius, and Miniellus (Mayden et al. 2006; Gidmark & Simons 2014). A subsequent study has questioned the monophyly of Alburnops and Hudsonius, but makes no taxonomic acts to synonymize these genera with others (Schönhuth et al. 2018). More work is forthcoming that is expected to further resolve the taxonomy of the group, and we tentatively retain the taxonomy recognized in Gidmark & Simons (2014). We follow Gidmark & Simons (2014) in synonymizing Moapa within Gila, and recognizing Acrocheilus (for Acrocheilus altacensis) and Klamathella (for Klamathella coerulack, previously placed in Gila) and Tiaroga for Tiaroga cobitis (previously placed in Rhinchithys). We do not recognize Pararhinichthys as a valid genus following studies that argue Pararhinichthys bowersi is an F₁ hybrid between Rhinchithys cataractae and Noemis micropogon (Poly & Sabaj 1998); however, if Pararhinichthys is determined to be distinct genus, it is an available name. Among East Asian phoxinines genera, Imoto et al. (2013) recovered Pseudaspius within a clade of Tribolodon, rendering Tribolodon paraphyletic based on mitogenomic data; given that Pseudaspius is the older name, Tribolodon could be a synonym of Pseudaspius. This result was also found by Kartavtsev et al. (2016) using mitochondrial sequences and Schönhuth et al. (2018) with both mitochondrial and nuclear sequences. None of these studies have made any taxonomic actions regarding Tribolodon.

**Esominae Tan & Armbruster new subfamily**

*Type genus:* Esomus Swainson 1839

**Diagnosis.** Esominae can be distinguished from all cypriniforms by the combined presence of long maxillary barbels extending past the pectoral-fin origin (vs. maxillary barbels, when present, not extending past the pectoral-fin origin) and possessing only a single row of teeth on the pharyngeal jaw (vs. multiple rows of teeth on the pharyngeal jaw). In many Esominae, extremely long maxillary barbels are present that extend past the pelvic-fin origin.

**Composition.** *Esomus ahli* Hora & Mukerji 1928, *Esomus altus* (Blyth 1860), *Esomus barbatus* (Jerdon
Remarks. We derived the diagnosis for *Esomus* based on information from Hora & Mukerji (1928) and Pasco-Viel et al. (2010). Additionally, morphological descriptions by Talwar & Jhingran (1991) and discussion by Liao et al. (2011) indicate Esominae members possess the following characters: mouth small and superior, lower jaw without symphyseal knob, eyes visible from ventral view, dorsal-fin insertion posterior to pelvic-fin insertion, dorsal fin with six or seven branched rays, anal fin with five branched rays, postcleithrum greatly reduced or absent, lateral line (when present) abruptly descending for first few scales anteriorly.

Classification of Genera of Cypriniformes

Gyrinocheiloidei

Gyrinocheilidae Gill 1905 (Type genus: *Gyrinocheilus* Vaillant 1902)

*Gyrinocheilus* Vaillant 1902 (syn. *Gyrinocheilops* Fowler 1937)

Catostomoidae

Catostomidae Agassiz 1850 (Type genus: *Catostomus* Lesueur 1817)

Catostominae Agassiz 1850 (Type genus: *Catostomus* Lesueur 1817)


*Chasmistes* Jordan 1878 (syn. *Lipomyzon* Cope 1881, *Pithecomyzon* Fowler 1913)

*Delistes* Seale 1896

*Xyrauchen* Eigenmann & Kirsch 1899

Erimyzontini Hubbs 1930

*Erimyzon* Jordan 1876

*Minytrema* Jordan 1878

Moxostomatini Bleeker 1863 (Type genus: *Moxostoma* Rafinesque 1820)


Thoburniini Hubbs 1930 (Type genus: *Thoburnia* Jordan & Snyder 1917)

*Hypentelium* Rafinesque 1818 (syn. *Hylomyzon* Agassiz 1855)

*Thoburnia* Jordan & Snyder in Jordan 1917

Cycleptinae Gill 1861 (Type genus: *Cycleptus* Rafinesque 1819)

*Cycleptus* Rafinesque 1819 (syn. *Rhytidostomus* Heckel 1843)

Ictiobinae Bleeker 1863 (Type genus: *Ictiobus* Rafinesque 1820)

*Carpiodes* Rafinesque 1820 (syn. *Sclerognathus* Valenciennes in Cuvier & Valenciennes 1844)


Myxocyprininae Fowler 1958 (Type genus: *Myxocyprinus* Gill 1877).

*Myxocyprinus* Gill 1877

Cobitoidei

Balitoridae Swainson 1839 (Type genus: *Balitora* Gray 1830)

Balitorinae Swainson 1839 (Type genus: *Balitora* Gray 1830)
Balitora Gray 1830 (syn. Sinohomaloptera Fang 1930)
Balitoropsis Smith 1945
Hemimyzon Regan 1911 (syn. Dienbienia Nguyen & Nguyen 2002)
Homaloptera van Hasselt 1823 (syn. Helgia Vinciguerra 1890)
Jinshaia Kottelat & Chu 1988
Lepturichthys Regan 1911
Metahomaloptera Chang 1944
Pseudohomaloptera Silas 1953
Sinogastromyzon Fang 1930
Homalopteroidinae Randall & Page 2015 (Type genus: Homalopteroides Fowler 1905)
Homalopteroides Fowler 1905 (syn. Chopraia Prashad & Mukerji 1929)
Homalopterula Fowler 1940
Balitoridae incertae sedis
Bhavania Hora 1920
Cryptotora Kottelat 1998
Ghatsa Randall & Page 2015
Neohomaloptera Herre 1944
Travancoria Hora 1941
Barbuccidae Kottelat 2012 (Type genus: Barbucca Roberts 1989)
Barbucca Roberts 1989
Botiidae Berg 1940 (Type genus: Botia Gray 1831)
Botiinae Berg 1940 (Type genus: Botia Gray 1831)
Ambastaia Kottelat 2012
Botia Gray 1831 (syn. Diacantha Swainson 1839, Hymenophysa McClelland 1839, often misspelled Hymenophysa)
Chromobotia Kottelat 2004
Sinibotia Fang 1936
Syncrossus Blyth 1860
Yasuhikotakia Nalbant 2002
Leptobotiinae Nalbant 2002 (Type genus: Leptobotia Bleeker 1870)
Leptobotia Bleeker 1870
Parabotia Dabry de Thiersant 1872
Cobitidae Swainson 1838 (Type genus: Cobitis Linnaeus 1758)
Acanthopsis van Hasselt 1823 (syn. Prostheacanthus Blyth 1860)
Aperioptus Richardson 1848 (syn. Acanthopsoides Fowler 1934, Neacanthopsis Smith 1945)
Bibarba Chen & Chen 2007
Canthophrys Swainson 1838 (syn. Somileptus Swainson 1839)
Koreocobitis Kim, Park & Nalbant 1997
Kottelatlimia Nalbant 1994
Lepidocephalus Bleeker 1858
Microcobitis Bohlen & Harant 2011
Misgurnus Lacepède 1803 (syn. Mesomisgurnus Fang 1935, Ussuria Nikolskii 1903)
Neoeucirrhichthys Bănărescu & Nalbant 1968
Pangio Blyth 1860 (syn. Apua Blyth 1860, Cobitophis Myers 1927, Eucirrhichthys Perugia 1892)
Paralepidocephalus Tchang 1935
Paramisgurnus Dabry de Thiersant 1872 (syn. Paramisgurnus Sauvage 1878)
Protocobitis Yang & Chen 1993
Sabanejewia Vladykov 1929
Theriodes Kottelat 2012
Ellopostomatidae Bohlen & Šlechtová 2009 (Type genus: Ellopostoma Vaillant 1902)
Ellopostoma Vaillant 1902
Gastromyzontidae Fowler 1905 (Type genus: Gastromyzon Günther 1874)
Annamia Hora 1932
Beaufortia Hora 1932
Erromyzon Kottelat 2004
Formosania Oshima 1919 (syn. Crossostoma Sauvage 1878)
Gastromyzon Günther 1874 (syn. Lepidoglanis Vaillant 1889)
Glaniopsis Boulenger 1899
Hypergastromyzon Roberts 1989
Katibasia Kottelat 2004
Liniparhomaloptera Fang 1935
Neogastromyzon Popta 1905
Paraprotomyzon Pellegrin & Fang 1935
Parhomaloptera Vaillant 1902
Plesiomyzon Zheng & Chen 1980
Protomyzon Hora 1932 (syn. Progastromyzon Hora & Jayaram 1952)
Pseudogastromyzon Nichols 1925 (syn. Labigastromyzon Tang & Chen 1996)
Vanmanenia Hora 1932 (syn. Homalosoma Boulenger 1901, Praeformosania Fang 1935)
Yaoshania Yang, Kottelat, Yang & Chen 2012
Nemacheilidae Regan 1911 (Type genus: Nemacheilus Bleeker 1863)
Aborichthys Chaudhuri 1913
Acanthocobitis Peters 1861
Afronemacheilus Golubtsov & Prokofiev in Prokofiev 2009
Barbatula Linck 1790 (syn. Cobites Swainson 1839, Orthrias Jordan & Fowler 1903)
Claea Kottelat 2011 (syn. Oreias Sauvage 1874)
Draconectes Kottelat 2012
Dzihunia Prokofiev 2001
Eidinemacheilus Segherloo, Ghaedrahmati & Freyhof 2016
Eonemachilus Berg 1938
Hedinichthys Rendahl 1933 (syn. Minihedinichthys Prokofiev 2017)
Heminoemacheilus Zhu & Cao 1987
Homatula Nichols 1925
Indoreonectes Rita & Bănărescu in Rita, Bănărescu & Nalbant 1978
Iskandaria Prokofiev 2009
Lefua Herzenstein 1888 (syn. Elxis Jordan & Fowler 1903, Octonema Herzenstein in Herzenstein & Warpachowski 1888)

Malihkaia Kottelat 2017

Mesonoemacheilus Bănărescu & Nalbant 1982

Micronemacheilus Rendahl 1944

Nemacheilus Bleeker 1863 (syn. Modigliania Perugia 1893, Pogononemacheilus Fowler 1937)

Nemachilichthys Day 1878

Neonoemacheilus Zhu & Guo 1985 (syn. Infundibulatus Menon 1987)

Oreonecetes Günther 1868 (syn. Octonema Martens 1868)


Paracanthocobitis Grant 2007

Paracobitis Bleeker 1863 (syn. Adiposia Annandale & Hora 1920, Pseudodon Kessler 1874)

Paranemacheilus Zhu 1983

Paraschistura Prokofiev 2009 (syn. Metaschistura Prokofiev 2009)

Petruichthys Menon 1987

Physoschistura Bănărescu & Nalbant 1982

Protonemacheilus Yang & Chu 1990

Pteronemacheilus Bohlen & Šlechtová 2011

Sasanidus Freyhof, Geiger, Golzarianpour & Patimar 2016

Schistura McClelland 1838 (syn. Acoura Swainson 1839, Longischistura Bănărescu & Nalbant 1995)

Sectoria Kottelat 1990

Seminemacheilus Bănărescu & Nalbant 1995

Speonectes Kottelat 1920

Sphaerophysa Cao & Zhu 1988

Sundoreonectes Kottelat 1990

Traccatichthys Freyhof & Serov 2001


Troglocobitis Parin 1983

Troglochilus Zhang, Zhao & Tang 2016

Tuberoschistura Kottelat 1990

Turcinoemacheilus Bănărescu & Nalbant 1964

Yumanilus Nichols 1925

Serpenticobitidae Kottelat 2012 (Type genus: Serpenticobitis Roberts 1997)

Serpenticobitis Roberts 1997

Vaillantellidae Nalbant & Bănărescu 1977 (Type genus: Vaillantella Fowler 1905)

Vaillantella Fowler 1905

Cyprinoidei

Acheilognathidae Bleeker 1863 (Type genus: Acheilognathus Bleeker 1859)

Acheilognathus Bleeker 1859 (syn. Acanthorhodeus Bleeker 1871, Paracheilognathus Bleeker 1863, Rhodeops Fowler 1910)

Paratanakia Chang, Chen & Mayden 2014

Pseudorhodeus Chang, Chen & Mayden 2014
Rhodeus Agassiz 1832 (syn. Pseudoperilampus Bleeker 1863)
Sinorhodeus Li, Liao & Arai 2017
Tanakia Jordan & Thompson 1914

Cyprinidae Rafinesque 1815 (Type genus: Cyprinus Linnaeus 1758)

Acrossocheilinae Yang et al. 2015 (Type genus: Acrossocheilus Oshima 1919)

Acrossocheilus Oshima 1919 (syn. Lissochilichthys Oshima 1920, Masticbarbus Tang 1942, Sinibarbus Sauvage 1874)
Folifer Wu 1977
Onychostoma Günther 1896 (syn. Scaphesthes Oshima 1919, Scaphiodontella Oshima 1920)

Barbinae Bleeker 1859 (Type genus: Barbus Daudin 1805)

Aulopyge Heckel 1841
Barbus Daudin 1805 (syn. Pseudobarbus Bielz 1853)
Capoeta Valenciennes 1842 (syn. Scaphiodon Heckel 1843)
Cyprinion Heckel 1843
Scaphiodonichthys Vinciguerra 1890 (syn. Scaphiodontopsis Fowler 1934)
Semiplotus Bleeker 1860

Cyprininae Rafinesque 1815 (Type genus: Cyprinus Linnaeus 1758)

Aaptosyax Rainboth 1991
Carassioides Oshima 1926
Carassius Jarocki 1822 (syn. Cyprinopsis Fitzinger 1832, Neocarassius Castelnau 1872)
Luciocyprinus Vaillant 1904 (syn. Fustis Lin 1932)
Procypris Lin 1933 (syn. Paraprocypsis Fang 1936)

Labeoninae Bleeker 1859 (Type genus: Labeo Cuvier 1816)

Garrini Bleeker 1863 (Type genus: Garra Hamilton 1822)

Discolabeo Fowler 1937
Paracrossochilus Popta 1904
Tariqilabeo Mirza & Saboohi 1990 (syn. Akrokolioplax Zhang & Kottelat 2006, Gonorhynchus McClelland 1838)

Labeonini Bleeker 1859 (Type genus: Labeo Cuvier 1816)

Altigena Burton (ex Lin) 1934 (syn. Vinalabeo Nguyen, Nguyen & Nguyen 2016)

Cirrhinus Oken 1817 (syn. Isocephalus Heckel 1843)
Gymnostomus Heckel 1843 (syn. Cirrhinchthys Bleeker 1863, Mrigala Bleeker 1860)
Incisilabeo Fowler 1937
Labeo Cuvier 1816 (syn. Abrostormus Smith 1841, Aera Bleeker 1860, Catla Valenciennes in Cuvier & Valenciennes 1844, Chrysophkekadion Bleeker 1860, Gibelion Heckel 1843,
Morulius Hamilton 1822, Nandina Gray 1831, Rohita Valenciennes in Cuvier & Valenciennes 1842, Rohitichthys Bleeker 1860, Tambra Bleeker 1860

Nukta Hora 1942
Speolabeo Kottelat 2017

‘Osteochilini’ (From genus Osteochilus Günther 1868)
Barbichthys Bleeker 1860
Crossocheilus Kuhl & van Hasselt 1823 (syn. Crossocheilichthys Bleeker 1860, Holotylognathus Fowler 1934)
Epalzeorhynchos Bleeker 1855
Henicorhynchus Smith 1945
Labiobarbus van Hasselt 1823 (syn. Cyrene Heckel 1843, Dangila Valenciennes in Cuvier & Valenciennes 1842)
Lobocheilos Bleeker 1853 (syn. Gobionichthys Bleeker 1859)
Osteochilus Günther 1868 (syn. Diplocheilos Bleeker 1860, Kantaka Hora 1942, Neorohita Fowler 1937)
Thynnichthys Bleeker 1859 (syn. Thynnichthyina Fowler 1937)

‘Semilabeonini’ (From genus Semilabeo Peters 1881)
Ageneiogarra Garman 1912
Cophecheilus Zhu, Zhang, Zhang & Han 2011
Discocheilus Zhang 1997 (syn. Discolabeo Chen in Chen & Lan 1992)
Discogobio Lin 1931
Fivepearlus Li, Yang, Li & Chen 2017
Hongshuia Zhang, Qiang & Lan 2008
Limichthys Zhang & Fang 2005
Mekongina Fowler 1937
Paraqianlabeo Zhao, Sullivan, Zhang & Peng 2014
Parasinilabeo Wu 1939 (syn. Pararectoris Su, Yang & Cui 2001)
Placocheilus Wu in Wu, Lin, Chen, Chen & He 1977
Prolixicheilus Zheng, Chen & Yang 2016
Pseudocrossocheilus Zhang & Chen 1997
Pseudogyrinocheilus Fang 1933
Psychidio Myers 1930 (syn. Varicogobio Lin 1931)
Qianlabeo Zhang & Chen 2004
Rectoris Lin 1935
Semilabeo Peters 1881 (syn. Amplolabrius Lin 1933)
Sinigarra Zhang & Zhou 2012
Sinocrossocheilus Wu 1977
Stenorynchoacrum Huang, Yang & Chen 2014
Vinagarra Nguyen & Bui 2009

Labeoninae incertae sedis
Diplocheilichthys Bleeker 1860
Longanalus Li 2006
Parapsilorhynchus Hora 1921
Protolabeo Zhang, Zhao & An 2010
Schismatorhynchos Bleeker 1855
Sinilabeo Rendahl 1933
‘Poropuntiinae’ (From genus *Poropuntius* Smith 1931)

*Albulichthys* Bleeker 1860  
*Amblyrhynchichthys* Bleeker 1860  
*Balantiocheilos* Bleeker 1860  
*Barbonymus* Kottelat 1999  
*Cosmochilus* Sauvage 1878 (syn. *Papillocheilus* Smith 1945)  
*Cyclocheilos* Bleeker 1859  
*Discherodontus* Rainboth 1989  
*Eirmotus* Schultz 1959  
*Hypsibarbus* Rainboth 1996  
*Mystacoleucus* Günther 1868 (syn. *Acanthonotus* Tickell in Day 1888, *Matsya* Day 1889)  
*Poropuntius* Smith 1931  
*Puntioplites* Smith 1929 (syn. *Adamacypris* Fowler 1934)  
*Sawbwa* Annandale 1918  
*Scaphognathops* Smith 1945 (syn. *Scaphognathus* Smith 1931)  
*Sikukia* Smith 1931 (syn. *Xenocheilichthys* Smith 1934)  

Probarbinae Yang et al. 2015 (Type genus: *Probarbus* Sauvage 1880)

*Catlocarpio* Boulenger 1898  
*Probarbus* Sauvage 1880

Schizothoracinae McClelland 1842 (Type genus: *Schizothorax* Heckel 1838)

*Aspiorynchus* Kessler 1879  
*Oreinus* McClelland 1838 (syn. *Englottogaster* Gistel 1848, *Opistocheilos* Bleeker 1860)  
*Percocypris* Chu 1935  
*Schizopyge* Heckel 1848 (syn. *Paraschizothorax* Tsao 1964)  

Schizopygopsinae Mirza 1991 (Type genus: *Schizopygopsis* Steindachner 1866)

*Chuanchia* Herzenstein 1891  
*Diptychus* Steindachner 1886  
*Gymnocypris* Günther 1868 (syn. *Rugogymnocypris* Yueh & Hwang 1964)  
*Gymnodiptychus* Herzenstein 1892  
*Herzensteinia* Chu 1935  
*Oxygymnocypris* Tsao 1964  
*Platypharodon* Herzenstein 1891  
*Ptychobarbus* Steindachner 1886  
*Schizopygopsis* Steindachner 1886

Smiliogastrinae Bleeker 1863 (Type genus: *Smiliogaster* Bleeker 1860)

*Barboides* Brüning 1929 (syn. *Raddabarbus* Thys van den Audenaerde 1971)  
*Clypeobarbus* Fowler 1936  
*Dawkinsia* Pethiyagoda, Meegaskumbura & Maduwage 2012  
*Desmopuntius* Kottelat 2013

Haludaria Pethiyagoda 2013 (syn. Dravidia Pethiyagoda, Meegaskumbura & Maduwage 2012)

Hampala Kuhl & van Hasselt 1823 (syn. Hampala Bleeker 1860, Heteroleuciscus Sauvage 1874)

Oliotius Kottelat 2013
Oreichthys Smith 1933
Osteobrama Heckel 1843 (syn. Smiliogaster Bleeker 1860)
Pethia Pethiyagoda, Meegaskumbura & Maduwage 2012
Pseudobarbus Smith 1841 (syn. Cheilobarbus Smith 1841, Gnathendalia Castelnau 1861, Oreodaimon Greenwood & Jubb 1967)
Puntigrus Kottelat 2013
Puntius Hamilton 1822
Rohtee Sykes 1839
Sahyadria Raghavan, Philip, Ali & Dahanukar 2013
Striuntius Kottelat 2013
Systomus McClelland 1838
Spinibarbinae Yang et al. 2015 (Type genus: Spinibarbus Oshima 1919)

Spinibarbichthys Oshima 1926
Spinibarbus Oshima 1919

Torinae Karaman 1971 (Type genus: Tor Gray 1834)

Acapoeta Cockerell 1910
Arabibarbus Borkenhagen 2014
Hypselobarbus Bleeker 1860 (syn. Gonoproktopterus Bleeker 1860)
Labeobarbus Rüppell 1835 (syn. Barbellion Whitley 1931, Barynotus Günther 1868, Dillonia Heckel 1847, Lanceabarbus Fowler 1936, Varicorhinus Rüppell 1835)
Lepidopygopsis Raj 1941
Mesopotamichthys Karaman 1971
Naziritor Mirza & Javed 1985
Osteochilichthys Hora 1942
Pterocapoeta Günther 1902
Sanagia Holly 1926
Tor Gray 1834

Cyprinidae incertae sedis

Barbopsis Di Caporiacco 1926 (syn. Eilichthys Pellegrin 1929, Zaccharinia Gianferrari 1934)
Caecobarbus Boulenger 1921
Caecocypris Banister & Bunni 1980
Chagunius Smith 1938
Coptostomabarbus David & Poll 1937
Eechathalakenda Menon 1999
Kalimantania Bănărescu 1980
Laocypris Kottelat 2000
Neobarynotus Bănărescu 1980
Parasikukia Doi 2000
Paraspinibarbus Chu & Kottelat 1989
Parator Wu, Yang, Yue & Huang 1963
Prolabeo Norman 1932
Prolabeops Schultz 1941
Pseudosinocyclocheilus Zhang & Zhao 2016
Rohtechthys Bleeker 1860
Schizocypris Regan 1914
Troglocyclocheilus Kottelat & Bréhier 1999
Typhlobarbus Chu & Chen 1982
Xenobarbus Norman 1923

Danionidae Bleeker 1863 (Type genus: Danio Hamilton 1822)

Chedrinae Bleeker 1863 (Type genus: Chedrus Swainson 1839)
Barilius Hamilton 1822 (syn. Pteropsarion Günther 1868)
Bengala Gray 1834 (syn. Megarasbora Günther 1868)
Cabdio Hamilton 1822 (syn. Aspidoparia Heckel 1847, Morara Bleeker 1860)
Chelaethiops Boulenger 1899 (syn. Anchovicypris Fowler 1936)
Engraulicyspris Günther 1894 (syn. Mesobola Howes 1984)
Leptocypris Boulenger 1900
Luciosoma Bleeker 1855 (syn. Trinematicthys Bleeker 1860)
Malayochela Bănărescu 1968
Nematabramis Boulenger 1894 (syn. Mearnsella Seale & Bean 1907)
Neobola Vinciguerra 1895
Opsaridium Peters 1854 (syn. Pelotrophus Günther 1864, Sagittabarilius Fowler 1936)
Raiamas Jordan 1919 (syn. Bola Günther 1868)
Rastrineobola Fowler 1936
Salmostoma Swainson 1839 (syn. Salmophasia Swainson 1839)
Securicula Günther 1868 (syn. Pseudoxygaster Bănărescu 1967)

Danioninae Bleeker 1863 (Type genus: Danio Hamilton 1822)
Betadevario Pramod, Fang, Rema Devi, Liao, Indra, Jameela Beevi & Kullander 2010
Chela Hamilton 1822 (syn. Cachius Günther 1868)
Danio Hamilton 1822 (syn. Brachydania Weber & de Beaufort 1916, Celestichthys Roberts 2007)
Danionella Roberts 1986
Inlecycris Howes 1980
Laubuka Bleeker 1859 (syn. Allochela Silas 1958)
Microdevario Fang, Norèn, Liao, Källersjö & Kullander 2009
Microrasbora Annandale 1918
Neocheila Silas 1958

Esominae new subfamily (Type genus: Esomus Swainson 1839)
Esomus Swainson 1839 (syn. Nuria Valenciennes in Cuvier & Valenciennes 1842, Pogonocharax Regan 1907)
Rasborinae Günther 1868 (Type genus: Rasbora Bleeker 1859)


*Boraras* Kottelat & Vidthyayanon 1993

*Brevibora* Liao, Kullander & Fang 2010

*Horadandia* Deraniyagala 1943

*Kottelatia* Liao, Kullander & Fang 2010

*Pectenocypris* Kottelat 1982


*Rasboroides* Brittan 1954

*Rasbosoma* Liao, Kullander & Fang 2010

*Trigonostigma* Kottelat & Witte 1999

Danionidae incertae sedis

*Thryssocypris* Roberts & Kottelat 1984

Gobionidae Bleeker 1863 (Type genus: *Gobio* Cuvier 1816)

Gobioninae Bleeker 1863 (Type genus: *Gobio* Cuvier 1816)

*Abbottina* Jordan & Fowler 1903 (syn. *Pseudogobiops* Berg 1914)

*Acanthogobio* Herzenstein 1892

*Biwia* Jordan & Fowler 1903

*Gobio* Cuvier 1816 (syn. *Bungia* Keyserling 1861)

*Gobiobota* Kreyenberg 1911 (syn. *Progobiobota* Chen & Cao 1982)

*Mesogobio* Bănărescu & Nalbant 1973


*Platysmacheilus* Lu, Luo & Chen 1977

*Pseudogobio* Bleeker 1860


*Xenophysogobio* Chen & Cao 1977

Sarcocheilichthyinae Kryzanowsky 1947 (Type genus *Sarcocheilichthys* Bleeker 1860)

*Coreoleuciscus* Mori 1935


*Gobiocypris* Ye & Fu 1983

*Ladislavia* Dybowski

*Paracanthobrama* Bleeker 1864 (syn. *Glabrobarbus* Fowler 1930)

*Pseudopungtungia* Mori 1935


*Pungtungia* Herzenstein 1892 (syn. *Zeza* Jordan & Fowler (ex Ishikawa) 1903)


Hemibarbus–Squalidus clade sensu Tang et al. 2011

*Belligobio* Jordan & Hubbs 1925 (syn. *Hemibarboidea* Wang 1935)

*Hemibarbus* Bleeker 1860 (syn. *Gobioharbus* Dybowski 1869)

Gobionidae incertae sedis
Coreius Jordan & Starks 1905 (syn. Coripareius Garman 1912)
Paraleucogobio Berg 1907
Placogobio Nguyen 2001

Leptobarbidae Bleeker 1864 (Type genus: Leptobarbus Bleeker 1859)
Leptobarbus Bleeker 1859 (syn. Filirasbora Fowler 1937)

Leuciscidae Bonaparte 1835 (Type genus: Leuciscus Cuvier 1816)
Lavinia Girard 1854 (syn. Lavininae Bleeker 1863)

Leuciscinae Bonaparte 1835 (Type genus: Leuciscus Cuvier 1816)
Abramis Cuvier 1816 (syn. Brama Bleeker (ex Klein) 1863, Sapã Kazanskii 1928, Zopa Fitzinger 1873)
Acanthobrama Heckel 1843 (syn. Acanthalburnus Berg 1916, Culticula Abbott 1901)
Achondrostoma Robalo, Almada, Levy & Doadrio 2007
Alburnoides Jeitteles 1861 (syn. Spirilinus Fatio 1882, Squalalburnus Berg 1932)
Alburnus Rafinesque 1820 (syn. Chalcalburnus Berg 1933)
Anaecypris Collares-Pereira 1983
Aspiolucius Berg 1907
Ballerus Heckel 1843
Blicca Heckel 1843
Capoetobrama Berg 1916
Chondrostoma Agassiz 1832 (syn. Chondrochilus Heckel 1843, Chondrorhynchus Heckel 1843, Machaerichilus Fitzinger 1873, Nasus Basilewsky (ex Cuvier) 1855)
Delminichthys Freyhof, Lieckfeldt, Bogutskaya, Pitra & Ludwig 2006
Iberochondrostoma Robalo, Almada, Levy & Doadrio 2007
Ladigesocypris Karaman 1972
Leucalburnus Berg 1916
Leucaspius Heckel & Kner 1857 (syn. Owslanka Dybowskii 1862)
Leuciscus Cuvier 1816 (syn. Aspiopsis Zugmayer 1912, Aspius Agassiz 1832, Aturius Dubalen 1878, Bathystoma Fitzinger 1873, Dobula Rafinesque 1820, Genghis Howes 1984, Idus Heckel 1843)
Leucos Heckel 1843
Mirogrex Goren, Fishelson & Trewavas 1973
Notemigonus Rafinesque 1819 (syn. Hemiplus Rafinesque 1820, Leucosomus Heckel 1843, Stilbe
DeKay 1842, Stilbius Gill 1865)
Pachychilon Steindachner 1882
Parachondrostoma Robalo, Almada, Levy & Doadrio 2007
Pelagius Kottelat & Freyhof 2007
Pelecus Agassiz 1835
Petroreuciscus Bogutskaya 2002
Phoxinellus Heckel 1843 (syn. Paraphoxinus Bleeker 1863)
Protochondrostoma Robalo, Almada, Levy & Doadrio 2007
Pseudochondrostoma Robalo, Almada, Levy & Doadrio 2007
Pseudophoxinus Bleeker 1860 (syn. Pararhodeus Berg 1907, Spinophoxinellus Karaman 1972)
Rutilus Rafinesque 1820 (syn. Ceniosiphon Bonaparte 1846, Gardnerus Bonaparte 1846, Liparus
Schulze 1892, Metallites Schulze 1890, Orfus Fitzinger 1873, Orthroleucos Derjavin 1937,
Pararutilus Berg 1912, Pigus Bonaparte 1846, Rubillus Fitzinger 1873)
Sarmarutilus Bianco & Ketmaier 2014
Scardinius Bonaparte 1837 (syn. Heegerius Bonaparte 1845)
Squalius Bonaparte 1837 (syn. Cephalopsis Fitzinger 1873, Cephalus Bonaparte 1846, Iberocypris
Doadrio 1890, Microlepis Bonaparte 1846)
Telestes Bonaparte 1840 (syn. Habrolepis Fitzinger 1873)
Tropidophoxinellus Stephanidis 1974
Vimba Fitzinger 1873 (syn. Leucabramis Smitt 1895)
Phoxininae Bleeker 1863 (Type genus: Phoxinus Rafinesque 1820)
Phoxinus Rafinesque 1820 (syn. Acahara Jordan & Hubbs 1925, Eulinneela Dybowski 1916,
Phoxinus Agassiz 1835)
Plagopterinae Cope 1874 (Type genus: Plagopterus Cope 1874)
Couesius Jordan 1878
Hemitremia Cope 1870
Lepidoma Cope 1874 (syn. Snyderichthys Miller 1945)
Margariscus Cockerell 1909
Meda Girard 1856
Plagopterus Cope 1874
Semotilus Rafinesque 1820 (syn. Cheilonemus Storer (ex Baird) 1855, Chilonemus Baird 1851)
Pogonichthyinae Girard 1858 (Type genus: Pogonichthys Girard 1854)
Agosia Girard 1856 (syn. Zophendum Jordan 1878)
Alburnops Girard 1856
Algansea Girard 1856 (syn. Xystrosus Jordan & Snyder 1899)
Aztecula Jordan & Evermann 1898
Campostoma Agassiz 1855
Clinostomus Girard 1856 (syn. Rhodopleuriscus Fowler 1944)
Codo Girard 1856
Cyprinella Girard 1856 (syn. Erogala Jordan in Jordan & Brayton 1878, Moniana Girard 1856)
Dionda Girard 1856
Ericymba Cope 1865
Erimonas Jordan 1924
Erimystax Jordan 1882
Exoglossum Rafinesque 1818 (syn. Maxillingua Rafinesque 1818, Parexoglossum Hubbs 1931)
Graodus Günther 1868
Hudsonius Girard 1856
Hybognathus Agassiz 1855 (syn. Algoma Girard 1856, Tirodon Hay 1882)
Hybopsis Agassiz 1854
Iotichthys Jordan & Evermann 1896
Lucilus Rafinesque 1820 (syn. Coccogenia Cockerell & Callaway 1909, Coccotis Jordan 1882, Hypsolepis Agassiz (ex Baird) 1854, Plagyrus Rafinesque 1820)
Lythrurus Jordan 1876
Macrhybopsis Cockerell & Allison 1909 (syn. Extrarius Jordan 1919)
Miellius Jordan 1888
Mylocheilus Agassiz 1855 (syn. Clarkina Jordan & Evermann 1927)
Nocomis Girard 1856 (syn. Ceratichthys Baird in Girard 1856)
Opsopoeodus Hay 1881 (syn. Trycherodon Forbes in Jordan & Gilbert 1883)
Oregonichthys Hubbs 1929
Phenacobius Cope 1867 (syn. Sarcidium Cope 1871)
Pimephales Rafinesque 1820 (syn. Ceraticthys Baird & Girard 1853, Cliola Girard 1856, Cochlognathus Baird & Girard 1854, Coliscus Cope 1871, Hyborhynchus Agassiz 1855, Hypargyrus Forbes in Gilbert 1884, Spinicephalus Lesueur in Vaillant 1896)
Platygobio Gill 1863
Pogonichthys Girard 1854 (syn. Symmetrurus Jordan 1878)
Pteronotropis Fowler 1935
Rhinchithys Agassiz 1849 (syn. Apocope Cope 1872, Argyreus Heckel 1843, Eritrema Cope & Yarrow 1875)
Richardsonius Girard 1856
Sypodon Garman 1881
Tampichthys Schönthuth, Doadrio, Dominguez-Dominguez, Hillis & Mayden 2008
Tiarog Girard 1856
Yuriria Jordan & Evermann 1896 (syn. Falcula Jordan & Snyder 1899, Falcularius Jordan & Snyder in Jordan 1903)
Pseudaspininae Bogutskaya 1990 (Type genus: Pseudaspius Dybowskii 1869)
Oreoleuciscus Warpachowski 1889 (syn. Acanthorutilus Berg 1912)
Pseudaspius Dybowskii 1869
Tribolodon Sauvage 1883
Paedocyprididae Mayden & Chen 2010 (Type genus: Paedocypris Kottelat, Britz, Tan & Witte 2006)
Paedocypris Kottelat, Britz, Tan & Witte 2006
Psilorhynchidae Hora 1926 (Type genus: Psilorhynchus McClelland 1838)
Psilorhynchus McClelland 1838 (syn. Psilorhynchoides Yazdani, Singh & Rao 1993)
Sundadanionidae Mayden & Chen 2010 (Type genus: Sundadanio Kottelat & Witte 1999)
Fangfangia Britz, Kottelat & Tan 2012
Sundadanio Kottelat & Witte 1999
Tanichthyidae Mayden & Chen 2010 (Type genus: Tanichthys Lin 1932)
Tanichthys Lin 1932
Tincidae Jordan 1878 (Type genus: Tinca Garsault 1764)
Tinca Garsault 1764
Xenocyprididae Günther 1868 (Type genus: Xenocypris Günther 1868)
Opsariichthyinae Rendahl 1928 (Type genus: Opsariichthys Bleeker 1863)
Candidia Jordan & Richardson 1909
Nipponocypris Chen, Wu & Hsu 2008
Opsariichthys Bleeker 1863
Zacco Jordan & Evermann 1902
Xenocypridinae Günther 1868 (Type genus: Xenocypris Günther 1868)
Ancherythroculter Yih & Wu 1964
Chanodichthys Bleeker 1860 (syn. Erythroculter Berg 1909, Leptocephalus Basilewsky 1855, Pseudoculter Bleeker 1860)
Ctenopharyngodon Steindachner 1866 (syn. Pristodon Dybowski 1877)
Culter Basilewsky 1855 (syn. Cultrichthys Smith 1938)
Distoechodon Peters 1881
Elopichthys Bleeker 1860 (syn. Gymnognathus Sauvage 1884, Scombrocypris Günther 1889)
Hainania Koller 1927
Hemiculterella Warpacowski 1888 (syn. Semiculter Chu 1935)
Hemigrammocypris Fowler 1910 (syn. Brevigobio Tanaka 1916)
Hypophthalmichthys Bleeker 1860 (syn. Abramocephalus Steindachner 1869, Aristichthys Oshima 1919, Cephalus Basilewsky 1855, Onychodon Dybowski 1872)
Ischikauia Jordan & Snyder 1900
Luciobrama Bleeker 1870
Macrochirichthys Bleeker 1859
Megalobrama Dybowski 1872 (syn. Parosteobrama Tchang 1930)
Metzia Jordan & Thompson 1914 (syn. Rasborinus Oshima 1920)
Mylopharyngodon Peters 1881 (syn. Leucisculus Oshima 1920, Myloleuciscus Garman 1912, Myloleucops Cockerell 1913, Myoleucus Günther 1873)
Ochetobius Günther 1868 (syn. Agenigobio Sauvage 1878)
Oxygaster van Hasselt 1823
Parabramis Bleeker 1864
Parachela Steindachner 1881 (syn. Grandisquamachela Fowler 1934)
Paralaubuca Bleeker 1864 (syn. Cultrops Smith 1938)
Plagiognathops Berg 1907 (syn. Plagiognathus Dybowski 1872)
Pseudobrama Bleeker 1870
Pseudohemiculter Nichols & Pope 1927
Pseudolaubuca Bleeker 1864 (syn. Parapeleucus Günther 1889)
Sinibrama Wu 1939
Squaliobarbus Günther 1868
Toxabramis Günther 1873
Xenocyprioide Chen 1982
Xenocypris Günther 1868
Xenocyprididae incertae sedis
Anabarilius Cockerell 1923 (syn. Nicholsiculter Rendahl 1928, Rohanus Chu 1935)
Araioypris Conway & Kottelat 2008
Atrilinea Chu 1935
Gymnodanio Chen & He 1992
Longiculter Fowler 1937
Pogobrama Luo 1995
Rasborichthys Bleeker 1859

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References

PHYLOGENETIC CLASSIFICATION OF CYPRINIFORMES


PHYLOGENETIC CLASSIFICATION OF CYPRINIFORMES

The phylogenetic classification of Cypriniformes has been extensively studied through various molecular and genetic approaches. This has provided insights into the evolution and vegetative adaptation of these fishes. For example, the genome sequencing of the grass carp (Ctenopharyngodon idellus) by Xu et al. (2014) and the common carp (Cyprinus carpio) by Xu et al. (2014) has contributed to our understanding of the genetic diversity and adaptation of these species. Similarly, the Sinocyclocheilus cavefish genome by Yang et al. (2016) has provided insights into cave adaptation.

Researchers have also used molecular phylogenetics to resolve the classification of cyprinid fishes. Yang et al. (2012a) and Yang et al. (2012b) have contributed to this field by providing phylogenetic placements of cyprinid genera and subfamilies. The systematics of the Labeonini inhabiting the karst regions in southwest China (Teleostei; Cypriniformes) has also been studied by Zheng et al. (2016).

Zhao et al. (2016) studied the origin and divergence of Gobioninae fishes (Teleostei; Cyprinidae) based on complete mitochondrial genome sequences. The molecular systematics of the Labeonini inhabiting the karst regions in southwest China (Teleostei; Cypriniformes) has been explored by Zheng et al. (2016).

In conclusion, the phylogenetic classification of Cypriniformes continues to be an active area of research, with ongoing efforts to understand the evolution and diversity of these fishes.