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Article

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Bleeker was right: Revision of the genus *Cyclocheilichthys* (Bleeker 1859) and resurrection of the genus *Anematichthys* (Bleeker 1859), based on morphological and molecular data of Southeast Asian Cyprininae (Teleostei, Cypriniformes)

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Abstract

The taxonomy within the order Cypriniformes is subject to frequent changes, thanks to the results coming from recent molecular phylogenies that help understand the Cypriniformes tree of life previously established through morphological characters. In this paper, we focus on species belonging to the Cyprininae – the largest sub-family among Cypriniformes – and we present both morphological and phylogenetic arguments to revise the taxonomy of the genus *Cyclocheilichthys*. For morphological investigations, we characterized external traits as well as the postcranial skeleton and the neurocranium. For molecular phylogenies, we used four markers, both mitochondrial and nuclear, to establish a phylogenetic tree. We studied four species currently assigned to the genus *Cyclocheilichthys* as well as the species *Cosmochilus harmandi* and *Puntioplites falcifer* and we show that the genus *Cyclocheilichthys* is non-monophyletic as *Cyclocheilichthys enoplos* is closer to *C. harmandi* and *P. falcifer* than *Cyclocheilichthys armatus*, *Cyclocheilichthys apogon* and *Cyclocheilichthys repasson*. Finally, we revise the genus *Cyclocheilichthys* and we propose to split this genus into two genera: genus *Cyclocheilichthys* with the species *Cyclocheilichthys enoplos* and genus *Anematichthys* with species *Anematichthys armatus*, *Anematichthys apogon* and *Anematichthys repasson*.

Key words: Cypriniformes, taxonomy, morphology, molecular phylogeny, *Cyclocheilichthys*

Introduction

Cypriniformes constitutes the largest order of freshwater fishes encompassing more than 3,000 extant species (Nelson 2006). The taxonomy of Cypriniformes has been the subject of a long debate since the 19th century; see Howes (1991) for a review. Recently, molecular phylogenies have brought much information on phylogenetic relationships among Cypriniformes (Saitoh *et al.* 2006, Mayden *et al.* 2009), but there are still many unresolved nodes in the Cypriniformes tree of life. The subfamily Cyprininae is the largest subfamily among Cypriniformes, with around 1,300 living species distributed within 110 genera (Yang *et al.* 2010). Although some classifications based on morphological characters (Howes 1991, Rainboth 1996) have been later validated by molecular phylogenies (Wang *et al.* 2007, Li *et al.* 2008, Yang *et al.* 2010), some clades like Semiploti and Osteobramae (according to Rainboth 1996) still lack solid confirmation by molecular studies. Recently published molecular investigations have shown that most species included in these two clades form a monophyletic group (Yang *et al.* 2010), with the exception of *Onychostoma*. This latter genus was moved into the Semiploti by Rainboth (1996), but recent molecular studies grouped *Onychostoma* together with *Schizothorax*, *Gymnocypris,* and *Spinibarbus* (Wang *et al.* 2007, Li *et al.* 2008, Yang *et al.* 2010) into a clade corresponding to Schizothoracin and Onychostoma-Cyprinion lineages by Howes (1991). A problem is that molecular studies dealing with the phylogeny of Cyprininae have poorly sampled species belonging to the sub-tribes Semiploti and Osteobramae (according to

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Rainboth 1996), thus involving important questions on the phylogenetic relationships within these two sub-tribes. The genus *Cyclocheilichthys* includes eight species (Rainboth 1996) which were assigned to this genus based on the presence of rows of parallel pores on the snout (Rainboth 1996, Kottelat 2001), but are morphologically divergent, emphasizing the need to confirm or disprove their monophyly. The present study proposes to revisit the positions of several species of the genus *Cyclocheilichthys* using both morphological and molecular data.

Morphological studies

Osteological preparations were carried out by manual cleaning, except one specimen of *Cyclocheilichthys enoplos* (AMNH 217316) was prepared using *Dermestes*. Specimens all come from the collections of the National Museum of Natural History of Paris (MNHN), except the above-cited specimen of *C. enoplos,* which was a loan from the American Museum of Natural History of New York (AMNH). Reference numbers for all studied specimens are provided in Table 1. Investigation of external characters included measurements of both standard length and height. Lateral-line tubes of the lateral-line scales were observed. Figures 1 and 2 show lateral views of one specimen for each species, as well as some other detailed characters. Characters of the neurocranium were investigated, and pictures were taken. Anatomical terminology has been established according to Ramaswami (1955), and abbreviations are explicated in the Appendix. For each species, plates show dorsal, lateral and ventral views of the neurocranium (Figs. 5,6,7). The fifth ceratobranchial, bearing the pharyngeal teeth, was extracted and pictured from various views (Fig. 4).

TABLE 1. Specimens used in this study for morphological and anatomical characters. All specimens are catalogued in the National Museum of Natural History in Paris (MNHN), except one specimen of C. enoplos from the American Museum of Natural History (AMNH).

Species	Catalog numbers
Cyclocheilichthys armatus	2012-0010, 2009-0258, 2009-0259
Cyclocheilichthys repasson	2012-0011
Cyclocheilichthys enoplos	2012-0012, 2012-0013, 2012-0014, AMNH 217316
Puntioplites falcifer	2011-1609, 2012-0015
Cosmochilus harmandi	2004-0163

Phylogenetic studies

Twenty-one species of Cypriniformes were used to infer a molecular phylogeny, including 14 species belonging to Osteobramae and Semiploti according to Rainboth (1996). The cobotid species, *Botia modesta*, was used as the outgroup. All samples were collected and fixed in ethanol 80 during field missions in Laos, in the Mekong basin (see Table 2 for origin of the specimens and sequence numbers on GenBank). DNA extraction was carried out with Qiagen DNA extraction kit. Gene amplification was carried out for four molecular markers commonly used in Cypriniformes phylogenetic studies: two mitochondrial markers—cytochrome b (cytb), cytochrome oxidase (coI); and two nuclear markers—recombination-activating gene 1 (rag1) and recombination-activating gene 2 (rag2). PCR was carried out following Rüber *et al.* (2007) for cytb, Perea *et al.* (2010) for coI, Chen & Mayden (2009) for rag1, Wang *et al.* (2007) for rag2. PCR products were sent to Beckman Coulter Genomics for purification and sequencing. Sequences obtained were cleaned and aligned with Seaview software (Galtier *et al.* 1996). Final alignments are as follows: 1,118 bp for cytb, 647 bp for coi, 947 bp for rag1 and 1,233 bp for rag2. Sequences were concatenated, giving a total of 3945 bp. The best model of evolution was chosen according to ModelTest software (Posada 2008). The selected model (GTR+G+I) was then used for a concatenated analysis of all sequences by Maximum Likelihood using PhyML software (Guindon & Gascuel 2003). Branch support analysis was carried out by bootstrap with 1,000 resampling. Phylogenetic analyses were also carried out with MrBayes software (Ronquist & Huelsenbeck 2003) for Bayesian methods, with 1,000,000 generations, a sampling frequency of 100, and a partitioned dataset for each marker and each base position, allowing independent models of evolution for each dataset. Branch supports of the consensus tree obtained were determined by posterior probabilities.

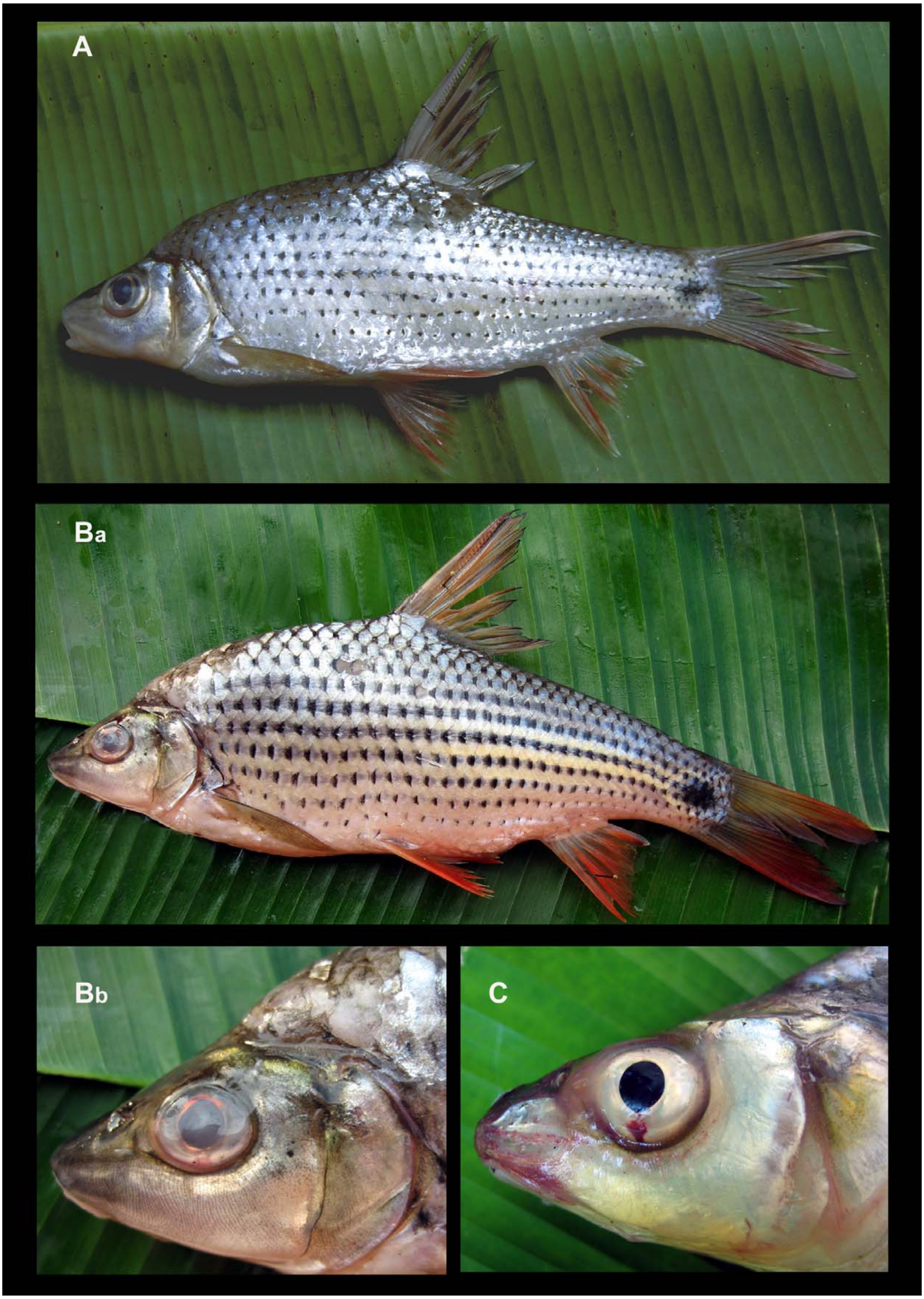

FIGURE 1. Lateral views of specimens. (A) *Cyclocheilichthys armatus* (MNHN 2012-0010, SL = 190 mm); (B) *Cyclocheilichthys repasson* (MNHN 2012-0011, SL= 190 mm). (a) Whole specimen. (b) Detailed picture of the head showing the rows of pores. (C) *Cyclocheilichthys enoplos*—detailed picture of the head showing the rows of pores, for comparison with *C. repasson*.

TABLE 2. Sequences used in this study for phylogenetic analyses with Genbank numbers. All specimens are from local markets in the Mekong Basin in Laos.

Species	MNHN catalog numbers	Province in Laos	Cytb	CoI	Rag1	Rag2
Barbonymus altus	2012-0070	Champassak	JQ34613	JQ34615	JQ346117	JQ346108
Barbonymus gonionotus	2012-0073	Champassak	JQ34613	JQ34615	JQ346120	JQ346109
Barbonymus scwhanenfeldii	2012-0084	Luang Prabang	JQ34615	JQ346171	JQ346130	-
Botia modesta	2012-0083	Khammouane	JQ34615	JQ346170	JQ346129	JQ346105
Cosmochilus harmandi	2012-0075	Champassak	JQ34614	JQ346163	JQ346115	JQ346095
Cyclocheilichthys apogon	2012-0074	Champassak	JQ34613	JQ34616	JQ346113	JQ34609
Cyclocheilichthys armatus	2012-0081	Khammouane	JQ34614	JQ346167	JQ346126	JQ346098
Cyclocheilichthys enoplos	2012-0014	Champassak	JQ34613	JQ346162	JQ346114	JQ346094
Cyclocheilichthys repasson	2012-0011	Khammouane	JQ34614	JQ346165	JQ346124	JQ346097
Hampala macrolepidota	2012-0077	Champassak	JQ34614	-	JQ346122	JQ346096
Hypophtalmichthys nobilis	2012-0076	Champassak	JQ34614	JQ346164	JQ346116	JQ346099
Hypsibarbus malcolmi	2012-0008	Khammouane	JQ34614	JQ346169	JQ346128	JQ346102
Hypsibarbus wetmorei	2012-0006	Champassak	JQ34613	JQ34615	JQ346121	JQ346103
Labeo rohita	2012-0072	Champassak	JQ34613	JQ34615	JQ346119	JQ346101
Mystacoleucus marginatus	2012-0079	Khammouane	JQ34614	JQ34616	JQ346123	JQ346104
Neolissochilus stracheyi	2012-0080	Khammouane	JQ34614	JQ346166	JQ346125	JQ346106
Osteochilus hasselti	2012-0082	Khammouane	JQ34614	JQ346168	JQ346127	JQ346111
Raiamas guttatus	2012-0078	Khammouane	JQ34614	JQ34615	-	JQ346110
Scaphognathops bandanensis	2012-0071	Champassak	JQ34613	JQ34615	JQ346118	JQ346100
Sikukia gudjeri	2012-0085	Khammouane	JQ34615	JQ346172	JQ346131	-
Puntioplites falcifer	2012-0069	Champassak	JQ3461	JQ346153	JQ34611	JQ346107

Results

1. Comparative anatomy between genera *Cyclocheilichthys* (Bleeker 1859), *Puntioplites* (Smith 1929) and *Cosmochilus* (Sauvage 1882)

1.1 External characters

On the one hand, *Cyclocheilichthys enoplos* (Bleeker 1849) is externally very different from *C. armatus* (Cuvier & Valenciennes 1842), *C. repasson* (Bleeker 1853) and *C. apogon* (Cuvier & Valenciennes 1842). *C. enoplos* is a large species, which measures at least up to 900mm (MNHN 2012-0013) whereas the three other species measure up to 300mm. *C. enoplos* has a more elongated body, with a large and long dorsal spine. Moreover, lateral-line scales display ramified lateral-line tubes in *C. enoplos*, a character shared with *Cosmochilus harmandi* (Sauvage 1878) but absent in *C. armatus, C. apogon* and *C. repasson* (Fig. 2). On the other hand, *C. armatus*, *C. repasson* and *C. apogon* are very close morphologically, with slight characters that can help distinguish them: the presence or absence of barbels and the number of scales around caudal peduncle.

Another character, which distinguishes *C. enoplos* from other *Cyclocheilichthys* is the extension of dorsal scales to the head; in *C. armatus, C. apogon* and *C. repasson*, dorsal scales reach the level of the orbit (Fig.1A–B), whereas in *C. enoplos* dorsal scales extend less anteriorly as in *Cosmochilus harmandi* and *Puntioplites falcifer* (Smith 1929) (Fig.2). Moreover, in *C. armatus, C. apogon* and *C. repasson,* there are rows of parallel pores, which are well underlined by small black dots, clearly visible under the eye (Fig.1B). In contrast, this character is absent in *C. enoplos* (Fig.1C).

As *C. armatus*, *C. apogon* and *C. repasson* are very similar, cranial and postcranial characters are shown only for *C. armatus* in the following sections.

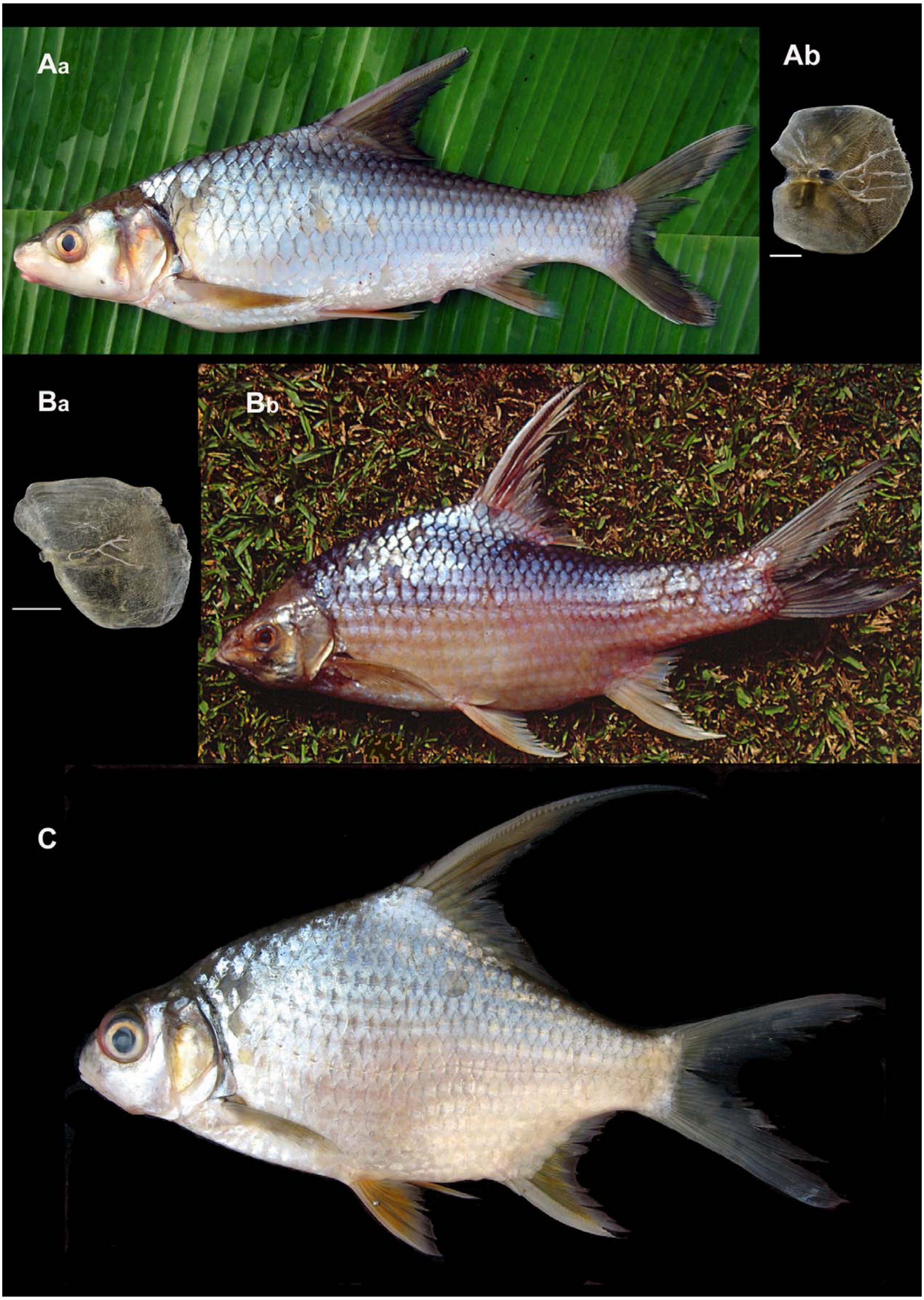

FIGURE 2. Lateral views of specimens. (A) *Cyclocheilichthys enoplos*. (a) MNHN 2012-0014, SL = 340 mm. (b) Lateral-line scale showing ramified tubes. (B) *Cosmochilus harmandi*. (a) Lateral-line scale showing ramified tubes. (b) MNHN 2004-0163, SL = 505 mm. (C) *Puntioplites falcifer* (MNHN 2011-1609, SL = 198 mm). Each scale bar represents 5 mm.

1.2 Post-neurocranium skeleton

1) *C. armatus*, as well as *C. enoplos* and *Cosmochilus harmandi*, have 5 supraneurals (Sne), but the most posterior one is not bound to the first pterygiophore of dorsal fin (Ptery 1) in *C. armatus* whereas it is bound in *C. enoplos* and *Cosmochilus harmandi* (Fig. 3). In *Puntioplites falcifer*, all four supraneurals are bound to one another and the last one is also bound to the first pterygiophore.

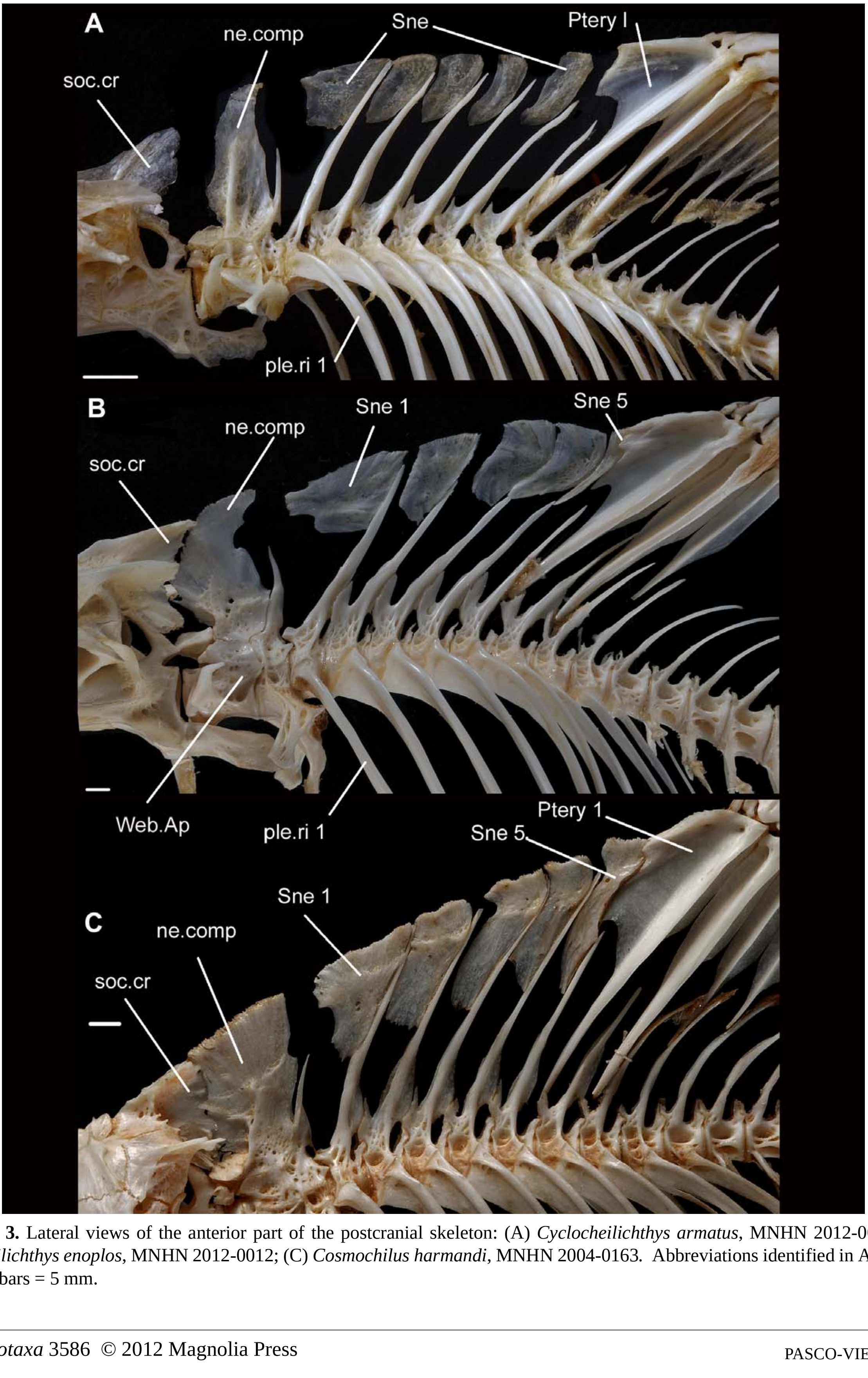

FIGURE 3. Lateral views of the anterior part of the postcranial skeleton: (A) *Cyclocheilichthys armatus*, MNHN 2012-0010; (B) *Cyclocheilichthys enoplos*, MNHN 2012-0012; (C) *Cosmochilus harmandi*, MNHN 2004-0163. Abbreviations identified in Appendix I. Scales bars = 5 mm.

2) In *C. enoplos*, *Cosmochilus harmandi* and *Puntioplites falcifer*, the neural complex (ne.comp) is bound to the supraoccipital crest (soc.cr) as there is a notch on the supraoccipital crest (see next paragraph) in which fits the neural complex, whereas in *C. armatus* there is no link between the neural complex and the supraoccipital crest (Fig. 3).

3) Pharyngeal bones (Fig. 4), which are the fifth ceratobranchial, are larger in *C. enoplos* and *Cosmochilus harmandi* than in *C. armatus*. On pharyngeal bones, *C. enoplos* and *Cosmochilus harmandi* have a large and rounded tooth at the second position on the main dental row — the row with five teeth — whereas the tooth at this position has a normal size, compared to other teeth, in *C. armatus*. Tooth shape is also different: *C. armatus* has spoon-shaped teeth, with a hook at the tip, whereas *C. enoplos* and *Cosmochilus harmandi* have flat spatula-like teeth (Pasco-Viel *et al.* 2010).

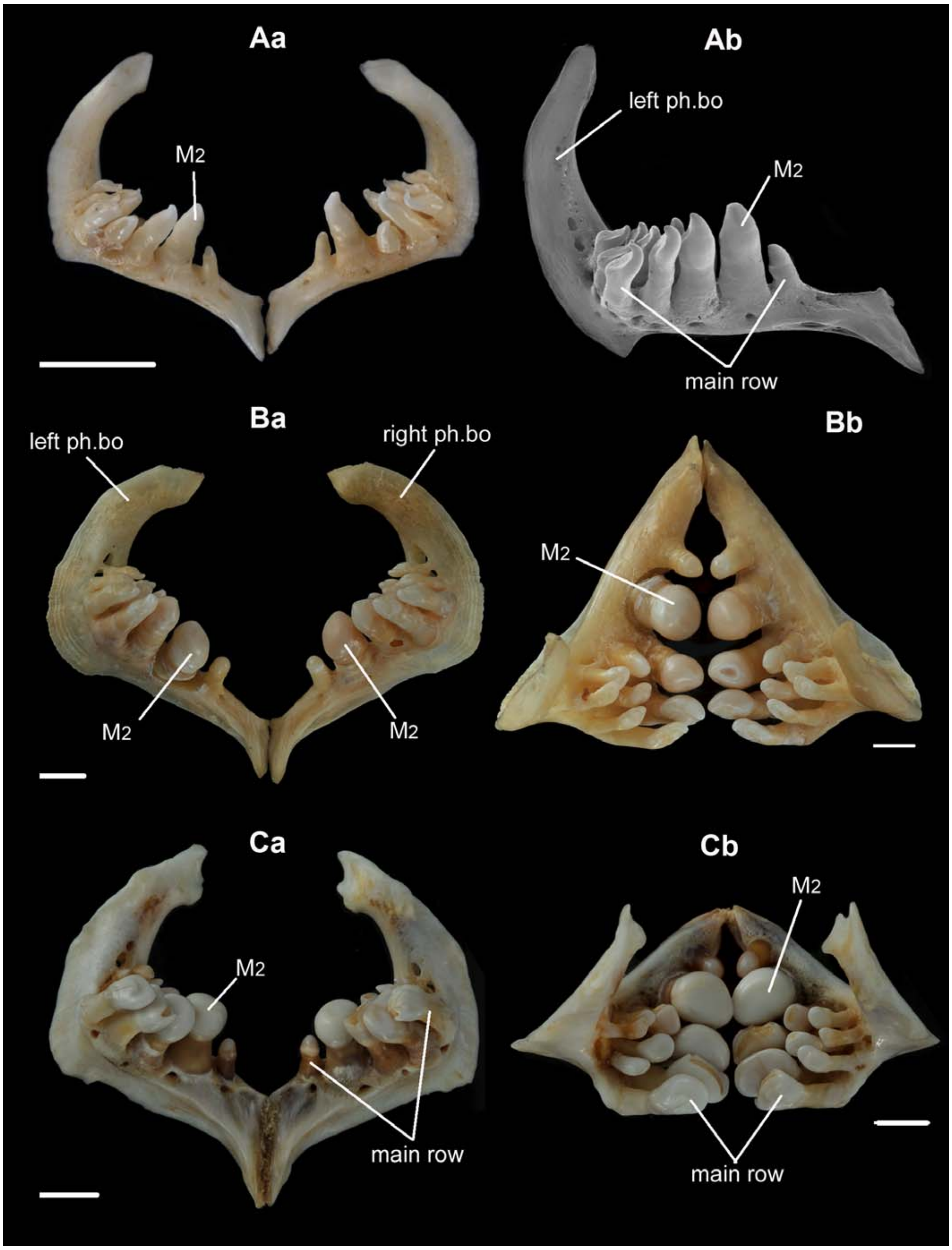

FIGURE 4. Pharyngeal bones. (A) *Cyclocheilichthys armatus*, MNHN 2012-0010. (a) Internal posterior view. (b) View of the left pharyngeal bone by scanning electron microscopy. (B) *Cyclocheilichthys enoplos*, MNHN 2012-0013. (a) Internal posterior view. (b) Dorsal view. (C) *Cosmochilus harmandi*, MNHN 2004-0163. (a) Internal posterior view. b) Dorsal view. Abbreviations identified in Appendix I. Scales bars = 5 mm.

1.3 Neurocranium

Several characters of the neurocranium allow *C. enoplos* to be distinguished from *C. armatus* and make *C. enoplos* closer to *Cosmochilus harmandi* and *Puntioplites falcifer.*

1) The supratemporal commissure (st.com), linking the two supratemporal sensory canals, is located at the border between the frontals (Fr) and parietals (Pa) in *C. armatus* whereas, as in most Cyprininae, it is located in the posterior part of the parietals in *C. enoplos*, *Cosmochilus harmandi* and *Puntioplites falcifer* (Fig. 5). This commissure represents the limit of insertion of the hypaxial muscles. The position of this commissure in *C. armatus* is more anterior on the cranial roof, reaching the orbit (Fig. 6), than in *C. enoplos*, *Cosmochilus harmandi* and *Puntioplites falcifer*, which explains the difference in extension of dorsal scales to the head (cf. External characters).

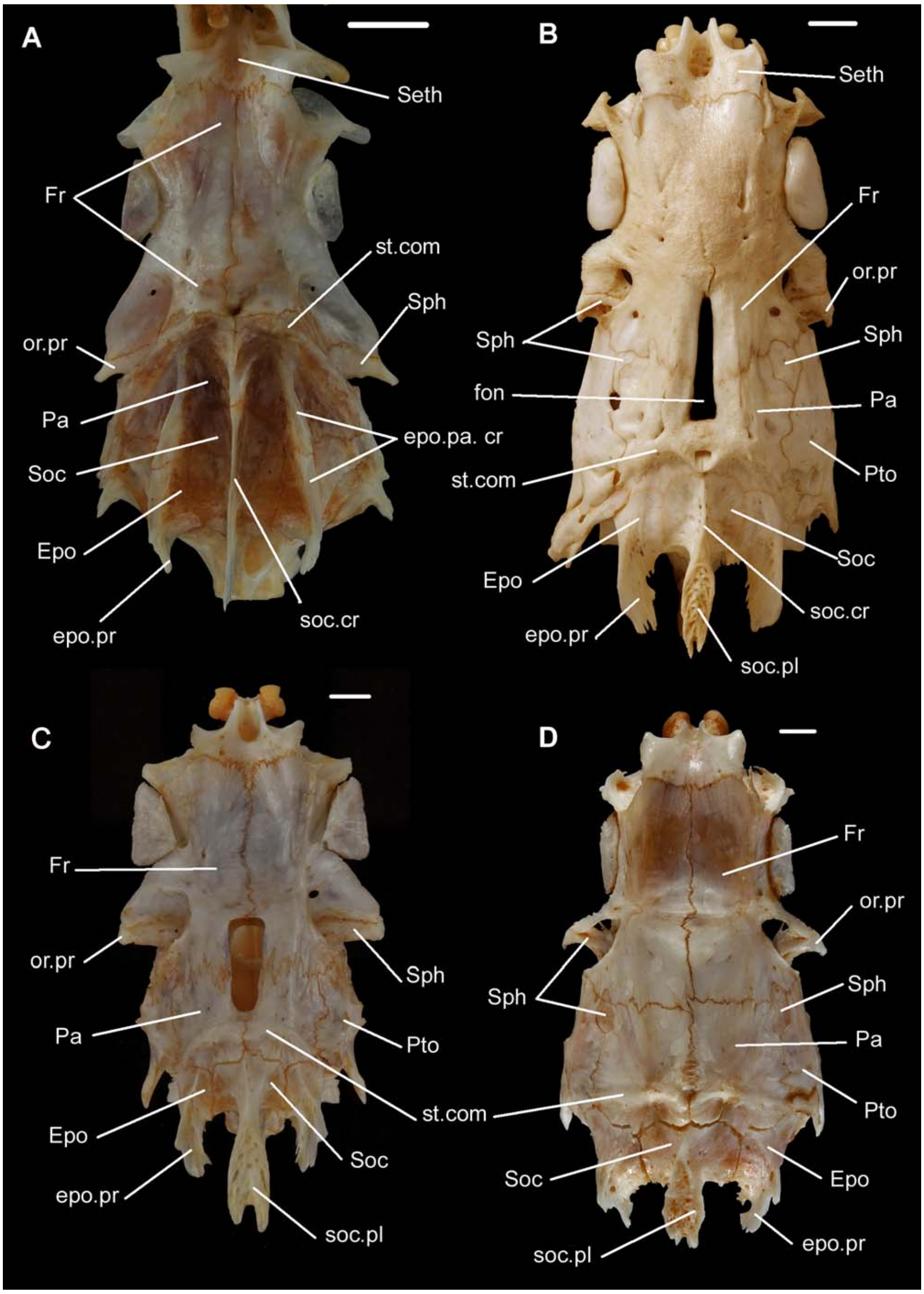

FIGURE 5. Dorsal views of the neurocranium: (A) *Cyclocheilichthys armatus*, MNHN 2012-0010; (B) *Cyclocheilichthys enoplos*, AMNH 217136; (C) *Puntioplites falcifer*, MNHN 2012-0015. (D) *Cosmochilus harmandi*, MNHN 2004-0163. Abbreviations identified in Appendix I. Scale bars = 5 mm.

2) There is a frontoparietal fontanelle (fon) in *C. enoplos* and *Puntioplites falcifer*, which is absent in *C. armatus* (Fig. 5).

3) In *C. armatus*, as in most Cyprinidae, sphenotics (Sph) are covered by bones of the cranial roof, and are thus dorsally visible only in the posterior indentation of the frontals (Fr), participating in the formation of the orbital processes (or.pr). However, in *C. enoplos* and *Cosmochilus harmandi*, sphenotics (Sph) are also visible on the cranial roof, between the frontals (Fr), the parietals (Pa) and the pterotics (Pto) (Fig. 5).

4) The supraoccipital crest (soc.cr) is very thin on all its surface in *C. armatus* and it is formed by both the supraoccipital (Soc) and the parietals (Pa), whereas in *C. enoplos*, *Cosmochilus harmandi* and *Puntioplites falcifer*, the supraoccipital crest, located only on the supraoccipital, is thicker on its dorsal edge, forming a plate (soc.pl), with a notch on its posterior end, in which fits the neural complex (ne.comp) (Fig. 5).

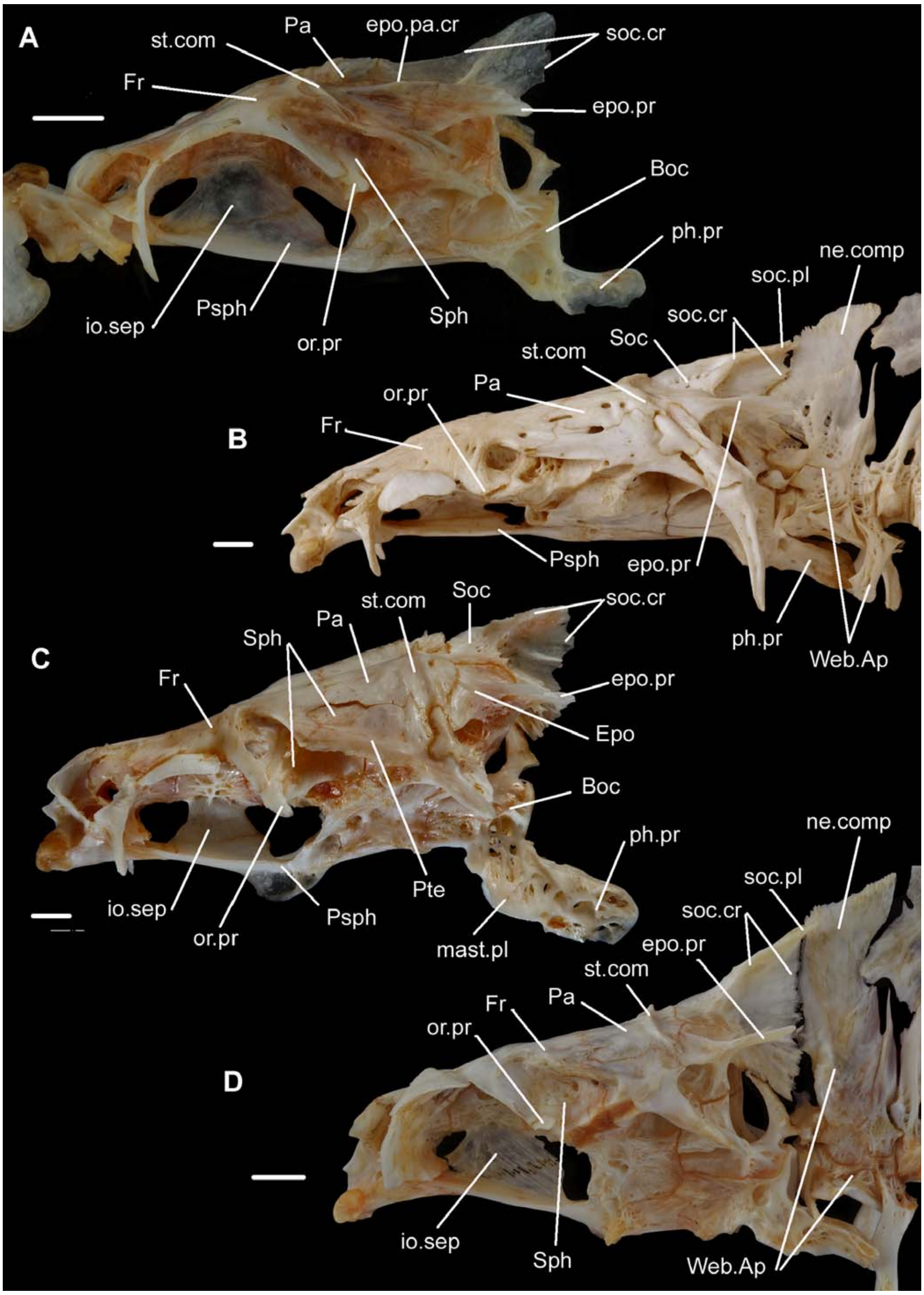

FIGURE 6. Lateral views of the neurocranium: (A) *Cyclocheilichthys armatus*, MNHN 2012-0010; (B) *Cyclocheilichthys enoplos*, AMNH 217136; (C) *Cosmochilus harmandi*, MNHN 2004-0163; (D) *Puntioplites falcifer*, MNHN 2012-0015. Abbreviations identified in Appendix I. Scale bars = 5 mm.

5) Epiotic processes (epo.pr) are large and well-developed posteriorly in *C. enoplos*, *Cosmochilus harmandi* and *Puntioplites falcifer,* whereas they are thin and short in *C. armatus*. Moreover, as for the supraoccipital crest, crests of the epiotic processes in *C. armatus* are extended to the parietals (Pa) forming long epiotico-parietal crests (epo.pa.cr) (Fig. 5).

6) Subtemporal fossae (sub.f), in which are inserted the *levator posterior* muscles of the pharyngeal bones, open ventrally between the prootics (Prot), pterotics (Pto) and exoccipitals (Exoc). These ventral openings are small and circular in *C. armatus*, whereas they are larger and with an oval shape in *C. enoplos*, *Cosmochilus harmandi* and *Puntioplites falcifer* (Fig. 7).

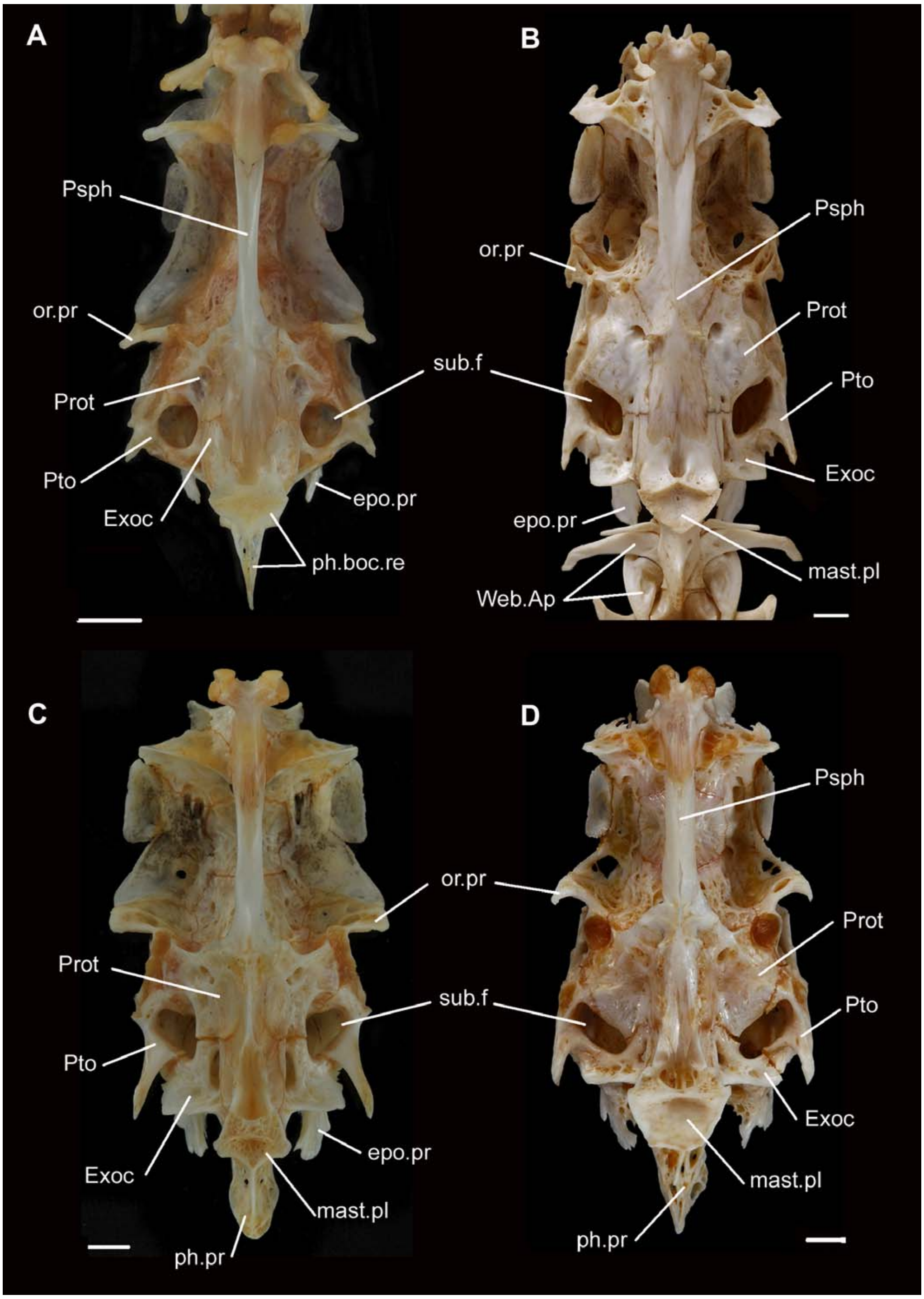

FIGURE 7. Ventral views of the neurocranium : (A) *Cyclocheilichthys armatus*, MNHN 2012-0010; (B) *Cyclocheilichthys enoplos*, AMNH 217136; (C) *Puntioplites falcifer*, MNHN 2012-0015. (D) *Cosmochilus harmandi*, MNHN 2004-0163. Abbreviations identified in Appendix I. Scale bars = 5 mm.

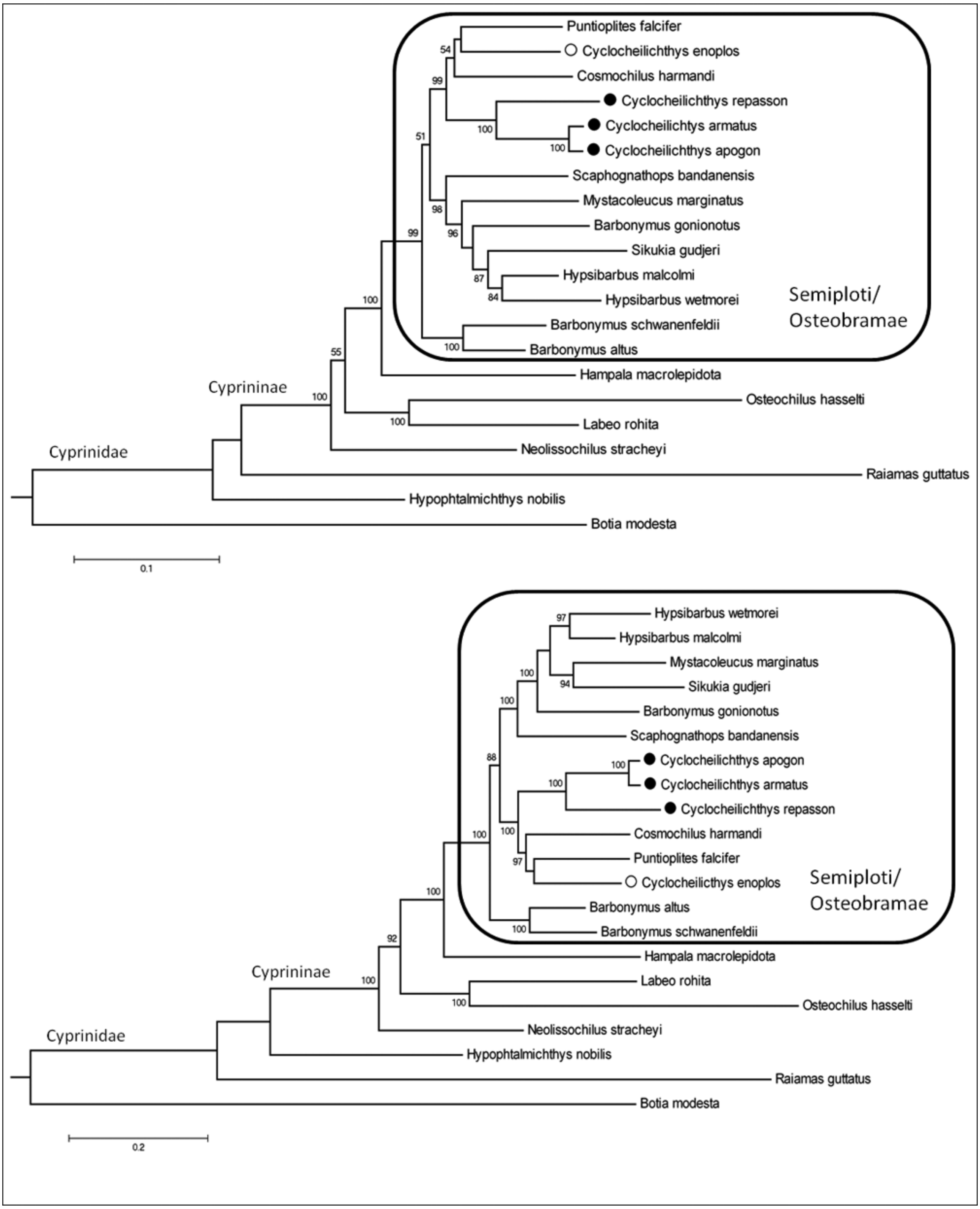

FIGURE 8. Phylogenetic trees including genera *Cyclocheilichthys*, *Cosmochilus* and *Puntioplites*. Upper: Maximum Likelihood analysis with bootstrap values indicated only if higher than 50%. Lower: Bayesian analysis with posterior probabilities indicated only if higher than 85%. *Botia modesta*, a cobitid species, was the outgroup. All other species are Cyprinoidea and all except *Raiamas guttatus* (a Rasborinae) and *Hypophthalmichthys nobilis* (a Leuciscinae) are Cyprininae species. Species within the grey rectangle represent the monophyletic group Semiploti/Osteobramae. Other species of Cyprininae represent the clades Tores, Labeonini and Systomi. Species formerly included in the genus *Cyclocheilichthys* are represented by circles. The difference in circle colors points out the non-monophyly of this genus. Species of the genus *Cyclocheilichthys* with black circles on this figure are assigned to the genus *Anematichthys*.

2. Phylogenetic studies

The phylogenies obtained (Fig. 8) by Maximum Likelihood and Bayesian methods first confirm the monophyly of the sub-family Cyprininae. Among Cyprininae, the first clade which diverges is the genus *Neolissochilus* which represents the subtribe Tores. Then, the second divergent clade is the tribe Labeonini represented in this analysis by genera *Labeo* and *Osteochilus*. The third divergent clade is the genus *Hampala*, which represents the subtribe Systomi. Finally, all other species in this analysis form a monophyletic clade. All of these species are members of the Semiploti and Osteobramae clades according to Rainboth (1996). Among this clade, *Barbonymus altus* and *B. scwhanenfeldii* form a monophyletic group that diverges early from all other species. Then, two monophyletic clades appear: one including genera *Cyclocheilichthys*, *Puntioplites* and *Cosmochilus*; another including genera *Scaphognathops*, *Mystacoleucus*, *Sikukia*, *Hypsibarbus*, as well as *Barbonymus gonionotus*.

Phylogenetic analyses unambiguously show the non-monophyly of the genus *Cyclocheilichtys* as *C. enoplos* is closer to *Puntioplites falcifer* and *Cosmochilus harmandi* whereas other species of *Cyclocheilichthys* included in this study form a monophyletic group. For convenience, we will refer to the group including *Cosmochilus harmandi*, *Puntioplites falcifer* and *Cyclocheilichthys enoplos* as the "*Cosmochilus* group". Thus, *C. armatus*, *C. apogon* and *C. repasson* form a monophyletic group that is the sister-group of the *Cosmochilus* group.

Even if bootstrap values are low for some branches in both analyses among the monophyletic clade Osteobramae/Semiploti, there are at least significant values to consider that *Cyclocheilichthys* is not currently a monophyletic genus, with *C. enoplos* being part of the *Cosmochilus* group whereas *C. armatus*, *C. apogon* and *C. repasson* form a monophyletic group.

Discussion

Splitting the genus *Cyclocheilichthys* (Bleeker 1859) into *Cyclocheilichthys* and *Anematichthys* (Bleeker 1859) for *Anematichthys armatus*, *Anematichthys apogon* and Ane*matichthys repasson*

The genus *Cyclocheilichthys* is formally cited first by Bleeker (1859) with the type species being *C. enoplos*. However, some species currently belonging to this genus were described earlier and assigned to the genus *Puntius*: *Puntius enoplos* (Bleeker 1849), *Puntius armatus* and *Puntius apogon* (Cuvier & Valenciennes 1842), *Puntius repasson* (Bleeker 1853). Kottelat (1999) investigated the origin of the genus *Cyclocheilichthys* and found a first citation by Bleeker (1859). Interestingly, Bleeker (1859) created two genera in the same publication: *Cyclocheilichthys*, with the type species *C. enoplos*, and *Anematichthys* with the type species being *A. apogon*—now named *C. apogon*. These two names were considered to be objective synonyms by Kottelat (1999). However, he found that in Bleeker (1859), *Cyclocheilichthys* was first cited as a genus and *Anematichthys* as a subgenus, hence the conclusion that *Cyclocheilichthys* has the priority to be used as the valid genus name. Roberts (1989) grouped former species of *Cyclocheilichthys* and *Anematichthys* under the same genus name – *Cyclocheilichthys*. However, he pointed out that *C. armatus*, *C. apogon* and *C. repasson* were closely related, whereas *C. enoplos* appeared very distinct. The only character used in keys to determine the genus *Cyclocheilichthys* is the high number of parallel rows of pores (Rainboth 1996, Kottelat 2001). However, this character is not present in *C. enoplos*, as shown above.

Our results show that there are both morphological and phylogenetic arguments to split the genus *Cyclocheilichthys* into two groups: one including *C. enoplos* and the other including *C. armatus*, *C. apogon* and *C. repasson*. As *C. enoplos* is closer to *Puntioplites* and *Cosmochilus* than to the other cited species of *Cyclocheilichthys*, it is necessary to give a new genus name, either for *C. enoplos* or for the three other species of *Cyclocheilichthys*. Considering that *C. enoplos* is the type species for the genus *Cyclocheilichthys* and that the genus name *Anematichthys* is still available and that the species type for this genus is *C. apogon*, we propose that *C. armatus*, *C. apogon* and *C. repasson* should be named *Anematichthys armatus*, *A. apogon* and *A. repasson*.

Other species of *Cyclocheilichthys* were not included in the present study. Concerning those other species, we can at least state that *C. furcatus*, considering its resemblance with *C. enoplos* (Roberts 1989, Kottelat 2001), should remain in the genus *Cyclocheilichthys*. However, further investigation will be needed for other species currently assigned to the genus *Cyclocheilichthys*.

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APPENDIX I: Abbreviations used in Figures 3–7

Boc	basioccipital
Epo	epiotic
epo.pr	epiotic process
epo.pa.cr	epiotico-parietal crest
Exoc	exoccipital
fon	fontanelle
Fr	frontal
Iorb	infraorbital
io.sep	interorbital septum
left ph.bo	left pharyngeal bone
M2	second dental position on the main row
mast.pl	masticatory plate
ne.comp	neural complex
op.f	optic foramen
or.pr	orbital process
Pa	parietal
ph.pr	pharyngeal process of basioccipital
ple.ri 1	pleural rib 1
Prot	prootic
Psph	parasphenoid
Ptery 1	pterygiophore 1 of dorsal fin
Pto	pterotic
right ph.bo	right pharyngeal bone
Seth	supraethmoid
Sne	supraneural
Soc	supraoccipital
soc.cr	supraoccipital crest
soc.pl	supraoccipital plate of supraoccipital crest
Sph	sphenotic
Sor	supraorbital
sub.f	subtemporal fossae
st.com	supratemporal commissure
Web.Ap	Weberian Apparatus