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## Limits and phylogenetic relationships of East Asian fishes in the subfamily Oxygastrinae (Teleostei: Cypriniformes: Cyprinidae)

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### Abstract

The cyprinid subfamily Oxygastrinae is composed of a diverse group of fishes that has been taxonomically and phylogenetically problematic. Their great variation in appearance, life histories, and trophic diversity resulted in uncertainty regarding their relationships, which led to their historical classification across many disparate subfamilies. The phylogenetic relationships of Oxygastrinae are resolved based on sequence data from four loci: cytochrome *b*, cytochrome *c* oxidase I, opsin, and recombination activating gene 1. A combined data matrix consisting of 4114 bp for 144 taxa was compiled and analyzed using maximum likelihood and parsimony optimality criteria. The subfamily Oxygastrinae is recovered as a monophyletic group that includes *Ancherythroculter*, *Aphyocypris*, *Candidia*, *Chanodichthys*, *Ctenopharyngodon*, *Culter*, *Distoechodon*, *Elopichthys*, *Hainania*, *Hemiculter*, *Hemiculterella*, *Hemigrammocypripis*, *Hypophthalmichthys*, *Ischikauia*, *Macrochirichthys*, *Megalobrama*, *Metzia*, *Mylopharyngodon*, *Nicholsicypris*, *Nipponocypris*, *Ochetobius*, *Opsariichthys*, *Oxygaster*, *Parabramis*, *Parachela*, *Paralauca*, *Parasabora*, *Parazacco*, *Plagiognathops*, *Pseudobrama*, *Pseudohemiculter*, *Pseudolauca*, *Sinibrama*, *Squaliobarbus*, *Toxabramis*, *Xenocyprionides*, *Xenocypris*, *Yaoshanicus*, and *Zacco*. Of these genera, the following were found to be monophyletic: *Aphyocypris*, *Distoechodon*, *Hypophthalmichthys*, *Nipponocypris*, *Opsariichthys*, *Parachela*, *Paralauca*, *Plagiognathops*, *Xenocyprionides*, and *Xenocypris*. The following genera were not monophyletic: *Metzia*, *Hemiculter*, *Toxabramis*, *Ancherythroculter*, *Chanodichthys*, *Culter*, *Megalobrama*. The remainder are either monotypic or were represented by only a single species. Four genera not examined in this study are provisionally classified in Oxygastrinae: *Anabarilius*, *Longiculus*, *Pogobrama*, and *Rasboraichthys*.

**Key words:** Cypriniformes, Cyprinidae, Oxygastrinae, phylogeny, systematics, taxonomy

## Introduction

The cyprinid subfamily Oxygastrinae (Teleostei: Ostariophysi: Cypriniformes) is a group of freshwater fishes distributed across eastern Eurasia and Southeast Asia. The recognition of this subfamily in its current usage follows Tang *et al.* (2013), who identified Oxygastrinae Bleeker 1860 as the senior available name for this taxonomically disorganized group. The subfamily has more than 40 genera and approximately 150 species (Howes, 1991; Rainboth 1991; Eschmeyer, 2012). This estimate of its diversity is based on the species classified in the subfamilies Cultrinae, Hypophthalmichthyinae, Squaliobarbinae, and Xenocypridinae (Howes 1991; Rainboth 1991; Nelson 1994, 2006), and taxa formerly placed in the subfamilies Alburninae and Danioninae that have been referred to this assemblage (Tang *et al.* 2010, 2013). Fishes of this subfamily show a wide range of trophic diversity (Bănărescu & Coad 1991; Sibbing 1991), including predatory piscivores (e.g., *Chanodichthys erythropterus*, *Elopichthys bambusa*, *Macrochirichthys macrochirus*), phytoplanktivores (e.g., *Hypophthalmichthys molitrix*), zooplanktivores (e.g., *H. nobilis*), macrophytic grazers (e.g., *Ctenopharyngodon idella*), and durophagous molluscivores (e.g., *Mylopharyngodon piceus*). Although these fishes are mostly small- to medium-sized, some can grow large in size, up to 2 m in length for *Elopichthys bambusa* (Nikolskii 1954; Bănărescu & Coad 1991) and over 70 kg for *Mylopharyngodon piceus* (Nico *et al.* 2005). Species like *C. idella*, *H. molitrix*, *H. nobilis*, and *M. piceus* also play important economic roles in aquaculture (Bănărescu & Coad 1991; Lin & Peter 1991; Nico *et al.* 2005; Kolar *et al.* 2007). These Asian carps have been introduced around the world (e.g., Mandrak & Cudmore 2004; Goren & Galil 2005; Povž & Šumer 2005; Britton & Davies 2007; Conover *et al.* 2007), either for aquaculture, as biological control agents, or both. In those countries where they have become established, they now pose problems as invasive pest species (e.g., Nico *et al.* 2005; Conover *et al.* 2007; Kolar *et al.* 2007).

**Systematics and taxonomic history.** The putative members of the recently recognized subfamily Oxygastrinae have had a long and torturous taxonomic history (Table 1). During most of that history, those species were rarely recognized as belonging to the same group and almost never called Oxygastrinae. Instead, they were distributed among a number of different groups that went by a host of junior names (e.g., Abramidina, Cultrinae, Squaliobarbinae, Xenocypridinae). As noted by Tang *et al.* (2013), the name Oxygastri fell into disuse after its initial erection (Bleeker 1860), with Bleeker (1863) himself renaming the group Smiliogastrini. Various studies of cyprinid systematics have shed some light on the nature of this group (e.g., Nikolskii, 1954; Bănărescu 1967; Gosline 1978; Cavender & Coburn 1992; Wang *et al.* 2007a). However, its composition and name remained uncertain until Tang *et al.* (2013) recognized Oxygastrinae Bleeker 1860 as the senior available name for this clade, synonymizing several junior family-group names and revising the classification of Cyprinidae to form a monophyletic subfamily Oxygastrinae. See Tang *et al.* (2013) for a more detailed discussion of the nomenclatural and taxonomic issues surrounding the family-group name Oxygastri Bleeker 1860.

Because this group was never well-established, tracing oxygastrines through the literature mostly involves following the history of other subfamilies, like Abramidina and, more recently, Alburninae, Cultrinae, and Xenocypridinae. Dybowski (1862) classified *Oxygaster* in the Alburniformes, noting that it was likely a member of the genus *Pelecus*, foreshadowing later uncertainty over the placement of *Pelecus* vis-à-vis cultrines (e.g., Bănărescu 1967). When Günther (1868) recognized Abramidina (a subgroup of his family Cyprinidae) with both European (e.g., *Abramis*, *Alburnus*) and Asian taxa (e.g., *Chela* [*Oxygaster* as a subgenus], *Culter*), it contained several genera that would eventually be recognized as cultrines and are now placed in Oxygastrinae (e.g., *Chanodichthys*, *Culter*, *Pseudolaubuca*). The composite nature of Günther's Abramidina was noted by later workers (e.g., Regan 1911; Kryzhanovsky 1947). Silas (1958: 62) stated "that the grouping is one more of convenience than a natural assemblage." He thought that some of its genera were closer to Leuciscinae and Rasborinae [=Danioninae]. However, Günther's name saw widespread use (e.g., Gill 1893; Berg 1912; Weber & de Beaufort 1916; Rendahl 1928; Chu 1935; Nichols 1938; Smith 1945; Silas 1958) until Nikolskii (1954) overhauled the classification of these fishes by moving the Asian species of Abramidina to the then recently erected Cultrinae (Kryzhanovsky 1947) and uniting the European taxa (including *Abramis*) with Leuciscinae. His Cultrinae included *Chanodichthys* (as *Erythroculter*), *Elopichthys*, *Hemiculter*, *Megalobrama*, *Opsariichthys*, *Parabramis*, *Plagiognathops*, and *Xenocypris*. Acceptance of Cultrinae for this group of fishes restricted to eastern Asia led to the decline in usage of Günther's Abramidina, though that name did remain in sporadic use (e.g., Yi & Wu 1964; Howes 1981, 1991; Bogutskaya 1990, 1991). Most subsequent workers (e.g., Bănărescu 1967; Gosline 1974, 1978; Howes 1991; Cavender & Coburn, 1992; Nelson 2006) would follow Nikolskii's (1954) decision to separate the

TABLE 1. Historical classifications of genera in the subfamily Cultrinae.

Nikolskii (1954)	Bănărescu (1967)	Gosline (1974)	Howes (1991)	Rainboth (1991)	Dai <i>et al.</i> (2005)	Wang <i>et al.</i> (2007a)
<i>Elopichthys</i>	<i>Anabarilius</i>	<i>Chela</i> <sup>2</sup>	<i>Ancherythroculter</i>	<i>Ancherythroculter</i>	<i>Anabarilius</i>	<i>Aristichthys</i> <sup>1</sup>
<i>Erythroculter</i> <sup>1</sup>	<i>Ancherythroculter</i>	<i>Culter</i>	<i>Chanodichthys</i>	<i>Chanodichthys</i>	<i>Ancherythroculter</i>	<i>Ctenopharyngodon</i>
<i>Hemiculter</i>	<i>Chela</i> <sup>2</sup>	<i>Erythroculter</i> <sup>1</sup>	<i>Culter</i>	<i>Culter</i>	<i>Culter</i>	<i>Culter</i>
<i>Megalobrama</i>	<i>Culter</i>	<i>Hemiculter</i>	<i>Erythroculter</i> <sup>1</sup>	<i>Hainania</i>	<i>Cultrichthys</i> <sup>1</sup>	<i>Cultrichthys</i> <sup>1</sup>
<i>Opsariichthys</i>	<i>Erythroculter</i> <sup>1</sup>	<i>Ischikauia</i>	<i>Ischikauia</i>	<i>Megalobrama</i>	<i>Hainania</i>	<i>Distoechodon</i>
<i>Parabramis</i>	<i>Hainania</i>	<i>Megalobrama</i>	<i>Longiculus</i>	<i>Parabramis</i>	<i>Hemiculter</i>	<i>Elopichthys</i>
<i>Plagiognathops</i>	<i>Hemiculter</i>	<i>Parabramis</i>	<i>Megalobrama</i>	<i>Sinibrama</i>	<i>Hemiculterella</i>	<i>Hemigrammocypripis</i>
<i>Xenocypris</i>	<i>Hemiculterella</i>		<i>Osteobrama</i> <sup>1</sup>	<i>Toxabramis</i>	<i>Ischikauia</i>	<i>Hypophthalmichthys</i>
	<i>Ischikauia</i>		<i>Parabramis</i>		<i>Macrochirichthys</i>	<i>Luciobrama</i>
	<i>Longiculus</i>		<i>Rohtee</i> <sup>1</sup>		<i>Megalobrama</i>	<i>Megalobrama</i>
	<i>Macrochirichthys</i>		<i>Sinibrama</i>		<i>Parabramis</i>	<i>Mylopharyngodon</i>
	<i>Megalobrama</i>				<i>Paralabaucha</i>	<i>Nicholsicypris</i>
	<i>Oxygaster</i>				<i>Pogobrama</i>	<i>Ochetobius</i>
	<i>Parabramis</i>				<i>Pseudohemiculter</i>	<i>Opsariichthys</i>
	<i>Parachela</i>				<i>Pseudolabaucha</i>	<i>Pseudobrama</i>
	<i>Paralabaucha</i>				<i>Rasborinus</i> <sup>1</sup>	<i>Pseudohemiculter</i>
	<i>Pelecus</i> <sup>2</sup>				<i>Sinibrama</i>	<i>Pseudolabaucha</i>
	<i>Pseudohemiculter</i>				<i>Toxabramis</i>	<i>Rasborinus</i> <sup>1</sup>
	<i>Pseudolabaucha</i>					<i>Sinibrama</i>
	<i>Pseudoxygaster</i> <sup>1,2</sup>					<i>Squaliobarbus</i>
	<i>Rasborichthys</i>					<i>Toxabramis</i>
	<i>Rasborinus</i> <sup>1</sup>					<i>Xenocypris</i>
	<i>Salmostoma</i> <sup>2</sup>					<i>Zacco</i>
	<i>Sinibrama</i>					
	<i>Toxabramis</i>					

<sup>1</sup> *Aristichthys* [= *Hypophthalmichthys*]; *Cultrichthys* [= *Culter*]; *Erythroculter* [= *Chanodichthys*]; *Cultrichthys* spp. and *Erythroculter* spp. are variably assigned to both *Chanodichthys* and *Culter* (Eschmeyer, 2012); *Pseudoxygaster* [= *Securicula*]; *Rasborinus* [= *Metzia*].

<sup>2</sup> Genera no longer classified with cultrine taxa (e.g., Howes, 1991; Nelson, 2006).

Note: Wang *et al.* (2007a) did not recognize the subfamily Cultrinae, but they did identify a similar monophyletic group that was classified as the tribe Xenocypridini in their subfamily Leuciscinae.

former members of Abramidina, placing the European species in the subfamily Leuciscinae and the Asian species mostly in the subfamilies Cultrinae and Danioninae. However, Günther's Abramidina would persist in the form of Alburninae, a subfamily that retained many European and Asian "abramidine" species (e.g., Howes 1991; Rainboth 1991; Nelson 1994).

The works of Bănărescu (1963, 1964, 1967, 1968a, b, 1969, 1970a, b, 1971a, b) further modified the classification of Cultrinae. Of these studies, Bănărescu (1967) had the greatest impact on cultrine systematics, where he recognized Cultrinae as including *Ancherythroculter*, *Chela*, *Culter*, *Erythroculter* [= *Chanodichthys*], *Hemiculter* (*Hainania* and *Pseudohemiculter* as synonyms), *Hemiculterella* (*Anabarilius* as synonym), *Ischikauia*, *Longiculter*, *Macrochirichthys*, *Megalobrama* (*Sinibrama* as synonym), *Oxygaster*, *Parabramis*, *Parachela*, *Paralaubuca*, *Pseudolaubuca*, *Pseudoxygaster* [= *Securicula*], *Rasborigichthys*, *Rasborinus* [= *Metzia*], *Salmostoma*, *Toxabramis*, and *Pelecus* (as the sole European representative). In that work, he also removed *Xenocypris* (*Distoechodon* and *Plagiognathops* as subgenera) from the subfamily, ascribing *Xenocypris* and *Pseudobrama* to Xenocypridinae, a subfamily which he thought was related to Cultrinae. However, the subfamily Danioninae was his choice for the closest relative of Cultrinae. Bănărescu noted some resemblance between cultrines and species of *Rohtee*, but placed *Rohtee* in the Barbinae [= Cyprininae]. Although species limits were well delimited in his view, Bănărescu felt generic limits were often arbitrary and inconsistent; this likely contributed to his uncertainty about generic relationships within Cultrinae. He divided the subfamily into three broad biogeographic groups: the Chinese group (with *Erythroculter*, *Culter*, *Ancherythroculter*, *Megalobrama*, *Parabramis*, *Hemiculter*, *Toxabramis*, *Ischikauia*, *Hemiculterella*, *Pseudolaubuca*, *Rasborigichthys*, *Rasborinus*); the South-East Asian group (the remaining genera minus *Pelecus*); and *Pelecus* (the only European taxon).

In his work on cyprinids, Gosline (1973, 1974, 1975, 1978) had reason to address the cultrine issue often. Corroborating Nikolskii (1954), Gosline (1974) found patterns of the cephalic lateral line that linked the European genera of Abramidina (*Abramis*, *Alburnoides*, *Blicca*, *Chalcalburnus* [= *Alburnus*], *Leucaspius*, *Pelecus*, and *Vimba*) with Leuciscinae, separating them from the Asian genera (*Chela*, *Culter*, *Erythroculter* [= *Chanodichthys*], *Hemiculter*, *Ischikauia*, *Megalobrama*, and *Parabramis*). This largely agreed with Bănărescu (1967) too, except that Gosline (1974) removed *Pelecus cultratus* from Cultrinae. Gosline also observed that *Elopichthys* + *Ochetobius* and *Hypophthalmichthys* + *Aristichthys* [= *Hypophthalmichthys*] represented specialized groups with no obvious close relatives. Gosline (1978) identified a cultrin-xenocypridin group of eastern and southeastern Asia as one of three major lineages within the subfamily Leuciscinae, one that was distinct from the leuciscin-abramidin-chondrostomin group of Europe and western Asia. However, Gosline could find no diagnostic characters uniting these two groups. In fact, he discovered two characters (number of pharyngeal tooth rows, presence/absence of connection between supraorbital and infraorbital sensory canals) that suggested separate evolutionary origins, which led him to agree with Nikolskii (1954): these fishes represented separate evolutionary radiations, one in Asia and one in Europe. Gosline (1978) hypothesized that the subsequent occupation of all major freshwater habitats by members of these two groups had produced analogous species which, although similar in appearance, were not closely related. He cited *Pelecus* as an example of a specific pelagic morphotype (cultrate abdomen, superior mouth, long pectorals) with an equivalent Asian counterpart in *Macrochirichthys*. Gosline mentioned *Chondrostoma* (European) and *Xenocypris* (Asian) as another pair displaying convergent evolution. He found the presence of a three-lobed swim bladder to be a diagnostic character for cultrins but he did report that the condition could vary (Gosline 1978: 10). Tchang (1931) originally recorded the presence of a third lobe in *Chanodichthys*, *Culter*, *Hemiculter*, *Hypophthalmichthys*, *Parabramis*, *Parapelecus* [= *Pseudolaubuca*], *Parosteobrama* [= *Megalobrama*], and *Xenocypris*; all of these were Chinese cyprinids that Gosline considered to be cultrins or derived from cultrin stock. Conversely, Tchang (1931) did not find this condition in any other Chinese cyprinids. Gosline (1978) did not find any instances of a third lobe reported for a non-cultrin cyprinid in the literature, nor did he find that type of swim bladder in any of the non-Chinese midwater genera that he personally examined, none of which were part of his cultrin stock. Liu (1940: 78) had also noted the presence of a tripartite air bladder in "a few genera of Abramidinae." Although no specific genera were named, presumably they included some of the ones discussed by Tchang (1931) and Gosline (1978).

Gosline (1978) saw clear cultrin affinities for certain eastern Asian groups of specialized cyprinids: *Aphyocypris*, *Hemigrammocypripis*, and *Tanichthys*; *Aristichthys* [= *Hypophthalmichthys*] and *Hypophthalmichthys*; *Opsariichthys* and *Zacco*. For *Aristichthys* and *Hypophthalmichthys*, Gosline based the connection on the presence of a three-lobed swim bladder. For *Opsariichthys* and *Zacco*, the cultrin association was indicated by the presence

of a foramen between the quadrate and metapterygoid. Said foramen is also found in *Salmostoma bacaila* (now classified as a danionine), *Paralauca harmandi*, *P. riveroi* (but not in *P. typus* or *P. barroni*), and *Macrochirichthys macrochirus* (Gosline 1975). This condition was often cited as evidence of the primitive position of *Opsariichthys* and *Zacco* within Cyprinidae (e.g., Regan, 1911; Greenwood *et al.* 1966; Hensel, 1970; Fink & Fink, 1981), because this character also occurs in Clupeidae, Characiformes, and Cobitidae *sensu stricto* (Ramaswami 1953; Gosline 1973). Gosline (1973) instead suggested that this fenestra may have evolved independently multiple times because of a possible functional constraint: providing additional space for the contraction of the *adductor mandibulae* muscles. He hypothesized that specific head/suspensorium configurations may lead to the evolution of such an opening, speculating that the extent of expansion in the cheek may also be a determining factor. Gosline (1975) noted that the occurrence of this character “in only certain long-jawed cyprinids” indicated that there was more to this than just providing space for muscle contraction, and the attendant increase in bite strength that comes with larger *adductor mandibulae*. Gosline (1975) suggested that this was tied to the limited space available in those species with compressed heads, like cultrins, noting that the opening was absent in genera like *Luciosoma* which also possess long jaws but have broader heads.

The work of Howes (1978, 1979, 1981, 1991) had important implications for the systematics of these fishes. Unlike previous classifications that placed them with other Asian genera, Howes (1978) grouped the monotypic *Luciobrama* and *Elopichthys* with *Aspiolucius*, *Aspius* [= *Leuciscus*], and *Pseudaspius* in an aspinine group within Leuciscinae. Howes (1978) based his conclusions on characters of the skull and jaws that differed between the two genera, as well as many putative synapomorphies *Elopichthys* appeared to share with aspinines. In particular, the various adaptations for piscivory were regarded as synapomorphies supporting the monophyly of the group. *Elopichthys* was considered unique among predatory cyprinids in evolving a pike-like morphology, where protrusibility of the upper jaw was sacrificed in favor of modifications to the jaw structure (Howes 1978: 62). In his examination of *Macrochirichthys macrochirus*, Howes (1979) remarked on the numerous similarities in morphology between *Oxygaster sensu lato* (included species referred to *Parachela* therein) and *Macrochirichthys*, similarities which prompted Howes to classify both genera in his cheline group (Howes 1979: 187), a group that also included *Chela*, *Parachela*, *Salmostoma*, and *Securicula*. These were the only six cultrine genera he recognized as forming a monophyletic group. Howes (1979) otherwise rejected the Cultrinae of Nikolskii (1954) and Bănărescu (1967) as non-monophyletic. Howes (1979: 186–187; fig. 41) recognized a clade which he informally named the oxygastrine lineage, comprising *Macrochirichthys*, *Oxygaster*, and *Parachela*, which he placed in his cheline group. All of the members of the cheline group were later moved into his subfamily Rasborinae [= Danioninae], as part of the bariliin group (Howes 1991). Of the remaining cultrine genera not grouped with the chelines, Howes (1979) recognized two additional groups, a cultrine group (*Culter*, *Erythroculter* [= *Chanodichthys*], *Ischikauia*, *Parabramis*, *Megalobrama*, *Paralauca*) and a hemicultrine group (*Hemiculter*, *Pseudolauca*, *Toxabramis*, and possibly *Rasborichthys* [in part]). He did not agree with prior hypotheses that the subfamily Cultrinae was related to the subfamilies Danioninae (Bănărescu 1967; Mirza 1975) and/or Xenocyprinidae (Bănărescu 1967), which may have been due to his contention that the latter two groups were not monophyletic (Howes 1979). Although primarily focused on danionine fishes, Howes (1980: 185) did briefly mention that aspinines, cultrines, and hemicultrines (including his Xenocyprinidae) were related in various ways to the three independent lineages that constituted what he considered to be a polyphyletic “Leuciscinae.” His cheline group, which included *Opsariichthys*, contradicted Gosline’s (1978) assertion that *Opsariichthys* and *Zacco* were related to cultrins. Howes (1980: 186) even speculated that *Zacco* was part of the alburnine lineage of “Leuciscinae,” a possibility he (Howes 1983: 97) later rejected, returning *Zacco* to its traditional place near *Opsariichthys* (e.g., Greenwood *et al.* 1966; Bănărescu 1968c; Hensel 1970; Gosline 1978; Fink & Fink 1981; Chen 1982).

In his work on *Ctenopharyngodon* and *Hypophthalmichthys*, Howes (1981) challenged prevailing opinion that the two genera were closely related, which also led him to disagree with Gosline (1978) on the use of the three-chambered swim bladder as an indicator of shared ancestry. Howes (1981) dismissed the diagnostic utility of the character because of its “mosaic distribution throughout the Cyprinidae.” He also discounted its significance because the presence of the third chamber could vary among individuals of the same species (e.g., Vasil’eva & Makeeva 2003; Shapovalov 2011), something that Gosline (1978) also had observed. Howes (1981) organized *Ctenopharyngodon*, *Mylopharyngodon*, and *Squaliobarbus* in a monophyletic squaliobarbine group, which he considered to be the sister group of all other barbelled cyprinids (i.e., subfamily Cyprininae). *Hypophthalmichthys*

along with Xenocypridinae (*Distoechodon*, *Plagiognathops*, and *Xenocypris*) formed the basal clade of his abramine group. Howes (1981) reversed his earlier statements (Howes 1979) that Xenocypridinae was polyphyletic and *Xenocypris* was related to the hemicultrine group. The classification of Howes (1991) had oxygastrine taxa scattered among most of the cyprinid subfamilies, though the majority were concentrated in Cultrinae and Danioninae (his Rasborinae, which he considered to be non-monophyletic). He again rejected the monophyly of the Cultrinae of Nikolskii (1954) and Bănărescu (1967). Howes (1991) restricted Cultrinae to *Ancherythroculter*, *Chanodichthys*, *Culter*, *Erythroculter* [= *Chanodichthys*], *Ischikauia*, *Megalobrama*, *Parabramis*, *Sinibrama*, and (questionably) *Longiculter*. This included most of the cultrine assemblage *sensu* Howes (1979). Howes (1991) also tentatively placed *Osteobrama* and *Rohtee* in Cultrinae on the basis of traits shared with *Parabramis* (e.g., presence of an enlarged dorsal ray). Although not addressed, it is apparent that his *Rohtee* included some species now recognized as *Osteobrama*, based on his discussion of *Rohtee cotio* [= *O. cotio*]. This cultrine classification of *Rohtee* was contrary to Bănărescu (1967) who had displaced *Rohtee* to Barbinae. Howes (1991) assigned other genera currently recognized as members of Oxygastrinae (Tang *et al.* 2013) to two different lineages of Rasborinae: *Oxygaster*, *Macrochirichthys*, and *Parachela* in the bariliin group; *Opsariichthys* and *Zacco sensu lato* (some species are currently assigned to *Nipponocypris*) in an unnamed assemblage. The squaliobarbin lineage *sensu* Howes (1981) was classified as part of the Cyprininae. His Alburninae included genera from the cultrine and hemicultrine lineages of Howes (1979): *Pseudolaubuca*, *Paralaubuca*, and *Hemiculter*. *Hemiculterella*, which Howes (1979) affiliated with *Pelecus* and Leuciscinae, was included in Alburninae (Howes 1991). Finally, the remaining oxygastrines were assigned to two different lineages of Leuciscinae: *Xenocypris*, *Plagiognathops*, *Distoechodon*, and *Hypophthalmichthys* of his abramine lineage; *Elopichthys* and *Luciobrama* of his aspinin lineage (Howes 1991).

Rainboth (1991) was one of the few modern authors to employ the original Bleeker name, as Oxygastrini, which he classified as a tribe of the subfamily Danioninae. In addition to *Oxygaster*, the tribe included *Aspidoparia* [= *Cabdio*], *Barilius*, *Luciosoma*, *Macrochirichthys*, *Opsariichthys*, *Opsarius*, *Parachela*, *Parazacco*, *Raiamas*, *Salmostoma*, *Securicula*, and *Zacco*. This work and that of Howes (1991) established the modern placement of *Oxygaster* within Danioninae (e.g., Nelson, 1994, 2006; Rainboth 1996; Menon 1999), contradicting Gosline (1975). Rainboth (1991) placed *Hemiculter*, *Heimculterella*, *Longiculter*, *Paralaubuca*, *Pseudohemiculter*, *Pseudolaubuca*, and *Rasborinus* [= *Metzia*] in Alburninae (his coverage was restricted to species of Southeast Asia) and *Ancherythroculter*, *Chanodichthys*, *Culter*, *Hainania*, *Megalobrama*, *Parabramis*, *Sinibrama*, and *Toxabramis* in Cultrinae. *Elopichthys*, *Luciobrama*, and *Ochetobius* were classified as leuciscines, in the tribe Aspiini. He also classified *Distoechodon*, *Hypophthalmichthys*, *Plagiognathops*, *Xenocyprionides*, and *Xenocypris* in the Leuciscinae, in the tribe Chondrostomini (also as Chondrostomatini therein), synonymizing Xenocypridinae with Chondrostomini. He followed Howes (1981) in recognizing Squaliobarbini as a tribe of Cyprininae, with the addition of *Atrilinea*. Rainboth (1991: 171) speculated that some species of *Rohtee sensu lato* (which included *Osteobrama* spp.) were likely members of the Cultrinae, which would agree with Howes (1991). Rainboth (1991) noted the implication of this: classification of *R. belangeri* [= *O. belangeri*], the type species of *Smiliogaster* [= *Osteobrama*], as a member of Cultrinae would mean that Smiliogastrini Bleeker 1863 would have priority over Cultrinae Kryzhanovsky 1947 (authorship given as Nikolskii 1954; Rainboth 1991: table 6.2).

Yue and Luo (1996) partitioned the Cultrinae into Anchidaniorine [sic], Cultrine, and Rasborine [= *Rasborinus*] groups. The first included only *Macrochirichthys* and *Paralaubuca*. The second was divided into a *Parabramis* branch with *Megalobrama* and *Parabramis*, and a *Culter* branch that appeared to include *Ancherythroculter*, *Culter*, and *Cultrichthys* [= *Chanodichthys*]. The third group was divided into a *Hemiculter* branch with *Hainania*, *Hemiculter*, *Hemiculterella*, *Pseudohemiculter*, *Pseudolaubuca*, and *Toxabramis*, and a *Rasborinus* branch with *Anabarilius*, *Ischikauia*, *Paralaubuca*, *Pogobrama*, *Rasborinus* [= *Metzia*], and *Sinibrama*. In Chen *et al.* (1998), putative oxygastrines were dispersed across five of the eight cyprinid subfamilies that were covered: Danioninae, Leuciscinae, Cultrinae, Xenocypridinae, and Hypophthalmichthyinae. The bulk of the taxa were located in Cultrinae, which included *Anabarilius*, *Ancherythroculter*, *Culter*, *Cultrichthys* [= *Chanodichthys*], *Hainania*, *Hemiculter*, *Hemiculterella*, *Macrochirichthys*, *Megalobrama*, *Parabramis*, *Paralaubuca*, *Pogobrama*, *Pseudohemiculter*, *Pseudolaubuca*, *Rasborinus* [= *Metzia*], *Sinibrama*, and *Toxabramis* (Luo & Chen 1998). Chen and Chu (1998) classified *Aphyocypris*, *Candidia*, *Nicholsicypris*, *Opsariichthys*, *Parazacco*, *Yaoshanicus*, and *Zacco* in Danioninae. *Ctenopharyngodon*, *Elopichthys*, *Luciobrama*, *Mylopharyngodon*, *Ochetobius*, and *Squaliobarbus* were assigned to Leuciscinae (Luo 1998). *Distoechodon*, *Pseudobrama*, *Xenocyprionides*, and

*Xenocypris* were recognized as members of Xenocyprinae (Liu & He 1998). Chen (1998) included *Aristichthys* [= *Hypophthalmichthys*] and *Hypophthalmichthys* in Hypophthalmichthyinae.

The lack of consensus on the composition and limits of the various groups that form Oxygastrinae can be blamed in part on an issue raised by Gosline (1975, 1978): many of these fishes bear striking resemblances to members of other cyprinid subfamilies. Some oxygastrine species (e.g., *Opsariichthys*, *Parachela*, *Zacco*) are difficult to distinguish from species of Danioninae (viz., *Opsarius*, *Salmostoma*, *Securicula*), whereas others can be mistaken for species of Leuciscinae (e.g., *Macrochirichthys-Pelecus*). These types of convergent similarities were noticed by Nikolskii (1954), who observed that Asian cultrines often had an analogous counterpart in the European fauna, with *Chanodichthys erythropterus* resembling the ziege (*Pelecus cultratus*), *Hemiculter leucisculus* resembling the bleak (*Alburnus alburnus*), and *Xenocypris macrolepis* resembling the savetta (*Chondrostoma* spp.). Gosline (1975) agreed that these resemblances were the result of convergent evolution due to similar life history, noting that Rasborinae [=Danioninae] and Cultrinae [=Oxygastrinae, in part] are both midwater groups, where “the term midwater is broadly interpreted ... to include the pelagic and/or surface-feeding forms of Brittan, 1961.” Despite being cognizant of this potential pitfall, Gosline (1975) still had difficulty in distinguishing between these two groups, placing *Salmostoma* and *Securicula* (as *Pseudoxygaster*), two danionine genera (Tang *et al.* 2010), in the Cultrinae. This type of confusion has contributed to the uncertain classification of many of these taxa (e.g., Howes 1979; Howes 1991; Rainboth 1991).

**Phylogenetic studies.** In one of the first cladistic analyses of Cyprinidae, Chen *et al.* (1984) established a framework for the relationships of the major lineages within the family, finding a sister-group relationship between Cultrinae and Xenocyprinae, but otherwise scattering oxygastrine taxa across several subfamilies. Although *Oxygaster* was not included, they did examine *Anabarilius*, *Chanodichthys* (as *Culter* and *Erythroculter*), *Hemiculter*, *Ischikauia*, *Macrochirichthys*, *Megalobrama*, *Parabramis*, *Pseudohemiculter*, *Pseudolaubuca*, and *Rasborinus* [= *Metzia*] among the cultrines, and *Aristichthys* [= *Hypophthalmichthys*], *Distoechodon*, and *Hypophthalmichthys* among the xenocyprines. They treated *Aphyocypris*, *Nicholsicypris*, *Opsariichthys*, and *Zacco* as danionines, and *Ctenopharyngodon*, *Elopichthys*, *Mylopharyngodon*, *Ochetobius*, and *Squaliobarbus* as leuciscines. Cavender and Coburn (1992) had another early application of cladistic methodology to cyprinid systematics, recovering relationships within Cyprinidae similar to those presented by Chen *et al.* (1984). Much like that earlier study, Cavender and Coburn’s lineages were represented as composite taxa, with individual terminals representing entire tribes. Cultrins and xenocypridins were recovered as sister groups within the subfamily Leuciscinae (Cavender & Coburn 1992: fig. 1). They recorded several synapomorphies uniting this group (e.g., modified pelvic girdle; modified first unbranched dorsal ray; diploid  $2n=48$ ) and noted a similar diploid number in *Elopichthys*, *Ochetobius*, and some species of *Zacco sensu lato*. Based on their results, Cavender and Coburn revised the classification of xenocypridins to include the subfamily of Chen *et al.* (1984) plus the Chinese major carps (*Ctenopharyngodon*, *Hypophthalmichthys*, *Mylopharyngodon*, and *Squaliobarbus*) of Howes (1981). Cavender and Coburn recovered *Opsariichthys* and *Zacco* with the cultrin-xenocypridin clade, a relationship which they noted was similar to Gosline’s (1978) hypothesis.

Numerous molecular studies have touched upon this group in one way or another (e.g., He *et al.* 2001, 2004, 2008; Wang *et al.* 2002, 2004, 2007a, 2008; Liu & Chen, 2003; Saitoh *et al.* 2006, 2011; Kong *et al.* 2007a, b, 2008; Rüber *et al.* 2007; Li *et al.* 2009; Mayden *et al.* 2008, 2009; Chen & Mayden, 2009; Fang *et al.* 2009; Bufalino & Mayden 2010; Mayden & Chen, 2010; Tang *et al.* 2010, 2013; Tao *et al.* 2010, 2013; Liao *et al.* 2011a). Liu and Chen (2003: figs. 3–5) recovered a clade uniting Cultrinae (including *Culter*, *Cultrichthys* [= *Culter*], *Megalobrama*, *Parabramis*, *Sinibrama*), Xenocyprinae (including *Distoechodon*, *Hemiculter*, *Pseudolaubuca*, *Xenocypris*), and Squaliobarbinae (*Ctenopharyngodon*, *Ochetobius*, *Squaliobarbus*); *Zacco platypus* was also examined but its relationships were unresolved. He *et al.* (2004) identified an “East Asian clade” of Leuciscinae which included species from their Cultrinae, Danioninae, Leuciscinae, and Xenocyprinae. This East Asian clade included *Aphyocypris*, *Aristichthys* [= *Hypophthalmichthys*], *Ctenopharyngodon*, *Cultrichthys*, *Distoechodon*, *Hemiculter*, *Hemigrammocypripis*, *Hypophthalmichthys*, *Ischikauia*, *Megalobrama*, *Mylopharyngodon*, *Ochetobius*, *Opsariichthys*, *Parabramis*, *Squaliobarbus*, *Xenocypris*, *Yaoshanicus*, and *Zacco*. *Tinca tinca*, a Eurasian species, was also recovered within this clade. Wang *et al.* (2007a) found a similar clade composed of *Aristichthys*, *Ctenopharyngodon*, *Culter*, *Cultrichthys*, *Distoechodon*, *Elopichthys*, *Hemigrammocypripis*, *Hypophthalmichthys*, *Luciobrama*, *Megalobrama*, *Mylopharyngodon*, *Nicholsicypris*, *Ochetobius*, *Opsariichthys*, *Pseudobrama*, *Pseudohemiculter*, *Pseudolaubuca*, *Rasborinus* [= *Metzia*], *Sinibrama*, *Squaliobarbus*, *Toxabramis*, *Xenocypris*,

and *Zacco*, but excluding *Tinca*. They recognized this monophyletic group as the tribe Xenocypridini, part of their subfamily Leuciscinae.

Tang *et al.* (2010) focused on the phylogeny of the subfamily Danioninae and found similar results: many putative danionine taxa (e.g., *Aphyocypris*, *Macrochirichthys*, *Parachela*, *Zacco*) are not part of Danioninae *sensu stricto*. This prompted Tang *et al.* (2010) to remove those genera from the subfamily. Almost all of these former danionines were recovered as part of a large but poorly understood clade of cyprinids that included a broad swath of fishes (*Aphyocypris*, *Candidia*, *Chanodichthys*, *Ctenopharyngodon*, *Hemigrammocycpris*, *Hypophthalmichthys*, *Ischikauia*, *Macrochirichthys*, *Megalobrama*, *Metzia*, *Nicholsicypris*, *Nipponocypris*, *Ochetobius*, *Opsariichthys*, *Parachela*, *Paralauca*, *Pararashora*, *Parazacco*, *Squaliobarbus*, *Xenocyprionides*, *Xenocypris*, *Yaoshanicus*, and *Zacco*) traditionally classified in disparate subfamilies. This enigmatic clade, whose taxonomic status remained unresolved in that study, also included members of the subfamilies Alburninae, Cultrinae, Hypophthalmichthyinae, Squaliobarbinae, and Xenocypridinae (Tang *et al.* 2010: fig. 1a), matching results from earlier molecular studies (e.g., Liu & Chen, 2003; Wang *et al.* 2007a). In a follow-up to that study, Tang *et al.* (2013) recovered *Oxygaster* as a member of this large, unnamed clade. Based on the phylogenetic position of *Oxygaster* and the implications for its associated family-group name (Oxygastrinae), Tang *et al.* (2013) synonymized the subfamilies Cultrinae, Hypophthalmichthyinae, Opsariichthyinae, Squaliobarbinae, and Xenocypridinae with Oxygastrinae. They recognized a revised Oxygastrinae as a subfamily with many taxa that had been classified in other subfamilies (e.g., Alburninae, Danioninae) and many that were historically difficult to classify (e.g., *Opsariichthys*, *Parachela*, *Zacco*).

**Current goals.** Taxon sampling was limited in Tang *et al.* (2013) because their aim was identifying the phylogenetic position of *Oxygaster*. Their revision of the cyprinid classification came about as a result of the placement of *Oxygaster* and the implications associated with that placement. In an effort to build upon that study, we have collected additional sequence data from as many potential representatives of Oxygastrinae as were available. Because the recognition of the subfamily Oxygastrinae is a recent development, its composition and relationships are poorly understood. Increasing taxon sampling will do much to improve our knowledge of the subfamily, while also testing its monophyly and the monophyly of its genera. This study is an attempt to lay the groundwork for the relationships within Oxygastrinae and the membership of this subfamily, while at the same time further testing the conclusions drawn by Tang *et al.* (2010, 2013). We seek to summarize the current knowledge of Oxygastrinae, consolidating into one subfamily genera that historically have been scattered across many different cyprinid subfamilies. Because these taxa have been distributed among groups that were not considered to be closely related, a full inventory of the fishes in this subfamily is not possible at this time, but this study is a first step in assessing the diversity within the group. Herein, we present a molecular phylogeny of Oxygastrinae and revise its composition to reflect the recently proposed nomenclatural changes. This phylogeny will provide guidance and serve as a foundation for future research.

## Materials and methods

Taxon sampling focused on genera and species that have been identified as putative oxygastrines by previous studies (e.g., Tang *et al.* 2010, 2013), as well as taxa historically classified in one of the following cyprinid subfamilies: Alburninae (in part), Cultrinae, Hypophthalmichthyinae, Squaliobarbinae, and Xenocypridinae. In addition to species of Oxygastrinae, we sampled each cyprinid subfamily: Acheilognathinae, Cyprininae, Danioninae, Gobioninae, Leptobarbinae, Leuciscinae, and Tincinae. We also included representative taxa from each of the other cypriniform families: Balitoridae, Botiidae, Catostomidae, Cobitidae, Ellopostomatidae, Gyrinocheilidae, Nemacheilidae, Psilorhynchidae, and Vaillantellidae. Additional taxa were drawn from non-cypriniform ostariophysan groups, with *Chanos chanos* serving as the root. We examined 144 taxa, consisting of 123 cyprinids (80 putative oxygastrines) and 21 non-cyprinid ostariophysan outgroups, representing 100 genera, including 40 putative oxygastrine genera. The non-oxygastrine taxa were chosen based on availability of GenBank sequences, with the bulk of the data taken from Tang *et al.* (2010). A full list of taxa examined with corresponding GenBank accession numbers is provided in the Appendix. Type information and synonymies follow Eschmeyer (2012).



Data collection followed the strategy presented in Tang *et al.* (2010), focusing on the same four target loci used therein: cytochrome *b* (cyt *b*), cytochrome *c* oxidase I (COI), exon 3 of recombination activating gene 1 (RAG1), and opsin (rhodopsin). These four genes in combination have shown promise in resolving relationships within the family Cyprinidae (Tang *et al.* 2010, 2011, 2013). Amplification and sequencing procedures used the PCR primers and followed the laboratory protocols described in Tang *et al.* (2010). Novel sequences collected for this study were deposited in GenBank (Appendix). Sequences were aligned according to codon positions and concatenated in a NEXUS-format file, which was converted by Mesquite 2.74 (Maddison & Maddison, 2010) into the file format appropriate for each tree search application.

Analyses were performed under maximum likelihood and parsimony optimality criteria. Maximum likelihood analyses were executed in the parallel version of RAxML 7.2.8 (Stamatakis, 2006) available through the CIPRES Science Gateway 3.1 (Miller *et al.* 2009), consisting of 100 independent searches, with a random starting tree for each search. The GTR+I+ $\Gamma$  model of nucleotide substitution was applied to the data (one of two models available in RAxML, both GTR variants). The topology with the best likelihood score was retained. Bootstrap values were calculated from 1000 replicates generated with GTR+CAT approximation for rapid bootstrapping (Stamatakis *et al.* 2008). Parsimony searches used the strategies outlined in Tang *et al.* (2010) for TNT 1.1 (Goloboff *et al.* 2008).

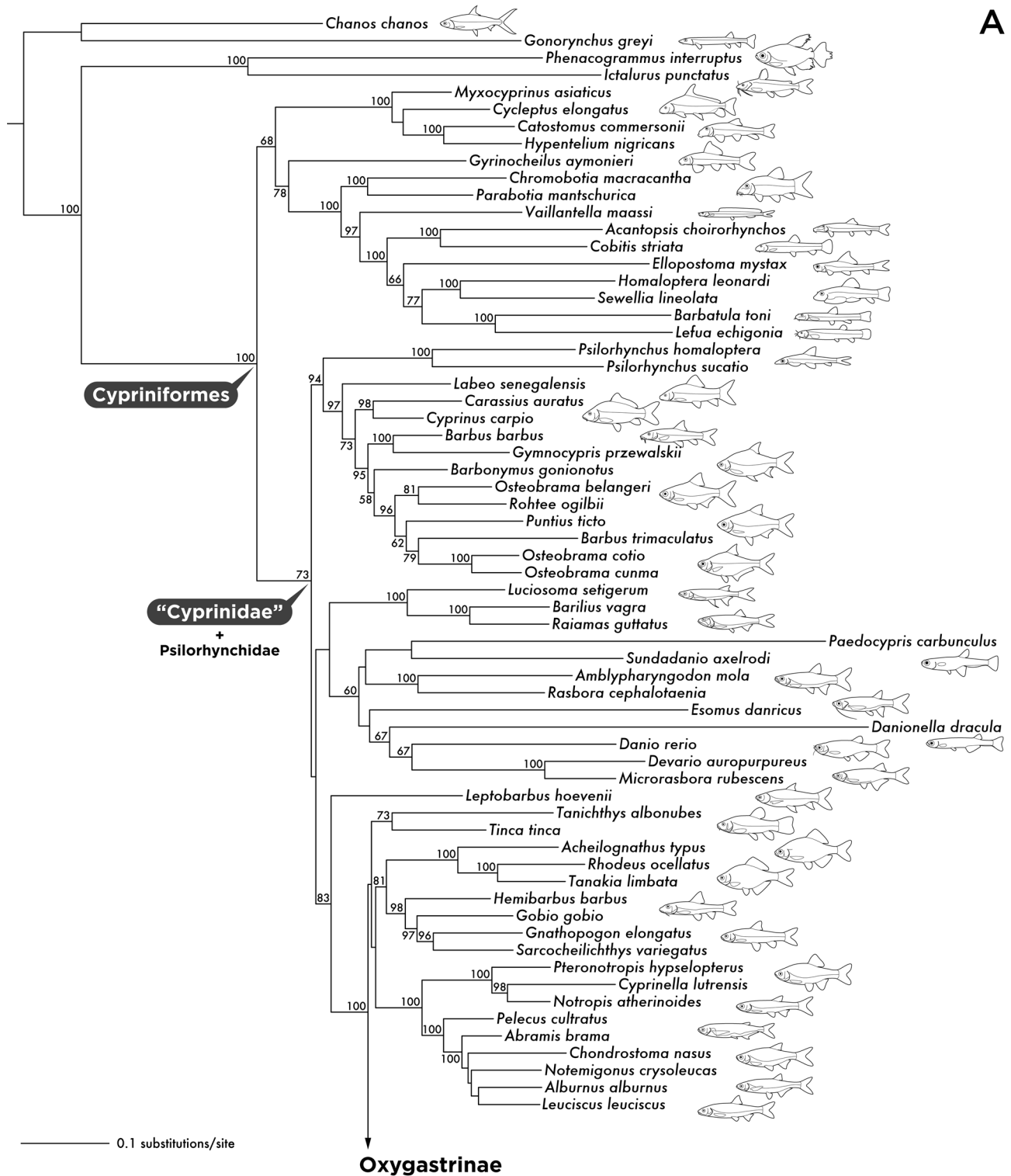
Because a number of taxa (19 oxygastrines and three outgroups) were only represented by sequence data downloaded from GenBank (almost all of which were incomplete for the four loci), we conducted additional likelihood and parsimony analyses to investigate the potential effects missing data had on our results. To that end, we created a reduced data matrix where those 22 terminals were deleted. These deletions reduced the number of terminals to 122, but left the number of base pairs per taxon the same. The searches performed using this abridged data set were identical to what was reported above for the analyses of the full data set, minus calculation of Bremer decay indices for the parsimony results.

## Results

The aligned data matrix consisted of 4114 base pairs (with 1893 parsimony-informative sites) for 144 terminals. The sequences included a complete 1140-bp sequence for cyt *b*, a 658-bp fragment of COI, a 1497-bp fragment of RAG1, and a 819-bp fragment of rhodopsin. Based on the alignment, a unique, single-codon deletion in cyt *b* of *Ictalurus punctatus* was the only indel observed in the data matrix. Maximum likelihood analyses recovered an optimal likelihood topology with  $\ln L = -111857.327$  (Fig. 1). Parsimony analyses converged on six most-parsimonious topologies (length = 26366 steps; CI = 0.154; RI = 0.469). With only six trees, the strict consensus topology is well resolved (Fig. 2), yielding only two polytomies within Oxygastrinae: a polytomy formed by *Hemiculterella macrolepis*, *Pseudolaubuca engraulis*, and a clade of *Hemiculter* (*H. lucidus* and *H. bleekeri*); a trichotomy of *Megalobrama amblycephala*, *M. pellegrini*, and *M. skolkovii*.

The subfamily Oxygastrinae *sensu* Tang *et al.* (2013) is recovered as a monophyletic assemblage with strong branch support in both likelihood and parsimony topologies. Within Oxygastrinae, there is support for the monophyly of the following genera: *Aphyocypris*, *Distoechodon*, *Hypophthalmichthys*, *Nipponocypris*, *Opsariichthys*, *Parachela*, *Paralaubuca*, *Plagiognathops*, *Xenocyprionides*, and *Xenocypris*. Conversely, *Ancherythroculter*, *Chanodichthys*, *Culter*, *Hemiculter*, *Megalobrama*, *Metzia*, and *Toxabramis* do not appear to be monophyletic. The likelihood topology (Fig. 1b) finds strong support for several major clades within the subfamily: an *Opsariichthys-Zacco* group that also includes *Candidia*, *Nipponocypris*, and *Parazacco*; an *Oxygaster* group that also includes *Aphyocypris*, *Macrochirichthys*, *Nicholsicypris*, *Parachela*, *Pararasbora*, and *Yaoshanicus*; and a large group containing the remaining genera minus *Hemigrammocypripis*, *Metzia*, and *Paralaubuca*. *Hemigrammocypripis* and *Metzia* form a clade, although *Metzia* does not appear to be monophyletic; and the species of *Paralaubuca* are recovered together in a monophyletic group. Both groups receive strong support for their monophyly, but their relationships to the other oxygastrine taxa are weakly supported, highlighted by their conflicting resolutions (Figs. 1b, 2b), where both of these clades are monophyletic but in distinctly different places. The parsimony tree also finds an *Opsariichthys-Zacco* group (but without *Parazacco*) and an *Oxygaster* group, with mostly similar relationships. The most obvious differences between the two topologies lie in the large crown clade, where there are many points of disagreement.

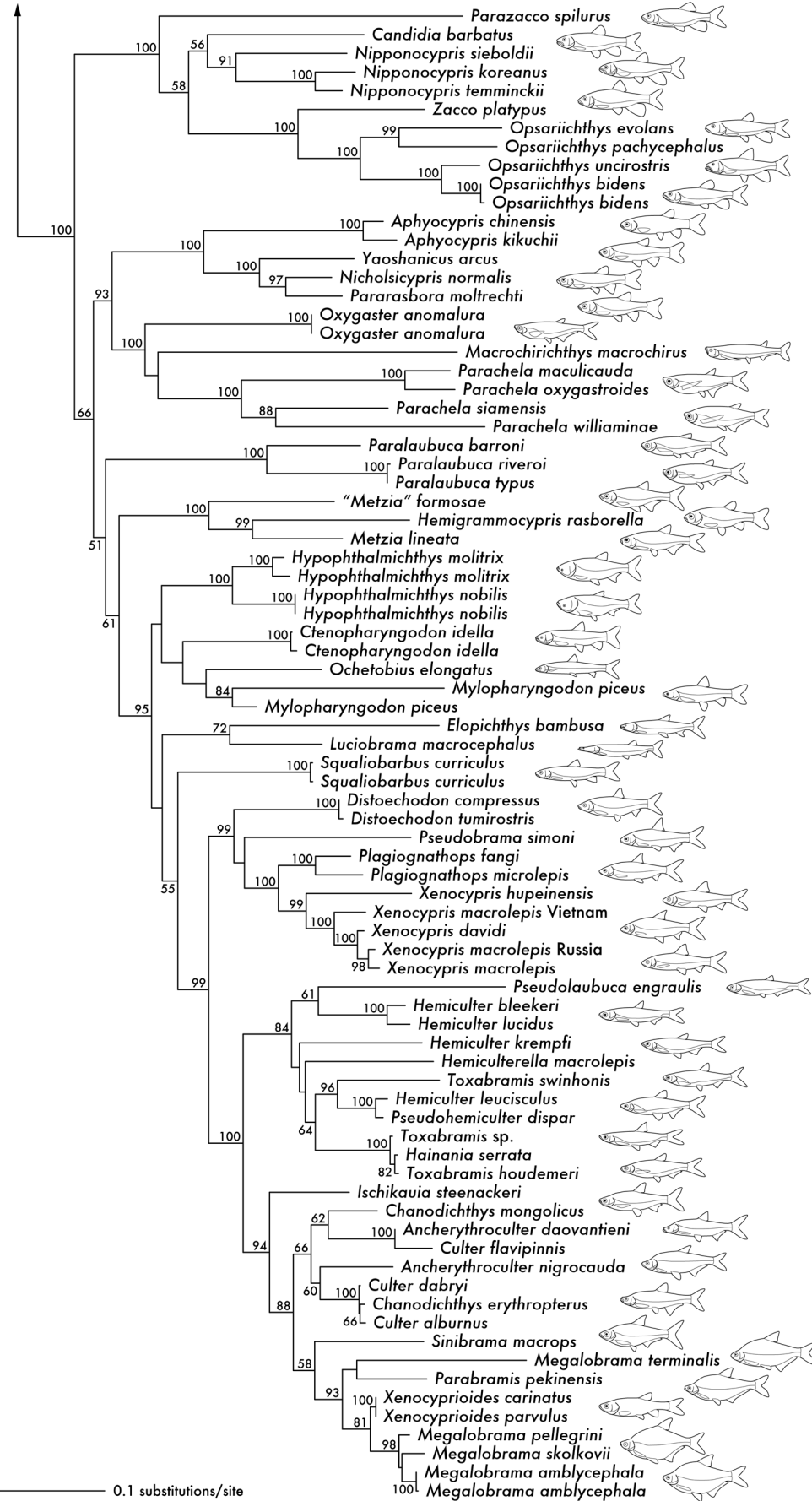
A



**FIGURE 1a.** The phylogenetic relationships of the subfamily Oxygastrinae (Teleostei: Cypriniformes: Cyprinidae), as represented by the tree topology with the best log likelihood score ( $\ln L = -111857.327$ ) recovered from 100 independent maximum likelihood searches. Bootstrap values are reported at each node (values below 50% are not shown). Relationships are shown for (a) outgroup taxa and (b) subfamily Oxygastrinae.

# Outgroups

B



**Reduced-taxa trees.** Maximum likelihood analyses of the reduced data matrix (122 terminals, after deleting the taxa that were drawn from GenBank) recovered a topology with  $\ln L = -107719.569$  (Fig. 3). Within Oxygastrinae, taking into account the taxa pruned from the larger tree, the two likelihood trees are nearly identical, diverging slightly in the position of *Elopichthys* and *Sinibrama*. Parsimony analyses of the same abridged matrix produced four most-parsimonious trees (length = 25370 steps; CI = 0.159; RI = 0.460) and the strict consensus is almost fully resolved within Oxygastrinae; the only polytomy is a trichotomy formed by *Megalobrama amblycephala*, *Parabramis*, and *Sinibrama* (Fig. 4). The relationships observed in this condensed parsimony tree more closely agree with the results of the likelihood analyses (Figs. 1, 3) than with the parsimony results based on the full data matrix (Fig. 2). The most notable difference is in the placements of *Paralaubuca*, which are different between the two parsimony trees, both of which differ from the likelihood trees, which are equivalent to each other.

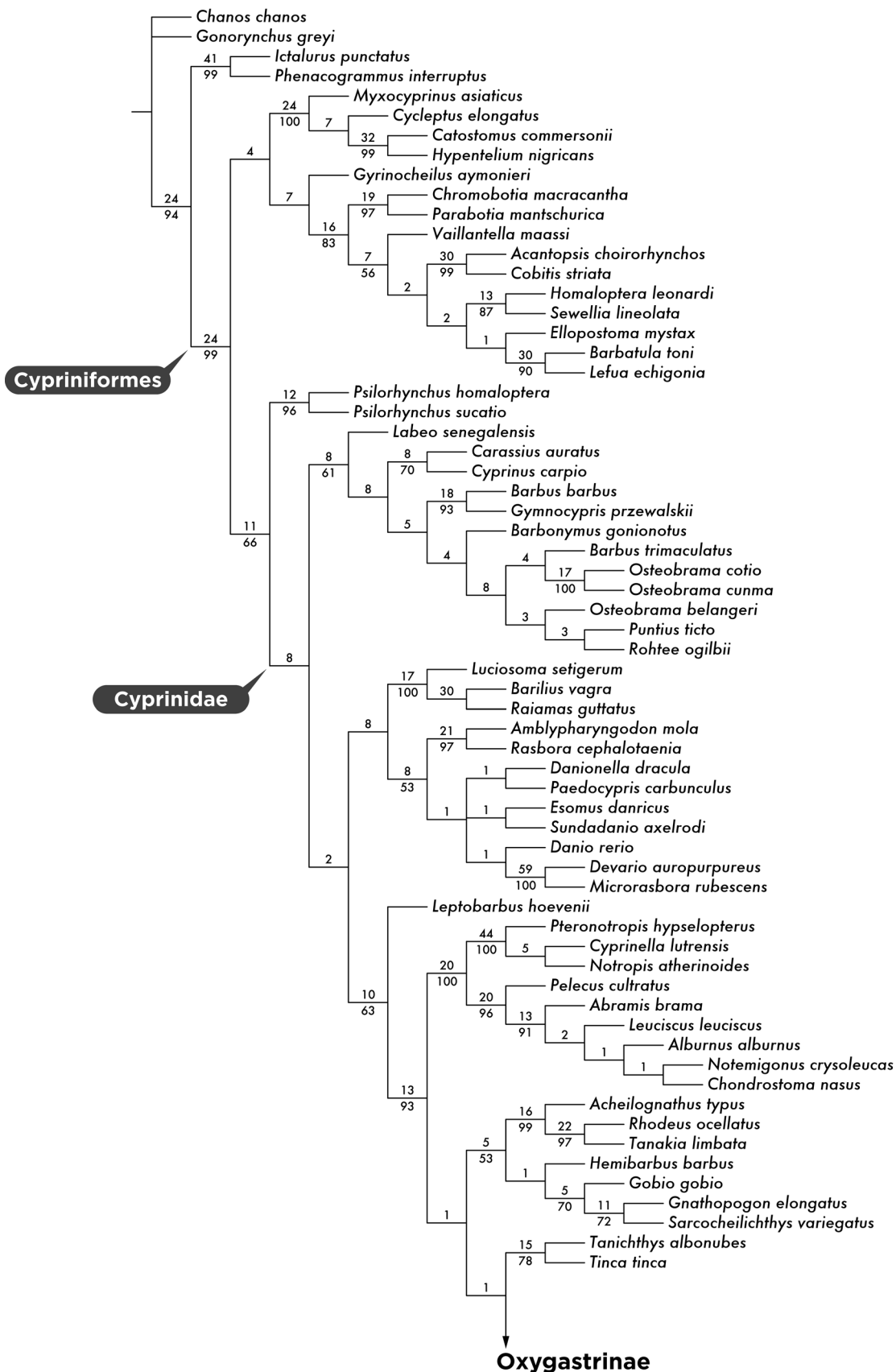
## Discussion

The recovery of a monophyletic subfamily Oxygastrinae corroborates the conclusions of Tang *et al.* (2013), which were logical extensions of earlier works that had recognized a similar grouping under different names (e.g., Nikolskii 1954; Bănărescu 1967; Gosline 1978; Cavender & Coburn 1992), as well as many recent molecular studies that all pointed to an ill-defined group of fishes with uncertain affinities to other cyprinid families (e.g., He *et al.* 2004; Saitoh *et al.* 2006, 2011; Kong *et al.* 2007a, b, 2008; Rüber *et al.* 2007; Wang *et al.* 2007a; Mayden *et al.* 2008; Chen & Mayden, 2009; Fang *et al.* 2009; Tang *et al.* 2010, 2011; Tao *et al.* 2010, 2013). For more information on the nomenclatural rationale for the recognition of Oxygastrinae as the family-group name for this clade see Tang *et al.* (2013), who detailed the various names that apply to the group and provided a partial synonymy for Oxygastrinae Bleeker 1860. Although the priority of Oxygastrinae is clear, the status of its junior synonyms is uncertain. As a result, recognition of tribes within Oxygastrinae is problematic (see below). Therefore, our classification covers the composition of Oxygastrinae but does not address family-group names below the level of subfamily.

Early phylogenies based on morphological characters identified the existence of this group. Chen *et al.* (1984) described two synapomorphies uniting a cultrine-xenocypridine clade broadly equivalent to Oxygastrinae: reduced bifurcation of the pelvic girdle and modified first accessory dorsal ray. Cavender and Coburn (1992) recorded a third synapomorphy for the group: diploid number of 48 chromosomes (Yu *et al.* 1989) versus the presumed ancestral state of 50 (Arai 1982). Arai (2011) appears to corroborate this, reporting  $2n=48$  in most species currently recognized as oxygastrines: his Cultrinae (minus *Osteobrama*), Hypophthalmichthyinae, Squaliobarbinae, and

**FIGURE 1b.** The phylogenetic relationships of the subfamily Oxygastrinae (Teleostei: Cypriniformes: Cyprinidae), as represented by the tree topology with the best log likelihood score ( $\ln L = -111857.327$ ) recovered from 100 independent maximum likelihood searches. Bootstrap values are reported at each node (values below 50% are not shown). Relationships are shown for (a) outgroup taxa and (b) subfamily Oxygastrinae.

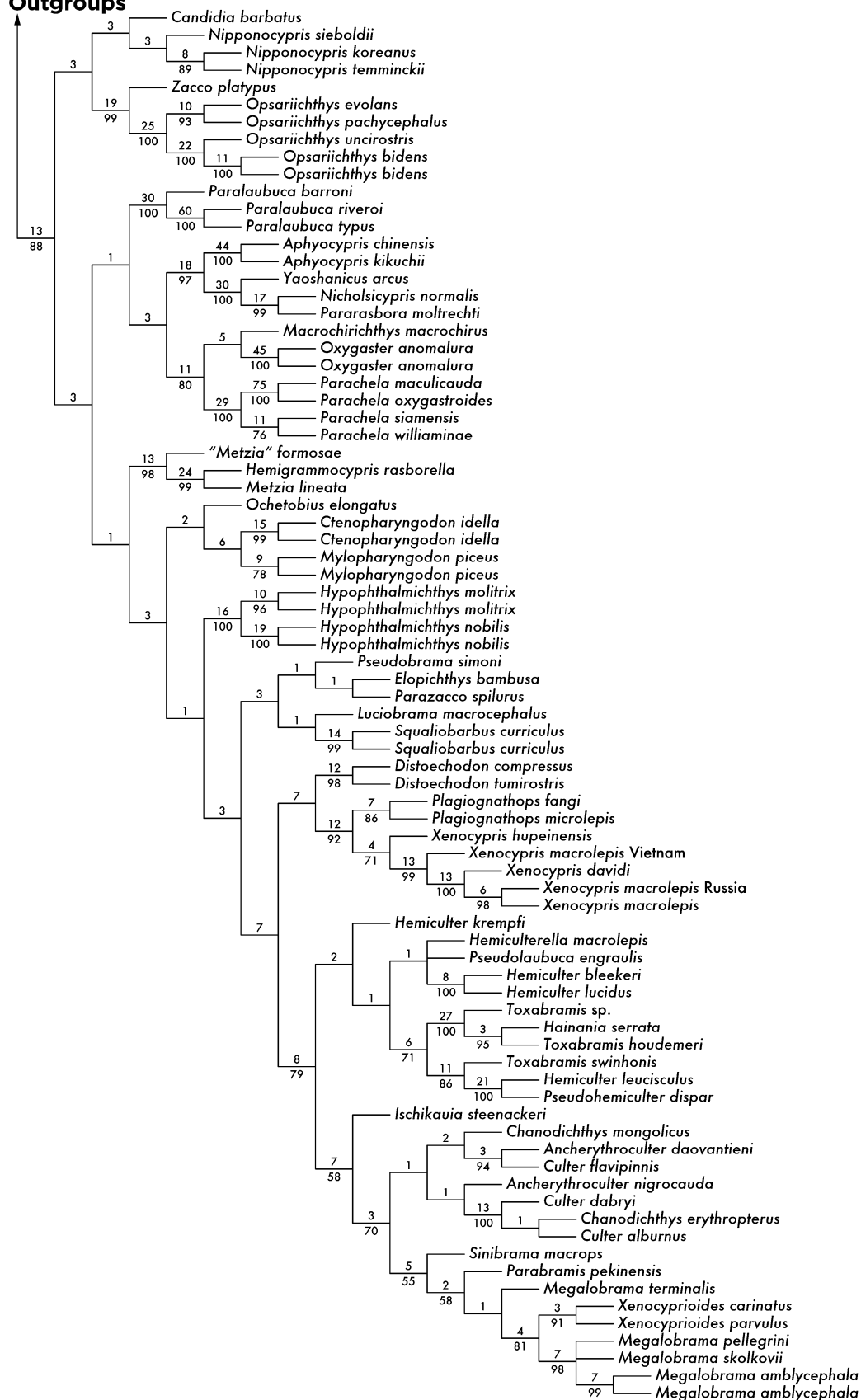
The illustrations (not drawn to scale) represent the following species, from top: (a) *Chanos chanos*, *Gonorynchus greyi*, *Phenacogrammus interruptus*, *Ictalurus punctatus*, *Myxocyprinus asiaticus*, *Hypentelium nigricans*, *Gyrinocheilus aymonieri*, *Chromobotia macracantha*, *Vaillantella maassi*, *Acantopsis choirorhynchus*, *Cobitis striata*, *Ellopostoma mystax*, *Sewellia lineolata*, *Barbatula toni*, *Lefua echigonia*, *Psilorhynchus sucatio*, *Labeo senegalensis*, *Cyprinus carpio*, *Barbus barbus*, *Barbonymus gonionotus*, *Osteobrama belangeri*, *Rohtee ogilbii*, *Osteobrama cotio*, *Luciosoma setigerum*, *Raiamas guttuatus*, *Paedocypris carbunculus*, *Rasbora cephalotaenia*, *Esomus danricus*, *Danionella dracula*, *Danio rerio*, *Devario auropurpureus*, *Leptobarbus hoevenii*, *Tinca tinca*, *Acheilognathus typus*, *Rhodeus ocellatus*, *Gobio gobio*, *Gnathopogon elongatus*, *Cyprinella lutrensis*, *Notropis atherinoides*, *Pelecus cultratus*, *Notemigonus crysoleucas*, *Alburnus alburnus*, *Leuciscus leuciscus*; (b) *Parazacco spilurus*, *Candidia barbata*, *Nipponocypris temminckii*, *Zacco platypus*, *Opsariichthys pachycephalus*, *Opsariichthys uncirostris*, *Opsariichthys bidens*, *Aphyocypris chinensis*, *Yaoshanicus arcus*, *Nicholsicypris normalis*, *Pararasbora moltrechti*, *Oxygaster anomalura*, *Macrochirichthys macrochirus*, *Parachela oxygastroides*, *Parachela williaminae*, *Paralaubuca barroni*, *Paralaubuca typus*, *Metzia formosae*, *Hemigrammocypripis rasborella*, *Metzia lineata*, *Hypophthalmichthys molitrix*, *Hypophthalmichthys nobilis*, *Ctenopharyngodon idella*, *Ochetobius elongatus*, *Mylopharyngodon piceus*, *Elopichthys bambusa*, *Luciobrama macrocephalus*, *Squaliobarbus curriculus*, *Distoechodon tumirostris*, *Pseudobrama simoni*, *Plagiognathops microlepis*, *Xenocypris macrolepis*, *Xenocypris davidi*, *Xenocypris macrolepis*, *Pseudolaubuca engraulis*, *Hemiculter bleekeri*, *Hemiculterella macrolepis*, *Hemiculter leucisculus*, *Pseudohemiculter dispar*, *Hainania serrata*, *Toxabramis houdemeri*, *Ischikauia steenackeri*, *Chanodichthys mongolicus*, *Ancherythroculter nigrocauda*, *Culter alburnus*, *Sinibrama macrops*, *Megalobrama terminalis*, *Parabramis pekinensis*, *Xenocyprionides carinatus*, *Megalobrama skolkovii*, and *Megalobrama amblycephala*.



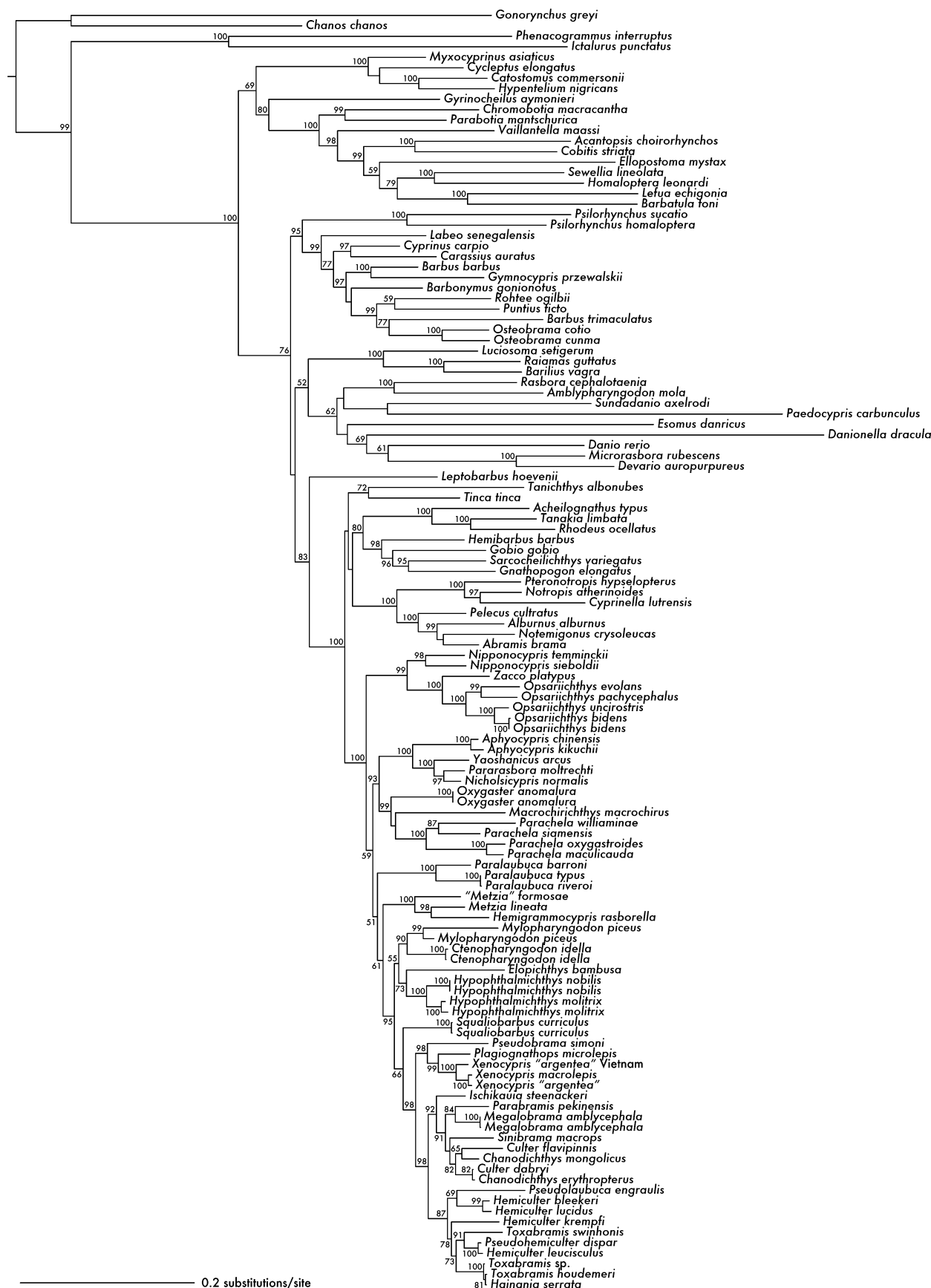
**FIGURE 2a.** The phylogenetic relationships of the subfamily Oxygastrinae, as represented by the strict consensus of six most-parsimonious trees (length = 26366 steps; CI = 0.154; RI = 0.469). Relationships are shown for (a) outgroup taxa and (b) subfamily Oxygastrinae. Bremer (above) and bootstrap (below) support values are displayed at each node (bootstrap values below 50% are not shown).

# Outgroups

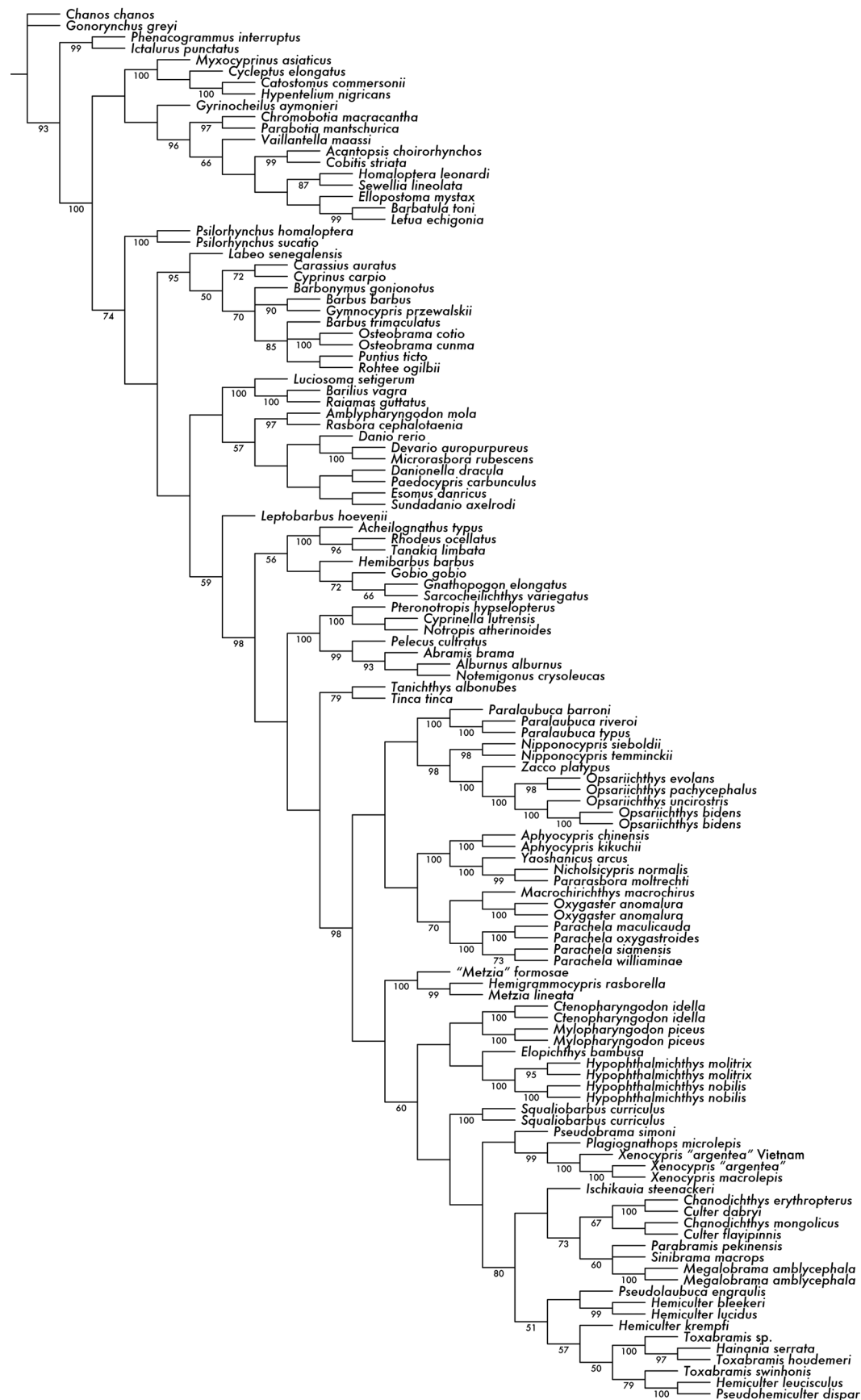
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**FIGURE 2b.** The phylogenetic relationships of the subfamily Oxygastrinae, as represented by the strict consensus of six most-parsimonious trees (length = 26366 steps; CI = 0.154; RI = 0.469). Relationships are shown for (a) outgroup taxa and (b) subfamily Oxygastrinae. Bremer (above) and bootstrap (below) support values are displayed at each node (bootstrap values below 50% are not shown).



**FIGURE 3.** The tree topology with the best log likelihood score ( $\ln L = -107719.569$ ) resulting from 100 independent searches of a data matrix with a subset of 122 taxa (of 144); terminals represented solely by sequences obtained from GenBank were removed. Bootstrap values are reported at each node (values below 50% are not shown).



**FIGURE 4.** The strict consensus of four most-parsimonious trees (length = 25370 steps; CI = 0.159; RI = 0.460) based on a data matrix with a subset of 122 taxa (of 144); terminals represented solely by sequences obtained from GenBank were removed. Bootstrap values are reported at each node (values below 50% are not shown).



Xenocyprinae, plus *Elopichthys*, *Hemigrammocypripis*, *Luciobrama*, *Ochetobius*, and *Zacco*. There are some exceptions, as Yu *et al.* (1989) reported: *O. bidens* has 74–76 chromosomes and *Zacco platypus* has 78. Cavender and Coburn (1992: 309) noted that, although the oxygastrine condition ( $2n=48$ ) was observed in other cyprinids, there were distinct differences: the longest chromosome pair in *Tinca* is metacentric (Cataudella *et al.* 1977); and acheilognathines have more acrocentric chromosomes. Cavender and Coburn (1992: 320) reported performing an additional parsimony analysis that included a composite terminal representing *Opsariichthys-Zacco*. The strict consensus topology of the resulting trees (not figured therein) resolved the *Opsariichthys-Zacco* taxon as the sister group to their cultrine-xenocypridin lineage, a result which supports our inclusion of *Opsariichthys* and its relatives in Oxygastrinae. Cavender and Coburn (1992) remarked that a three-lobed swim bladder, a character Gosline (1978) suggested as a synapomorphy for cultrins, was also found in xenocypridins, which would make it a potential fourth synapomorphy for their cultrine-xenocypridin clade, though they did not indicate it as such.

Molecular studies (e.g., Wang *et al.* 2002, 2004, 2007a; Liu & Chen 2003; He *et al.* 2004; Tao *et al.* 2010, 2013) have identified a similar cultrine-xenocypridine clade which is broadly congruent with what we are recognizing as the subfamily Oxygastrinae. He *et al.* (2001) first referred to this group as an East Asian clade of Leuciscinae *sensu lato*, following the classifications of Chen *et al.* (1984) and Cavender and Coburn (1992), who divided Cyprinidae into two large subfamilies: Cyprininae and Leuciscinae. However, He *et al.*'s (2001) use of *Opsariichthys* and *Zacco* as outgroups predictably skewed the resulting phylogeny and affected the composition of the East Asian clade that they recovered. Subsequent studies, with expanded taxon sampling and non-cyprinid outgroups, have consistently recovered an East Asian clade that conforms to the demarcation of Oxygastrinae.

**Classification.** The subfamily Oxygastrinae is hereby recognized as comprising the following genera: *Anabarilius*, *Ancherythroculter*, *Aphyocypris*, *Candidia*, *Chanodichthys*, *Ctenopharyngodon*, *Culter*, *Distoechodon*, *Elopichthys*, *Hainania*, *Hemiculter*, *Hemiculterella*, *Hemigrammocypripis*, *Hypophthalmichthys*, *Ischikauia*, *Longiculter*, *Luciobrama*, *Macrochirichthys*, *Megalobrama*, *Metzia*, *Mylopharyngodon*, *Nicholsicypris*, *Nipponocypris*, *Ochetobius*, *Opsariichthys*, *Oxygaster*, *Parabramis*, *Parachela*, *Paralauca*, *Pararashbora*, *Parazacco*, *Plagiognathops*, *Pogobrama*, *Pseudobrama*, *Pseudohemiculter*, *Pseudolauca*, *Rasborichthys*, *Sinibrama*, *Squaliobarbus*, *Toxabramis*, *Xenocyprionides*, *Xenocypris*, *Yaoshanicus*, and *Zacco*. Included in this group are the entirety of the subfamilies Squaliobarbinae and Xenocyprinae *sensu* Nelson (2006) and the entirety of the subfamily Cultrinae *sensu* Rainboth (1991). All of the taxa in the clade labeled “Former Danioninae” by Tang *et al.* (2010: fig. 1a) were recovered in Oxygastrinae. Our revised classification — recognition of Oxygastrinae via the inclusion of Alburninae (in part), Cultrinae, Danioninae (in part), Hypophthalmichthyinae, Squaliobarbinae, and Xenocyprinae — concurs with and elaborates upon the changes introduced in Tang *et al.* (2013).

The classification provisionally includes four genera not examined in this study: *Anabarilius*, *Longiculter*, *Pogobrama*, and *Rasborichthys*. Their inclusion is based on previous literature. Bănărescu (1967) originally considered *Anabarilius* a subgenus of *Hemiculterella*, before recognizing it as a distinct genus of Cultrinae (Bănărescu & Coad 1991; Bănărescu, 1997). Various workers (Arai 1982; Yue & Luo 1996; Luo & Chen 1998) have identified *Anabarilius* as a member of Cultrinae along with other genera that now are reassigned to Oxygastrinae. In a morphological parsimony analysis, Dai *et al.* (2005) recovered *Anabarilius* in Cultrinae. Gan *et al.* (2009), in describing a new species of *Metzia*, remarked on similarities shared among *Anabarilius* and three oxygastrine genera: *Metzia*, *Ischikauia*, and *Hemiculterella*. Arai (2011) reported that species of *Anabarilius* have a diploid number of 48, which matches the chromosome number found in almost all other oxygastrine taxa (see above). Takeuchi and Hosoya (2011) discovered a synapomorphy (metapterygoid elongated dorsally) that unites *Anabarilius* with *Chanodichthys*, *Culter*, *Hemiculter*, *Ischikauia*, *Megalobrama*, *Sinibrama*, and *Toxabramis*. Howes (1991) provisionally placed *Longiculter* in Cultrinae. Rainboth (1991, 1996) classified it in Alburninae, but the subfamily included other eastern Asian taxa that are referred to Oxygastrinae herein (e.g., *Hemiculter*, *Paralauca*). There have been few studies of the monotypic genus *Pogobrama* since its original description: Yue and Luo (1996) found it sister to *Sinibrama* in their phylogeny of Cultrinae; Luo and Chen (1998) classified *Pogobrama* as a member of Cultrinae. Based on the information in those two previous studies, Dai *et al.* (2005) was able to code character states for 28 morphological characters (of 75 total in their data matrix) and resolved it as the sister group of *Sinibrama*. Oshima (1920) indicated that *Rasborichthys* is most closely related to *Rasborinus* [= *Metzia*], an oxygastrine taxon. Bănărescu (1967) classified *Rasborichthys* as a member of Cultrinae. Gosline (1974) linked it with *Aphyocypris* and *Hemigrammocypripis*. Howes (1979: 197) considered *Rasborichthys* a

possible member of his hemicultrine group, whose other members were *Hemiculter*, *Pseudolaubuca*, and *Toxabramis*. The classification and phylogenetic relationships of *Anabarilius*, *Longiculter*, *Pogobrama*, and *Rasboraichthys* merit further examination.

*Atrilinea*, a genus which contains only three species restricted to China, may be a member of Oxygastrinae. Historically, the classification of *Atrilinea* has been uncertain: Bănărescu and Coad (1991) placed it among their danionines, a group that also included *Ochetobius* and *Xenocyprionides*; Rainboth (1991) placed it within Cyprininae, but as a member of the tribe Squaliobarbini, which also included *Ctenopharyngodon*, *Mylopharyngodon*, and *Squaliobarbus*; Luo (1998) designated the genus as a member of Leuciscinae *sensu lato*, which also included oxygastrine genera like *Ctenopharyngodon*, *Elopichthys*, *Luciobrama*, *Mylopharyngodon*, *Ochetobius*, and *Squaliobarbus*. In the only phylogenetic analysis to include the genus, Chen (1987) recovered *Atrilinea* in a *Ctenopharyngodon* group composed primarily of oxygastrines (*Squaliobarbus*, *Ctenopharyngodon*, *Mylopharyngodon*, *Elopichthys*, *Ochetobius*, and *Luciobrama*) plus one lone leuciscine genus (*Phoxinus*). The phylogeny of Chen (1987) suggests the possible inclusion of *Atrilinea* in Oxygastrinae. However, without more evidence, we have chosen to leave *Atrilinea incertae sedis* within Cyprinidae. Additional study of *Atrilinea* will be necessary before its placement can be resolved.

Excluded from Oxygastrinae are *Osteobrama* and *Rohtee*. Howes (1991) provisionally placed both genera in Cultrinae on the basis of similarities shared with *Parabramis*. Rainboth (1991) suggested that some species of *Rohtee* (none named) were part of Cultrinae. Arai (2011) also classified *Osteobrama* in his Cultrinae. Our results disagree; we find *Osteobrama* and *Rohtee* to be members of the subfamily Cyprininae (Fig. 1a), which agrees with other workers (e.g., Regan 1911; Bănărescu 1967) who assigned the two genera to Cyprininae (or an equivalent taxonomic group). Although not explicitly stated, Tilak and Husain (1989) discussed both genera and their systematic position in the context of their association with *Mystacoleucus*, a genus of Cyprininae *sensu lato* (Regan 1911; Smith 1945; Shan *et al.* 2000; Li *et al.* 2008; Yang *et al.* 2010). Following Vishwanath and Shantakumar (2007), *Osteobrama cunma* is treated as a separate species, distinct from *O. cotio*. See below for discussion of family-group names based on *Osteobrama* and its synonyms.

*Pelecus* has been moved into and out of the cultrines. Dybowski (1862) first associated *Pelecus* with this group. Among later workers, Bănărescu (1967, 1969) and Sorescu (1968, 1970) were proponents of a *Pelecus*-Cultrinae relationship. Some of their contemporaries (e.g., Nikolskii 1954; Gosline 1974, 1978; Howes 1979) disagreed and classified *Pelecus* as a leuciscine. Bogutskaya (1991) concurred that it is a leuciscine. Despite affiliating it with leuciscines, Howes (1979) also proposed a *Hemiculterella* relationship for *Pelecus*. The leuciscine affinities of *Pelecus* have been confirmed by molecular phylogenies (e.g., Saitoh *et al.* 2006, 2011; Mayden *et al.* 2009; Perea *et al.* 2010). The historical link between *Pelecus*-Cultrinae seems to stem from misleading similarities that arose due to convergence, a potential hazard predicted by earlier workers (Nikolskii 1954; Gosline 1975, 1978; Howes 1979).

We have followed Tang *et al.* (2013) in recognizing a single subfamily Oxygastrinae rather than further subdividing these fishes into multiple subfamilies. Tang *et al.* (2013) discussed some of the nomenclatural difficulties and implications that would be involved: the most commonly used name for this group, Cultrinae, is only recently proposed (Kryzhanovsky, 1947); Hypophthalmichthyina Günther 1868 and Xenocypridina Günther 1868 are simultaneous and it is unclear if a first reviser ever decided priority between the two family-group names. Therefore, recognition of Cultrinae would be heavily dependent on the phylogenetic position of *Culter alburnus*, which would determine whether the name Cultrinae could have priority. Usage of Hypophthalmichthyinae and/or Xenocypridinae rests on the aforementioned unresolved nomenclatural question, which in turn is contingent on the positions of *Hypophthalmichthys molitrix* and *Xenocypris macrolepis*. The distribution of clades within Oxygastrinae creates other potential problems. Because of the positions of *Paralaubuca* and the *Hemigrammocypripis-Metzia* clade (Fig. 1b), each would require the erection of their own family-group name or they would have to be subsumed into a larger clade that encompasses both *Hypophthalmichthys* and *Xenocypris*, where the ambiguity over priority of their respective family-group names becomes an issue. For all of the reasons enumerated in Tang *et al.* (2013), we have avoided recognizing tribes within Oxygastrinae. The current extent of our taxonomic knowledge precludes a more detailed classification.

**Nomenclature.** The inclusion of *Elopichthys bambusa* provides insight into the status of the family-group name Elopichthyini Berg 1912, an issue Tang *et al.* (2013) did not address because the monotypic *Elopichthys* was not sampled in their phylogeny. We found *Luciobrama* to be the sister group of *Elopichthys*. Some previous

workers have linked *Elopichthys* to *Ochetobius*, a genus we also recovered in Oxygastrinae, but not immediately related to either *Elopichthys* or *Luciobrama*. Gosline (1974, 1978) thought that *Elopichthys*, *Luciobrama*, and *Ochetobius* formed its own distinct, specialized cyprinid group, commenting that they are East Asian cultrins which resembled leuciscins (Gosline 1978). Howes (1978) disagreed and grouped *Elopichthys* and *Luciobrama* in his aspinine group along with the leuciscine genera *Aspiolucius*, *Aspius*, and *Pseudaspius*, based on putative synapomorphies tied to their piscivorous habits. Our results suggest that *Elopichthys* is not closely related to leuciscines and the similarities cited by Howes are the result of convergent evolution imposed by the functional constraints of piscivory. Other molecular studies seem to corroborate this conclusion, recovering relationships linking *Elopichthys* to taxa classified as Oxygastrinae (Kong *et al.* 2007a, b, 2008; Rüber *et al.* 2007; Wang *et al.* 2007a; He *et al.* 2008; Bufalino & Mayden 2010; Tao *et al.* 2010, 2013). More work will be needed to fully determine the relationships of *Elopichthys*, but there can be little doubt that *Elopichthys* is part of the larger oxygastrine assemblage. We hereby synonymize Elopichthyini Berg 1912 with Oxygastrinae Bleeker 1860.

We found the eastern Asian members of the subfamily Alburninae (Howes 1991; Rainboth 1991) in Oxygastrinae, but we found *Alburnus alburnus* and its closest relatives (restricted to Europe and western Asia) outside of Oxygastrinae. As a result, the family-group name Alburninae Girard 1858, which would have priority over Oxygastrinae Bleeker 1860, does not apply to this group. *Alburnus* is recovered as part of the subfamily Leuciscinae Bonaparte 1839, as the sister group of *Leuciscus leuciscus*, which calls the status of Alburninae into question. This corresponds with previous phylogenies that have found European alburnines to be more closely related to leuciscines than any eastern Asian cyprinids (e.g., Briolay *et al.* 1998; Gilles *et al.* 1998, 2001; Zardoya & Doadrio 1999; Zardoya *et al.* 1999; Hänfling & Brandl 2000; Durand *et al.* 2002a, b; Liu *et al.* 2002; Liu & Chen 2003; He *et al.* 2004; Saitoh *et al.* 2006, 2011; Rüber *et al.* 2007; Fang *et al.* 2009; Perea *et al.* 2010). The European alburnine species do not form a monophyletic group either (*Pelecus* is the sister group of all sampled leuciscines), further confusing the issue. It is likely Alburninae will have to be placed in the synonymy of Leuciscinae, but that is beyond the scope of this study.

The family-group name Chondrostomi Agassiz 1855 has been linked to the group we are calling Oxygastrinae. Agassiz (1855) originally established the tribe for European and North American cyprinids. Berg (1912) later placed *Xenocypris* and *Plagiognathops* in his Chondrostomini. Nichols (1938) included *Xenocypris* in his Chondrostomatinae; he may have considered other oxygastrine genera part of this subfamily, but he did not list all putative members. The formation used by Nichols (1938) employs the correct stem of *Chondrostoma* (Steyskal 1980). Rainboth (1991: 172) expanded Chondrostomatini to include all species previously placed in Xenocypridinae. Our results show that the name Chondrostomi does not apply to oxygastrines because *Chondrostoma nasus*, the type species of the type genus, is recovered in the same clade as *Leuciscus*, along with *Alburnus*. The inclusion of *Chondrostoma* in the leuciscine assemblage has been supported by numerous systematic studies (e.g., Zardoya & Doadrio 1999; Zardoya *et al.* 1999; Hänfling & Brandl 2000; Gilles *et al.* 2001; Durand *et al.* 2002a, b; Liu *et al.* 2002; Rüber *et al.* 2007; Thai *et al.* 2007; Perea *et al.* 2010). As with Alburninae, the status of Chondrostomi is tied to Leuciscinae and cannot be resolved by our study. Addressing the nomenclatural issues surrounding Leuciscinae and all of its potential junior synonyms will have to await further research.

Although the family-group name Abramidina Günther 1868 has fallen out of use, it has historical ties to oxygastrines (see above). Much like Alburninae and Chondrostomi, Abramidina appears to be in the synonymy of Leuciscinae: *Abramis brama*, the type and only species of *Abramis*, is recovered among the leuciscines. Nikolskii (1954) was the first to consolidate the European abramidines with the leuciscines, breaking up Abramidina. This affiliation between abramidines and leuciscines has been the prevailing consensus in cyprinid classification since then (e.g., Bănărescu 1967; Gosline 1974, 1978; Howes 1991; Cavender & Coburn, 1992; Nelson 2006). The relationship has been corroborated by many recent works (Briolay *et al.* 1998; Gilles *et al.* 1998, 2001; Zardoya & Doadrio 1999; Zardoya *et al.* 1999; Liu *et al.* 2002; He *et al.* 2004; Rüber *et al.* 2007; Sasaki *et al.* 2007; Fang *et al.* 2009; Perea *et al.* 2010).

Osteobramae Bleeker 1863 and Smiliogastrini Bleeker 1863 are two other family-group names that have been linked to oxygastrine fishes because of the occasional inclusion of the genus *Osteobrama* (see above). The phylogenetic positions of *Osteobrama cotio*, the type species of *Osteobrama*, and *O. belangeri*, the type species of *Smiliogaster* [= *Osteobrama*], indicate that neither pertain to the oxygastrine group. Instead, the two species of *Osteobrama* examined are recovered among the species of Cyprininae *sensu lato* but do not form a monophyletic

group. Neither *Osteobrama* nor *Rohtee* are closely related to the oxygastrines of eastern Asia.

*Cultrichthys* Smith 1938, which appears with some frequency in the literature (e.g., Cunha *et al.* 2002; Dai & Yang 2003; Liu & Chen 2003; Dai *et al.* 2005; Thai *et al.* 2007; Wang *et al.* 2007a; Fang *et al.* 2009; Liao *et al.* 2011a), is a synonym of *Culter* Basilewsky 1855 because *Cultrichthys brevicauda*, the type species of *Cultrichthys*, is a synonym of *Culter alburnus*, the type species of *Culter* (Kottelat 2006). However, not all species of *Cultrichthys* were referred to *Culter*, some (e.g., *C. erythropterus*, *C. mongolicus*) were placed in *Chanodichthys* (Kottelat 2006).

*Xenocypris macrolepis* Bleeker 1871 should be used instead of *X. argentea*, a senior synonym that is in widespread use (e.g., Saitoh *et al.* 2006, 2011; Mayden *et al.* 2009; Tang *et al.* 2010, 2013). Even though *Xenocypris argentea* Günther 1868 has priority, it is permanently invalid because it is a junior secondary homonym that was replaced before 1961 and whose substitute name is currently in use (Art. 59.3; ICZN 1999); see Kottelat (2001: 44) for a detailed discussion of this issue. The results of our phylogenetic analysis also raise some doubt as to whether *X. macrolepis* as it is currently constituted represents a single species (see below).

**Conflict and missing data.** The maximum likelihood and parsimony topologies are largely congruent, but there are a few notable areas of conflict. *Parazacco spilurus* is recovered as sister to *Elopichthys* in the parsimony tree. *Paralaubuca*, monophyletic in both trees, appears as the sister group to the *Aphyocypris-Oxygaster* clade in the parsimony tree (Fig. 2b) and as the sister group to a large clade of all oxygastrines excluding the *Opsariichthys-Zacco* and *Aphyocypris-Oxygaster* groups in the likelihood tree (Fig. 1b). *Hypophthalmichthys* is monophyletic in both analyses but is sister to the *Ctenopharyngodon-Mylopharyngodon-Ochetobius* clade in the likelihood topology and sister to a large crown clade of oxygastrines in the parsimony topology. *Pseudobrama simoni* falls outside of the *Xenocypris* clade in the parsimony tree. Some areas of disagreement (e.g., *Parazacco*) can probably be attributed to incomplete data representation.

Removal of taxa with widespread missing data suggests that the parsimony analysis was more sensitive to the effects of missing data. This is based on the observation that the condensed parsimony tree (Fig. 4) is similar to the condensed (Fig. 3) and full (Fig. 1) likelihood trees, yet all three differ substantially from the full parsimony tree (Fig. 2) when it comes to the relationships within Oxygastrinae. For example, *Pseudobrama* is recovered with *Plagiognathops* and *Xenocypris* in both reduced-taxa trees (Figs. 3, 4), matching the full likelihood tree (Fig. 1b). The exclusion of GenBank-only taxa also stabilized the phylogenetic position of *Hypophthalmichthys*, resulting in congruent relationships in both condensed trees (Figs. 3, 4) that match the full likelihood tree. However, incomplete data cannot be the only explanation of the differences observed between the two optimality criteria, because the placement of *Paralaubuca* remained inconsistent even after deletion of the GenBank-only taxa. The remainder of the discussion will focus on the phylogenetic relationships recovered by the maximum likelihood analysis (Fig. 1).

**Phylogeny of Oxygastrinae.** The taxon sampling for putative oxygastrines is far from complete, but certain distinct clades can be observed. There is strong support for a clade that is composed of *Opsariichthys* and its closest relatives; this lineage is the sister group to the remaining oxygastrines. These species historically have been closely associated because of their overall similarity (e.g., Bănărescu 1968c; Gosline 1978; Chen 1982). Often, they have been identified as the most primitive cyprinids on the basis of a quadrate-metapterygoid fenestra that they share with non-cyprinid relatives (e.g., Regan 1911; Greenwood *et al.* 1966; Hensel 1970; Fink & Fink 1981). Although Nikolskii (1954) moved *Opsariichthys* into Cultrinae (i.e., Oxygastrinae), the general consensus remained that *Opsariichthys* and its relatives were allied with danionines (e.g., Bănărescu 1968c; Howes 1991; Rainboth 1991; Nelson 1994, 2006) and not cultrines. Gosline (1973, 1975), one of the few dissenters, suggested that the quadrate-metapterygoid fenestra was not indicative of a primitive link to other ostariophysans but instead the condition had evolved independently multiple times within Cyprinidae. Phylogenetic studies have since confirmed Nikolskii's classification and Gosline's contention that *Opsariichthys* and *Zacco* are not primitive cyprinids (e.g., Saitoh *et al.* 2006, 2011; Fang *et al.* 2009; Mayden *et al.* 2009; Tang *et al.* 2010, 2013). Furthermore, a flurry of recent studies have made several taxonomic changes to this group. Wang *et al.* (2007b) found *Zacco sensu lato* to be non-monophyletic, with two putative *Zacco* species (*Z. sieboldii* and *Z. temminckii*) more closely related to *Candidia* than *Z. platypus*, the type species. To resolve this, they referred the displaced *Zacco* species to *Candidia*, while placing *Zacco* in the synonymy of *Opsariichthys*, but retaining *Parazacco* as a distinct genus. Several of these changes were overturned by Chen *et al.* (2008), who found results similar to those of Wang *et al.* (2007b), but chose instead to retain *Zacco* as a separate genus and erected the genus *Nipponocypris*

for those putative *Zacco* species more closely related to *Candidia*. Wang *et al.* (2011) did not recognize *Nipponocypris* and treated species assigned to that genus as members of *Candidia*. Liao *et al.* (2011b) resurrected Opsariichthyinae Rendahl 1928, using the name for what had been labeled “ex-Rasborinae” by Fang *et al.* (2009), a group that included *Candidia*, *Opsariichthys*, *Parazacco*, and *Zacco*. The clade that contained “ex-Rasborinae” also included four other genera (*Aphyocypris*, *Hemigrammocypripis*, *Parachela*, and *Yaoshanicus*) that were designated *incertae sedis* (Fang *et al.* 2009). Liao *et al.* (2011b) appears to have expanded Opsariichthyinae to include *Aphyocypris* and *Parachela* as well as *Metzia* and *Macrochirichthys*, two genera that were not part of the phylogeny presented by Fang *et al.* (2009: fig. 2). Liao *et al.* (2011b) did not address the taxonomic status of *Hemigrammocypripis* or *Yaoshanicus* relative to Opsariichthyinae.

There is strong support for a clade that includes *Aphyocypris*, *Macrochirichthys*, *Nicholsicypris*, *Oxygaster*, *Parachela*, *Pararasbora*, and *Yaoshanicus*. This group can be further divided into two sister clades: one with *Aphyocypris*, *Nicholsicypris*, *Pararasbora*, and *Yaoshanicus*, and the other with *Macrochirichthys*, *Oxygaster*, and *Parachela*, each of which is supported by robust bootstrap values (Fig. 1b). The general consensus has been that *Aphyocypris*, *Nicholsicypris*, *Pararasbora*, and *Yaoshanicus* are closely related (e.g., Rüber *et al.* 2007; Fang *et al.* 2009; Tang *et al.* 2010, 2013). Although not explicitly stated, by treating *Nicholsicypris normalis* as *Pararasbora normalis*, Chen *et al.* (2009) considered *Nicholsicypris* Chu 1935 a synonym of *Pararasbora* Regan 1908. Subsequently, Liao *et al.* (2011c) placed *Nicholsicypris*, *Pararasbora*, and *Yaoshanicus* in the synonymy of *Aphyocypris*. Takeuchi *et al.* (2011) discovered a synapomorphy of the cephalic lateral line system (infraorbital and supraorbital canals separated) that united *Aphyocypris sensu stricto*, *Hemigrammocypripis*, and *Metzia*. Takeuchi *et al.* (2011) identified a second synapomorphy uniting *Aphyocypris sensu stricto* and *Hemigrammocypripis* (temporal and preopercular canals separated), though they remarked that this latter character may be homoplastic as separation of these two canals is a common condition in cyprinids. Their conclusions agree with our results concerning a close relationship between *Hemigrammocypripis* and *Metzia*, but conflict regarding the relationship of *Aphyocypris* to those genera. The recovery of a clade composed of *Macrochirichthys*, *Oxygaster*, and *Parachela* is consistent with the tree reported in Tang *et al.* (2013), which should be expected considering much of our data are shared with that study. The existence of this clade corroborates the placement of *Oxygaster* first reported by Tang *et al.* (2013), which provided the impetus for recognizing Oxygastrinae. A link between *Oxygaster* and one or both of these two genera had been suggested before (e.g., Weber & de Beaufort 1916; Smith 1945; Bănărescu 1969), though often as components of a larger grouping. Howes (1979: 198) specifically recognized an oxygastrine group comprising only these three genera. The species in this group are not well known and have been the subject of few systematics-oriented studies, as evidenced by the nomenclatural issues surrounding *Oxygaster* (Tang *et al.* 2013).

The *Hemigrammocypripis*-*Metzia* clade is recovered with strong branch support, a result that concurs with Wang *et al.* (2007a) and Tang *et al.* (2010). A sister-group relationship between *Hemigrammocypripis* and *M. lineata* also receives strong support, which renders *Metzia* non-monophyletic, something also reported by Tang *et al.* (2010). The paraphyly of *Metzia* supports Kottelat (2001: 29) who stated that *Metzia formosae* and *M. lineata* “belong to distinct genera” and recognized the former species as “*Metzia*” *formosae*. Gan *et al.* (2009) found evidence to support Kottelat’s (2001) distinction, noting that the number of lateral line scales and position of the mouth distinguished *M. formosae* and *M. longinasus* from the remaining species of *Metzia*. The former two species, which they termed *formosae*-like species, would require a new genus-group name because the species they called *mesembrinum*-like include the type species, *Metzia mesembrinum*. However, they refrained from erecting a new genus without a phylogenetic analysis. The placement of *Hemigrammocypripis* introduces another complication: *Hemigrammocypripis* Fowler 1910 would have priority over *Metzia* Jordan and Thompson 1914.

There is robust support for a large clade that contains the remaining oxygastrines. Within this clade, there is support for a lineage that includes *Distoechodon*, *Plagiognathops*, *Pseudobrama*, and *Xenocypris*. This *Xenocypris* group has some of the best support in the entire tree, with all but one node receiving bootstrap support  $\geq 98\%$  (Fig. 1b). These four genera have been classified together as the subfamily Xenocypridinae before (e.g., Bănărescu 1967; Bogutskaya 1991). Most recently, Zhao *et al.* (2009) placed all four genera in Xenocypridinae and excluded *Xenocyprionides* from the subfamily. Howes (1981) had united *Distoechodon*, *Plagiognathops*, and *Xenocypris* (*Pseudobrama* was not examined) on the basis of shared characters of the gill arches and basioccipital, but he was unable to resolve the relationships among the three genera. He explicitly stated that they were not closely related to oxygastrine taxa like *Hemiculter* and *Ochetobius*, instead he considered them part of his abramine group, which included *Abramis*, *Chondrostoma*, and *Rutilus*, genera acknowledged to be leuciscines (e.g., Perea *et al.* 2010). Our

recovery of *X. hupeinensis* sister to the other representatives of *Xenocypris* corroborates Shan (1998), who referred that species from *Distoechodon* to *Xenocypris*, a move followed by subsequent workers (Xiao *et al.* 2001; Zhao *et al.* 2009). An interesting result is that we find *X. davidi* mixed in with representatives of *X. macrolepis*, which matches the relationships presented by Xiao *et al.* (2001: fig. 2). Investigating this issue is outside the scope of this study, but it does warrant further research. Sister to *Xenocypris* is a monophyletic *Plagiognathops*. We follow Shan (1998), who treated *Xenocypris fangi* as a member of *Plagiognathops*, because this generic assignment preserves monophyly for *Xenocypris*, as otherwise its sister relationship with *P. microlepis*, the type species of *Plagiognathops*, would cause problems. Based on morphological characters, she found a clade comprising these four genera with the same relationships as we recovered herein. Using molecular data, Xiao *et al.* (2001) found relationships among these four genera that are consistent with the phylogeny of Shan (1998) and our phylogeny.

This *Xenocypris* group is sister to the remainder of the subfamily, a large group which could be considered core “cultrines” as the term has been used in literature (e.g., Howes 1991; Rainboth 1991; Nelson 2006). Dai *et al.* (2005) resolved a similar clade on the basis of five synapomorphies, theirs was composed of *Ancherythroculter*, *Culter*, *Cultrichthys*, *Hainania*, *Hemiculter*, *Hemiculterella*, *Macrochirichthys*, *Megalobrama*, *Parabramis*, *Paralaubuca*, *Pseudohemiculter*, *Pseudolaubuca*, *Sinibrama*, and *Toxabramis*. Where our phylogenies diverge is in their inclusion of *Macrochirichthys* and *Paralaubuca*, both of which are oxygastrine genera but are remote from *Culter* and *Hemiculter*; this discrepancy may be due to their use of *Ctenopharyngodon* and *Mylopharyngodon* as outgroups, two genera that are more closely related to *Culter* and its relatives than either *Macrochirichthys* or *Paralaubuca* (Fig. 1b). Takeuchi and Hosoya (2011) described a dorsally elongated metapterygoid as a synapomorphy uniting a clade of *Anabarilius*, *Chanodichthys*, *Culter*, *Hemiculter*, *Ischikauia*, *Megalobrama*, *Sinibrama*, and *Toxabramis* (their Cultrinae), which is comparable to the crown group of Oxygastrinae we recovered. Within the crown clade, the clear delineation of genera seen in the rest of Oxygastrinae begins to break down. *Ancherythroculter*, *Chanodichthys*, *Culter*, *Hemiculter*, *Megalobrama*, and *Toxabramis* all appear to be polyphyletic. *Xenocyprionides*, whose two members are sister species, is the only genus in this clade that is monophyletic. The position of *Xenocyprionides* confirms its affinity with oxygastrines (e.g., Xiao *et al.* 2001; Cunha *et al.* 2002; Fang *et al.* 2009; Tang *et al.* 2010, 2013) and demonstrates that it is not closely related to danionines as previously suggested (Bănărescu & Coad 1991; Zhao *et al.* 2009). We found support for two large clades within the crown group: one comprising *Hemiculter* and its relatives (e.g., *Pseudohemiculter*, *Pseudolaubuca*, *Toxabramis*) and the other comprising *Culter* and its relatives (e.g., *Chanodichthys*, *Ischikauia*, *Megalobrama*). The *Hemiculter* clade has a generic composition equivalent to the *Hemiculter* branch of Yue and Luo (1996) and is similar to the hemicultrine group of others (e.g., Howes 1979; Dai & Yang 2003). The *Culter* clade corresponds to the cultrine groups identified by previous authors (Howes 1979; Yue & Luo 1996). Dai *et al.* (2005) described four synapomorphies (fused second and third vertebral centra; 20 or more branched anal-fin rays; convex anterior margin of first anal pterygiophore; 23 or more caudal vertebrae) uniting *Ancherythroculter*, *Chanodichthys* (as *Cultrichthys*), *Culter*, *Megalobrama*, *Parabramis*, and *Sinibrama*. Takeuchi and Hosoya (2011) reported three morphological synapomorphies uniting *Chanodichthys*, *Culter*, *Ischikauia*, *Megalobrama*, and *Sinibrama*: narrow third infraorbital, large quadrate foramen, third supraneural extended dorsally. The cultrine groups circumscribed by both studies are consistent with the *Culter* clade recovered herein.

## Conclusions

Phylogenetic studies, both molecular (e.g., Wang *et al.* 2002, 2004, 2007a; Liu & Chen 2003; He *et al.* 2004; Saitoh *et al.* 2006, 2011; Kong *et al.* 2007a, b, 2008; Thai *et al.* 2007; Chen & Mayden 2009; Fang *et al.* 2009; Tang *et al.* 2010, 2013) and morphological (e.g., Chen *et al.* 1984, 2005; Cavender & Coburn 1992), have agreed on a clade similar in composition to the one presented herein as the cyprinid subfamily Oxygastrinae. However the traditional classification of these fishes across numerous subfamilies prevented their recognition as a single cohesive group. Following Nikolskii (1954), subsequent workers (e.g., Bănărescu 1967; Gosline 1978) were able to piece together an outline for the group, laying the groundwork for later studies, including this one, that have better delineated the limits of the subfamily. It is now clear that this assemblage encompasses a broad swath of East Asian cyprinids that have historically been classified as members of multiple subfamilies. The evidence that these genera do not belong to any other established cyprinid subfamilies and that together they form a natural group is

compelling. However, much more work on the phylogenetic relationships within Oxygastrinae is clearly needed as its diversity is far greater than the representative sampling used herein. More detailed revisionary work will be needed to clarify the species relationships and monophyly of many of the “core” cultrine genera (e.g., *Chanodichthys*, *Culter*, *Hemiculter*, *Megalobrama*). Furthermore, there are some genera (e.g., *Atrilinea*, *Rasboraichthys*) whose subfamilial affiliations remain ambiguous and will require investigation. Nonetheless, the recognition of Oxygastrinae as a distinct subfamily with a well-defined composition represents an important step forward in our understanding of cyprinid systematics.

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**APPENDIX.** Taxa examined for this study, with GenBank accession numbers. Institutional abbreviations as follows: AMS=Australian Museum; CBM-ZF=Natural History Museum and Institute, Chiba; IHB=Institute of Hydrobiology, Chinese Academy of Sciences; KUN-P=Kinki University-Pisces Collection; STL=Saint Louis University; UAIC=University of Alabama Ichthyological Collection; USNM=United States National Museum.

Classification	Taxon	Catalog No.	Source	RAG1	Rh	Cyt <i>b</i>	COI
Gonorynchiformes	<i>Chanos chanos</i>	N/A	GenBank	AY430207	FJ197072	AB054133	AB054133
	<i>Gonorynchus greyi</i>	AMS-I.33768-001	New South Wales, Australia	EU409606	EU409632	AB054134	AB054134
Characiformes	<i>Phenacogrammus interruptus</i>	N/A	GenBank	FJ197124	FJ197073	AB054129	AB054129
Siluriformes	<i>Ictalurus punctatus</i>	N/A	GenBank	DQ492511	AF028016	AF482987	AF482987
Cypriniformes							
Cobitoidea							
Balitoridae	<i>Homaloptera leonardi</i>	N/A	Moon River, Thailand	EU711130	FJ197027	AB242165	AB242165
	<i>Sewellia lineolata</i>	CBM-ZF-11315	Aquarium	HM224068	EU409635	AP011292	AP011292
Botiidae	<i>Chromobotia macracantha</i>	CBM-ZF-11438	Aquarium	EU711137	FJ197037	AB242163	AB242163
	<i>Parabotia mantschurica</i>	CBM-ZF-11432	K. Saitoh	EU711138	FJ197038	AB242170	AB242170
Catostomidae							
Catostominae							
	<i>Catostomus commersonii</i>	STL 814.04	Illinois, USA	EU409612	FJ197032	AB127394	AB127394
	<i>Hypentelium nigricans</i>	UAIC 12136.04	Youghiogheny River, Maryland, USA	EU711134	FJ197033	AB242169	AB242169
Cyprinodontidae							
	<i>Cyprinus elongatus</i>	UAIC 12497.21	Duck River, Tennessee, USA	EU409613	FJ197035	AB126082	AB126082
	<i>Myoxocypris asiaticus</i>	N/A	Aquarium	EU711136	FJ197036	AB223007	AB223007
Cobitidae							
	<i>Acanthopsis choirohynchus</i>	STL uncataloged	Aquarium	EU711139	FJ197039	AB242161	AB242161
	<i>Cobitis striata</i>	CBM-ZF-10606	Lake Biwa, Japan	EF458303	HM223938	AB054125	AB054125
Ellopostomatidae							
	<i>Ellopostoma mystax</i>	UAIC 14301.02	Tapi River Basin, Thailand	FJ650417	FJ650477	JN003323	JN003347

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APPENDIX. (Continued)

Classification	Taxon	Catalog No.	Source	RAG1	Rh	Cyt <i>b</i>	COI
Gyrinocheilidae							
	<i>Gyrinocheilus aymonieri</i>	UAIC 12928.03	N/A	EU292682	FJ197071	AB242164	AB242164
Nemacheilidae							
	<i>Barbatula toni</i>	CBM-ZF-11288	Hokkaido, Japan	EU711133	FJ197030	N/A	N/A
		N/A	Ussuri River, Russia	N/A	N/A	AB242162	AB242162
	<i>Lefua echigonia</i>	N/A	Hino, Shiga, Japan	EF458305	FJ197028	AB054126	AB054126
Vaillantellidae							
	<i>Vaillantella maassi</i>	CBM-ZF-11437	Aquarium	EU711132	FJ197031	AB242173	AB242173
Cyprinioidea							
Cyprinidae							
Acheilognathinae							
	<i>Acheilognathus typus</i>	CBM-ZF-11423	Hanamaki, Iwate, Japan	EU292688	FJ197042	AB239602	AB239602
	<i>Rhodeus ocellatus</i>	N/A	Yao, Osaka, Japan	EU711142	FJ197043	AB070205	AB070205
	<i>Tanakia limbata</i>	CBM-ZF-11178	Okayama, Japan	HM224070	HM223952	HM224309	HM224190
Cyprininae							
	<i>Barboromys gonionotus</i>	CBM-ZF-11230	Kampong Chhnang, Cambodia	N/A	FJ531344	N/A	N/A
		N/A	Moon River, Thailand	EU711146	N/A	AB238966	AB238966
	<i>Barbus barbus</i>	N/A	Danube River, Austria	EU711147	FJ197049	AB238965	AB238965
	<i>Barbus trimaculatus</i>	N/A	Maputo, Mozambique	EU711148	FJ197050	AB239600	AB239600
	<i>Carassius auratus</i>	N/A	GenBank	DQ196520	L11863	AB006953	AB111951
	<i>Cyprinus carpio</i>	N/A	GenBank	AY787040	U02475	X61010	X61010
	<i>Gymnocypris przewalskii</i>	N/A	Qinghai Lake, Qinghai, China	EU711149	FJ197051	AB239595	AB239595
	<i>Labeo senegalensis</i>	N/A	Ouémé and Iguidi Rivers, Benin	EU711151	FJ197053	AB238968	AB238968
	<i>Osteobrama belangeri</i>	N/A	GenBank	N/A	N/A	N/A	HQ116652
	<i>Osteobrama cotio</i>	CBM-ZF-11308	Aquarium	KF029702	KF029646	AP011260	AP011260
	<i>Osteobrama cumma</i>	CBM-ZF-11564	Myanmar	KF029703	KF029647	KF029688	KF029669
	<i>Puntius ticto</i>	N/A	GenBank	EU711152	FJ197054	AB238969	AB238969
	<i>Rohtee ogilbii</i>	CBM-ZF-11154	Aquarium	KF029704	N/A	AP011362	AP011362

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APPENDIX. (Continued)

Classification	Taxon	Catalog No.	Source	RAG1	Rh	Cyt <i>b</i>	COI
Danioninae							
	<i>Amblypharyngodon mola</i>	CBM-ZF-11790	Koshi Barrage, Nepal	HM224019	HM223899	HM224256	HM224137
	<i>Barilius vagra</i>	UAIC 14179.07	Aquarium	HM224022	HM223901	HM224259	HM224140
	<i>Danio rerio</i>	N/A	GenBank	U71093	L11014	AC024175	AC024175
	<i>Danionella dracula</i>	UAIC 14169.47	Aquarium	EF452841	HM223913	EF452741	EF452887
	<i>Devario auropurpureus</i>	CBM-ZF-11324	Aquarium	EU292708	HM223915	HM224275	HM224156
	<i>Esomus danricus</i>	UAIC 14169.04	Aquarium	HM224044	HM223926	HM224287	HM224168
	<i>Luciosoma setigerum</i>	CBM-ZF-11273	Aquarium	EU292704	FJ531352	AP011423	AP011423
	<i>Microsabora rubescens</i>	UAIC 14167.06	Aquarium	EF452844	EF452913	EF452744	EF452890
	<i>Paedocypris carbunculus</i>	UAIC 14180.63	Aquarium	GQ365218	GQ365226	HM224326	HM224209
	<i>Raiamas guttatus</i>	CBM-ZF-11363	Aquarium	HM224092	HM223977	AP011222	AP011222
	<i>Rasbora cephalotaenia</i>	CBM-ZF-11443	Aquarium	HM224099	HM223984	AP011430	AP011430
	<i>Sundadanio axelrodi</i>	UAIC 14300.01	Aquarium	EU292711	GQ365228	HM224383	HM224253
Gobioninae							
	<i>Gnathopogon elongatus</i>	CBM-ZF-11430	Lake Biwa, Japan	EU711153	FJ197055	AB218687	AB218687
	<i>Gobio gobio</i>	N/A	Planá, Czech Republic	EU292689	FJ197056	AB239596	AB239596
	<i>Hemibarbus barbus</i>	N/A	Sarugaishi River, Japan	EU711154	FJ197057	AB070241	AB070241
	<i>Sarcocheilichthys variegatus</i>	CBM-ZF-10604	Lake Biwa, Japan	EU711157	FJ197060	AB054124	AB054124
Leptobarbinae							
	<i>Leptobarbus hoevenii</i>	CBM-ZF-11225	Kampong Chhnang, Cambodia	FJ531249	FJ531351	AP011286	AP011286
Leuciscinae							
	<i>Abramis brama</i>	STL	Lake Yazkhan,	EU711103	KF029648	Y10441	KF029670
	<i>Alburnus alburnus</i>	775.01/uncataloged	Turkmenistan/GenBank	EU711143	FJ197044	AB239593	AB239593
	<i>Chondrostoma nasus</i>	N/A	Saône River, Lyon, France	N/A	N/A	AF533760	N/A
	<i>Cyprinella lutrensis</i>	UAIC 11405.07	Frio River, Texas, USA	EU711158	FJ197061	AB070206	AB070206
	<i>Leuciscus leuciscus</i>	N/A	GenBank	HM560407	N/A	HM560100	HM560272
	<i>Notemigonus crysoleucas</i>	N/A	St. Catharines, Ontario, Canada	EF452831	FJ197062	U01318	EF452854
	<i>Notropis atherinoides</i>	UAIC 10485.06	Wisconsin, USA	HM224059	HM223942	HM224297	HM224179
	<i>Pelecus cultratus</i>	N/A	Lake Balaton, Hungary	EU711144	FJ197045	AB239597	AB239597
	<i>Pteronotrops hypselopterus</i>	UAIC 12730.02	Alabama, USA	HM224065	HM223948	HM224303	HM224185

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# APPENDIX. (Continued)

Classification	Taxon	Catalog No.	Source	RAG1	Rh	Cyt <i>b</i>	COI
Oxygastrinae							
	<i>Ancherythroculter daovantieni</i>	N/A	GenBank	N/A	N/A	DQ464975	N/A
	<i>Ancherythroculter nigrocauda</i>	N/A	GenBank	N/A	N/A	AY493869	N/A
	<i>Aphyocypris chinensis</i>	CBM-ZF-11424	Tanushimaru, Fukuoka, Japan	EU292692	FJ197066	AB218688	AB218688
	<i>Aphyocypris kikuchii</i>	CBM-ZF-12285	Aquarium	N/A	N/A	AP012123	AP012123
	<i>Candidia barbatus</i>	N/A	GenBank	N/A	EU919559	AY58200	N/A
	<i>Chanodichthys erythropterus</i>	UAIC 14381.01	GenBank	KF029705	KF029649	KF029689	N/A
		N/A	GenBank	N/A	N/A	N/A	HQ536348
	<i>Chanodichthys mongolicus</i>	UAIC 14382.01	N/A	EU711145	FJ197047	AP009060	AP009060
	<i>Ctenopharyngodon idella</i>	IHB 0411070	Wuhan, Hubei, China	EF178284	HM223939	EU391390	EU391390
	<i>Ctenopharyngodon idella</i>	IHB uncataloged		GU217832	N/A	N/A	KF029671
	<i>Culter alburnus</i>	N/A	GenBank	GU217839	GU218595	GU190362	GU190362
	<i>Culter dabryi</i>	KUN-P 40632	Wuhan, Hubei, China	N/A	N/A	AP012111	AP012111
	<i>Culter flavipinnis</i>	UAIC 14246.02	Red River, Thailand	KF029706	KF029650	KF029690	KF029672
	<i>Distoechodon compressus</i>	N/A	GenBank	N/A	N/A	AF374407	N/A
	<i>Distoechodon tumirostris</i>	N/A	GenBank	N/A	N/A	DQ026431	DQ026431
	<i>Elopichthys bambusa</i>	CBM-ZF-11514	Mai Chau, Hoa Binh, Vietnam	KF029707	KF029651	KF029691	KF029673
	<i>Hainania serrata</i>	UAIC 14246.01	Red River, Thailand	KF029708	KF029652	KF029692	KF029674
	<i>Hemiculter bleekeri</i>	IHB 0411061		KF029709	KF029653	KF029693	KF029675
	<i>Hemiculter krempfi</i>	UAIC 15279.01	Vietnam	N/A	N/A	KF029694	N/A
	<i>Hemiculter leuciscus</i>	CBM-ZF-11621	Vinh Phuc, Vietnam	KF029710	KF029654	AP012110	AP012110
	<i>Hemiculter lucidus</i>	UAIC 14391.01	Russia	EU711119	KF029655	KF029695	N/A
	<i>Hemiculterella macrolepis</i>	N/A	GenBank	N/A	N/A	EF151094	N/A
	<i>Hemigrammocypripis rasborella</i>	CBM-ZF-11669	Shiga, Japan	HM224045	HM223927	AP011422	AP011422
	<i>Hypophthalmichthys molitrix</i>	IHB 0411072	Wuhan, Hubei, China	KF029712	KF029656	N/A	N/A
		N/A	GenBank	N/A	N/A	EU315941	EU315941
	<i>Hypophthalmichthys molitrix</i>	IHB 0807219	Wuhan, Hubei, China	KF029711	N/A	N/A	KF029676
	<i>Hypophthalmichthys nobilis</i>	IHB 0411071	Wuhan, Hubei, China	HM224058	HM223941	EU343733	EU343733
	<i>Hypophthalmichthys nobilis</i>	IHB uncataloged	Wuhan, Hubei, China	GU217834	N/A	N/A	KF029677
	<i>Ischikauia steenackeri</i>	N/A	Lake Biwa, Japan	EU292687	EU409648	AB239601	AB239601

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# APPENDIX. (Continued)

Classification	Taxon	Catalog No.	Source	RAG1	Rh	Cyt b	COI
	<i>Luciobrama macrocephalus</i>	N/A	GenBank	GU217842	GU218598	N/A	N/A
	<i>Macrochirichthys macrochirus</i>	CBM-ZF-11207	Kandal, Cambodia	EU409630	EU409659	AP011234	AP011234
	<i>Megalobrama amblycephala</i>	IHB uncataloged	Liangzihu, Hubei, China	KF029713	KF029657	DQ026433	DQ026433
	<i>Megalobrama amblycephala</i>	CBM-ZF-11345	Aquarium	EU409620	EU409647	AP011219	AP011219
	<i>Megalobrama pellegrini</i>	N/A	GenBank	N/A	N/A	AF051869	N/A
	<i>Megalobrama skolkovii</i>	N/A	GenBank	N/A	N/A	AF051871	N/A
	<i>Megalobrama terminidis</i>	N/A	GenBank	N/A	N/A	AF475156	N/A
	<i>Metzia formosae</i>	UAIC 14266.03	Hanoi, Vietnam	HM224066	HM223949	HM224304	HM224186
	<i>Metzia lineata</i>	UAIC 14266.02	Hanoi, Vietnam	HM224067	HM223950	HM224305	HM224187
	<i>Mylopharyngodon piceus</i>	IHB uncataloged		GU217831	N/A	N/A	KF029678
	<i>Mylopharyngodon piceus</i>	CBM-ZF-11254	Saitama, Japan	N/A	KF029658	AP011216	AP011216
	<i>Nicholsicypris normalis</i>	CBM-ZF-11304	Aquarium	EU711123	HM223937	AP011396	AP011396
	<i>Nipponocypris koreanus</i>	N/A	GenBank	N/A	N/A	N/A	HQ536538
	<i>Nipponocypris sieboldii</i>	CBM-ZF-11165	Okayama, Japan	EU292713	FJ197069	AB218898	AB218898
	<i>Nipponocypris temminckii</i>	CBM-ZF-11175	Shimane, Japan	EF452849	EF452918	EF452750	EF452897
	<i>Ochetobius elongatus</i>	N/A	GenBank	GU217841	GU218597	AF309506	N/A
	<i>Opsariichthys bidens</i>	IHB 805651	Tumen, Jilin, China	KF029714	KF029659	N/A	KF029679
	<i>Opsariichthys bidens</i>	UAIC 14398.01	Aquarium	HM224074	HM223957	HM224313	HM224195
	<i>Opsariichthys evolans</i>	CBM-ZF-12275	Aquarium	N/A	EU919564	AP012120	AP012120
	<i>Opsariichthys pachycephalus</i>	CBM-ZF-11684	Aquarium	HM224075	HM223958	HM224314	HM224196
	<i>Opsariichthys uncirostris</i>	CBM-ZF-11177	Fukuoka, Japan	EF452847	EF452916	EF452748	EF452894
	<i>Oxygaster anomalura "IM33"</i>	USNM 394000	Kalimantan Selatan, Indonesia	HQ009863	HQ009865	HQ009867	HQ009869
	<i>Oxygaster anomalura "IM36"</i>	USNM 394000	Kalimantan Selatan, Indonesia	HQ009864	HQ009866	HQ009868	HQ009870
	<i>Parabramis pekinensis</i>	Uncataloged		KF029715	KF029660	KF029696	KF029680
	<i>Parachela maculicauda</i>	UAIC 14167.21	Aquarium	HM224060	HM223943	HM224298	HM224180
	<i>Parachela oxygastroides</i>	CBM-ZF-11326	Aquarium	HM224061	HM223944	HM224299	HM224181
	<i>Parachela siamensis</i>	UAIC 14175.06	Nong Khai, Thailand	HM224062	HM223945	HM224300	HM224182
	<i>Parachela williaminae</i>	UAIC 14269.08	Mekong River, Thailand	HM224063	HM223946	HM224301	HM224183
	<i>Paralabuca barroni</i>	STL uncataloged	Mekong River, Thailand	KF029716	KF029661	KF029697	KF029681
	<i>Paralabuca riveroi</i>	STL uncataloged	Mekong River, Thailand	KF029717	KF029662	KF029698	KF029682
	<i>Paralabuca typus</i>	CBM-ZF-11203	Kandal, Cambodia	EU409619	EU409646	AP011211	AP011211

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# APPENDIX. (Continued)

Classification	Taxon	Catalog No.	Source	RAG1	Rh	Cyt <i>b</i>	COI
	<i>Parasbora moltrechti</i>	CBM-ZF-12276	Aquarium	N/A	N/A	AP012122	AP012122
	<i>Parazacco spilurus</i>	N/A	GenBank	N/A	N/A	AY958195	N/A
	<i>Plagiognathops fangi</i>	N/A	GenBank	N/A	N/A	AF036205	N/A
	<i>Plagiognathops microlepis</i>	IHB 2603062	Poyang Lake, Jiangxi, China	N/A	KF029663	N/A	KF029683
		UAIC 15516.01	Russia	N/A	N/A	KF029699	N/A
	<i>Pseudobrama simoni</i>	KUN-P 40634	Wuhan, Hubei, China	N/A	N/A	AP011364	AP011364
	<i>Pseudohemiculter dispar</i>	UAIC 14246.06	Red River, Thailand	KF029718	KF029664	KF029700	KF029684
	<i>Pseudolabuca engraulis</i>	IHB 807108	Poyang Lake, Jiangxi, China	N/A	KF029665	N/A	KF029685
	<i>Sinibrama macrops</i>	CBM-ZF-12273	Aquarium	N/A	N/A	AP012112	AP012112
		IHB 0807101	Yongfu, Guangxi, China	N/A	KF029666	N/A	N/A
	<i>Squaliobarbus curriculus</i>	IHB 0807079	Tengxian, Guangxi, China	KF029719	N/A	N/A	KF029686
	<i>Squaliobarbus curriculus</i>	IHB 0411051	Guangxi, China	HM224069	HM223951	HM224308	HM224189
	<i>Toxabramis houdemeri</i>	CBM-ZF-11622	Yên Mỹ, Hưng Yên, Vietnam	KF029720	KF029667	AP011333	AP011333
	<i>Toxabramis</i> sp.	UAIC 14313.04	Krông Ana River, Vietnam	N/A	KF029668	KF029701	KF029687
	<i>Toxabramis swinhonis</i>	KUN-P 40633	Wuhan, Hubei, China	N/A	N/A	AP011334	AP011334
	<i>Xenocyprionoides carinatus</i>	N/A	GenBank	N/A	N/A	AF036201	N/A
	<i>Xenocyprionoides parvulus</i>	N/A	GenBank	N/A	N/A	AF036207	N/A
	<i>Xenocypris davidi</i>	N/A	GenBank	N/A	N/A	GQ289558	GQ289558
	<i>Xenocypris hupeinensis</i>	N/A	GenBank	N/A	N/A	AF036165	N/A
	<i>Xenocypris macrolepis</i>	UAIC 14410.01		EU711160	FJ197064	AP011283	AP011283
	<i>Xenocypris macrolepis</i>	Uncataloged	Amur River, Russia	N/A	N/A	AP009059	AP009059
	"Russia"						
	<i>Xenocypris macrolepis</i>	CBM-ZF-11411	Vĩnh Phúc, Vietnam	HM224071	HM223953	HM224310	HM224191
	"Vietnam"						
	<i>Yaoshanicus arcus</i>	CBM-ZF-11355	Aquarium	FJ531254	FJ531361	AP011398	AP011398
	<i>Zacco platypus</i>	CBM-ZF-11160	Okayama, Japan	EF452848	EF452917	EF452749	EF452896
Tincinae							
	<i>Tanichthys albonubes</i>	CBM-ZF-11334	Aquarium	FJ531253	FJ531359	AP011397	AP011397
	<i>Tinca tinca</i>	N/A	Saône River, Fारेins, France	EU711162	FJ197070	AB218686	AB218686
Psilorhynchidae							
	<i>Psilorhynchus homaloptera</i>	IHB uncataloged	Aquarium	FJ531250	FJ531354	DQ026436	DQ026436
	<i>Psilorhynchus sucatio</i>	CBM-ZF-11322	Aquarium	FJ531251	FJ531355	AP011288	AP011288