



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

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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, including 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, Barbuccidae, Botiidae, Cobitidae, Ellopostomatidae, Gastromyzontidae, Serpenticobitidae, Nemacheilidae, 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 Cyprinoidei. 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 Cyprinoidei (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 Ictiobinae, Cycleptinae, Myxocyprinae, 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 modification 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 Myxocyprinae, 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. Erimyzontini is occasionally spelled Erimyzonini (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, Barbuccidae, 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* (= Barbuccidae + 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 & Bănărescu (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 *Ellopostoma*. In some older classification schemes, Nemacheilidae and *Ellopostoma* were considered together with Balitoridae *sensu lato* (e.g. Siebert 1987), but most recent classification schemes consider the nemacheilids and ellopostomatids 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). *Ellopostoma* 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 *Ellopostoma* in a polytomy with Nemacheilidae and Balitoridae *sensu lato*, while Chen *et al.* (2009) recover *Ellopostoma* as sister to Nemacheilidae. Schönhuth *et al.* (2018) recover Cobitidae as more closely related to Balitoridae, Gastromyzontidae, and Nemacheilidae than *Ellopostoma*, however this was not strongly supported. For a description and diagnosis for Ellopostomatidae, 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 (*Ambastaia*, *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 leptobotiines 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 lato* (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: *Bhavana* Hora 1920, *Cryptотора* Kottelat 1998, *Ghatsa* 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 Lefuini (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; Rüber *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, Psilorhynchidae (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 clade 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 Paedocypridae, is unique among cypriniforms and can be easily distinguished by numerous apomorphic characters (Kottelat *et al.* 2006).

Acheilognathidae, the bitterlings, are distinguished from other cyprinoids 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 three 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 cyprinoid 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 *Fangfangia* 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, barb, and their allies. This group still includes a large diversity of cyprinoid 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, barb, labeonins, garrins, oreinins, 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, Probarbinae, Torinae, Smiliogastrinae, Cyprininae, Acrossocheilinae, Spinibarbinae, 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 Probarbinae, Acrossocheilinae, and Spinibarbinae. 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: Labeoina and Garraina. Yang *et al.* (2012a) divide the Labeoninae into four subgroups: Labeoina, Garraina, ‘Semilabeoina’, and ‘Osteochilina’. The Labeoina and Garraina *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*), Garrini (using the stem *Garr-*, 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*, *Parapsilorhynchus*, and *Sinilabeo* as *incertae sedis* within Labeoninae. Yang *et al.* (2012a) also comment that the status of *Schismatorhynchus* requires further investigation, and we tentatively recognize *Schismatorhynchus* 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 Garrini.

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

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 napoensis* 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 *Prolixicheilus*, *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 *Discherodontus* 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 *Discherodontus* is part of the ‘Poropuntiinae’. Yang *et al.* (2015) classified *Chagunius* in Smiliogastrinae, however they recovered it in variable places including grouped with the Smiliogastrinae from mitogenome data (80% bootstrap support), sister to ‘Poropuntiinae’ by RAG1 (although with less than 50% support), and sister to *Aptosyax* 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 Spinibarbinae, Acrossocheilinae, Schizopygopsinae, Torinae, and Barbinae, while coalescent-based analysis placed it more closely-related to the clade formed by Smiliogastrinae + ‘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 the Smiliogastrinae. Yang *et al.* (2015) do not present explicit morphological diagnoses for these barb groups. As part of recognizing a monophyletic *Barbus* and Smiliogastrinae, 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 *Pterocapoeta*, *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 *Varicorhinus*, and the closely-related genera *Acapoeta* and *Sanagia*. *Eechathalakenda* 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 Smiliogastrinae, 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 Spinibarbinae. 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 Smiliogastrinae, 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 basimi, 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*, *Platysmacheilus*, 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 Xenocyprididae 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 Oxygastrinae (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 *Rasborichthys* 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, rasborine, 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*, *Rhynchocypris*, and *Tribolodon*), the Laviniinae 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 Laviniinae. *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*, *Aztecuela*, *Ericymba*, *Graodus*, *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 alutaceus*) and *Klamathella* (for *Klamathella coerulea*, previously placed in *Gila*) and *Tiaroga* for *Tiaroga cobitis* (previously placed in *Rhinichthys*). We do not recognize *Pararhinichthys* as a valid genus following studies that argue *Pararhinichthys bowersi* is an F₁ hybrid between *Rhinichthys cataractae* and *Nocomis micropogon* (Poly & Sabaj 1998); however, if *Pararhinichthys* is determined to be distinct genus, it is an available name. Among East Asian phoxinin 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

1849), *Esomus caudiocellatus* Ahl 1924, *Esomus danrica* (Hamilton 1822), *Esomus longimanus* (Lunel 1881), *Esomus malayensis* (Matte & Reichelt 1908), *Esomus metallicus* Ahl 1924, *Esomus thermoicos* (Valenciennes 1842) and the possibly valid species *Esomus lineatus* Ahl 1923, *Esomus malabaricus* Day 1867 and *Esomus manipurensis* Tilak & Jain 1990.

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)

Catostomoidei

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

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

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

Catostomus Lesueur 1817 (syn. *Acomus* Girard 1856, *Decactylus* Rafinesque 1820, *Minomus* Girard 1856, *Notolepidomyzon* Fowler 1913, *Pantosteus* Cope in Cope & Yarrow 1875, *Stomocatus* Bonaparte 1839)

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

Deltistes Seale 1896

Xyrauchen Eigenmann & Kirsch 1899

Erimyzontini Hubbs 1930

Erimyzon Jordan 1876

Minytrema Jordan 1878

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

Moxostoma Rafinesque 1820 (syn. *Lagochila* Jordan & Brayton 1877, *Megapharynx* Legendre 1942, *Placopharynx* Cope 1870, *Ptychostomus* Agassiz 1855, *Quassilabia* Jordan & Brayton in Jordan 1878, *Scartomyzon* Fowler 1913, *Teretulus* 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)

Ictiobus Rafinesque 1820 (syn. *Amblodon* Rafinesque 1819, *Bubalichthys* Agassiz 1855, *Megastomatobus* Fowler 1913)

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*
Bhavana Hora 1920
Cryptотора 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)
Acantopsis 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)
Cobitis Linnaeus 1758 (syn. *Acanestrinia* Băcescu 1962, *Acanthopsis* Agassiz 1832, *Acantophthalmus* van
 Hasselt 1823, *Beyshehiria* Erk'akan, Atalay-Ekmekçi & Nalbant 1999, *Bicanestrinia* Băcescu 1962,
Choia Kim, Park & Nalbant 1997, *Cobitinula* Hankó 1924, *Iberocobitis* Băcescu 1962, *Iksookimia*
 Nalbant 1993, *Kichulchoia* Kim, Park & Nalbant 1999, *Niwaella* Nalbant 1963)
Koreocobitis Kim, Park & Nalbant 1997
Kottelatlimia Nalbant 1994
Lepidocephalichthys Bleeker 1863 (syn. *Cobitichthys* Bleeker 1858, *Enobarbichthys* Whitley 1931,
Enobarbus Whitley 1928, *Jerdonia* Day 1871, *Madrasia* Nalbant 1963, *Platacanthus* Day 1865)
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)
Sewellia Hora 1932 (syn. *Diardichthys* Roberts 1998, *Parasewellia* Nguyen & Nguyen in Nguyen 2005)
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
Afromacheilus 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)
- Oreonectes* Günther 1868 (syn. *Octonema* Martens 1868)
- Oxynoemacheilus* Bănărescu & Nalbant 1966 (syn. *Ilanemacheilus* Coad & Nalbant 2005, *Nun* Bănărescu & Nalbant in Bănărescu, Nalbant & Goren 1982)
- Paracanthocobitis* Grant 2007
- Paracobitis* Bleeker 1863 (syn. *Adiposia* Annandale & Hora 1920, *Pseudodon* Kessler 1874)
- Paranemachilus* 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 2012
- Sphaerophysa* Cao & Zhu 1988
- Sundoreonectes* Kottelat 1990
- Traccatichthys* Freyhof & Serov 2001
- Triplophysa* Rendahl 1933 (syn. *Deuterophysa* Rendahl 1933, *Didymophysa* Whitley 1950, *Diplophysa* Kessler 1874, *Diplophysoides* Fowler 1958, *Indotriplophysa* Prokofiev 2010, *Labiatoophysa* Prokofiev 2010, *Paradidymophysa* Prokofiev 2017, *Qinghaichthys* Zhu 1981, *Tarimichthys* Prokofiev 2010, *Tauphysa* Rendahl 1933)
- Troglocobitis* Parin 1983
- Troglonectes* Zhang, Zhao & Tang 2016
- Tuberoschistura* Kottelat 1990
- Turcinoemacheilus* Bănărescu & Nalbant 1964
- Yunnanilus* 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
Luciobarbus Heckel 1843 (syn. *Aspiobarbus* Berg 1933, *Bertinichthys* Whitley 1953, *Bertinius* Fang 1943, *Messinobarbus* Bianco 1998)
Scaphiodonichthys Vinciguerra 1890 (syn. *Scaphiodontopsis* Fowler 1934)
Semiplotus Bleeker 1860
- Cyprininae Rafinesque 1815 (Type genus: *Cyprinus* Linnaeus 1758)
Aptosyax Rainboth 1991
Carassioides Oshima 1926
Carassius Jarocki 1822 (syn. *Cyprinopsis* Fitzinger 1832, *Neocarassius* Castelnau 1872)
Cyprinus Linnaeus 1758 (syn. *Carpio* Heckel 1843, *Laichowcypris* Nguyen & Doan 1969, *Laichowcypris* Mai (ex Hoa & Hoa) 1978, *Mesocyprinus* Fang 1936, *Mesocyprinus* Cheng 1950)
Luciocyprinus Vaillant 1904 (syn. *Fustis* Lin 1932)
Procypris Lin 1933 (syn. *Paraprocypris* Fang 1936)
Sinocyclocheilus Fang 1936 (syn. *Anchicyclocheilus* Li & Lan 1992, *Gibbibarbus* Dai 1988)
- Labeoninae Bleeker 1859 (Type genus: *Labeo* Cuvier 1816)
Garrini Bleeker 1863 (Type genus: *Garra* Hamilton 1822)
Discolabeo Fowler 1937
Garra Hamilton 1822 (syn. *Discognathichthys* Bleeker 1860, *Discognathus* Heckel 1843, *Hemigarra* Karaman 1971, *Hemigrammocapoeta* Pellegrin 1927, *Horalabiosa* Silas 1954, *Iranocypris* Bruun & Kaiser 1944, *Lissorhynchus* Bleeker 1860, *Mayoa* Day 1870, *Neotylognathus* Kosswig 1950, *Phreatichthys* Vinciguerra 1924, *Platycara* McClelland 1838, *Tylognathoides* Tortonese 1938, *Typhlogarra* Trewavas 1955)
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)
Bangana Hamilton 1822 (syn. *Mirolabeo* Chu & Wang 1963, *Rohitodes* Bleeker 1860, *Tylognathus* Heckel 1843)
Cirrhinus Oken 1817 (syn. *Isocephalus* Heckel 1843)
Gymnostomus Heckel 1843 (syn. *Cirrhinichthys* Bleeker 1863, *Mrigala* Bleeker 1860)
Incisilabeo Fowler 1937
Labeo Cuvier 1816 (syn. *Abrostomus* Smith 1841, *Acra* Bleeker 1860, *Catla* Valenciennes in Cuvier & Valenciennes 1844, *Chrysophekadion* 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)
- Epalzeorhynchus* Bleeker 1855
- Henicorhynchus* Smith 1945
- Labio barbatus* 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
- Linichthys* 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
- Pseudogyriinocheilus* Fang 1933
- Ptychidio* 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
- Longanulus* Li 2006
- Parapsilorhynchus* Hora 1921
- Protolabeo* Zhang, Zhao & An 2010
- Schismatorhynchus* 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)

Cyclocheilichthys Bleeker 1859 (syn. *Anematischthys* Bleeker 1859, *Oxybarbus* Vaillant 1893, *Siaja* Bleeker 1859)

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)

Aspiorhynchus Kessler 1879

Oreinus McClelland 1838 (syn. *Englottogaster* Gistel 1848, *Opistocheilos* Bleeker 1860)

Percocypris Chu 1935

Schizopyge Heckel 1848 (syn. *Paraschizothorax* Tsao 1964)

Schizothorax Heckel 1838 (syn. *Aspiostoma* Nikolskii 1897, *Paraschizothorax* Bleeker 1863,

Paratylognathus Sauvage 1880, *Racoma* McClelland & Griffith in McClelland 1842,

Schizothoraichthys Misra 1962, *Tetrostichodon* Tchang, Yueh & Hwang 1964)

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

Chuanchia Herzenstein 1891

Diptychus Steindachner 1866

Gymnocypris Günther 1868 (syn. *Rugogymnocypris* Yueh & Hwang 1964)

Gymnodiptychus Herzenstein 1892

Herzensteinia Chu 1935

Oxygymnocypris Tsao 1964

Platypharodon Herzenstein 1891

Ptychobarbus Steindachner 1866

Schizopygopsis Steindachner 1866

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

Barbodes Bleeker 1859 (syn. *Cephalakompsus* Herre 1924, *Mandibularca* Herre 1924, *Ospatulus* Herre 1924, *Spratellicypris* Herre & Myers 1931)

Barboides Brüning 1929 (syn. *Raddabarbus* Thys van den Audenaerde 1971)

Clypeobarbus Fowler 1936

Dawkinsia Pethiyagoda, Meegaskumbura & Maduwage 2012

Desmopuntius Kottelat 2013

- Enteromius* Cope 1867 (syn. *Afropuntio* Karaman 1971, *Agrammobarbus* Pellegrin 1935, *Beirabarb* Herre 1936, *Estevea* Whitley 1953, *Hemigrammocapoeta* Estève 1952, *Hemigrammopuntius* Pellegrin 1923, *Mannichthys* Schultz 1942, *Nicholsopuntius* Pellegrin 1933, *Parapuntius* Karaman 1971, *Vanderbiltella* Fowler 1936)
- 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
- Systemus* 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
- Carasobarbus* Karaman 1971 (syn. *Kosswigobarbus* Karaman 1971, *Pseudotor* Karaman 1971)
- Hypselobarbus* Bleeker 1860 (syn. *Gonoproktopterus* Bleeker 1860)
- Labeobarbus* Rüppell 1835 (syn. *Barbellion* Whitley 1931, *Barynotus* Günther 1868, *Dillonia* Heckel 1847, *Lanceobarbus* Fowler 1936, *Varicorhinus* Rüppell 1835)
- Lepidopygopsis* Raj 1941
- Mesopotamichthys* Karaman 1971
- Naziritor* Mirza & Javed 1985
- Neolissochilus* Rainboth 1985 (syn. *Lissochilus* Weber & de Beaufort 1916)
- Osteochilichthys* Hora 1942
- Pterocapoeta* Günther 1902
- Sanagia* Holly 1926
- Tor* Gray 1834
- Cyprinidae *incertae sedis*
- Barbopsis* Di Caporiacco 1926 (syn. *Eilichthys* Pellegrin 1929, *Zaccarina* 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
Rohteichthys 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)
Engraulicypris Günther 1894 (syn. *Mesobola* Howes 1984)
Leptocypris Boulenger 1900
Luciosoma Bleeker 1855 (syn. *Trinematichthys* 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)
Opsarius McClelland 1838 (syn. *Allodanio* Smith 1945, *Bendilisis* Bleeker 1860, *Chedrus* Swainson 1839, *Pachystomus* Heckel 1843, *Paradaniops* Nguyen & Doan 1969, *Perilampus* McClelland 1838, *Shacra* Bleeker 1860, *Schacra* Günther 1868)
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. *Brachydanio* Weber & de Beaufort 1916, *Celestichthys* Roberts 2007)
Danionella Roberts 1986
Devario Heckel 1843 (syn. *Danioides* Chu 1935, *Daniops* Smith 1945, *Eustira* Günther 1868, *Parabarilius* Pellegrin & Fang 1940, *Paradanio* Day 1865, *Rambaibarnia* Fowler 1934)
Inlecycpris Howes 1980
Laubuka Bleeker 1859 (syn. *Allochela* Silas 1958)
Microdevario Fang, Norén, Liao, Källersjö & Kullander 2009
Microrasbora Annandale 1918
Neochela 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)

Amblypharyngodon Bleeker 1860 (syn. *Brachygramma* Day 1865, *Mola* Heckel 1848, *Mola* Blyth 1860)

Boraras Kottelat & Vidthayanon 1993

Brevibora Liao, Kullander & Fang 2010

Horadandia Deraniyagala 1943

Kottelatia Liao, Kullander & Fang 2010

Pectenocypris Kottelat 1982

Rasbora Bleeker 1859 (syn. *Parluciosoma* Howes 1980)

Rasboroides Brittan 1954

Rasbosoma Liao, Kullander & Fang 2010

Trigonopoma 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)

Gobiobotia Kreyenberg 1911 (syn. *Progobiobotia* Chen & Cao 1982)

Mesogobio Bănărescu & Nalbant 1973

Microphysogobio Mori 1934 (syn. *Huigobio* Fang 1938, *Rostrigobio* Taranetz 1937)

Platysmacheilus Lu, Luo & Chen 1977

Pseudogobio Bleeker 1860

Romanogobio Bănărescu 1961 (syn. *Rheogobio* Bănărescu 1961)

Saurogobio Bleeker 1870 (syn. *Armatogobio* Taranetz 1937, *Gobiosoma* Dybowski 1872, *Longurio* Jordan & Starks 1905)

Xenophysogobio Chen & Cao 1977

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

Coreoleuciscus Mori 1935

Gnathopogon Bleeker 1860 (syn. *Leucogobio* Günther 1896, *Otakia* Jordan & Snyder 1900)

Gobiocypris Ye & Fu 1983

Ladislavia Dybowski 1869

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

Pseudopungtungia Mori 1935

Pseudorasbora Bleeker 1860 (syn. *Fundulichthys* Bleeker 1860, *Micraspius* Dybowski 1869)

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

Rhinogobio Bleeker 1870 (syn. *Megagobio* Kessler 1876, *Rhinogobioides* Rendahl 1928)

Sarcocheilichthys Bleeker 1860 (syn. *Barbodon* Dybowski 1872, *Chilogobio* Berg 1914, *Exoglossops* Fowler & Bean 1920, *Georgichthys* Nichols 1918)

Hemibarbus–*Squalidus* clade *sensu* Tang *et al.* 2011

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

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

Squalidus Dybowski 1872 (syn. *Parasqualidus* Doi 2000, *Sinigobio* Chu 1935)

- 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. *Filirashora* Fowler 1937)
- Leuciscidae Bonaparte 1835 (Type genus: *Leuciscus* Cuvier 1816)
- Laviniinae Bleeker 1863 (Type genus: *Lavinia* Girard 1854)
Acrocheilus Agassiz 1855
Chrosomus Rafinesque 1820 (syn. *Parchrosomus* Gasowska 1979, *Pfrille* Jordan 1924)
Eremichthys Hubbs & Miller 1948
Evarra Woolman 1894
Gila Baird & Girard 1853 (syn. *Moapa* Hubbs & Miller 1948, *Myloleucus* Cope 1872, *Protoporus* Cope 1872, *Siboma* Girard 1856, *Temeculina* Cockerell 1909, *Tigoma* Girard 1856)
Hesperoleucus Snyder 1913 (syn. *Endemichthys* Hopkirk 1974)
Klamathella Miller 1945
Lavinia Girard 1854 (syn. *Luxilinus* Jordan 1885)
Mylopharodon Ayres 1855
Orthodon Girard 1856
Ptychocheilus Agassiz 1855
Relictus Hubbs & Miller 1972
Siphateles Cope 1883 (syn. *Leucidius* Snyder 1917)
- Leuciscinae Bonaparte 1835 (Type genus: *Leuciscus* Cuvier 1816)
Abramis Cuvier 1816 (syn. *Brama* Bleeker (ex Klein) 1863, *Sapa* 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. *Spiralinus* Fatio 1882, *Squalalburnus* Berg 1932)
Alburnus Rafinesque 1820 (syn. *Chalcalburnus* Berg 1933)
Anaocypris 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, *Machaerochilus* 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
Leucaspis Heckel & Kner 1857 (syn. *Owsianka* Dybowski 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
Pelagus Kottelat & Freyhof 2007
Pelecus Agassiz 1835
Petroleuciscus 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. *Cenisophius* Bonaparte 1846, *Gardonus* Bonaparte 1846, *Liparus* Schulze 1892, *Metallites* Schulze 1890, *Orfus* Fitzinger 1873, *Orthroleucos* Derjavin 1937, *Pararutilus* Berg 1912, *Pigus* Bonaparte 1846, *Rubellus* 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 1980, *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. *Achahara* Jordan & Hubbs 1925, *Eulinmeela* Dybowski 1916, *Phoxinus* Agassiz 1835)
Plagopterinae Cope 1874 (Type genus: *Plagopterus* Cope 1874)
Couesius Jordan 1878
Hemitremia Cope 1870
Lepidomeda 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
Alganssea Girard 1856 (syn. *Xystrosus* Jordan & Snyder 1899)
Aztecula Jordan & Evermann 1898
Campostoma Agassiz 1855
Clinostomus Girard 1856 (syn. *Rhodopleuriscus* Fowler 1944)
Codoma Girard 1856
Cyprinella Girard 1856 (syn. *Erogala* Jordan in Jordan & Brayton 1878, *Moniana* Girard 1856)
Dionda Girard 1856
Ericymba Cope 1865
Erimonax 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
Luxilus Rafinesque 1820 (syn. *Coccogenia* Cockerell & Callaway 1909, *Coccotis* Jordan 1882, *Hypsolepis* Agassiz (ex Baird) 1854, *Plargyrus* Rafinesque 1820)
Lythrurus Jordan 1876
Macrhybopsis Cockerell & Allison 1909 (syn. *Extrarius* Jordan 1919)
Miniellus Jordan 1888
Mylocheilus Agassiz 1855 (syn. *Clarkina* Jordan & Evermann 1927)
Nocomis Girard 1856 (syn. *Ceraticthys* Baird in Girard 1856)
Notropis Rafinesque 1818 (syn. *Alburnellus* Girard 1856, *Azteca* Jordan & Evermann 1896, *Chriope* Jordan 1878, *Episema* Cope & Jordan in Jordan 1877, *Erinemus* Jordan 1876, *Hydrophlox* Jordan in Jordan & Brayton 1878, *Minnilus* Rafinesque 1820, *Nazatexico* Whitley 1931, *Nototropis* Jordan 1877, *Opsopoea* Jordan & Evermann 1896, *Orcella* Jordan & Evermann 1896, *Orcula* Jordan & Evermann 1900, *Paranotropis* Fowler 1904, *Photogenis* Cope 1867)
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
Rhinichthys Agassiz 1849 (syn. *Apocope* Cope 1872, *Argyreus* Heckel 1843, *Eritrema* Cope & Yarrow 1875)
Richardsonius Girard 1856
Stypodon Garman 1881
Tampichthys Schönhuth, Doadrio, Dominguez-Dominguez, Hillis & Mayden 2008
Tiaroga Girard 1856
Yuriria Jordan & Evermann 1896 (syn. *Falcula* Jordan & Snyder 1899, *Falcularius* Jordan & Snyder in Jordan 1903)
Pseudaspininae Bogutskaya 1990 (Type genus: *Pseudaspius* Dybowski 1869)
Oreoleuciscus Warpachowski 1889 (syn. *Acanthorutilus* Berg 1912)
Pseudaspius Dybowski 1869
Rhynchocypris Günther 1889 (syn. *Czekanowskiella* Dybowski 1916, *Eupallasella* Dybowski 1916, *Lagowskiella* Dybowski 1916, *Moroco* Jordan & Hubbs 1925)
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
 Parazacco Chen 1982 (syn. *Carinozacco* Zhu, Wang & Ni 1982)
 Zacco Jordan & Evermann 1902
 Xenocypridinae Günther 1868 (Type genus: *Xenocypris* Günther 1868)
 Ancherythroculter Yih & Wu 1964
 Aphyocypris Günther 1868 (syn. *Aphyocyprionides* Tang 1942, *Caraspius* Nichols 1925, *Fusania*
 Jordan & Starks 1905, *Nicholsicypris* Chu 1935, *Pararashora* Regan 1908, *Phoxiscus* Oshima
 1919, *Yaoshanicus* Lin 1931)
 Chanodichthys Bleeker 1860 (syn. *Erythroculter* Berg 1909, *Leptocephalus* Basilewsky 1855,
 Pseudoculter Bleeker 1860)
 Ctenopharyngodon Steindachner 1866 (syn. *Pristiodon* 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
 Hemiculter Bleeker 1860 (syn. *Cultricus* Oshima 1919, *Kendallia* Evermann & Shaw 1927,
 Siniichthys Bănărescu 1970)
 Hemiculterella Warpachowski 1888 (syn. *Semiculter* Chu 1935)
 Hemigrammocypripis 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, *Myloleucus* Günther 1873)
 Ochetobius Günther 1868 (syn. *Agenigobio* Sauvage 1878)
 Oxygaster van Hasselt 1823
 Parabramis Bleeker 1864
 Parachela Steindachner 1881 (syn. *Grandisquamachela* Fowler 1934)
 Paralabuca Bleeker 1864 (syn. *Cultrops* Smith 1938)
 Plagiognathops Berg 1907 (syn. *Plagiognathus* Dybowski 1872)
 Pseudobrama Bleeker 1870
 Pseudohemiculter Nichols & Pope 1927
 Pseudolabuca Bleeker 1864 (syn. *Parapelecus* Günther 1889)

Sinibrama Wu 1939
Squaliobarbus Günther 1868
Toxabramis Günther 1873
Xenocyprionides Chen 1982
Xenocypris Günther 1868
 Xenocyprididae *incertae sedis*
Anabarilius Cockerell 1923 (syn. *Nicholsiculter* Rendahl 1928, *Rohanus* Chu 1935)
Araiocypris Conway & Kottelat 2008
Atrilinea Chu 1935
Gymnodanio Chen & He 1992
Longiculter Fowler 1937
Pogobrama Luo 1995
Rasborschichthys Bleeker 1859

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