Universidade Estadual de Londrina

GUSTAVO WILLAMOWIUS VITURI

EVOLUÇÃO DO TAMANHO DO CORPO E COMPORTAMENTO ‘HEAD-STAND’ NA SUPERFAMÍLIA NEOTROPICAL ANOSTOMOIDEA (OSTARIOPHYSI:CHARACIFORMES)

Londrina
2019

Programa de Pós-Graduação
Ciências Biológicas

CAPES

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Dissertação apresentada ao Programa de Pós-Graduação em Ciências Biológicas da Universidade Estadual de Londrina, como requisito parcial à obtenção do título de Mestre em Ciências Biológicas (Biodiversidade e Conservação de Habitats Fragmentados).

Orientador: Prof. Dr. José Luís Olivan Birindelli
Co-Orientador: Prof. Dr. Oscar Akio Shibatta

Londrina
2019

Ficha de identificação da obra elaborada pelo autor, através do Programa de Geração Automática do Sistema de Bibliotecas da UEL

Vituri, Gustavo Willamowius.
Evolução do Tamanho do Corpo e Comportamento 'Head-stand' na Superfamília Neotropical Anostomoidea (Ostariophysi:Characiformes) / Gustavo Willamowius Vituri. - Londrina, 2019.
53 f. : il.

Orientador: José Luís Olivan Birindelli.
Coorientador: Oscar Akio Shibatta.
Dissertação (Mestrado em Ciências Biológicas) - Universidade Estadual de Londrina, Centro de Ciências Biológicas, Programa de Pós-Graduação em Ciências Biológicas, 2019.
Inclui bibliografia.

1. Macroevolução - Tese. 2. Characiformes - Tese. 3. Tamanho do corpo - Tese. 4. Comportamento - Tese. I. Birindelli, José Luís Olivan. II. Shibatta, Oscar Akio. III. Universidade Estadual de Londrina. Centro de Ciências Biológicas. Programa de Pós-Graduação em Ciências Biológicas. IV. Título.

Universidade
Estadual de Londrina

201711510042

CENTRO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

DEFESA DE DISSERTAÇÃO DE MESTRADO

Discente: Gustavo Willamowius Vituri

Título: Evolução do tamanho do corpo e comportamento ‘head-stand na Superfamília Neotropical Anostomoidea (Ostariophysi:Characiformes)

Data da Defesa: 26 de Fevereiro de 2019 – 14:00 hs, na sala do Centro de Ciências Biológicas n° 10 da Universidade Estadual de Londrina.

Banca Examinadora		**Parecer**
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AGRADECIMENTOS

Ao meu orientador Prof. José Luís Olivan Birindelli e Co-Orientador Prof. Oscar Akio Shibatta por me inserirem no meio da ictiologia, demonstrando suas interconexões com as demais áreas da biologia. Ao Prof. Birindelli que me orientou de maneira empática e serena, provendo suporte e atenção em momentos difíceis e frente a obstáculos que me pareciam insuperáveis.

Ao Gabriel Rosa e Lenice Souza Shibatta pela incalculável ajuda na superação de obstáculos encontrados ao longo do desenvolvimento do trabalho nos tópicos de Estatísticas e Filogenia Molecular respectivamente.

Aos Profs. Ana Paula Magnoni, Brian Sidlauskas, Cristiano Moreira, Fernando Camargo Jerep, Marcos Robalinho Lima e Gabriel Silva, pelas correções e sugestões apresentadas durante as banca de qualificação e defesa assim como durante a fase inicial do presente trabalho.

A CAPES pela bolsa de mestrado usufruída. Ao CNPQ por fornecer auxílios que indiretamente ajudaram na construção do presente estudo (número do processo 420255/2016-8, JLOB).

Aos meus pais e família pelo apoio e confiança em mim depositados e por possibilitarem minha entrada e permanência na universidade.

A Ana Flávia Gonçalves de Campos pela companhia durante os altos e baixos experimentados durante a graduação; por toda ajuda e apoio cedidos de bom grado.

E a todos que participaram direta ou indiretamente do presente estudo, assim como da minha vida acadêmica, incluindo os colegas de programa de Pós-Graduação, os colegas e técnicos do laboratório.

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RESUMO

O tamanho do corpo é um caráter importante para a ecologia das espécies e está ligado ao comportamento, anatomia e fisiologia. O comportamento headstand, que consiste no peixe manter a cabeça voltada para baixo e o corpo em um ângulo de aproximadamente 45º em relação ao substrato, não é bem explorado em Anostomoidea (Characiformes), diferentemente de outras ordens de peixes que apresentam este comportamento. Para estudar a evolução do comportamento headstand e do tamanho do corpo e a relação entre ambos, foram utilizados uma árvore filogenética resultante de análise Bayesiana e dados de comprimento padrão máximo e presença do comportamendo headstand de 266 espécies de Anostomoidea. A distribuição de classes de tamanho do corpo e estatísticas exploratórias mostraram grande diversidade de tamanhos de corpo em Anostomoidea, assim como uma associação entre a riqueza das famílias e a diversidade de tamanhos do corpo. O teste do λ de Pagel confirmou o sinal filogenético do tamanho do corpo (λ = 0,886). Nenhuma tendência geral do tamanho do corpo foi encontrada para toda Anostomoidea com o mapeamento de caráter contínuo e reconstrução do estado ancestral de caráter. O comportamento headstand surgiu independentemente três vezes ao longo da evolução de Anostomoidea e apresenta sinal filogenético, de acordo com o teste D de Fritz e Purvis (D = -1,04). Testes T filogenéticos evidenciaram igualdade entre o tamanho do corpo dos headstanders de Chilodontidae e Anostomidae (p-valor = 0,615) e diferença entre headstanders e não headstanders (p-valor = 0,0032). É possível que o comportamento headstand, conciliado a modificações morfológicas, evoluiu como uma resposta a necessidades ecológicas causadas por mudanças para tamanhos menores de corpo.

Palavras-chave: Comprimento padrão. Comportamento. Macroevolução. Tamanho do corpo.

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ABSTRACT

Body size is an important character to the ecology of species, and it is linked to behavior, anatomy, and physiology. The headstand behavior, that consists in the fish pointing its head down and maintaining its body in a 45º angle with the substrate, is not well explored in Anostomoidea (Characiformes), unlike the other fish orders that present it. To study the evolution of headstand behavior, body size and the relation between both, we used a phylogenetic tree resultant of Bayesian analysis and data for maximum standard length and headstand behavior presence for 266 Anostomoidea species. Body size class distribution and summary statistics showed great body size diversity in Anostomoidea and an association between family richness and body size diversity. Pagels λ test confirmed the phylogenetic signal of body size (λ = 0.886). No general body size trend for Anostomoidea was found with continuous character mapping and ancestral character state reconstruction. Headstand behavior evolved three independent times throughout the evolution of Anostomoidea and presented phylogenetic signal, according to Fritz and Purvis’ D test (D = -1.04). Phylogenetic T-tests evidenced body size equality among Chilodontidae and Anostomidae headstanders (p-valor = 0.615) and difference between headstanders and non-headstanders (p-valor = 0,0032). It is possible that the headstand behavior, along with morphological modification, evolved in response to new ecological needs caused by body size shifting to smaller sizes.

Keywords: Behavior. Body size. Macroevolution. Standard length.

LISTA DE ABREVIATURAS

MLS	Maximum standard Length
PDB	Phylogenetic data block
sd	Standard deviation
TDB	Total data Block

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INTRODUCTION

Headstand behavior in fishes consists in the animal assuming an inclined position, head downwards, at an angle of approximately 45º with the substrate (Géry, 1997; Vari & Williams, 1987; Winterbottom 1980). This behavior is found in other freshwater fish orders, such as in *Xiphophorus nezahualcoyotl* Rauchenberger, Kallman & Morizot 1990 (Ciprinodontiformes: Poeciliidae), which the male presents the headstand behavior as an agonistic response to other males presence or performing the female courtship (Lyons & Morris, 2008). Also, as an agonistic response, the headstand behavior is expressed in territory defense in *Chromidotilapia guntheri* (Sauvage, 1882) (Perciformes: Cichlidae) (Myrberg Jr., 1965). In *Micropterus salmoides* Lacépède, 1802 and *Lepomis macrochirus* Rafinesque, 1919 (Centrarchiformes: Centrarchidae) the headstand behavior is used to accomplish interspecific signaling. In this case, *M. salmoides and L. macrochirus* assume headstanding pose while stationary, signaling to small cleaning fishes their availability to be cleaned (Sulak,1975).

In the Characiformes order, the headstand behavior is exclusive to small fishes from Anostomoidea, belonging to Chilodontidae and members of Anostomidae (Anostominae and *Abramites*) (Géry, 1997; Vari & Williams, 1987; Winterbottom, 1980). These fishes are popularly known as headstanders, and unlike the other cited fish orders, there are no behavioral studies focusing on the understanding of the headstanding behavior in Anostomoidea. This lack of scientific literature is only partially counteracted by seldom published information that generalizes the headstand behavior presence for genera or even for the entire family as well as speculates about its origins, biological and ecological functions.

For Anostomidae headstanders it is proposed that the behavior is expressed while resting (Vari & Williams, 1987) or feeding (Géry, 1977; Santos & Rosa, 1998) and that it is linked to feeding strategies (Géry, 1977) or morphological traits linked to feeding, such as mouth position (Winterbottom, 1980). On the other hand, Chilodontidae headstanders are supposed to express the behavior while swimming (Géry, 1977) or while swimming and resting, and it is apparently linked to anatomical modifications in the axial skeleton, anterior ribs and associated ligamentous tissues (Vari et al., 1995). Studies have yet to explore the link between the occurrence of headstand behavior in Anostomidae and Chilodontidae, but it is presumed to be due to convergence caused by similar evolutionary ecological pressure and not to phylogenetic proximity (Géry, 1977).

Behavioral traits usually have a lower phylogenetic signal (Blomberg et al., 2003), and its distribution across taxa will often not correlate with the topology of the phylogenetic tree (Freckleton et al., 2002). Conversely, body size is a character known to have strong phylogenetic signal, ensuring that phylogenetically related species will have a similar body size (Blomberg et al., 2003; Felsenstein, 1985; Havey & Pagel, 1991).

Body size is of great importance in animal ecology (Brown et al., 1993; Cardillo et al., 2005) once it is correlated with physiology, species interaction, life history and species biomechanics (Peters, 1986) and especially with diet and feeding (Romanuk, 2011). However, only recently this character has been a frequent target in fish studies. For example, the association between body size and ecological traits such as migratory behavior and trophic position (Bloom et al., 2018). Another example is exploring body size frequency and phylogenetic gradients as well as the tendency of groups to a body size optima (Steele & López-Fernández, 2014).

Some studies have shown that on an evolutionary scale, body size reduction in freshwater fishes is a common phenomenon (Bennett & Conway, 2010; Griffiths, 2012; Lavoué et al., 2010). Body size shifting to extreme values at the course of evolution can lead to changes in anatomy, physiology, and behavior of the species, especially in the case of body size reductions, given the relevance that the character has to the ecology of fish species ecology (Griffiths, 1986; Hanken & Wake, 1993).

In the present study, we explore the phylogenetic distribution of body size in the Neotropical freshwater superfamily Anostomoidea by looking for a correlation between the phylogeny topology and the character distribution among Anostomoidea species. Furthermore, we investigate the character mapping and ancestral state reconstruction looking for body size tendencies in major clades. We also aim to bring light to the headstand topic for Anostomoidea by studying the emergence of the character within the superfamily, testing if this complex behavior evolved independently in Anostominae, *Abramites,* and Chilodontidae, as proposed by Géry (1977). Moreover, the study intends to determine if body size is linked to the presence of headstand behavior since Anostomoidea headstanders appears to have relatively small body sizes.

MATERIAL E METHODS

Anostomoidea phylogenetic reconstruction

No ultrametric phylogenetic tree file containing branch lengths for all Anostomoidea was found in the literature. Therefore, the present study collected molecular sequence data of three mitochondrial genes (16s, COI and Cytb) and three nuclear genes (Myh6, Rag1, and Rag2) from stored data in GenBank online database.

Altogether, the six genes summed 165 Anostomoidea species belonging to 23 of all 28 genera contemplated by the superfamily, each gene presenting a specific number of species (Table 1). Data for six outgroups species belonging to Parodontidae, Characidae and Serrassalmidae, were sampled from Genbank. The outgroup species were chosen based on the most recent literature for Anostomidae (Melo, 2015), Chilodontidae (Melo et al., 2014), Curimatidae (Melo et al., 2018) and Prochilodontidae (Frable et al., 2016) phylogenetic trees.

Table 1. Summary information for sequence matrices used in the present study.

Genes matrices	Species	Length (bp)	BMNSE
16s	139	614	GTR+I+G
COI	158	635	TrN+I+G
Cytb	160	1019	GTR+I+G
Myh6	152	741	TIM+I+G
Rag1	154	1454	TIM2ef+I+G
Rag2	132	1001	TrNef+I+G

Species number, total length of sequence and model of nucleotide sequence evolution presented for each gene matrix used in the Bayesian analysis. BMNSE: Best model of nucleotide sequence evolution using Bayesian Information Criterion (BIC), JModelTest 2.

Sequences were aligned using Muscle extension in Mega 7 followed by the trimming of the sequences endings. For this study the sequence of only one individual was used for each species contained in each gene matrix; the criterion for selection was how complete the sequence was. All the other individuals with less complete sequences were discarded.

The best model of nucleotide sequence evolution was obtained for each gene matrix using Bayesian information criterion (BIC) with JModelTest2 (Table 1) offered in CIPRES Science Gateway in XSEDE. All six genes matrices were imported separately to Beauti2, and each model of nucleotide sequence evolution was attributed to the respective gene matrix. Yule model was used as the tree prior, and Relaxed Clock Log Normal was used as clock model for all gene's matrices. The resulting .xml file from Beauti2 was used to run the Bayesian analysis using Beast2. The analyses ran for 100 million generations, sampling every 10000th generation.

Tracer 1.7.1 was used to verify the effectiveness of sample size on achieved results, obtaining a score equal or higher than 200 in all parameters and establishing a 10% burn-in (1000 trees). Maximum credibility tree was generated using TreeAnotator2, and posterior probability support values were added with Figtree.

Comparing the phylogenetic tree obtained with the most recent phylogenetic super-tree for Anostomoidea was used as an acceptance criterion. To create the super-tree, all the most recent phylogenetic trees for Anostomidae (Melo, 2015), Chilodontidae (Melo et al., 2014), Curimatidae (Melo et al., 2018) and Prochilodontidae (Frable et al., 2016), as well as for the relationship between families (Melo, 2015). To compare both trees, a tanglegram was made using the Dendextend package in Rstudio, showing share branches, unique branches and respective species position in both trees. The construction of the supertree was made using Mesquite software, importing all the species used by each literature and reconstructing the topology of the tree by hand with the branch manipulation tools.

Data sampling

Maximum standard length (SL) was chosen to represent species body size, following other studies (Fu et al., 2004; Steele & Lopez-Fernández, 2014). Data for maximum standard length were obtained for 266 species from species descriptions, taxonomic revisions, and other published scientific material. Museum material was eventually analyzed, and the specimens and lots cited. Data for the presence of the headstanding behavior were searched in the literature (Géry, 1977; Winterbottom, 1980; Vari et al., 1995) for all used species. The presence of the headstanding behavior was extended to congeners when information was unavailable for each congener species. All data for 266 Anostomoidea species and outgroups species on maximum standard length and headstanding behavior presence were compiled, and species used for Anostomoidea phylogenetic reconstruction were highlighted (S1 Table). Different analyses were conducted with the data for the entirety of 266 Anostomoidea species, denominated full data block (FDB), and the 161 species used for the phylogenetic reconstruction, denominated phylogenetic data block (PDB).

Statistical Analyses

Since FDB contemplates a more representative data for Anostomoidea and contemplates all species of PDB, it was used for summary statistics (mean, median, standard deviation, first and third quartile), considering all genera as monophyletic groups. This data block was also used to study the occupation of body size classes for all four families contained in Anostomoidea. The square root criterion was chosen to determine the number and range of classes. This criterion was selected once it generates a greater number of classes when compared to Sturges rule and the inequality criterion.

Phylogenetic signal testing was conducted for body size and headstand behavior using PDB. Pagel's Lambda test was applied to the continuous trait (maximum standard length) since it is specific for this type of data sets. The presentation of a λ value close to 0 indicates a weak or inexistent phylogenetic signal, while results close to 1 indicates a strong phylogenetic signal (Fleckleton et al., 2002). For headstand behavior presence, Fritz and Purvis' D test was used. This test is specific to binary characters, such as headstand behavior. A character with a weak phylogenetic signal will present a D value close to or greater than 1, on the other hand, a character with the strong phylogenetic signal is found when D is close to or less than 0 (Fritz & Purvis 2010).

Continuous character mapping and ancestral character state reconstruction were performed using contMap function from Phytools package in Rstudio with log-transformed standard length data. Parsimony analysis was used to track the headstand behavior presence and absence for internal branches of the phylogeny, therefore testing the hypothesis of independent evolution of the character at Anostominae, *Abramites,* and Chilodontidae.

To determine if there is an association between body size and headstanding behavior, two-tailed phylogenetic T-tests were used to check for the statistically significant difference between maximum standard length means among headstanders and non-headstanders. Tests were conducted using Phytools package in Rstudio and the groups used for comparisons were: *Abramites* plus Anostominae (Anostomidae headstanders), other Anostomidae (Anostomidae non-headstanders), Chilodontidae, Curimatidae, and Prochilodontidae. Statistical difference test was also tested between all headstanders and all non-headstanders groups.

RESULTS

The Bayesian analysis resulted in a wholly resolved topology with 87.81% of posterior probability supports greater than 95% (Appendix 2). Results support the monophyly of Anostomidae, Chilodontidae, Curimatidae and Prochilodontidae and the phylogenetic relationship of (Anostomidae (Prochilodontidae (Chilodontidae, Curimatidae), composing Anostomoidea. From 23 genera, only four were presented as polyphyletic (*Curimatella*, *Cyphocharax*, *Hypomasticus,* and *Leporinus*).

Graphical comparison using Tanglegram shows the resemblance between the Bayesian analysis resulted tree and the most recent Anostomoidea super-tree (Figure 1). Families Chilodontidae and Prochilodontidae presented fewer dissimilarities, with few exclusive branches and corresponding subtrees with large species number. The Curimatidae family shown elevated numbers of exclusive branches for both trees but good similarities within small subtrees and Anostomidae exhibited the most disagreement between trees among the families.

Applying the square root criterion for FDB maximum standard length data, it was possible to recover 16 body size classes with a 30mm range each. Family maximum standard length values were then distributed into the given classes and presented graphically (Figure 2). Body size class distribution also demonstrated broader distributions in richer families. Combined with body size boxplots for each infra-family groups, body class distribution demonstrates the body size trend for each family. Chilodontidae and Curimatidae have distribution concentrated in small size classes while Prochilodontidae shows a distribution concentrated in higher size classes. On the other hand, the distribution of body size in Anostomidae covers the entire size classes, even though peaks in small and medium-size classes are present.

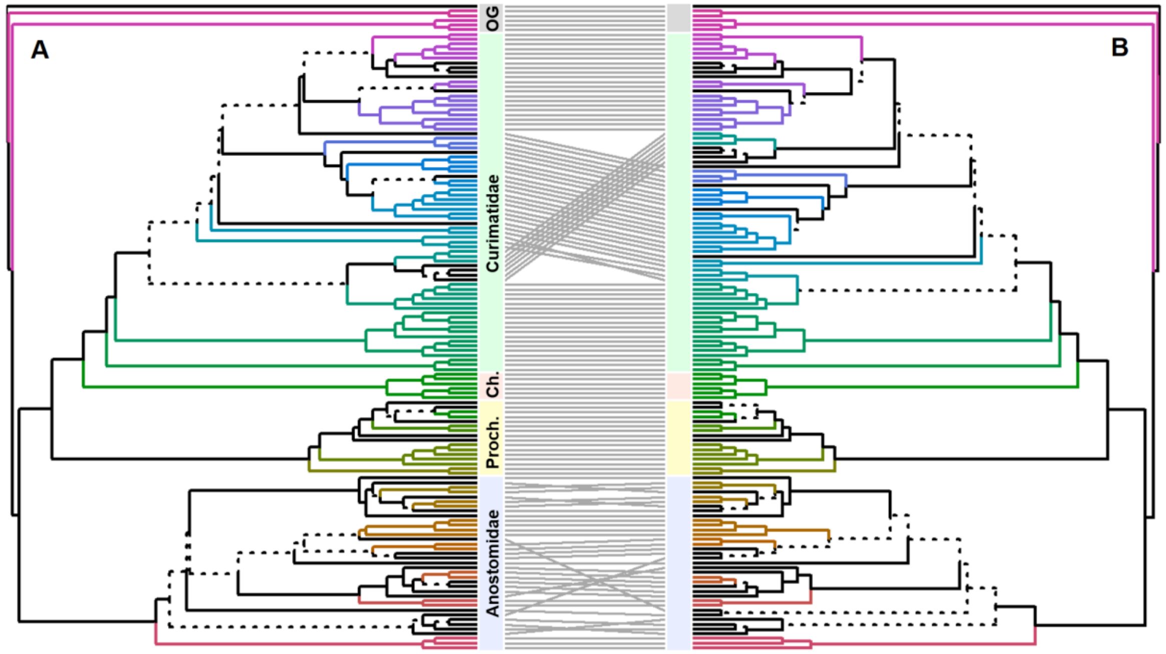

Figure 1. Anostomoidea Bayesian analysis tree and super-tree Tanglegram. Graphical comparison between Anostomoidea Bayesian analysis tree and super-tree generated with Dendextend Rstudio package. Colored lined represent identical sub-tress from both trees. Dashed lines denote a tree-exclusive branch. Black lines are common branches with divergent topology among trees. A: Anostomoidea Bayesian analysis resultant tree; B: Anostomoidea Super-tree from most recent literature; Proch.: Prochilodontidae; Ch.: Chilodontidae; OG: Outgroup species.

Phylogenetic signal tests performed for PDB data shown strong phylogenetic signal in maximum standard length character (λ = 0,886) and for headstand behavior presence (D = - 1,04). These results indicate that variations in body size between species included in the same infra-family groups are generally smaller than variations among species from different infra-family groups. It also represents a correlation between both characters' phylogenetic distribution and the topology of the phylogenetic tree.

Ancestral character state reconstruction results recovered were untransformed from $\log_{10}$, and continuous character mapping was expressed graphically (Figure 3). The value found for the node linking all Anostomoidea families was 163 mm of maximum standard length. For the node linking all the Anostomidae the value recovered was 180 mm, followed by a slight decrease in Anostominae and *Leporellus* groups. An increase in the internal nodes of the monophyletic group containing all other Anostomidae infra-familiar groups except Anostominae and *Leporellus* groups was also detected, especially in the basal nodes of *Megaleporinus* (222) and *Schizodon* (234 mm) groups.

For the node linking (Prochilodontidae (Chilodontidae, Curimatidae) a value of 157 mm was found, followed by an increase in Prochilodontidae basal node. All basal nodes in Prochilodontidae presented considerable increases: *Ichthyoelephas* basal node = 303 mm, *Semaprochilodus* basal node = 294 mm, *Prochilodus* basal node = 311 mm. A decrease was found in the node linking Chilodontidae and Curimatidae (143 mm) followed by further decreases in the Chilodontidae basal node (116 mm) and Curimatidae basal node (134 mm). In the Chilodontidae, a tiny increase was spotted in the *Caenotropus* basal node (120 mm) and a decrease in the *Chilodus* basal node (80 mm).

The Curimatidae presented increases of maximum standard length in all base nodes of the paraphyletic group formed by *Curimata* (basal node = 167 mm), *Potamorhina* (basal node = 196 mm), *Cyphocharax spilotus* group (basal node = 141 mm) and *Psectrogaster* (basal node = 164 mm) infra-familiar groups. For the remaining monophyletic group composed of *Pseudocurimata* (basal node = 130 mm), *Cyphocharax nigripinnis* group (basal node = 119 mm), *Cyphocharax multilineatus*, *Stendachnerina* (basal node = 114 mm) and *Cyphocharax* stricto sensu (basal node = 105 mm), all basal nodes values suffered decreases.

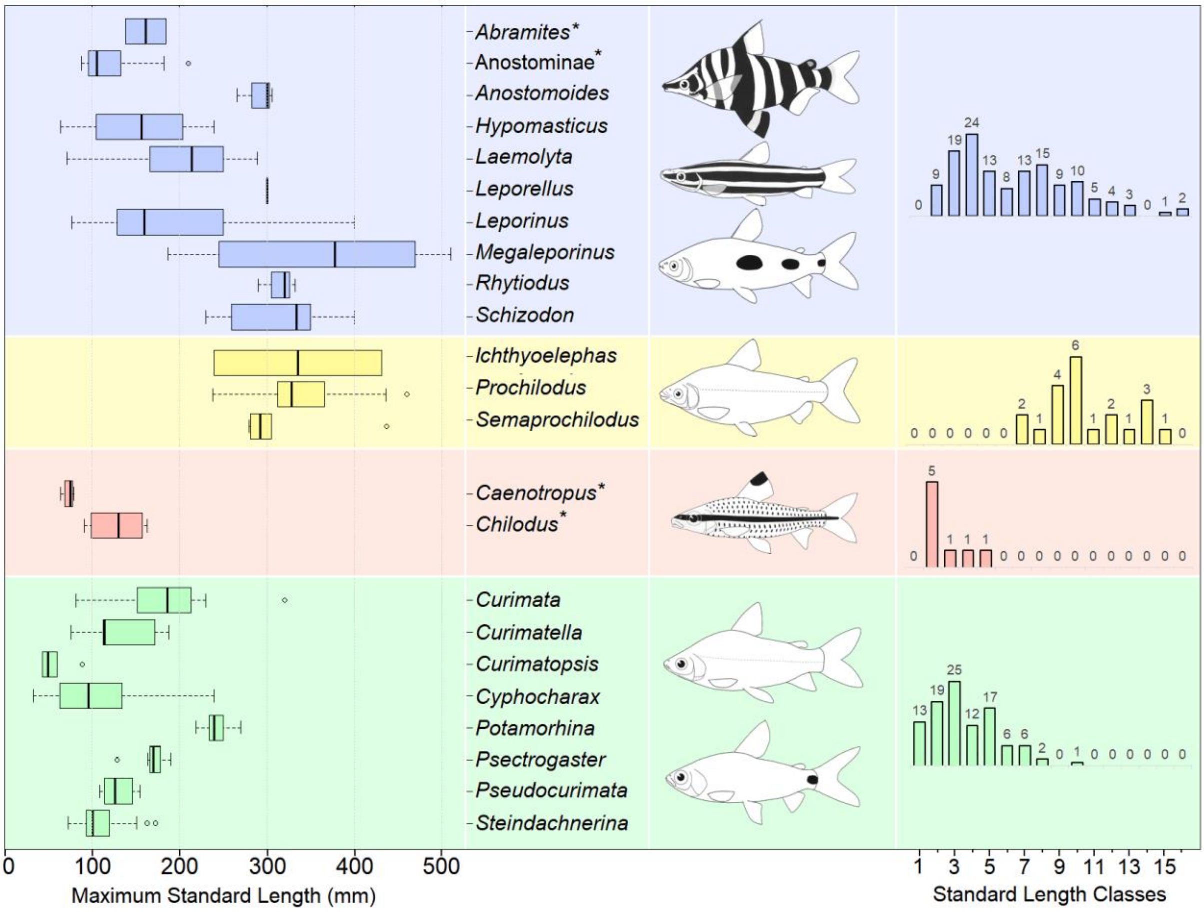

Figure 2. Anostomoidea body-size distribution among families and genera. Data from FDB. Anostomoidea infra-family body size distribution exhibited as individual boxplots. Anostomoidea families body-size class distribution exhibited as bars plot. Representatives of each family are given under each family name; illustrations not to scale. Presence of headstand behavior indicated with an asterisk next to infra-family group names. Boxplots distribution outliers indicated by individual dots on the left and right of each plot upper and lower limit. Number of species contained in each body size class indicated as numbers above bars.

Parsimony analysis showed that headstand behavior is absent in basal Anostomoidea and that it appears independently three times, one in Abramites, one in Anostominae and another in Chilodontidae, achieving the current phylogenetic distribution of the behavior in the Anostomoidea (Figure 3).

Phylogenetic mean comparison tests show that body size among Anostomidae headstanders (mean = 125.5 mm, sd = 26.7 mm) and Chilodontidae (mean = 100.8 mm, sd = 37.4 mm) are statistically similar (T-value = -0.519, p-value = 0.615). Statistical difference was found in all headstanders (mean = 109 mm, sd = 35.1 mm) versus all non-headstanders (mean = 203.5 mm, sd = 107.2 mm) comparison (T-value = -2.9835, p-value = 0.0032) and the less inclusive pairwise comparisons also found difference between Anostomidae headstanders and Prochilodontidae (mean = 333.8 mm, sd = 67.7 mm) (T-value = 4.9289, p-value=0.00005), Anostomidae headstanders and Anostomidae non-headstanders (mean = 252.4 mm, sd = 99.5 mm) (T-value = 3.1658, p-value = 0.0024), Chilodontidae and Prochilodontidae (T-value = 7.2371, p-value = <0.00001), Chilodontidae and Anostomidae non-headstanders (T-value = -5.176, p-value= <0.00001). No statistical difference was detected in the comparison between Chilodontidae and Curimatidae (mean = 131.6 mm, sd = 55.3 mm) (T-value = 1.0672, p-value = 0.289) and Anostomidae headstanders and Curimatidae (T-value = 0.1536, p-value=0.8783).

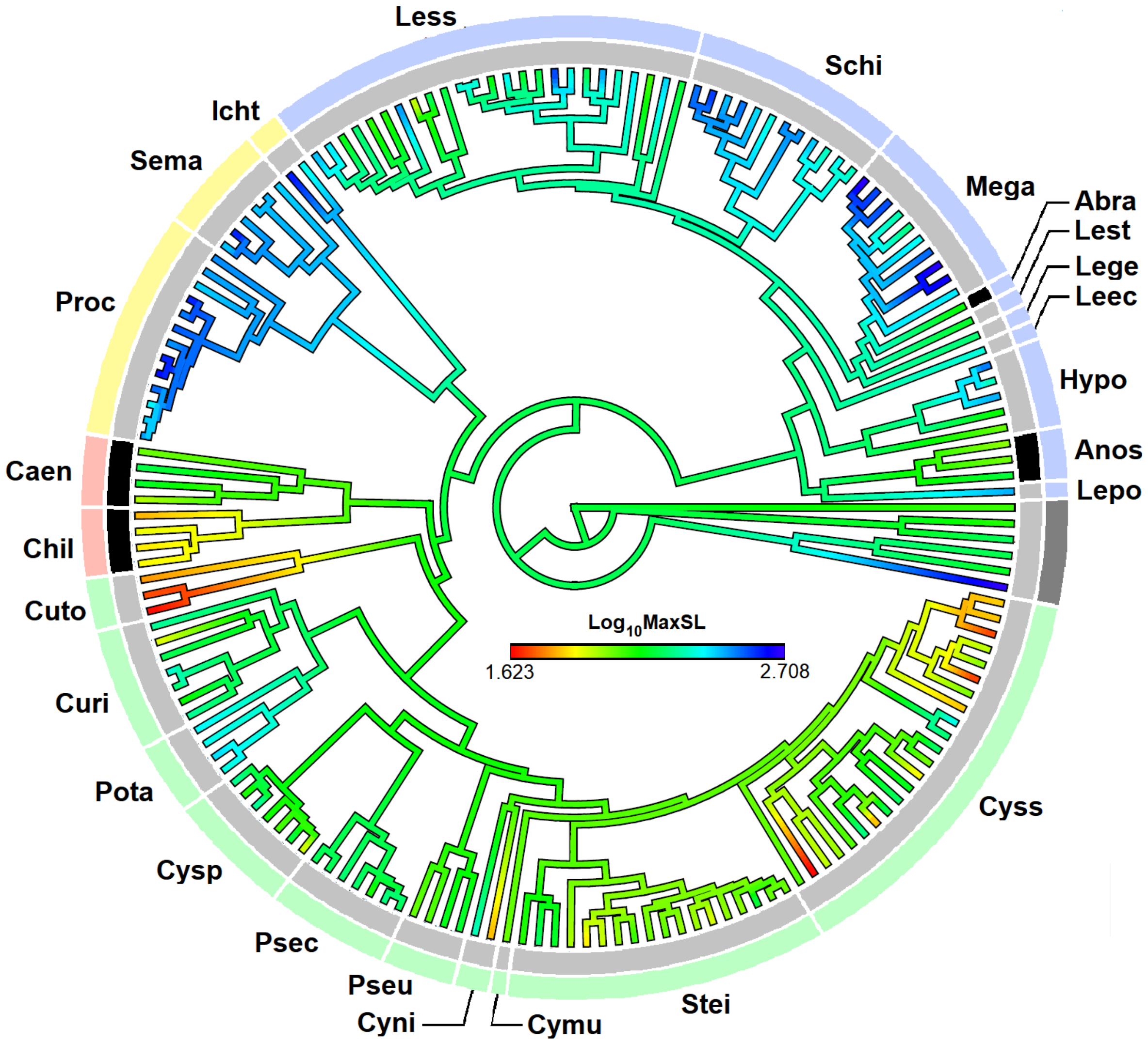

Figure 3. Body size phylogenetic character mapping. Character mapping and ancestral character state reconstruction generated with Phytools Rstudio Package. Each outer ring color refers to one Anostomoidea family, with Anostomidae (blue), Chilodontidae (red), Curimatidae (green) and Prochilodontidae (yellow). Presence of headstand behavior is presented by the color black in the infra-family group section in the inner ring. Log10MaxSL: log-transformed maximum standard length values. Infra-family groups abbreviatures in alphabetic order as follows: *Abramites* (Abra), Anostominae (Anos), *Caenotropus* (Caen), *Chilodus* (Chil), *Curimata* (Curi), *Curimatopsis* (Cuto), *Cyphocharax spilotus* group (Cysp), *C.* stricto sensu (Cyss), *Hypomasticus* (Hypo), *Ichthyolephas* (Icht), *Leporellus* (Lepo), *Leporinus ecuadorensis* (Leec), *L. geminis* (Lege), *L. striatus* (Lest), *L.* stricto sensu (Less), *Megaleporinus* (Mega), *Potamorhina* (Pota), *Prochilodus* (Proc), *Psectogaster* (Psec), *Pseudocurimata* (Pseu), *Schizodon* (Schi), *Semaprochilodus* (Sema) and *Steindachnerina* (Stei).

DISCUSSION

Our results demonstrate that the Anostomoidea superfamily carry great diversity in body size character, as species range from small Curimatidae like *Cyphocharax signatus* (33 mm of maximum SL) to large Anostomidae like *Megaleporinus obtusidens* (510 mm of maximum SL), whereas other species fulfill the wide gap between these species with intermediates body sizes. In the family’s context this body size diversity appears to be associated to family richness, especially in Anostomidae, the richest family, in which body size distribution among size classes occupied 14 of 16 classes while Chilodontidae, the least rich family, occupied only 4 of 16 body size classes. Results indicating this association were expected since body size is known to influence and be influenced by ecology (Brown et al., 1993; Cardillo et al., 2005; Peters, 1986) especially diet and feeding (Romanuk, 2011). Therefore, it is expected that richer families present major diversity in ecological trends, reflecting in greater body size divergence. Interestingly the Prochilodontidae presented same body size class occupation as the Curimatidae, which possesses five times the number of species. This discrepancy may be due to ecological constraint pressures throughout evolution among the Curimatidae species, culminating in a convergence in body size. The exact opposite may have occurred in the Prochilodontidae, with a wide range of sizes emerging due to extremely different ecological pressures throughout evolution (Brown et al., 1993; Cardillo et al., 2005). Unlike results for families, richness of infra-family groups appears not to be associated with body size diversity, as seen in the following comparisons: Anostominae group (n=14, MSL sd=35.9 mm) and *Megaleporinus* group (n=10, MSL sd=120.6 mm) or *Cyphocharax* (n=41, MSL sd=53.9 mm), *Steindachnerina* group (n=19, MSL sd=25.9 mm) and *Curimatella* group (n=5, MSL sd=46.2 mm).

Finding phylogenetic signal in the maximum standard length shows that this character is distributed as expected, with lower divergences within species from the same infra-family group than among infra-family groups (Blomberg et al., 2003; Felsenstein, 1985; Havey & Pagel, 1991). However, even if that is true for most groups, discrepancies occurred in groups like the *Leporinus* stricto sensu, in which mean of maximum standard length is 192 mm but included much larger species (e.g., *Leporinus friderici* with 400 mm), or the *Curimata* group with mean of 192.8 mm that included *Curimata mivartii* with 320 mm. It is possible that these divergences in body size inside groups are due to specific ecological features of each species. In that case, *Leporinus friderici* and *Curimata mivartii* would have evolved occupying an ecological niche distinct from most closely related species of each group.

The character mapping and ancestral state reconstruction are not conclusive about a tendency for the body size in all Anostomoidea. Our results indicate that body size for ancestral nodes in Anostomidae and Curimatidae presented intermediary-small values, with greater body sizes as well as tiny ones evolving in more terminal branches. However, Prochilodontidae and Chilodontidae showed tendencies to increase and decrease in body size towards terminal branches, respectively.

Different from that proposed by Blomberg et al. (2003) and Freckleton et al. (2002) for phylogenetic signal in behavioral characters, Fritz and Purvis’ D statistic for headstand behavior denotes a great phylogenetic signal for the character in question. Unlike the species that present the headstand behavior in the orders Ciprinodontiformes, Perciformes and Centrarchiformes, in which behavioral studies were conducted (Sulak, 1975; Lyons & Morris, 2008; Myrberg JR, 1965), little ethological information is known about Anostomoidea headstanders. This lack of scientific information about its real phylogenetic distribution for Anostomoidea, leading to extrapolations of its presence to genera or subfamilies, impact the results for phylogenetic signal in this character. The results of our parsimony analysis results corroborate the literature hypothesis of headstand behavior emergence (Géry, 1977), in which the current distribution of headstand behavior is a result of convergence. Therefore the behavior appeared three times independently throughout the group's evolution.

Headstand behavior appears to be somehow connected to smaller body sizes, based on the results of the phylogenetic T-tests. These results indicate that a headstander fish will present a small body size, but not all small-sized fish will present the behavior as seen in the family Curimatidae. We propose that throughout evolution a body size reduction in response to some ecological pressure, as the exploration of new habitats or the need to use new food resources (Brown et al., 1993; Cardillo et al., 2005), lead to the emergence of headstand behavior (Griffiths, 1986; Hanken & Wake, 1993). Since it is known that body size shifting in an evolutionary scale is common and can lead to modifications of anatomic and behavioral traits (Griffiths, 1986; Hanken & Wake, 1993), it is possible that the evolution of the headstand behavior in these small-sized fishes occurred along with anatomical modifications, such as mouth position in Anostominae species (Winterbottom, 1980) and modification in the axial skeleton and anterior ribs in the family Chilodontidae (Vari et al., 1995).

CONCLUSION

The Anostomoidea carry great diversity in body size, as species range from tiny curimatids smaller than 35 mm SL to giant anostomids of over 500 mm SL. The diversity of body sizes within groups seems to be associated with family richness. The maximum standard length for the ancestral of Anostomoidea was 163 mm.

Chilodontidae showed a tendency for small body sizes whereas Prochilodontidae showed a tendency for larger body sizes. The Anostomidae showed the most comprehensive range of body sizes and included small body-sized (Anostominae), and large body-sized clades (*Megaleporinus* and *Schizodon*). On the other hand, the Curimatidae presented very few body sizes, as compared to the other families, especially considering its species diversity, what could be due to different ecological pressures throughout evolution.

Even though the headstand behavior evolved three times independently in Anostomoidea, in Chilodontidae, Anostominae, and *Abramites,* it shows strong Phylogenetic signal, if we consider that all species of these groups exhibit this unusual behavior. Finally, our results indicate an association between headstand behavior and small-sized fishes. The appearance of this behavior may have been a consequence of body size reduction and may have occurred alongside morphological modifications.

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APPENDIXES

APPENDIX 1 Table. Behavior and standard length data for each species in the Full Data Block and Phylogenetic Data Block followed by a reference.

Infra-family group	Species	Maximum SL (mm)	Reference	Headstand behavior	Reference
Abramites	*Abramites hypselonotus* †	138	[1]	Present	[1, 83]
	Abramites eques	185	[2]	Present	[83]
Anostomoides	*Anostomoides atrianalis*	266	mzusp32421	Absent	-
	Anostomoides laticeps	300	[3]	Absent	-
	Anostomoides passionis	306	[4]	Absent	-
Anostomus	*Anostomus anostomus* †	107	[5]	Present	[5, 83]
	Anostomus brevior	91	[6]	Present	[5, 83]
	Anostomus longus	104	nmhn1961-1128	Present	[5, 83]
	Anostomus ternetzi †	100	[5]	Present	[5, 83]
Gnathodolus	*Gnathodolus bidens*	114	[7]	Present	[5, 83]
Hypomasticus	*Hypomasticus despaxi*	100	[8]	Absent	-
	Hypomasticus julii	201	[9]	Absent	-
	Hypomasticus lineomaculatus	64	[8]	Absent	-
	Hypomasticus megalepis †	109	Fmnh53367	Absent	-
	Hypomasticus mormyrops †	207	Mzusp48502	Absent	-
	Hypomasticus pachycheilus †	157	[9]	Absent	-
	Hypomasticus thayeri †	240	Mzusp62747	Absent	-
Laemolyta	*Laemolyta fernandezi* †	213	[10]	Absent	-
	Laemolyta garmani †	215	[10]	Absent	-
	Laemolyta macra	71	[11]	Absent	-
	Laemolyta orinocensis	166	[12]	Absent	-
	Laemolyta proxima †	250	[10]	Absent	-
	Laemolyta taeniata †	289	[10]	Absent	-
Leporellus	*Leporellus vittatus*	300	[12]	Absent	-
Leporinus	*Leporinus acutidens*	330	[6]	Absent	-
	Leporinus affinis †	262	[13]	Absent	-

Leporinus agassizi †	234	[8]	Absent	-
Leporinus altipinnis †	316	[14]	Absent	-
Leporinus amae	135	mzuel5393	Absent	-
Leporinus amazonicus	250	[15]	Absent	-
Leporinus amblyrhynchus †	274	[16]	Absent	-
Leporinus apollo	134	[17]	Absent	-
Leporinus arcus	309	fmnh53795	Absent	-
Leporinus arimaspi	190	[18]	Absent	-
Leporinus aripuanaensis	234	[19]	Absent	-
Leporinus badueli	105	[12]	Absent	-
Leporinus bahiensis	304	ufscar-não catalogado	Absent	-
Leporinus bistriatus	111	[12]	Absent	-
Leporinus bleheri †	142	[20]	Absent	-
Leporinus boehlkei †	158	[9]	Absent	-
Leporinus britskii	155	[21]	Absent	-
Leporinus brunneus †	256	[22]	Absent	-
Leporinus copelandii †	353	Mzusp47902	Absent	-
Leporinus cylindriformis	199	[23]	Absent	-
Leporinus desmotes †	171	[13]	Absent	-
Leporinus ecuadorensis †	230	Bmnh1971.2.11.2214	Absent	-
Leporinus fasciatus †	293	[13]	Absent	-
Leporinus friderici †	400	[24]	Absent	-
Leporinus geminis †	180	[25]	Absent	-
Leporinus gomesi	150	[26]	Absent	-
Leporinus gossei	250	[6]	Absent	-
Leporinus granti	145	[26]	Absent	-
Leporinus guttatus	125	[27]	Absent	-
Leporinus jamesi	250	[28]	Absent	-
Leporinus jatuncochi †	85	[13]	Absent	-
Leporinus klausewitzi	299	fmhn104019	Absent	-
Leporinus lacustris †	150	[29]	Absent	-

Leporinus lebailli	218	[30]	Absent	-
Leporinus maculatus	129	Impa31089	Absent	-
Leporinus marcgravii	119	[27]	Absent	-
Leporinus melanopleura	105	[31]	Absent	-
Leporinus melanopleurodes	129	[31]	Absent	-
Leporinus melanostictus	280	[24]	Absent	-
Leporinus microphthalmus †	118	[9]	Absent	-
Leporinus moralesi	105	mzusp51126	Absent	-
Leporinus multimaculatus	110	[32]	Absent	-
Leporinus nattereri	268	impa4043	Absent	-
Leporinus niceforoi	144	Mcz95471	Absent	-
Leporinus nigrotaeniatus	160	Cas70628	Absent	-
Leporinus nijsseni	145	mzups48506	Absent	-
Leporinus octofasciatus †	312	[16]	Absent	-
Leporinus octomaculatus †	129	[27]	Absent	-
Leporinus ortomaculatus	142	Bmnh1942.7.27.196-197	Absent	-
Leporinus parae †	229	[33]	Absent	-
Leporinus paranensis †	163	[34]	Absent	-
Leporinus parvulus	77	[35]	Absent	
Leporinus pearsoni †	160	Ansp143800	Absent	-
Leporinus piau †	250	Ansp171809	Absent	-
Leporinus pitingai	315	[12]	Absent	-
Leporinus punctatus	150	[36]	Absent	-
Leporinus reticulatus †	136	[27]	Absent	-
Leporinus santosi	135	[38]	Absent	-
Leporinus sexstriatus	80	[9]	Absent	-
Leporinus spilopleura	265	[3]	Absent	-
Leporinus steindachineri †	303	Nmw68405	Absent	-
Leporinus steyermarki	127	fmnh45701	Absent	-
Leporinus striatus †	151	[38]	Absent	-
Leporinus subniger	140	[12]	Absent	-

	Leporinus taeniatus †	222	Mnrj18056	Absent	-
	Leporinus taeniofasciatus	129	[12]	Absent	-
	Leporinus tigrinus †	180	[39]	Absent	-
	Leporinus trimaculatus †	232	[9]	Absent	-
	Leporinus tristriatus	180	[38]	Absent	-
	Leporinus uatumaensis	102	[12]	Absent	-
	Leporinus unitaeniatus	125	[25]	Absent	-
	Leporinus vanzoi	118	[40]	Absent	-
	Leporinus venerei †	136	[33]	Absent	-
	Leporinus yophorus	222	ansp135435	Absent	-
Megaleporinus	*Megaleporinus brinco* †	187	[41]	Absent	-
	Megaleporinus conirostris †	375	[41]	Absent	-
	Megaleporinus elongatus †	384	[41]	Absent	-
	Megaleporinus garmani †	208	[41]	Absent	-
	Megaleporinus macrocephalus †	470	[42]	Absent	-
	Megaleporinus muyscorum †	260	[41]	Absent	-
	Megaleporinus obtusidens †	510	[41]	Absent	-
	Megaleporinus piavussu †	380	[41]	Absent	-
	Megaleporinus reinhardti †	245	[41]	Absent	-
	Megaleporinus trifasciatus †	500	[43]	Absent	-
Petulanos	*Petulanos intermedius*	92	[5]	Present	[5]
	Petulanos plicatus	104	[5]	Present	[5]
	Petulanos spiloclistron	104	[5]	Present	[5]
Pseudanos	*Pseudanos gracilis*	182	[44]	Present	[5]
	Pseudanos trimaculatus †	157	[44]	Present	[5]
	Pseudanos varii	210	[44]	Present	[5]
	Pseudanos winterbottomi	152	[45]	Present	[5]
Rhytiodus	*Rhytiodus argenteofuscus* †	320	[43]	Absent	-
	Rhytiodus lauzannei	290	[46]	Absent	-
	Rhytiodus microlepis †	332	[43]	Absent	-
Sartor	*Sartor elongatus*	91	[07]	Present	[5, 83]

	Sartor respectus	88	[05]	Present	[5, 83]
	Sartor tucuruiense	112	impa38579	Present	[5, 83]
Schizodon	*Schizodon altoparanae*	230	[12]	Absent	-
	Schizodon australis	334	[09]	Absent	-
	Schizodon borellii †	347	[47]	Absent	-
	Schizodon corti	400	[48]	Absent	-
	Schizodon fasciatus †	400	[28]	Absent	-
	Schizodon intermedius †	290	[49]	Absent	-
	Schizodon isognathus	350	[12]	Absent	-
	Schizodon jacuiensis	250	[12]	Absent	-
	Schizodon knerii †	235	[50]	Absent	-
	Schizodon nasutus	375	[29]	Absent	-
	Schizodon platae	260	[51]	Absent	-
	Schizodon scotorhabdotus †	271	[50]	Absent	-
	Schizodon vittatus †	350	[3]	Absent	-
Synaptolaemus	*Synaptolaemus latofasciatus*	109	[52]	Present	[5, 83]
Chilodus	*Chilodus fritillus* †	73	[53]	Present	[56, 83]
	Chilodus gracilis †	64	[54]	Present	[56, 83]
	Chilodus punctatus †	79	[55]	Present	[56, 83]
	Chilodus zunevei †	77	[54]	Present	[56, 83]
Caenotropus	*Caenotropus labyrinthicus* †	152	[56]	Present	[56, 83]
	Caenotropus maculosus †	108	[56]	Present	[56, 83]
	Caenotropus mestomorgmatos †	163	[56]	Present	[56, 83]
	Caenotropus schizodon †	91	[57]	Present	[56, 83]
Curimata	*Curimata aspera*	212	[58]	Absent	-
	Curimata cyprinoides †	230	[3]	Absent	-
	Curimata inornata †	136	[58]	Absent	-
	Curimata incompta †	167	[59]	Absent	-
	Curimata knerii †	177	[58]	Absent	-
	Curimata mivartii	320	[2]	Absent	-
	Curimata roseni †	195	[43]	Absent	-

	Curimata vittata †	196	[43]	Absent	-
Curimatella	*Curimatella alburna* †	188	[43]	Absent	-
	Curimatella dorsalis †	114	[60]	Absent	-
	Curimatella immaculata †	76	[61]	Absent	-
	Curimatella lepidura †	113	[61]	Absent	-
	Curimatella meyeri †	172	[43]	Absent	-
Curimatopsis	*Curimatopsis cryptica* †	50	[62]	Absent	-
	Curimatopsis evelynae	40	[62]	Absent	-
	Curimatopsis macrolepis †	60	[62]	Absent	-
	Curimatopsis microlepis	89	[62]	Absent	-
	Curimatopsis myersi †	43	[12]	Absent	-
Cyphocharax	*Cyphocharax abramoides* †	213	[63]	Absent	-
	Cyphocharax aninha	39	[64]	Absent	-
	Cyphocharax aspilos †	180	[62]	Absent	-
	Cyphocharax biocellatus	69	[63]	Absent	-
	Cyphocharax boiadeiro †	49	[66]	Absent	-
	Cyphocharax corumbae †	117	[67]	Absent	-
	Cyphocharax derhami	89	[68]	Absent	-
	Cyphocharax festivus †	63	[60]	Absent	-
	Cyphocharax gangamon	47	[63]	Absent	-
	Cyphocharax gilbert †	126	[60]	Absent	-
	Cyphocharax gillii †	100	[11]	Absent	-
	Cyphocharax gouldingi †	88	[60]	Absent	-
	Cyphocharax helleri †	96	[69]	Absent	-
	Cyphocharax laticlavus	53	[69]	Absent	-
	Cyphocharax leucostictus †	105	[60]	Absent	-
	Cyphocharax magdalenae †	240	[2]	Absent	-
	Cyphocharax meniscaprorus	57	[63]	Absent	-
	Cyphocharax mestomyllon †	42	[63]	Absent	-
	Cyphocharax microcephalus †	169	[63]	Absent	-
	Cyphocharax modestus †	162	[63]	Absent	-

	Cyphocharax multilineatus †	109	[60]	Absent	-
	Cyphocharax nagelii	163	[60]	Absent	-
	Cyphocharax nigripinnis †	65	[63]	Absent	-
	Cyphocharax notatus †	147	[43]	Absent	-
	Cyphocharax oenas †	48	[63]	Absent	-
	Cyphocharax pantostictos	98	[63]	Absent	-
	Cyphocharax pinnilepis	101	[70]	Absent	
	Cyphocharax platanus †	134	[63]	Absent	-
	Cyphocharax plumbeus †	178	[63]	Absent	-
	Cyphocharax punctatus	43	[60]	Absent	-
	Cyphocharax saladensis †	67	[60]	Absent	-
	Cyphocharax sanctigabrielis †	67	[71]	Absent	-
	Cyphocharax santacatarinae †	201	[63]	Absent	-
	Cyphocharax signatus	33	[63]	Absent	-
	Cyphocharax spilotus †	82	[63]	Absent	-
	Cyphocharax spiluropsis †	90	[63]	Absent	-
	Cyphocharax spilurus	104	[60]	Absent	-
	Cyphocharax stilbolepis	108	[60]	Absent	-
	Cyphocharax vanderi †	68	[63]	Absent	-
	Cyphocharax vexillapinnus	63	[63]	Absent	-
	Cyphocharax voga †	196	[60]	Absent	-
Potamorhina	*Potamorhina altamazonica* †	270	[72]	Absent	-
	Potamorhina laticeps †	250	[73]	Absent	-
	Potamorhina latior †	240	[43]	Absent	-
	Potamorhina pristigaster	219	[72]	Absent	-
	Potamorhina squamoralevis †	234	[72]	Absent	-
Psectrogaster	*Psectrogaster amazonica* †	190	[3]	Absent	-
	Psectrogaster ciliata †	129	[74]	Absent	-
	Psectrogaster curviventris †	171	[74]	Absent	-
	Psectrogaster essequibensis †	169	[74]	Absent	-
	Psectrogaster falcata †	168	[74]	Absent	-

	Psectrogaster rhomboides †	178	[74]	Absent	-
	Psectrogaster rutiloides †	178	[43]	Absent	-
	Psectrogaster saguiru	164	[74]	Absent	-
Pseudocurimata	*Pseudocurimata boehlkei* †	109	[75]	Absent	-
	Pseudocurimata boulengeri †	146	[76]	Absent	-
	Pseudocurimata lineopunctata †	114	[76]	Absent	-
	Pseudocurimata patiae	125	[75]	Absent	-
	Pseudocurimata peruana	127	[75]	Absent	-
	Pseudocurimata troschelii †	155	[76]	Absent	-
Steindachnerina	*Steindachnerina amazonica* †	99	[77]	Absent	-
	Steindachnerina argentea †	93	[77]	Absent	-
	Steindachnerina atratoensis	83	[77]	Absent	-
	Steindachnerina bimaculata †	173	[43]	Absent	-
	Steindachnerina binotata	133	[77]	Absent	-
	Steindachnerina biornata	73	[60]	Absent	-
	Steindachnerina brevipinna †	109	[60]	Absent	-
	Steindachnerina conspersa †	128	[60]	Absent	-
	Steindachnerina corumbae	117	[67]	Absent	-
	Steindachnerina dobula †	163	[77]	Absent	-
	Steindachnerina elegans †	106	[77]	Absent	-
	Steindachnerina fasciata †	96	[60]	Absent	-
	Steindachnerina gracilis †	73	[60]	Absent	-
	Steindachnerina guentheri †	111	[77]	Absent	-
	Steindachnerina hypostoma †	98	[77]	Absent	-
	Steindachnerina insculpta †	106	[60]	Absent	-
	Steindachnerina leucisca †	151	[77]	Absent	-
	Steindachnerina notonota †	98	[77]	Absent	-
	Steindachnerina notograptos	106	[78]	Absent	-
	Steindachnerina planiventris †	87	[60]	Absent	-
	Steindachnerina pupula †	99	[77]	Absent	-
	Steindachnerina quasimodoi †	123	[60]	Absent	-

	Steindachnerina seriata †	83	[79]	Absent	-
	Steindachnerina varii	94	[60]	Absent	-
Prochilodus	*Prochilodus argenteus* †	436	[80]	Absent	-
	Prochilodus brevis †	270	[80]	Absent	-
	Prochilodus britskii †	238	[80]	Absent	-
	Prochilodus costatus †	420	[80]	Absent	-
	Prochilodus hartii †	333	[80]	Absent	-
	Prochilodus lacustris †	324	[80]	Absent	-
	Prochilodus lineatus †	460	[80]	Absent	-
	Prochilodus magdaleane †	312	[80]	Absent	-
	Prochilodus mariae †	366	[80]	Absent	-
	Prochilodus nigricans †	365	[80]	Absent	-
	Prochilodus reticulatus †	279	[80]	Absent	-
	Prochilodus rubrotaeniatus †	320	[80]	Absent	-
	Prochilodus vimboides †	328	[80]	Absent	-
Ichthyoelephas	*Ichthyoelephas humeralis* †	240	[80]	Absent	-
	Ichthyoelephas longirostris †	431	[80]	Absent	-
Semaprochilodus	*Semaprochilodus brama* †	303	[80]	Absent	-
	Semaprochilodus insignis †	305	[80]	Absent	-
	Semaprochilodus kneri †	282	[80]	Absent	-
	Semaprochilodus laticeps †	437	[80]	Absent	-
	Semaprochilodus taeniurus †	281	[80]	Absent	-
	Semaprochilodus varii †	280	[80]	Absent	-
Outgroup	*Apareiodon affinis* †	170	[16]	Absent	-
	Parodon nasus †	127	[81]	Absent	-
	Bricon Pesu †	120	[6]	Absent	-
	Catoprion mento †	150	[82]	Absent	-
	Colossoma macopomum †	510	[43]	Absent	-
	Metynnis lippincottianus †	164	[43]	Absent	-

Species from PDB highlighted with † in front of the species name. Data collected from museum specimens is referenced with the specimen museum code. SL: standard length.

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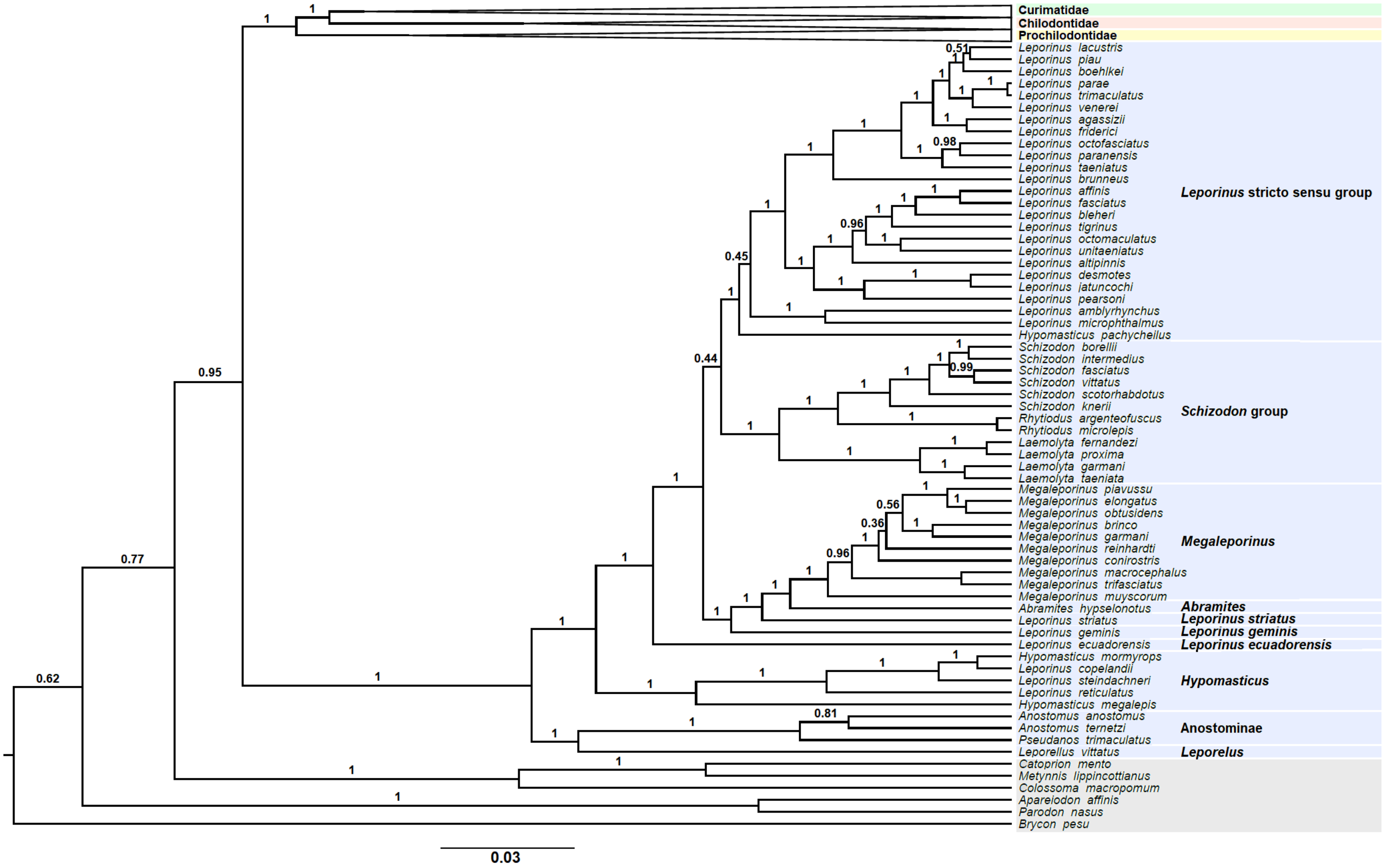
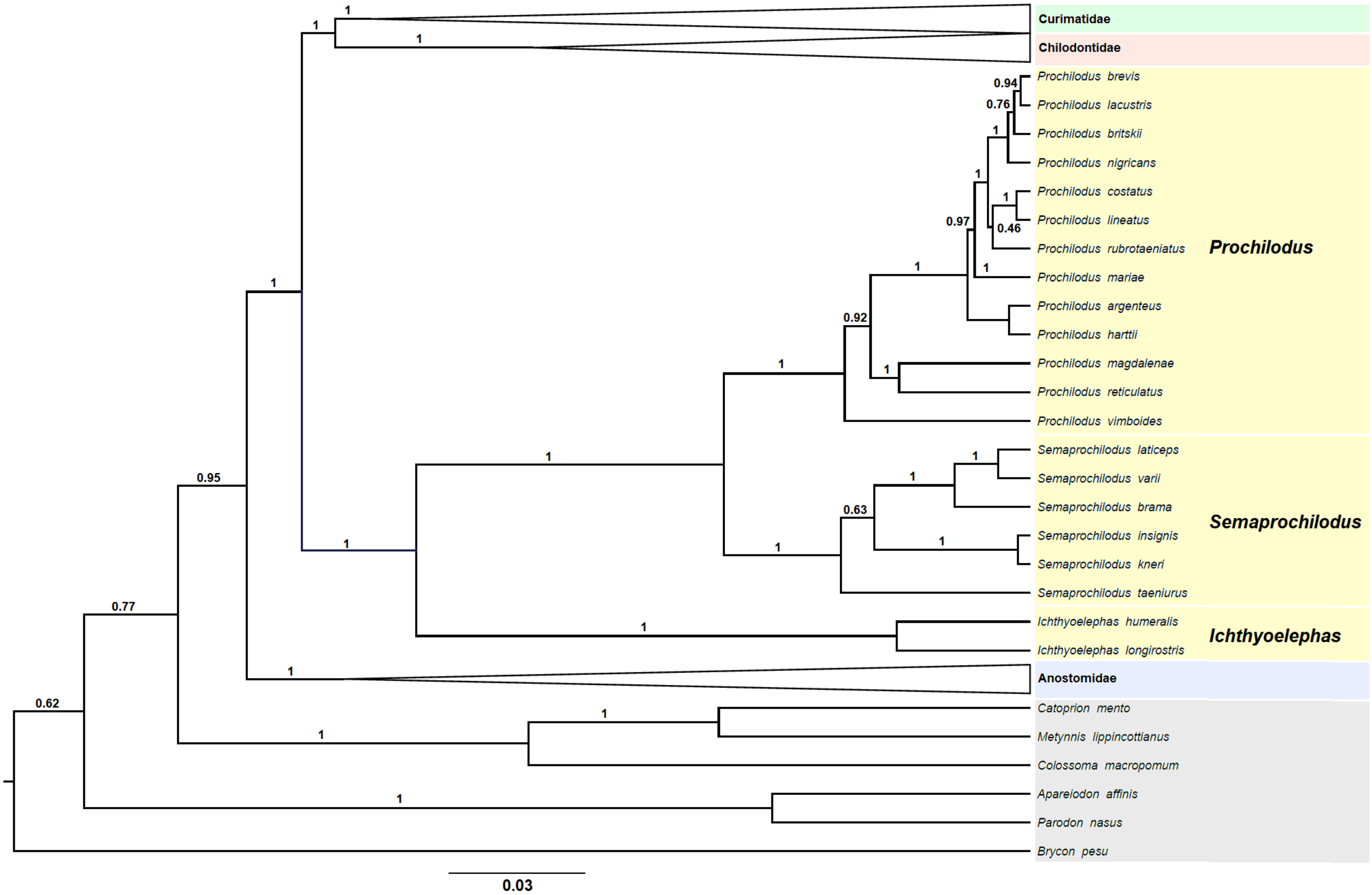
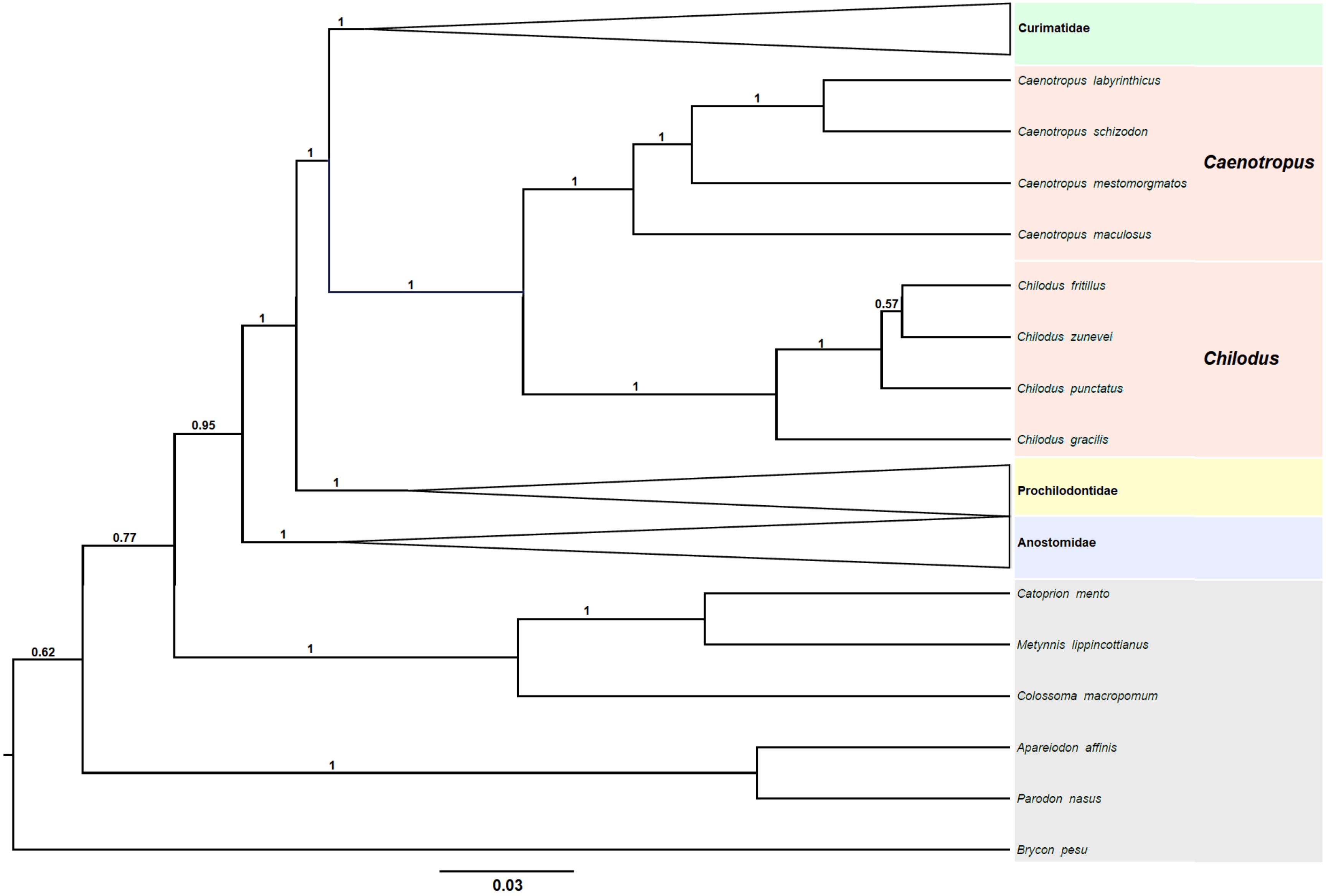
APPENDIX 2. Expanded families subtrees from Anostomoidea.



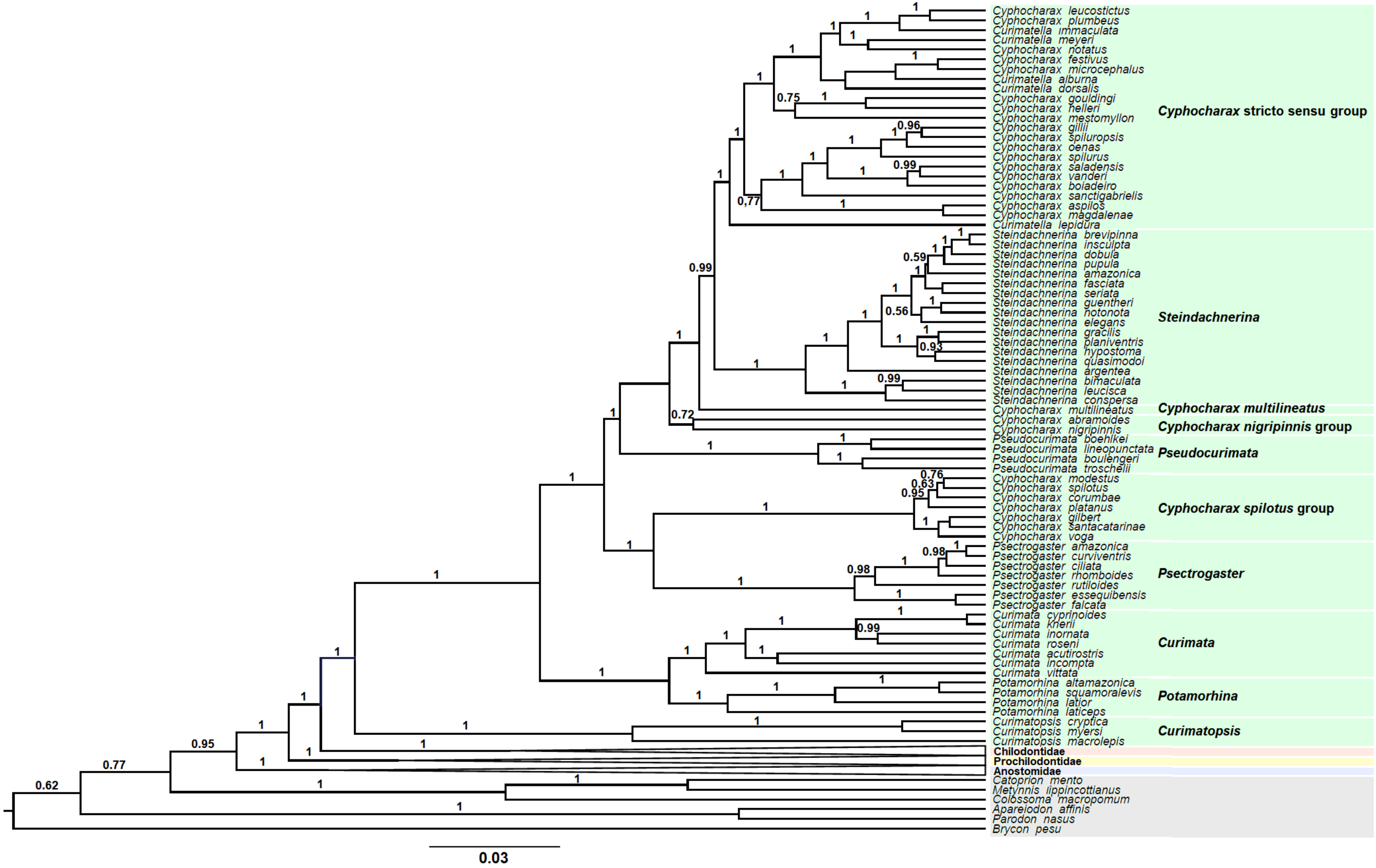
Expanded Anostomidae sub-tree from Anostomoidea. Anostomidae detail from Anostomoidea resultant tree from Bayesian Analysis. Numbers above branches represent posterior probability support values. Names in front of species represent infra-family group given by the author.



Expanded Prochilodontidae sub-tree from Anostomoidea. Prochilodontidae detail from Anostomoidea resultant tree from Bayesian Analysis. Numbers above branches represent posterior probability support values. Names in front of species represent infra-family group given by the author.



Expanded Chilodontidae sub-tree from Anostomoidea. Chilodontidae detail from Anostomoidea resultant tree from Bayesian Analysis. Numbers above branches represent posterior probability support values. Names in front of species represent infra-family group given by the author.



Expanded Curimatidae sub-tree from Anostomoidea. Curimatidae detail from Anostomoidea resultant tree from Bayesian Analysis. Numbers above branches represent posterior probability support values. Names in front of species represent infra-family group given by the author.

APPENDIX 3. Exploratory statistics of FDB data.

Family groups	Infrafamily groups	N	Mean (mm)	SD	Median (mm)	Max (mm)	Min (mm)	1º quartile	3º quartile
Anostomoidea		266	183.6	100.8	157.5	510	33	105	250
Anostomidae		135	210.1	97.1	190	510	64	129	272.5
	Abramites †	2	161.5	33.2	161.5	185	138	149.75	173.25
	Anostominae †	16	119.8	35.9	105.5	210	88	98	123.5
	Anostomoides	3	290.6	21.5	300	306	266	283	303
	Hypomasticus	7	154	65.1	157	240	64	104.5	204
	Laemollyta	6	200.6	75.6	214	289	71	177.75	241.25
	Leporellus	1	300	0	300	300	300	300	300
	Leporinus	74	190.7	76	160	400	77	130.25	250
	Megaleporinus	10	351.9	120.6	337.5	510	187	248.75	448.5
	Rythiodus	3	314	97	320	332	290	305	326
	Schizodon	13	314.7	61.4	334	400	230	260	350
Chilodontidae		8	100.8	37.4	85	163	64	76	119
	Caenotropus †	4	128.5	34.4	130	79	64	70.75	77.5
	Chilodus †	4	73.2	6.6	75	163	91	103.75	154.75
Curimatidae		102	124.0	58.4	109	320	33	83	167.75
	Curimata	8	187.8	69.4	186	320	82	159.25	204.5
	Curimatella	5	132.6	46.2	114	188	76	113	172
	Curimatopsis	5	56.4	19.7	50	89	43	43	60
	Cyphocharax	41	104.1	53.9	96	240	33	63	134
	Potamorhina	5	242.6	18.9	240	270	219	234	250
	Psectrogaster	8	168.3	17.8	170	190	129	167	178
	Pseudocurimata	6	129.3	17.9	126	155	109	116.75	141.25
	Steindachnerina	24	108.4	25.9	102.5	173	73	93.75	118.50
Prochilodontidae		21	333.8	67.7	320	460	238	281	366
	Ichthyolephas	2	335.5	135	335.5	431	240	287.75	383.25
	Prochilodus	13	342.3	65.7	328	460	238	312	366
	Semaprochilodus	6	314.6	60.9	292.5	437	280	281.25	304.5

Summary statistics of body size for Anostomoidea and its families and infra-family groups. Presence of headstand behavior indicated with † next to infra-family group names — number of species (N); Standard deviation (SD).