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RIANNE CAROLINE DE OLIVEIRA

Phylogenetic systematics of *Mesonauta* Günther 1862 (Cichliformes: Cichlidae: Cichlinae)

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Tese apresentada ao Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais, do Departamento de Biologia, Centro de Ciências Biológicas da Universidade Estadual de Maringá, como requisito parcial para obtenção do título de Doutor em Ecologia e Limnologia.
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Orientador: Prof. Dr. Weferson Júnio da Graça
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BANCA EXAMINADORA

Prof. Dr. Weferson Júnio da Graça
Universidade Estadual de Maringá (Presidente)

Prof.ª Dr.ª Renata Rúbia Ota
Universidade Federal da Grande Dourados, MS (UFGD)

Dr. Thomaz Mansini Carrenho Fabrin
Universidade Tecnológica Federal do Paraná (Pós-doutorando UTFPR)

Prof.ª Dr.ª Alessandra Valéria de Oliveira
Universidade Estadual de Maringá (UEM)

Dr. Augusto Frota
Universidade Estadual de Maringá (Pós-doutorando PEA/UEM)

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Sistemática filogenética de *Mesonauta* Günther 1862 (Cichliformes: Cichlidae: Cichlinae)

RESUMO

Ciclídeos tornaram-se modelos para o estudo da história evolutiva de peixes da região Neotropical. Muitos autores têm tentado recuperar a filogenia do grupo com dados morfológicos e moleculares, apresentando resoluções satisfatórias entre muitos gêneros. Entretanto, as relações de parentesco intragenéricas ainda permanecem obscuras para vários gêneros, o que pode dificultar até mesmo a delimitação das espécies. *Mesonauta* apresenta seis espécies válidas, muito apreciadas pelos aquaristas. Atualmente não há nenhuma proposta filogenética de relações entre suas espécies e o gênero apresenta ampla distribuição geográfica e variações fenotípicas, com possíveis espécies novas não descritas. Foram delimitadas as espécies do gênero, a partir de dados moleculares e morfométricos de espécimes conservados e depositados em coleções ictiológicas. Das seis espécies descritas anteriormente, o COI delimita espécies diferentes, uma vez que duas delas (*Mesonauta egregius* e *M. guyanae*) não foram corroboradas pela análise de delimitação e duas são supostas espécies novas, mostrando seis diferentes espécies: *Mesonauta mirificus*, *M. festivus*, *Mesonauta* sp. "Pantanal", *M. acora, Mesonauta* sp. "Amapá" and *M. insignis*. Os resultados mostraram uma nova base para estudos dentro do gênero e novas pesquisas são necessárias para entender a ampla distribuição de *M. mirificus*. Foi testado o monofiletismo de *Mesonauta* e as relações entre as espécies, com a construção de cladogramas baseados em caracteres moleculares (COI, 16S) utilizando três métodos filogenéticos, dos quais dois clados principais foram recuperados. Uma espécie nova de *Mesonauta* foi descrita da bacia do rio Amapá Grande, baseada em características morfológicas e moleculares, em uma região afetada pela presença de mercúrio. Este é o primeiro passo na investigação da filogenia molecular de *Mesonauta*, que mostrou relações intragenéricas baseadas em dados moleculares, possibilitou a descrição de uma espécie nova do gênero e forneceu informações para futuras pesquisas sobre a história evolutiva do grupo.

Palavras-chave: biodiversidade; Cichlidae; evolução; taxonomia integrativa; região Neotropical.

Phylogenetic systematics of *Mesonauta* Günther 1862 (Cichliformes: Cichlidae: Cichlinae)

ABSTRACT

Cichlids have evolved into models for studying the evolutionary history of Neotropical fish. Many authors attempted to recover the group's phylogeny using morphological and molecular data, presenting satisfying solutions across a wide range of genera. However, intrageneric relationships remain obscure in a number of genus, potentially complicating species delimitation. *Mesonauta* presents six distinct species that are highly valued by aquarists. Currently, there is no proposed phylogenetic relationship between its species; however, it has a wide geographic distribution and phenotypic variations, with the possibility of new species not yet described. Species of the genus were delimited using molecular and morphometric data from preserved and deposited species in ichthyological collections. From the six previously described species, COI delimitate different species, since two of them (*Mesonauta egregius* and *M. guyanae*) were not corroborated by delimitation analysis and two are putative new species, showing six different species: *M. mirificus*, *M. festivus*, *Mesonauta* sp. "Pantanal", *M. acora*, *Mesonauta* sp. "Amapá" and *M. insignis*. The results showed a new basis for studies within the genus and further research is needed to understand the wide distribution of *M. mirificus*. *Mesonauta*'s monophyly was tested and the relationships between species by constructing concatenated cladograms based on molecular characters (COI, 16S) using three phylogenetic methods, from which two main clades were recovered a new species of *Mesonauta* was described from the Amapá Grande river basin, based on morphological and molecular characteristics, in a region affected by the presence of mercury. This is the first step in investigating the molecular phylogeny of Mesonauta, which showed intrageneric relationships based on molecular data, enabled the description of a new species of the genus and provided information for future research on the evolutionary history of the group.

Keywords**:** biodiversity; Cichlidae; evolution; integrative taxonomy; Neotropical Region.

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SUMMARY

1 INTRODUCTION

Cichlinae are the second most diverse subfamily in the Neotropical region, with roughly 600 known species (Fricke *et al*., 2023). Cichlids have been frequently utilized as a model to explore diversification patterns and evolutionary history (Arbour and López-Fernández, 2014; Ilves *et al*., 2018). Cichlini, Retroculini, Astronotini, Chaetobranchini, Geophagini, Cichlasomatini, and Heroini were proposed as seven tribes (López-Fernández *et al*., 2010; Ilves *et al*., 2018) being Geophagini, Cichlasomatini, and Heroini the most diverse tribes in Cichlinae (Ilves *et al*., 2018). Despite efforts to resolve evolutionary relationships, several topologies continue to be ambiguous. This is owing to methodological differences (López-Fernández *et al*., 2010; Říčan *et al*., 2016), in addition to other limitations such as a small dataset (Friedman, 2013). This variation can be seen in Heroini, where the clades were not well supported (López-Fernández *et al*., 2010; Říčan *et al*., 2016).

Mesonauta Günther 1862, belongs to the Heroini and is found throughout South America in the Amazon Basin, Paraguay Basin, Orinoco Basin, and the Guianas (Kullander & Silfvergrip, 1991; Kullander, 2003). Phylogenetic analyses of Neotropical cichlids used few species per genus to demonstrate the group's evolutionary history in depth (López-Fernández et al., 2010; Ilves *et al*., 2018). From the six species described in the genus, only *M. insignis* (Heckel 1840) and *M. egregius* Kullander & Silfvergrip 1991 were included in those analyses; as a result, the relationship between *Mesonauta* species remains unknown, with only information on intergeneric relationships. Previous research discovered close relationships between *Pterophyllum*, *Symphysodon*, *Uaru*, *Heros*, and *Mesonauta* (Kullander, 1998; López-Fernández *et al*., 2010; Ilves *et al*., 2018), however, their relationship is different in these studies.

In a morphological analysis, *Symphysodon* was considered a sister group of a clade that included *Heros* and *Uaru*, which is sister group of *Mesonauta* and *Pterophyllum*, supported by eleven synapomorphies, five of which were related to body height (Kullander, 1998). Later, an informal clade known as Mesonautines, consisting of *Mesonauta*, *Uaru*, *Symphysodon*, and *Heros*, was suggested based on molecular analyses (López-Fernández *et al*., 2010; Ilves *et al*., 2018). Unlike the clade presented by López-Fernández *et al*. (2010), *Mesonauta* was discovered as sister group of a clade that included *Heros* as sister of *Symphysodon* and *Uaru* (Ilves *et al*., 2018).

Günther (1862) described *Mesonauta* to include species that correspond to the definition of *Heros* Heckel (1840), but have 8-9 spines in the anal fin (vs. 5-7 in the *Heros* species) and the origin of the pelvic fin located anteriorly to the vertical that passes through the origin of the dorsal (*vs*. posteriorly). *Mesonauta* was created to include *M. insignis*, *M. festivus* (Heckel, 1840), and *M. acora* (Castelnau, 1855). Despite the fact that other authors only recognized *M. festivus* and included it in *Cichlasoma*, as explained by Kullander & Silfvergrip (1991), *Mesonauta* was revisited and rediagnosed by Kullander (1986), who also acknowledged the validity of the three previously described species, albeit without providing a useful diagnosis for *M. acora*. Following that, Kullander & Silfvergrip (1991) published a comprehensive review of the genus, rediagnosing *M. acora* and describing two new species, *M. egregius* and *M. mirificus*. Finally, Schindler (1998) described *M. guyanae* Schindler, 1998 from the Essequibo River basin. After these two works, none described any species, however there are still doubts about the correct identification of *Mesonauta* species due to two factors: (1) *M. insignis* is a putative species complex (Kullander, 1986) and (2) a lack of adequate material (*i.e.* juveniles or poorly preserved specimens) prevented the description of additional species from the Guianas and the Rio Solimões-Amazonas (Kullander & Silfvergrip, 1991).

Molecular analysis has been used in several studies to delimit species and to recover phylogeny (Ilves *et al.*, 2018). In such cases, a range of genes could be chosen according to their characteristics. For example, COI is a mitochondrial gene used as DNA barcode in a wide range of species delimitation studies, (Hebert *et al.*, 2003; Pereira *et al.*, 2011a; 2011b; 2013).

Because of the greater volume of data, molecular analyses can elucidate issues from species boundaries to suprageneric relationships (McMahan *et al.*, 2015). This enables the identification of new species and new synonyms, as well as polyphyletic genus. As a result, the molecular approach provides answers that morphology alone is incapable of providing. However, morphology has crucial and applicable characteristics in the identification of synapomorphies. Together, molecular and morphological methods play an integrated role that allows for the incorporation of a diverse set of data capable of improving taxonomic resolution. Aside from elucidating taxonomic issues, the study of aquatic organism phylogeny has the potential to improve understanding of these issues through ecological applications (e.g. establishment of non-native species that are phylogenetically distant from the natives (see Mcknight *et al.*, 2017).

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2 SPECIES DELIMITATION IN NEOTROPICAL FISHES OF *Mesonauta* Günther 1862 (CICHLIFORMES: CICHLIDAE)

ABSTRACT

From Neotropical cichlids, *Mesonauta* accomplishes six described species, but putative new species are referred to this genus. Considering that understanding the boundaries of each species could help in phylogenetic context, here we use DNA-barcode technique to 1) delimit species within *Mesonauta*, 2) to test the *M. insignis* species complex, and 3) discuss the *Mesonauta* species distribution. The Maximum Likelihood tree used under the three delimitation methods does not corroborate the six species previously described and the nine morphotypes, four for *M. mirificus* and remaining for the other five availabe species. According to the mitochondrial data used herein, despite some differences in coloration pattern, the genus is composed by six OTUs: 1) *Mesonauta mirificus*, widely distributed from several tributaries from Amazon River basin, Tapajós, Moa, Negro and Xingu Rivers, including *M. guyanae* from Suriname, Takutu, Branco and Oiapoque Rivers; *Mesonauta festivus*, composed by two OTUs: 2) *M. festivus* from Guaporé River basin and a putative new species 3) *Mesonauta* sp. "Pantanal" from Paraguay River basin; 4) *M. acora,* distributed in the Tocantins-Araguaia and Xingu River basins; a putative new species 5) *Mesonauta* sp. "Amapá", from Amapá Grande River basin and Jeju River; and 6) *M. insignis,* from upper Negro and Venezuelan Orinoco River, including *M. egregius* from Colombian Orinoco River. No molecular differences were found between *Mesonauta egregius* described from the Orinoco River basin and *M. insignis* and between *M. mirificus* and *M. guyanae* from Amazon/Suriname River basin. Further, PCA analysis and color pattern are insufficient to differentiate *M. festivus* from *Mesonauta* sp. "Pantanal". These findings offer a unique perspective on cichlid diversity and provide the basis for future research focusing on the widely distributed *Mesonauta mirificus*.

Keywords: COI, Cichlid diversity, OTU, Putative new species.

2.1 Introduction

Mesonauta Günther 1862 is a monophyletic Heroini genus with a great body depth and an oblique bar that extends ascending from the snout and eye areas to the end of the dorsal fin (Ilves *et al*., 2018). It is distinguished from its sister group *Heros* Heckel (1840) by having more spines on the anal fin and a different color pattern. *Mesonauta* species distribution encompasses the Amazon-Orinoco-Guyana (AOG) region, the Paraguay and Tocantins-Araguaia River basins (Kullander & Silfvergrip 1991).

In the most recent review of *Mesonauta* a new diagnosis was proposed for *M. insignis* (Heckel 1840), *M. festivus* (Heckel 1840) and *M. acora* (Castelnau 1855), and two new species were described (Kullander & Silfvergrip 1991). Since the 90's, only one species was described. Currently, the genus has six valid species widely distributed in different Amazon sub-basins: *M. insignis* in the upper Rio Negro and Rio Orinoco; *M. festivus* in the Paraguay River and Bolivian Amazon, Jamari River and lower Tapajós River; *M.* acora in the Tocantins-Araguaia and Xingu Rivers; *M. egregius* Kullander & Silfvergrip 1991 in the Colombian Orinoco; *M. mirificus* Kullander & Silfvergrip 1991 in the Peruvian Amazon (Kullander & Silfvergrip 1991); and *M. guyanae* in the Essequibo River basin (Schindler, 1998).

Mesonauta insignis is a putative species complex (Kullander, 1986) and certainly there are more species to be described, which have not yet been described due to the lack of adequate material (*sensu* Kullander & Silfvergrip 1991). Additionally, lots analyzed herein yield nine different morphospecies, at least four for *M. mirificus* and other five corresponding to the remaining available species cited above. Taxonomic problems can cause errors in identification and, as explained by Kullander (1986), difficulties in defining the geographic distribution of a species. In this way, species delimitation studies provide resolutions to the problems mentioned above, by describing and delimiting the geographic range of species.

Several studies use DNA barcode to delimit and identify species, with successful tree resolutions and genetic distance to enforce the species identification (Serrano *et al*., 2018; Zhang *et al*., 2021, Oliveira *et al*., 2023). For example, partial sequences of the mitochondrial cytochrome c oxidase subunit I (COI) is widely used to assist in identification of fish species (Pereira *et al*., 2011a; 2011b; 2013). In this context, COI are here used for test species delimitation in *Mesonauta*. The aim of the present study is to use molecular data to: (1) delimit the species of *Mesonauta*; (2) verify if there is more than one species in *M. insignis*; and (3) discuss the *Mesonauta* species distribution according to COI data and delimitation analyzes.

2.2 Material and Methods

2.2.1 Molecular data

2.2.1.1 Sampling and sequencing.

From DNA taken from tissue samples of 152 *Mesonauta*, one *Pterophyllum*, and six *Heros* species, we were able to get partial sequences of the COI gene. Five, from the 152 sequences, are from *Mesonauta egregius* were retrieved from the GenBank database (Appendix A).

The voucher specimens were preserved at 70º GL ethanol after being fixed in 10% formalin. Samples that were kept and held at 95º GL ethanol were used to extract tissue samples. Ivanova et al. (2006) were followed in the extraction of whole DNA. Polymerase chain reaction (PCR) was used to amplify the COI's DNA barcode area posteriorly. The primers FISH-F6 (5'-ACYAAYCACAAAGAYATTGGCA-3') and FISH-R7

(5'-TARACTTCTGGRTGDCCRAAGAAYCA-3') were outlined by Jennings et al. (2019). The PCR was performed on a thermocycler with a final volume of 12.5 µl containing 7.85 µl distilled water (ddH2O), 0.30 µl deoxynucleotide triphosphate (dNTP) (2 mM), 1.25 µl PCR buffer (10×), 0.4 µl $MgCl_2$ (50 mM), 0.25 µl each primer, 2 µL DNA (200 ng) and 0.20 µl Taq DNA polymerase PHT (Phoneutria). PCR was performed under the following conditions: an initial denaturation at 95º C for 5 min, followed by 30 cycles including denaturation at 95ºC for 60 s, annealing (primer hybridization) at 52º C for 45 s and nucleotide extension at 68ºC for 1 min, with a final extension at 68º C for 10 min. The PCR products were amplified and checked on a 1% agarose gel before being purified using ExoSAP-IT (USB Corporation, Cleveland, OH, USA) according to the manufacturer's protocol.

Using the BigDye Terminator v3.1 Cycle Sequencing Ready Reaction kit (Applied Biosystems, Austin, TX, USA), we sequence both DNA strands in a final volume of 7 µl that contains 3.9 µl distilled water, 1.05 µl buffer 5×, 0.7 µl BigDye mix, and 0.35 µl primer (10 mM). DNA was isolated by ethanol precipitation and sequenced at the Instituto de Biociências at the Universidade Estadual Paulista "Júlio de Mesquita Filho", UNESP, Botucatu, using the 3500-Genetic Analyzer (Applied Biosystems) at IBTEC.

2.2.1.2 Molecular delimitation analysis.

Pterophyllum scalare and *Heros efasciatus* sequences were used as outgroups in the analysis. Sequences of the aforementioned species obtained from GenBank followed their morphological identification as suggested by their respective studies. The electropherogram peaks of each sequence were visualized in Bioedit (Hall, 1999) to check whether they corresponded to their respective nitrogenous bases. Sequences were then edited (if any difference in electropherogram and sequences appeared) and aligned using MEGA X (Kumar *et al*., 2018), using the Clustal W algorithm (Thompson *et al*., 1994) with verification for stop codons. Genetic distances (between and within groups) are calculated in MEGA X, separating the morphospecies. As delimitation analysis recovered two OTUs for *Mesonauta festivus*, a posterior analysis were calculated to verify the genetic distance between specimens from Guaporé River basin and from Paraguai River basin.

For species delimitation, four approaches were used: two methods based in trees, the Poisson Tree Process (PTP; Zhang *et al.*, 2013) analysis and General Mixed Yule Coalescent Model (GMYC; Pons *et al.*, 2006; Fujisawa & Barraclough, 2013) analysis, with difference that the latter calculate the posterior probability; and two methods based in distances, the Automatic Barcode Gap Discovery (ABGD; Puillandre *et al.*, 2012) analysis, and the Assemble Species by Automatic Partitioning (ASAP; Puillandre *et al.*, 2021), with difference the latter shows a score value to choose the best partition.

A maximum likelihood (ML) analysis was performed in MEGA-X v10.2.1 (Kumar *et al.*, 2018) using the best nucleotide substitution model (K2+I, lowest BIC score: 7449,725 with 317 parameters), five random searches and 1,000 bootstrap replicates and other parameters at default, showing the best tree. Additionally, genetic distances (Kimura 1980) between and within groups were calculated with the Kimura 2-parameter model (K2P) and 1,000 bootstrap replicates in MEGA-X v10.2.1 (Kumar *et al.*, 2018). The resulting ML tree was used as an input tree for PTP analysis performed on the PTP web server (species.h–its.org/server) using 10,000,000 MCMC generations with 0.1 burn-in rate.

In addition, the ABGD analysis was performed on the ABGD web server (bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html), inserting the fasta file with the aligned sequences, using Kimura (K2P; 2.0) distance model and other parameters at default (Pmin = 0.001; Pmax = 0.1).

Complementary, the ASAP analysis was performed on the ASAP web server (https://bioinfo.mnhn.fr/abi/public/asap/), inserting the fasta file with the aligned sequences, using Kimura (K80; 2.0).

For GMYC analysis, a Bayesian inference was performed to construct a phylogenetic tree, inserting the with the fasta file with unique haplotypes, HKY+I nucleotide evolutionary substitution model, an uncorrelated relaxed clock and a speciation birth-death model (Yule process), on an arbitrary timescale, using BEAUTi and BEAST v.1.8.4 (Drummond *et al.*, 2012). The nucleotide evolutionary substitution model differs from that used in ML analysis once BEAUTi does not present the Kimura 2-parameters model. Two analyses were conducted, one using all *Mesonauta* sequences and one using the 47 unique haplotypes. The latter were used to run the analysis because some errors, such as oversplitting (Pentinsaari *et al*. 2017), are caused when identical sequences are inserted because terminal branches, when are zero length, lead to an infinite coalescent calculate (Fujisawa & Barraclough, 2013; Monaghan *et al*. 2009). A random tree was used as a starting tree for the MCMC searches with a run of 100 million generations, and a tree sampled every 10,000 generations. Following that, Tracer v1.7.2 (Rambaut *et al*., 2018) was used to investigate the distribution of log-likelihood scores and the identification of the stationary phase for each search (to determine whether more runs were necessary to achieve convergence). In the burn-in procedure, the sampled topologies below the asymptote were removed (10%), and the remaining trees were used to construct a 50% majority-rule consensus tree in TreeAnnotator v1.8.4. (included in BEAST). The resultant ultrametric tree was displayed in FigTree v1.4.3 (Rambaut, 2019) and a newick archive exported was employed as an input file for the GMYC analysis done using a single threshold method at the GMYC webserver (species.h–its.org/gmyc/R).

A map of distribution was made under Quantum-GIS program v.3.18.2-Zürich, with locations of analyzed specimens, most of them with COI sequences extracted.

2.2.1.3 Genetic Diversity

DnaSP.6.12 (Rozas *et al*., 2017) was used to examine the genetic diversity of the aligned COI sequences for the number of haplotypes, number of segregating sites (S), haplotype diversity (Hd), nucleotide diversity (π), and average number of nucleotide differences (k).

The minimum spanning network approach, as implemented in Population Analysis with Reticulate Trees, PopA.RT v.1.7 (Leigh and Bryant 2015) a web-based software package, was used to build a genealogical relationship between the haplotypes and the genealogical link with more closely related Rivers was validated using CO1 sequences

2.2.1.4 Morphological analysis

Morphometric data were collected in accordance with Ota et al. (2021, supplementary material 1) and Deprá et al. (2022) of specimens over 42.0 mm SL (Pires et al., 2015). A total of 30 measurements were taken from the left side of 13 specimens of *Mesonauta festivus* from Guaporé/Madeira River basins(UFRO-ICT 6042, UFRO-ICT 11166, UFRO-ICT 6726, MCP 38477, LBP 10824, AMNH 229313, UFRO-ICT 24382), 40 specimens of *Mesonauta festivus* from Paraguay River basin (LBP 1982, LBP 13638, LBP 14019, LBP 3802, LBP 14000, LBP 7594, LBP 10773, LBP 13529, LBP 10135, LBP 10127, LBP 13683, NUP 175, NUP 12592, NUP 5999) and 10 specimens of *M. acora* (Araguaia, NUP 8182, NUP 8204, LBP 4908; Xingu, MNRJ 25082) for comparative purposes. The measurements in percentage of standard length and additionally pre-dorsal in percentage of pre-pelvic fin (Appendix B) were used to run a principal component analysis (PCA; Jolliffe, 2002) using Past v4.03 (Hammer, Harper, & Ryan, 2001).

2.3 Results

2.3.1 Molecular analysis

New COI sequences were obtained from 147 specimens of *Mesonauta* and five additional sequences of *Mesonauta egregius* were downloaded from GenBank, totalizing 161 sequences in the final matrix (152 *Mesonauta*, six *Heros* and one *Pterophyllum*) (Appendix C).

After alignment and editing, the final matrix of *Mesonauta* species had 476 characters, with 336 conserved and 140 variable sites (of which 103 were parsimony-informative), with 22.3% adenine, 29.2% cytosine, 31.6% thymine and 16.9% guanine.

The estimated index of substitution saturation (Iss) performed in DAMBE 5.2.31 (Xia and Xie 2001) showed that the data was not saturated (*i.e.* Iss.c > Iss). Genetic distances of the COI gene between *Mesonauta* morphospecies and other outgroup species are presented in Table 1. Distances between groups are larger than within groups in all groups analyzed.

Table 1. Genetic K2P distance between and within groups in *Mesonauta* species. Standard errors between groups are presented in blue color. In the main diagonal the intraspecific values. d = distance, S.E. = standard error within groups. Values of interspecific distance < 2% are highlighted, showing the non-divergence between groups. *Mesonauta festivus* shows high genetic distance within groups.

Morphospecies		**Between groups**												**Within groups**	
		1	2	3	4	5	6	7	8	9	10	11	12	d	S.E.
1	*Mesonauta* sp. "Amapá"		0,012	0,012	0,013	0,013	0,014	0,013	0,012	0,013	0,020	0,021	0,023	0,000	0,000
2	*Mesonauta mirificus* (Moa)	0,060		0,002	0,004	0,0023	0,011	0,012	0,012	0,013	0,019	0,020	0,025	0,004	0,002
3	*Mesonauta mirificus* (Purus)	0,063	0,007		0,003	0,002	0,011	0,012	0,012	0,013	0,019	0,020	0,025	0,006	0,002

4	*Mesonauta guyanae* (Takutu)	0,066	0,012	0,010		0,003	0,012	0,012	0,013	0,014	0,020	0,020	0,026	0,006	0,002
5	*Mesonauta mirificus* (Negro)	0,064	0,008	0,006	0,008		0,011	0,012	0,012	0,013	0,020	0,020	0,025	0,005	0,002
6	*Mesonauta egregius*	0,072	0,057	0,057	0,062	0,058		0,005	0,012	0,014	0,019	0,019	0,025	0,001	0,001
7	*Mesonauta insignis*	0,069	0,062	0,064	0,069	0,065	0,012		0,012	0,014	0,019	0,020	0,025	0,003	0,001
8	*Mesonauta festivus*	0,069	0,072	0,073	0,078	0,075	0,070	0,070		0,013	0,018	0,018	0,022	0,016	0,004
9	*Mesonauta acora*	0,069	0,074	0,077	0,078	0,078	0,089	0,091	0,076		0,018	0,018	0,024	0,000	0,000
10	*Heros* sp.	0,155	0,149	0,151	0,150	0,152	0,142	0,148	0,136	0,138		0,007	0,023	0,004	0,002
11	*Heros efasciatus*	0,160	0,149	0,148	0,147	0,149	0,144	0,151	0,142	0,132	0,024		0,024	n/c	n/c
12	*Pterophyllum scalare*	0,209	0,235	0,232	0,240	0,234	0,227	0,225	0,201	0,218	0,204	0,213		n/c	n/c

Table 2. Genetic K2P distance between and within groups in *Mesonauta festivus* from Guaporé and Paraguai River basins. Standard errors between groups are presented in blue color. In the main diagonal the intraspecific values. d = distance, S.E. = standard error within groups.

Delimitated group		**Between groups**		**Within groups**	
		1	2	d	S.E.
1	*Mesonauta festivus* (Guaporé)		0,008	0,002	0,001

2	*Mesonauta festivus* (Paraguai) = *Mesonauta* sp. “Pantanal”	0,030		0,001	0,001

Table 3. Genetic K2P distance between and within groups of unique haplotypes of *Mesonauta*. Standard errors between groups are presented in blue color. In the main diagonal the intraspecific values. d = distance, S.E. = standard error within groups. Values of interspecific distance < 2% are highlighted, showing the non-divergence between groups. *Mesonauta festivus* shows high genetic distance within groups.

Species		**N haplotypes**	**N sequences**	**Between groups**										**Within groups**	
				1	2	3	4	5	6	7	8	9	10	d	S.E.
1	*Mesonauta sp. "Amapá"*	1	3		0,012	0,012	0,013	0,013	0,012	0,013	0,022	0,022	0,024	n/c	n/c
2	*Mesonauta mirificus*	24	80	0,064		0,003	0,011	0,011	0,012	0,013	0,020	0,020	0,025	0,009	0,002
3	*Mesonauta guyanae*	3	17	0,065	0,010		0,011	0,012	0,013	0,013	0,020	0,021	0,026	0,010	0,004
4	*Mesonauta egregius*	2	7	0,074	0,059	0,060		0,004	0,011	0,015	0,019	0,020	0,025	0,004	0,003
5	*Mesonauta insignis*	3	13	0,069	0,064	0,065	0,013		0,011	0,015	0,020	0,020	0,025	0,007	0,003
6	*Mesonauta festivus*	8	28	0,069	0,074	0,077	0,069	0,069		0,013	0,019	0,019	0,022	0,016	0,004
7	*Mesonauta acora*	1	4	0,069	0,078	0,077	0,091	0,091	0,075		0,020	0,020	0,025	n/c	n/c
8	*Heros sp.*	3	5	0,156	0,151	0,151	0,145	0,150	0,137	0,138		0,007	0,024	0,006	0,003

9	*Heros efasciatus*	1	1	0,160	0,148	0,148	0,146	0,151	0,143	0,132	0,024		0,024	n/c	n/c
10	*Pterophyllum*	1	1	0,209	0,234	0,238	0,229	0,226	0,202	0,218	0,204	0,213		n/c	n/c

The ML tree inferred through MEGA-X recovered the six groups consistent with the genetic distance analysis (Table 1), once morphotypes of *Mesonauta mirificus* from different River basins and *M. guyanae* have low genetic divergence (cutoff < 2%), and exhibited strong node support for each species (Fig. 1).

2.3.1.1 Delimitation analysis

The ABGD analysis resulted in nine partitions that ranged from 3 (P = 0.059) to 45 (P = 0.001) lineages, with four partitions (P = 0.004–0.0021) resulting in 8 lineages, six of them from *Mesonauta* species and two from the outgroup. The ASAP analysis resulted in 10 partitions that ranged from 2 (score = 4.0) to 48 (score=8.5) lineages, with two partitions with 8 lineages (lowest score = 2.5) (see Appendix D for details in the delimitation analyses).

With the exception of GMYC and morphological analysis, all species delimitation analyses (PTP, ABGD, ASAP and genetic distance) corroborate the separation of *Mesonauta* species into six groups (Figs. 1-2): *Mesonauta mirificus* and *M. guyanae* represent a single OTU (1) *Mesonauta mirificus*, widely distributed from Amazon River basin, Suriname, Oiapoque, Tapajós, Moa, Negro and Xingu Rivers; (2) *Mesonauta festivus* splited into two OTUs: (2) *Mesonauta festivus* from Guaporé and Madeira River basin and *Mesonauta festivus* from Paraguai River basin, herein named (3) *Mesonauta* sp. “Pantanal”; (4) *M. acora* from Tocantins-Araguaia and Xingu River basin; (5) *Mesonauta* sp. “Amapá” from Amapá Grande and Jeju River basin; *M. egregius* and *M. insignis* represent a single OTU, herein named (6) *M. insignis* from Orinoco and Negro River basins.

GMYC analysis recovered four lineages: 36 to the mtDNA-based *M. mirificus*, 5 to the morphotype of *M. insignis*, 3 to the morphotype of *M. egregius*; 3 to *Mesonauta* sp. “Pantanal”; 6 to *M. festivus*, 2 to *M. acora* and 3 to the outgroup *Heros efasciatus*. When unique haplotypes were used only for GMYC, the method recovered four lineages, lumping *Mesonauta festivus* from Guaporé and Paraguai (*Mesonauta* sp. “Pantanal”) River basins, the *M. insignis* and *M. egregius*, and the *M. acora* and *Mesonauta* sp. “Amapá” (Appendi D, fig..

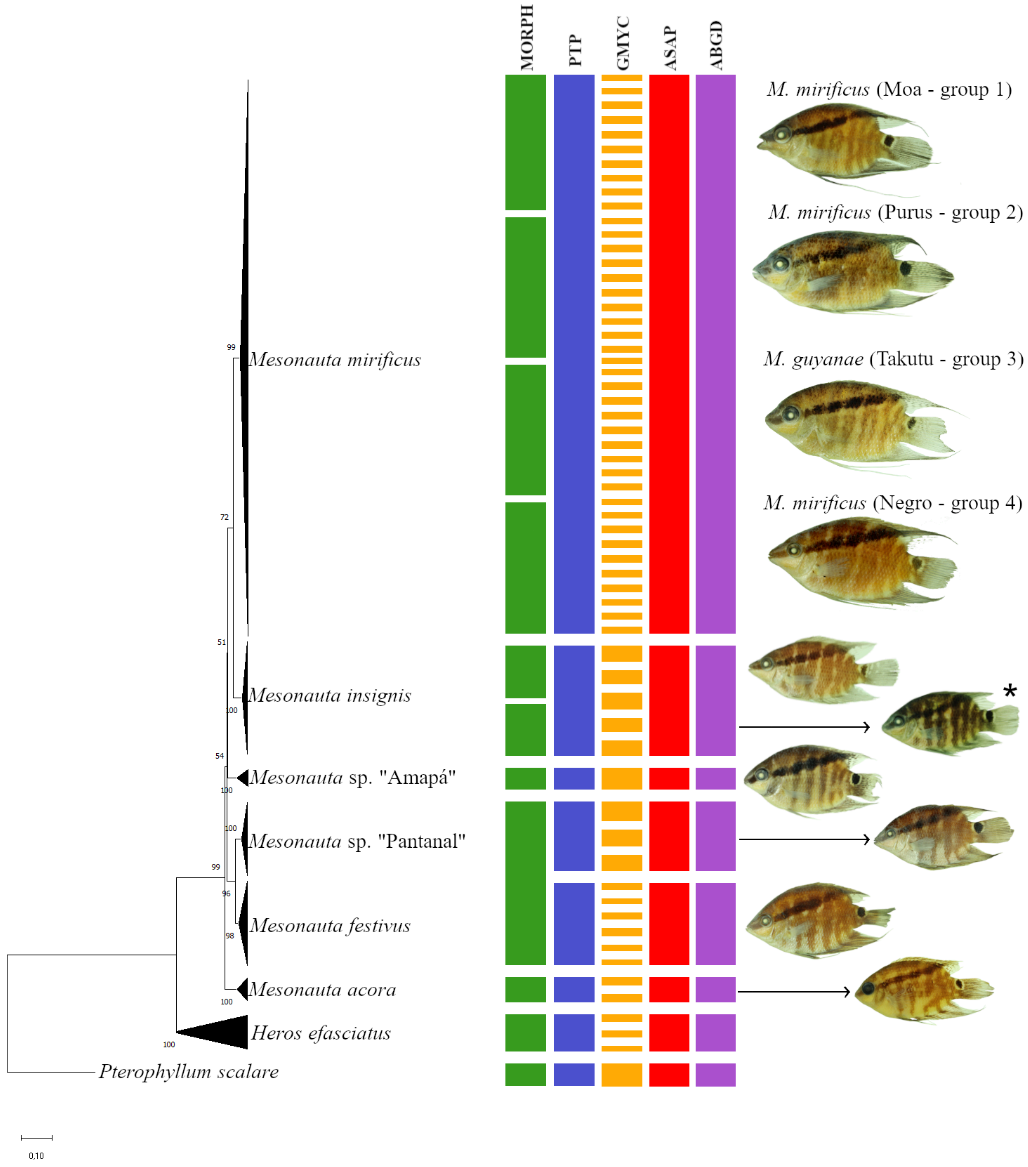

Figure 1. Maximum likelihood COI tree of *Mesonauta* species, showing the delimitation methods and photographs of *Mesonauta* morphotypes. The four morphotypes of

Mesonauta mirificus do not represent entire intragroups or monophyletic clades; Note that *M. insignis* is represented by two morphotypes, *M. insignis* above and (*) *M. egregius* below, but in most of delimitation analysis and genetic distance it was recovered as a single species (see remarks and Appendix D, Fig. D1 for more details).

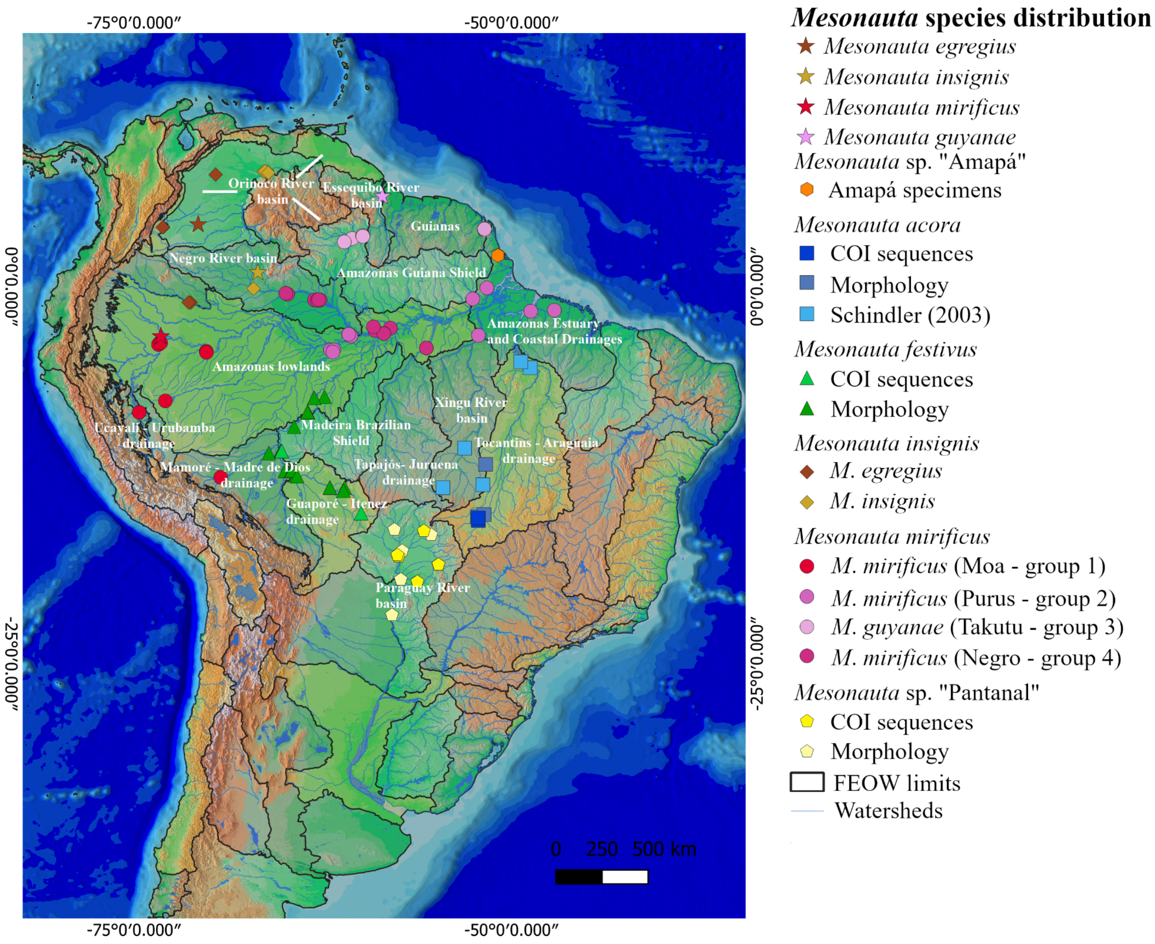

Figure 2. Distribution of *Mesonauta* species from the AOG region, Paraguay and Araguaia River basins. Colored stars (★) represent the approximate type-locality of *Mesonauta* species from Kullander & Silfvergrip (1991) and Schindler (1998). *Mesonauta acora* is described from Araguaia River, no types known; *Mesonauta festivus* is described from Guaporé River, no types known.

2.3.1.2 Haplotype network

A total of 154 sequences of *Mesonauta* were used providing 38 haplotypes from COI sequences analysis. The overall haplotype diversity was 0.946, and nucleotide diversity was 0.04227. The average number of nucleotide differences (*k*) was 16,73712 overall. Most of the Amazonian haplotypes are grouped (purple-ellipsed, *Mesonauta mirificus* clade) and had the most significant number of haplotypes (26) (Fig. 3), with one of the haplotypes composed by 23 individuals (higher frequency), shared by specimens from Manacapuru River, Tapajós River and Alenquer.

The Paraguayan populations (orange-ellipsed, *Mesonauta* sp. “Pantanal” clade) have two haplotypes, one from Taquari River and other from Paraguai/Cuiabá Rivers, and were well connected to the Guaporé/Madeira populations (green-ellipsed, *Mesonauta festivus* clade), which present four haplotypes, one of them shared with Madeira specimens and two other haplotypes with one specimen each.

The Araguaia population (light-pink-ellipsed, *Mesonauta acora* clade) has a single haplotype with four individuals, connected to the *Mesonauta guyanae* clade (blue-ellipsed).

The Amapá Grande population has one haplotype which is shared with the Guamá specimen (Jeju River, specifically) forming the *Mesonauta* sp. “Amapá” clade.

Specifically Negro River specimens are divided into five haplotypes, one belonging to upper Negro River (i.e. region of São Gabriel da Cachoeira) from *Mesonauta insignis* clade (red-ellipsed), closer related to three haplotypes from Orinoco River; four haplotypes distributed among the *Mesonauta insignis* clade, in which one is shared with specimens from Oiapoque, other shared with specimens from Amazon River basin, one haplotype of one specimen connected to five other haplotypes, and the last one linked to the larger haplotype from *Mesonauta mirificus* clade.

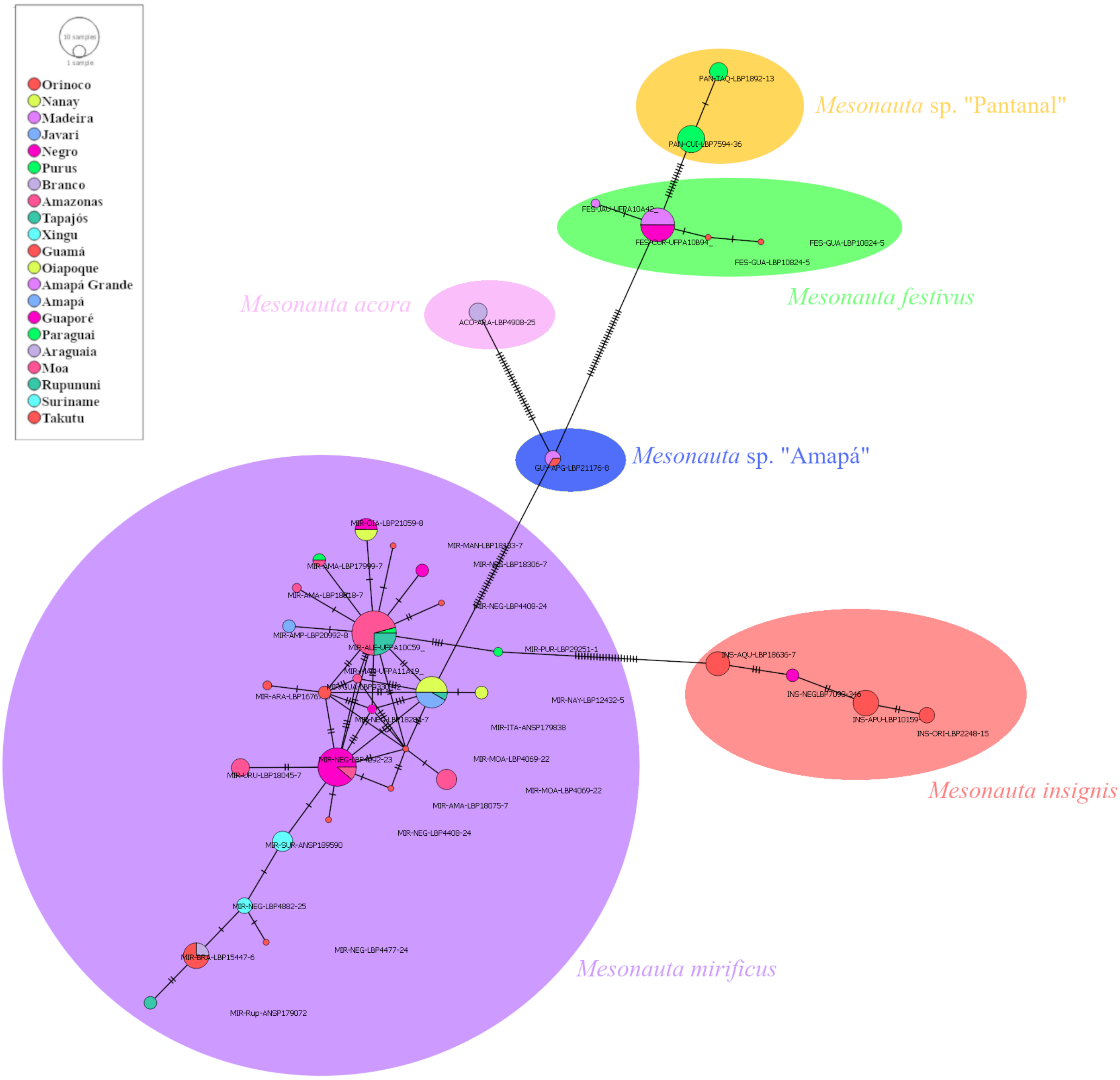

Figure 3. Minimum spanning network based on the *CO1* sequences of *Mesonauta* species. The larger ellipses represent the species clades.

2.3.2 Morphological analysis

2.3.2.1 Morphometrics

The morphometric PCA indicated some changes in morphospace but with superposition between *Mesonauta festivus* from the Guaporé and *Mesonauta* sp. “Pantanal” from Paraguay River (Fig. 4). Aspects of morphology that rely largely on the first two principal components are body depth (PC1 = 0.445), dorsal-anal distance (PC1 = 0.402), dorsal-pelvic (PC1 = 0.368), predorsal/prepelvic distance (PC1 = -0.490), snout length (PC2 = 0.452) Lacrimal depth (PC2 = 0.368), Cheek depth (PC2 = 0.348), Orbital width (PC2 = -0.303), Snout-anal distance (PC2 = -0.287), Snout-pelvic distance (PC2 = -0.297); (Appendix E). For all studied specimens, PC1 explains 51,97% of the variation while PC2 explains 27,81% of the variation. Coloration patterns and counts demonstrated no substantial difference between *M. festivus* and *Mesonauta* sp. Pantanal.

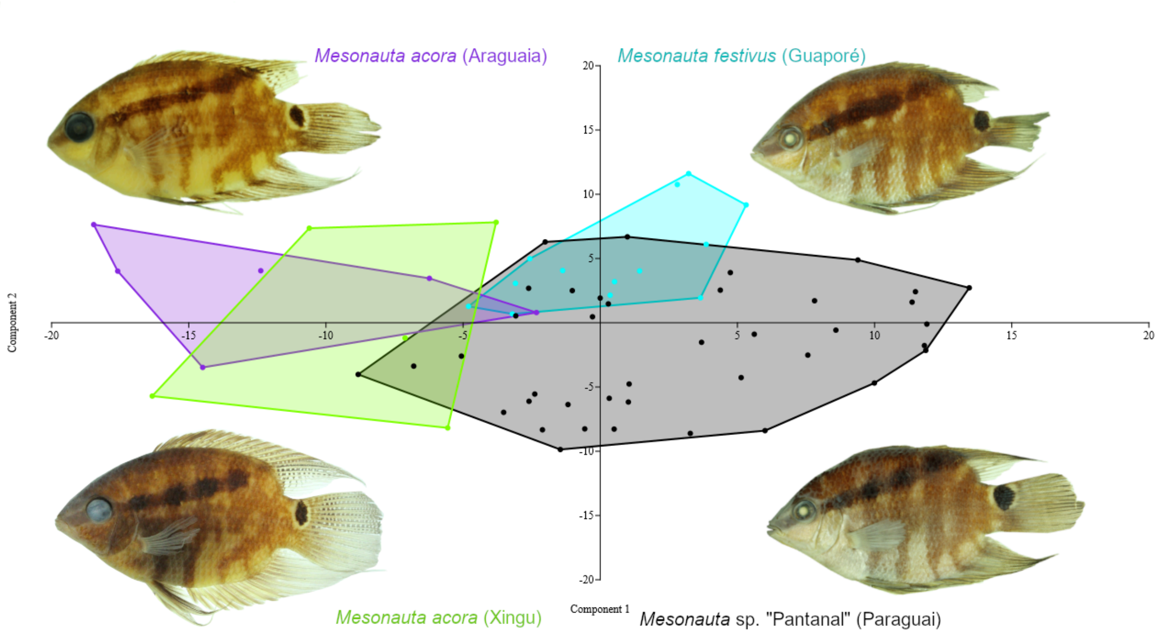

Figure 4. Principal component analysis (PCA) of morphological data and preserved specimens of *Mesonauta festivus* and *Mesonauta* sp. "Pantanal", and comparative *Mesonauta acora* from Araguaia and Xingu basins.

2.3.2.2 Color pattern characterization and COI groups remarks

Mesonauta acora: the coloration pattern in adult and juvenile specimens is similar to the presented by Kullander and Silfvergrip (1991), with a mottled pattern between bars 3-5, and a rupture in the bar. Distribution: present study - Araguaia and Xingu Rivers; Kullander and Silfvergrip (1991), and Schindler (2003) - Tocantins-Araguaia and Xingu Rivers. Type-locality - Araguaia River.

Mesonauta festivus: specimens from Guaporé River basin present the color pattern identical to species description, with bars 3-4 united, forming an "X", with no reticulate pattern. The specimens from Tapajós River basin (which are supposed to pertain to *M. festivus*) are described below in *M. mirificus*, because of the differentiation in color pattern and mtDNA segregation. Distribution: present study - Guaporé-Madeira system and Madre de Dios River; Kullander and Silfvergrip (1991) Guaporé, Paraguai, Madre de Dios, Tapajós. Type-locality - Guaporé River.

Mesonauta sp. "Pantanal": the delimitation analysis separated specimens from Paraguay River basin from those from Guaporé River basin, however, their have similar color pattern, indiscernible between both, also presenting bars 3-4 united, forming and "X", with no reticulate pattern. Distribution: present study - Paraguay River basin.

Mesonauta sp. "Amapá": differently from *Mesonauta guyanae* coloration pattern (bar 5 divided above in two bars), specimens from Amapá Grande River presents bars 4-7 straight and not divided, and caudal fin pigmented, while live specimens from Jeju River present bars 5 and 6 divided above in two bars. Distribution: present study - Amapá Grande River and Jeju.

Mesonauta insignis: the delimitation analyzes united specimens of *M. insignis* and *M. egregius* (Genbank sequences) from Orinoco River basin and *M. egregius* (Aquarium trade - Colombia). *M. insignis* present bars 6-7 joined at the bottom as it was in species description, while Aquarium specimen present bar 6 slightly divided above into two bars. Specimens from Genbank present the *M. egregius* color pattern, with bar 6 also divided above in two. Distribution: present study, Kullander and Silfvergrip (1991) - Orinoco and Negro Rivers (São Gabriel da Cachoeira section). Type-locality - Upper Negro River.

Mesonauta mirificus: Here, we address specimens of *Mesonauta mirificus* and those that have been morphologically determined to be *M. guyanae*. Molecular study indicates that both belong to a single species. As a result, we divide into *M. mirificus* morphotypes once this species was previously stated. Some groups show specimens from the same locality not clustering right together, resulting in polyphyletic groups (see Appendix D for more details). This is the case of *Mesonauta mirificus* species from Purus, Negro, Xingu, Tapajós, Manacapuru, Amazonas, Urubu, Preto do Eva, and Guamá, while there are monophyletic lineages from Moa, Oiapoque, Itaya-Javari-Ucayali-Nanay and Takutu-Branco Rivers. Color patterns differ among some groups (see Appendix E for more details): (1) specimens from Moa, Itaya-Javari-Ucayali-Nanay Rivers are similar to each other, presenting bar 6 divided above in two (*M. mirificus* pattern); (2) specimens from Purus resembles those from Manacapuru and Guamá Rivers, with a "grid" color pattern, where bars 3-4 are slightly united (*M. festivus* pattern), bar 5 is divided above in two (*M. guyanae* pattern), and present a reticulate pattern, i.e., scales with dark borders; (3) Takutu-Branco and Oiapoque specimens present bar 5 divided above in two (*M. guyanae* pattern); (4) Specimens from Negro, Tapajós, Amazonas and Urubu have bars 6-7 joined at the bottom (*M. insignis* pattern), 5 divided above (*M. guyanae* pattern) and with reticulate pattern. Those from Xingu and Preto do Eva Rivers are too young to define the coloration pattern. Due to discrepancies in color pattern and its broad distribution, *Mesonauta mirificus* species groups need more investigation. Distribution: present study - Amazon River basin, Suriname, Oiapoque, Tapajós, Moa, Itaya, Javari, Ucayali, Nanay, Negro, Takutu, Branco and Xingu Rivers. Kullander and Silfvergrip (1991) - Ucayali, Napo, Ampiyacu; type locality of *M. mirificus* - Rio Mazán, near the mouth of the Napo River. Schindler (2004) - from Yarinacocha on the middle Ucayali (Pucallpa, Peru) to Isla Mocagua, above Leticia on the Amazon in Peru, the lower reaches of various

Rivers in Ecuador part of the Amazon system. Type locality of *M. guyanae* - Essequibo River, Rockstone, Guyana.

2.4 Discussion

Delimitation analysis plus genetic distance results do support two of the earlier morphological five species proposed in Kullander and Silfvergrip's (1991) revision of *Mesonauta* species and Schindler's (1998) *Mesonauta guyanae* species description. Previous research in cichlids also indicated a discrepancy between molecular and morphological delimitation (Willis *et al*., 2012). While certain groups showed high levels of molecular diversification (for example, *Mesonauta festivus* from the Guaporé River basin vs. *Mesonauta* sp. "Pantanal" from the Paraguay River basin), but with low morphological difference, others from distant regions have low values of genetic distance whereas present discrepancies in coloration pattern, which is the case of *M. mirificus*. The Haplotype network revealed a different number of haplotypes per species.

The different approaches of species delimitation yielded divergent findings, however the majority of the delimitation analysis delineated six *Mesonauta* groups, diverging from the species described before by the recovery of *M. acora* and a putative new species *Mesonauta* sp. "Amapá", the union in a single OTU the *M. insignis* with *M. egregius* and *M. mirificus* with *M. guyanae*, the split of *M. festivus* into two OTUs, one of them being a putative new species *Mesonauta* sp. "Pantanal" from the Paraguai River basin, each explained posteriorly. When majority of the species delimitation methods are in agreement, this is probably an operational taxonomic unit (OTU) recovered (Ramirez *et al*., 2023). Moreover, when interspecific genetic divergence is more than 2%, it is considered a suitable threshold for species delimitation (de Carvalho *et al*., 2011; Pereira *et al*., 2011a; 2011b; 2013). Herein COI was used to delimit species, but with morphological incongruence. Some studies show that DNA-barcode reveals the minimal source of variation necessary to separate species and delimited several groups with high precision (Serrano et al., 2018; Zhang et al., 2021, Oliveira et al., 2023). In contraposition, others properly showed concerns in the use of one-locus delimitation (DeSalle & Goldstein, 2019). It is necessary to emphasize that molecular data is a part of the species delimitation input, once morphological data, as measurements, color pattern, and others should be investigated to separate species.

The most divergent delimitation analysis was GMYC, which oversplitting could be caused by some factors. As reported by Pentinsaari *et al.* (2017) oversplitting occurs by errors during dating the ultrametric tree. Zhang *et al.* (2013) demonstrated this by observing a higher count of OTUs in 3/5 of the data sets when the ultrametric tree was analyzed under PTP *vs*. employing ML tree as input. When we also tested the ultrametric tree under PTP analysis, the same scenario occurred with our data set. The analysis, for example, split *Mesonauta festivus* from the Guaporé River basin into two OTUs as in the GMYC delimitation. As GMYC tends to oversplit when equal sequences are used (Fujisawa & Barraclough, 2013; Monaghan *et al.* 2009), when using the unique haplotypes to run the analysis, the number of species decreases.

Mesonauta insignis was not recovered as a species complex. In the present study, *M. insignis* occurs in the Upper Negro river and Orinoco River basin, and *M. egregius* occurs in the upper Meta river (Orinoco basin). Both species are clustered, forming a unique OTU and also have identical COI haplotypes. Although both species are nested together in delimitation analyzes, the difference in color pattern reveal two morphological sympatric species proposed by Kullander & Silfvergrip (1991). In Říčan *et al.* (2023), the authors showed biogeographic patterns of a northern group of *Bujurquina* species with a wide ancestral area fragmented by vicariance (separation of Orinoco from North-Western Amazon at 7.9 Ma). Same is possible to occur with *Mesonauta insignis*, in which haplotypes from Orinoco River basin are not shared, but related to *Mesonauta mirificus* haplotypes from Purus River (Amazon River basin). Further, *M. insignis* is present in both basins, which is in agreement of other cichlid species occurrence (Willis *et al*., 2010), once (besides dispersal decrease with this separation), the Casiquiare channel enabled the move of some fish species between Upper Negro and Upper Orinoco basins (Winnemiller *et al*., 2008).

Except for GMYC, *Mesonauta acora* was recovered as an OTU in all delimitation analyzes and represents a single haplotype from Araguaia River basin, which is also compatible with morphological analysis. Voucher specimens observed from mtDNA and together with only morphological analyzed specimens (i.e. Xingu's River basin specimens), revealed similarities in morphology, color pattern and distribution corresponding to the species revision (Kullander & Silfvergrip (1991). The specimen with the COI sequence from the Xingu River basin analyzed clustered with *Mesonauta mirificus* specimens, and because it is a young specimen, it is difficult to determine to which species it is meant to belong morphologically.

Occurrences of *Mesonauta festivus* were recorded in Paraguay, Guaporé, Mamoré, Madeira, and lower Tapajós (sensu Kullander & Silfvergrip, 1991). Other cichlids, such as *Apistogramma trifasciata*, *Aequidens plagiozonatus*, *Bujurquina vitatta*, were recorded in Paraguay/Guaporé River basins (Steinhäuser, 2017). However, differently and unexpected, delimitation analyzes divided *Mesonauta festivus* into two OTUs, *Mesonauta festivus*, restricted to the Guaporé/Madeira River basin and *Mesonauta* sp. "Pantanal", restricted to the Paraguay River basin. Moreover, specimens from Tajapós were genetically different, clustering together with *Mesonauta mirificus* (see below). The similarities in color pattern, measurements and counts reveals a single morphological species, since they are morphologically indistinguishable, they are classified as cryptic species. The two locations (Guaporé-Paraguay) have been shown to have fauna interchange due to vicariance and dispersal events for some groups of fishes (Costa, 2010; Hubert & Renno, 2006) and are considered areas of endemism. For example, in *Bujurquina*, a vicariant event occurred at 10.2 Ma, where its southern group divided into Paraguay-Paraná vs. Madre de Dios-upper Ucayali. (Říčan et al., 2023). During the Late Miocene (c. 10 Ma), uplift of the Northern Andes and the Vaupés Arch caused the Amazon River to invade the Purus arch, connecting the Western Amazon river basins and enhancing species interchange (Cassemiro *et al*., 2022). This resulted in dispersal events between the Western Amazon and La Plata, as well as between Upper Madeira and Upper Paraguay (Cassemiro *et al*., 2022). On the other hand, since *Mesonauta* sp. "Pantanal" doesn`t present specimens collected in the upper Paraguay, additional research is needed to determine which most likely causes the splitting into the two species.

Mesonauta sp. "Amapá" was recovered as a single OTU in all delimitation analysis, and represents one haplotype shared by two localities, Jeju and Amapá Grande River. Furthermore, the color pattern differs from the *M. guyanae* described (see color pattern section). Although specimens from Amapá Grande River clustered together with the Jeju in the ML analysis, both have some differences in color pattern that need to be more investigated. *Mesonauta guyanae*, described from the Essequibo River, has been occurring in the Amazon River basin according to the original description (Schindler, 1998). Also, Schindler (2003) mentioned the occurrence of specimens that resemble *M. guyanae* in Guamá River basin. However, our results show no molecular difference between *M. guyanae* and *M. mirificus*, since specimens from Suriname, which were supposed to be *M. guyanae*, were clustered together with the *M. mirificus* specimens (see below).

The *Mesonauta mirificus* is described from Peru's Napo River (Kullander & Silfvergrip, 1991). However, the ML analysis revealed that specimens from Peru (e.g. Ucayali/Nanay Rivers) and from Moa River clustered together with a variety of specimens found throughout the Amazon River basin. Specimens from Peru show the morphological *M. mirificus* color pattern, with bar 6 divided above in two, while specimens from other locations show a different configuration of bars and other color patterns. The Haplotype network revealed 26 different populations, with mixed locations. For example, specimens from Takutu and Branco Rivers are inside of the same haplotype, whereas specimens from Negro River are divided into several haplotypes. A range of reasons, such as introgression, hybridization, recent speciation, or insufficient lineage sorting (Zhang et al., 2021) could explain the considerable morphological variance in coloration patterns with low genetic differences. The same occurs in the *Mesonauta insignis*, where Orinocoan and Colombian *M. egregius* specimens are clustered together with *M. insignis* from Orinoco and Negro Rivers. Carvalho *et al.* (2019) revealed cichlid species that have recent diversification or cases of hybridization, could not be detected under single-locus species-discovery (SLSD), and it is possible that those species are in the "gray zone" of speciation, showing genetic divergence between 0.5–2% (Roux *et al.*, 2016).

2.5 Conclusions

When compared to morphological examination, the COI was able to delimit most previously known species; nevertheless, it is possible that delimitation analysis using COI understimate the diversity within the *Mesonauta mirificus vs. M. guyanae*, and *M. insignis vs. M. egregius*. We underline the importance of morphology in confirming newly identified species delimitation conclusions, as well as the ongoing use of integrated taxonomic approaches. The findings offer a new perspective into cichlid diversity and lay the framework for future research, with an emphasis on the widespread *Mesonauta mirificus*, to better understand the group's population dynamics and evolution.

Data availability

All data supporting the conclusions can be accessed on the supplementary material.

Conflict of interest

The authors declare no conflict of interest.

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3 MOLECULAR PHYLOGENY OF *Mesonauta* GÜNTHER 1862 (CICHLIFORMES: CICHLIDAE)

ABSTRACT

Heroini accomplishes several Central and South-American cichlids forming a monophyletic clade. Despite intergeneric relationships within the tribe being well-resolved, some genera still lack phylogenetic resolution. Here we recover the *Mesonauta* phylogeny using molecular data from two mitochondrial genes, the cytochrome c oxidase subunit 1 (COI) and the non-coding 16S ribosomal rRNA (16S) gene. The combined data was analyzed under three methods: maximum likelihood (ML), bayesian inference (BI) and maximum parsimony (MP). Results show *Mesonauta* as monophyletic, with six main monophyletic groups: Clade (A) is composed by 1) *Mesonauta festivus* from Guaporé River basin as sister to 2) *Mesonauta* sp. "Pantanal" from Paraguay River basin, both as the sisters to a group composed by 3) *M. acora* from Tocantins-Araguaia and Xingu River basins as sister group to 4) *Mesonauta* sp. "Amapá" from Amapá Grande River basin. Clade (B) is composed by 5) *Mesonauta insignis* from Orinoco and Upper Negro River basins as sister to 6) *M. mirificus* widely distributed in the Amazon River basin. Further, clade (A) is a sister group to Clade (B). Previous study in delimitation investigation has suggested that *Mesonauta insignis* comprehends *M. egregius*, while *M. mirificus* comprehends *M. guyanae*. This is the first step on the study on *Mesonauta* molecular phylogeny which highlighted the intrageneric relationship according to molecular data, and also provided data for future studies on the evolution of the group.

3.1 Introduction

Phylogenetic studies use morphological or molecular characters to construct trees with satisfactory topologies. However, incongruences found between topologies in the different works may occur due to the differences in the methodologies used (López-Fernández *et al.* 2010; Říčan *et al.*, 2016) and also due to the small number of loci or morphological characters used (e.g. Friedman *et al.*, 2013). For this reason, integrative taxonomy is appreciated for resolving these biases, so that they provide a greater range of data to be investigated (Pante *et al.*, 2015, Ramirez *et al.,* 2017). In addition to being significant for reconstructing the phylogeny of a group, integrated analyzes allow the delimitation of possible species that, in some cases, only the alpha taxonomy would have difficulty in defining.

On the other hand, it is possible to recover phylogeny at genera level using only molecular data, and multilocus analysis has been used for this purpose (Willis *et al.*, 2012; Ilves *et al.*, 2018). Molecular phylogenies were employed in cichlids to reconstruct trees in a broader context (e.g. Cichlid phylogeny, see Ilves *et al.*, 2018). Heroini is a well-supported clade among the seven Cichlinae tribes proposed by Ilves *et al.* (2018) with five nominal clades. Among them, "mesonautines" comprises only South America's Heroini fish diversity, including *Mesonauta* Günther 1862 sister to *Heros*, and them as sister to *Symphysodon* and *Uaru*. *Mesonauta* includes six currently valid species: *M. insignis* (Heckel 1840), *M. festivus* (Heckel 1840), *M. acora* (Castelnau 1855), *M. egregius* Kullander & Silfvergrip 1991, *M. mirificus* Kullander & Silfvergrip 1991, and *M. guyanae* Schindler 1998. They are appreciated by aquarists for their striking coloration, change of color during parental care (Pires *et al.*, 2015) and agonistic reproductive behavior (Sarmento, 2017).

In the Ilves *et al.* (2018) cichlid phylogeny, only two *Mesonauta* species were included in the analysis, thus, the study does not clarify the phylogenetic relationships of the species within the genus. The difficulty in determining *Mesonauta* relationships may be caused by the group's difficulties in sampling sequences and delimiting species. Once delimitation is proposed by (Oliveira *et al.*, 2024), the intrageneric relationships can be studied.

In this context the aim of this study is to study *Mesonauta* in order to 1) test *Mesonauta* monophyly and 2) reconstruct the reliable relationship evidencing the intrageneric clades using two different loci, the mitochondrial coding cytochrome c oxidase subunit I (COI) and the mitochondrial non-coding 16S ribosomal rRNA (16S). Both genes have been extensively used and are reliable to propose the main phylogeny hypothesis in a multilocus landscape (Zou *et al*., 2011; Willis *et al*., 2012; Zhang *et al*., 2021).

3.2 Material and Methods

3.2.1 Molecular data

3.2.1.1 Sampling and sequencing.

Molecular data included in the analysis comprises two loci: the mitochondrial coding gene cytochrome c oxidase subunit 1 (COI) and the mitochondrial non-coding 16S ribosomal rRNA (16S). The molecular dataset comprised 32 terminal taxa, 26 of them of *Mesonauta*. Outgroup species (Table 1) corresponds to the sequences of COI and 16S extracted from Genbank whose voucher we have not examined. Tissue samples were extracted from samples preserved and stored at 95º GL ethanol. Voucher specimens were fixed in 10% formalin and then stored at 70º GL ethanol.

Table 1. Sequences of outgroup species extracted from Genbank database.

Acession number	**Genbank name**	**Current status**	**Reference**
DQ119220.1 - COI DQ119191.1 - 16S	*Uaru amphiacanthoides*	*Uaru amphiacanthoides*	Chakrabarty (2006)
DQ119219.1 - COI DQ119190.1 - 16S	*Hypselecara temporalis*	*Hypselecara temporalis*	Chakrabarty (2006)

DQ119218.1 - COI DQ119189.1 - 16S	*Heros efasciatus*	*Heros efasciatus*	Chakrabarty (2006)
DQ119197.1 - COI DQ119168.1 - 16S	*Nandopsis octofasciata*	*Rocio octofasciata*	Chakrabarty (2006)
DQ119195.1 - COI DQ119166.1 - 16S	*Herotilapia multispinosa*	*Herotilapia multispinosa*	Chakrabarty (2006)

Total DNA was extracted following Ivanova *et al*. (2006). The DNA region of the COI was amplified by polymerase chain reaction (PCR) using the primers FISH-F6 (5’-ACYAAYCACAAAGAYATTGGCA-3’) and FISH-R7 (5’-TARACTTCTGGRTGDCCRAAGAAYCA-3’) described by Jennings *et al*. (2019), and the DNA region of 16S was amplified by PCR using the primers 16SF (5’-GAC TTG AAA AACCAYCGTTGT-3’) and 16SR (5’-CGTTTGGGAGTTAGDGGTGGGAGTTAGAATC -3’) according to Palumbi (1996). The PCR was performed on a thermocycler with a final volume of 12.5 µl containing 7.85 µl distilled water (ddH2O), 0.30 µl deoxynucleotide triphosphate (dNTP) (2 mM), 1.25 µl PCR buffer (10×), 0.4 µl MgCl2 (50 mM), 0.25 µl each primer, 2 µL DNA (200 ng) and 0.20 µl Taq DNA polymerase PHT (Phoneutria). The following conditions were used for COI PCR: an initial denaturation at 95º C for 5 min, followed by 30 cycles including denaturation at 95ºC for 60 s, annealing (primer hybridization) at 52º C for 45 s and nucleotide extension at 68ºC for 1 min, with a final extension at 68º C for 10 min. The following conditions were used for 16S PCR: an initial denaturation at 94º C for 5 min, followed by 40 cycles including denaturation at 94ºC for 30 s, annealing (primer hybridization) at 48º C for 45 s and nucleotide extension at 72ºC for 45 s, with a final extension at 72º C for 10 min. The PCR products were amplified and checked on a 1% agarose gel before being purified using ExoSAP-IT (USB Corporation, Cleveland, OH, USA) in line with the manufacturer's instructions.

We use the BigDye Terminator v3.1 Cycle Sequencing Ready Reaction kit (Applied Biosystems, Austin, TX, USA) in a final volume of 7 µl containing 0.35 µl primer (10 mM), 1.05 µl buffer 5×, 0.7 µl BigDye mix and 3.9 µl distilled water to sequence both DNA strands from COI and from 16S genes. DNA was purified using ethanol precipitation and sequenced using the 3500-Genetic Analyzer (Applied Biosystems) at IBTEC, at the Instituto de Biociências at Universidade Estadual Paulista "Júlio de Mesquita Filho", UNESP, Botucatu, São Paulo, Brazil.

The sequences were processed using Mega-X v10.2.1 (Kumar *et al.*, 2018), which included aligning through the ClustalW algorithm (Thompson *et al.*, 1994), translation of coding regions to account for stop codons and correction of the reading frame. Alignments were inspected by eye and ends were trimmed when there were gaps in many taxa, to decrease the amount of missing data and non-homologous sites. Ending gaps (-) were converted to missing data (?) but gaps along the sequences in 16S were maintained. Sequences are in Appendix F.

3.2.1.2 Phylogenetic analyses

Maximum Likelihood (ML) and Bayesian Inference (BI) were used to examine the sequences. The concatenated matrix in fasta format was used as input for ML, and the analysis was performed using IQ-tree (Minh *et al.*, 2020) (best-fit model was selected inside the software); output was utilized on Figtree to examine the tree constructed. Branch support for the ML analysis was calculated by resampling the Ultrafast Bootstrap implementation in IQtree 1,000 times.

BEAST v.1.8.4 was used for the BI analysis (Drummond *et al.*, 2012). On an arbitrary timescale, the fasta file was placed into BEAUti, which used the HKY+I (the available model into BEAUTi) nucleotide evolutionary substitution model, an uncorrelated relaxed clock, and a speciation birth-death model (Yule process). For the MCMC searches, a random tree with 100 million generations was employed, and the tree was sampled every 10,000 generations. On Tracer v1.7.2 (Rambaut *et al*., 2018) occurred the investigation of the distribution of log-likelihood scores as the identification of the stationary phase for each search (to determine whether more runs were necessary to achieve convergence, e.g. ESS > 200). On TreeAnnotator v1.8.4 (included in BEAST) the burn-in procedure was performed, where the sampled topologies below the asymptote were removed (25%), and the remaining trees were used to construct a majority-rule consensus tree. The output ultrametric tree was visualized in FigTree v1.4.3 (Rambaut, 2019).

The TNT 1.1, where parsimony analyses were carried out (Goloboff *et al*., 2003, 2008) with the input of .tnt files (Appendix F). Fifth state was defined as gaps in 16S alignments. All of the molecular features were given the same weight (EW) while doing the main parsimony analyses. However, we also utilized extended implied weighting (XIW; Goloboff, 2014) to investigate the influence of cladistic congruence between the various data sources while accounting for their inherent characteristics (*i.e*., kind of data, varying amounts of missing data in each partition). In XIW analysis, the non-coding gene 16S was weighted by average homoplasy, and the first, second, and third codon positions of the coding genes (COI) were weighted differently based on their average homoplasy. In the WIW analysis, a "mild" constant k = 12 was chosen because it has been suggested for larger data sets (e.g. Goloboff *et al*., 2008b, 2017). This is due to the fact that it does not downweight putative homoplastic characters as much as lower k-values (e.g. default k=3).

Searches using traditional heuristic searches The Tree Bisection Reconnection (TBR) method was used for conventional searches. The number of replications was fixed once the top score was acquired at least 50 times, ensuring a reasonably thorough search. The number of trees per replication was chosen to prevent overflow (*i.e*., trees generated by the replication that could not be saved due to restricted memory). In traditional parsimony analyses, an initial TBR run with 10,000 replications, retaining 100 trees each replication, was followed by additional TBR branch swapping runs on the trees held in memory until the number of most parsimonious trees (henceforth MPT) reached stationarity. A strict consensus tree was created by combining the most parsimonious trees. Each node's support was calculated via bootstrap index resampling. Positions of nucleotides are according to sequenced material and character transformations positions are presented for MP analysis and comments in the discussion section.

3.2.1.3 Character reconstructions and synapomorphies

Character reconstructions were performed using the parsimony as criterion of optimality in order to define synapomorphies for each group. For that, the most parsimonious weighted tree from the most parsimonious analysis was used as input to through optimization of all molecular data, an output with the list of the common synapomorphies and the list of character transformations was obtained. The polarization of the character states was performed by the method of outgroup comparison (Nixon & Carpenter, 1993), using the South American cichlid *Hypselecara temporalis* as the root, since it has been recovered as sister group of all "Mesonautines" (*sensu* Ilves *et al*., 2018).

3.3 Results

3.3.1 Data heterogeneity and complementarity

Tha alignments derived from the molecular sequences herein extracted (2 genes, 1064 bp; Appendix H), both loci have the same taxon coverage but varied in relation to the amount of missing data (16S present some gaps).

3.3.2 Main hypothesis and multiple alternatives

Multiple hypotheses on the relationships between *Mesonauta* were produced by combining the datasets (primarily inside *Mesonauta mirificus*). The investigation of various optimality criteria for tree searches, such as parsimony, model-based ML and BI analysis, and statistics, is another reason for different hypotheses. We also investigated a few weighting strategies under parsimony (e.g., equal weighting *vs*. extended implied weighting).

The combined dataset-based tree that emerges from the ML approach (Figure 1) serves as the basis for both taxonomy and phylogenetic discussion. The molecular data's fully resolved topology is provided via ML analysis. The only significant distinction between the consensus topology produced by the Bayesian Inference (Figure 2) and the ML tree is the polytomy inside *Mesonauta mirificus*.

Nonetheless, parsimony studies of the combined datasets carried out here produced topologies that were the same regardless of how the data or parameters were handled. The resulting consensus tree (Figure 3, right) based on the analysis of all molecular characters and the equal weighting (EW) and extended implied weighting (XIW) scheme (53 nodes in both) agrees well with the ML tree about the ingroup relationships between the *Mesonauta* and recovers all of these groups. Appendix G presents the lists of synapomorphies and character transformations across the topology for both trees shown in Figure 3, as the character reconstructions were carried out using the Parsimony criterion.

3.3.2.1 Maximum-likelihood analysis

Mesonauta was recovered as a monophyletic clade. Intrageneric relationships were shown for the first time, as follows: Clade (A) is composed by *Mesonauta festivus* as sister to

Mesonauta sp. “Pantanal”, both as the sisters to a group composed by *M. acora* as sister group to *Mesonauta* sp. “Amapá”. Clade (B) is composed by *Mesonauta insignis* as sister to *M. mirificus*. Clade (A) is a sister group to Clade (B).

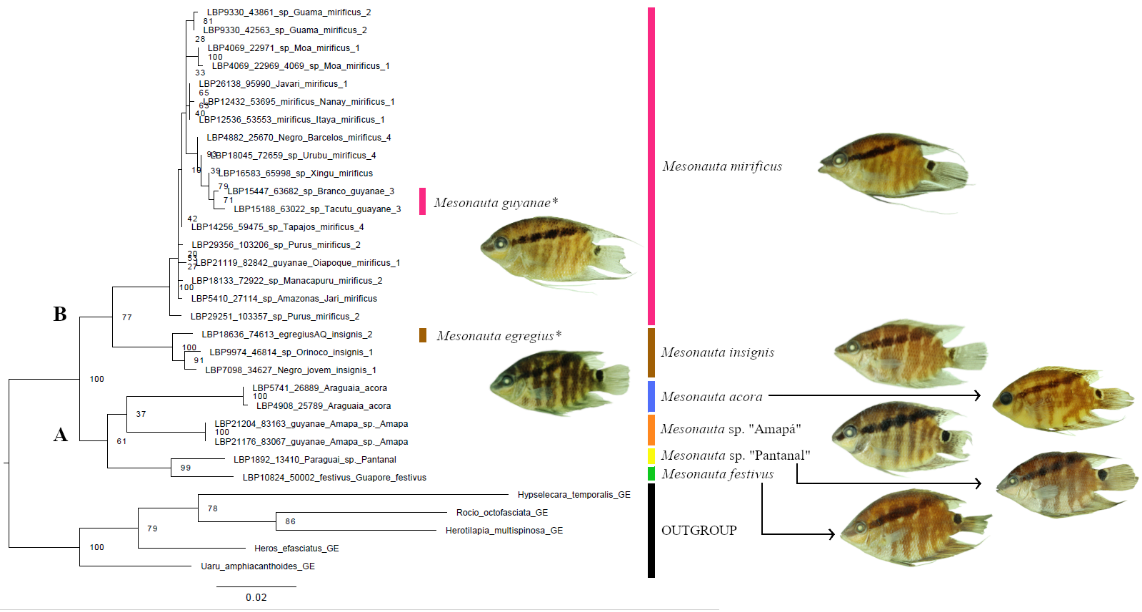

Figure 1 - Maximum-Likelihood tree of *Mesonauta* species using concatenated mitochondrial COI and 16S. Node numbers are Bootstrap values. Colored bars show the delimitation analysis carried out by (Oliveira *et al*., 2024), from where (*) *Mesonauta guyanae* specimens are grouped with *Mesonauta mirificus* and *Mesonauta egregius* specimen is grouped with *Mesonauta insignis*.

3.3.2.2 Bayesian analysis

Mesonauta was also recovered as a monophyletic clade in Bayesian analysis. Intrageneric relationships were the same as the ML analysis, but *Mesonauta mirificus* intragroups, which are shown without polytomies in BI analysis.

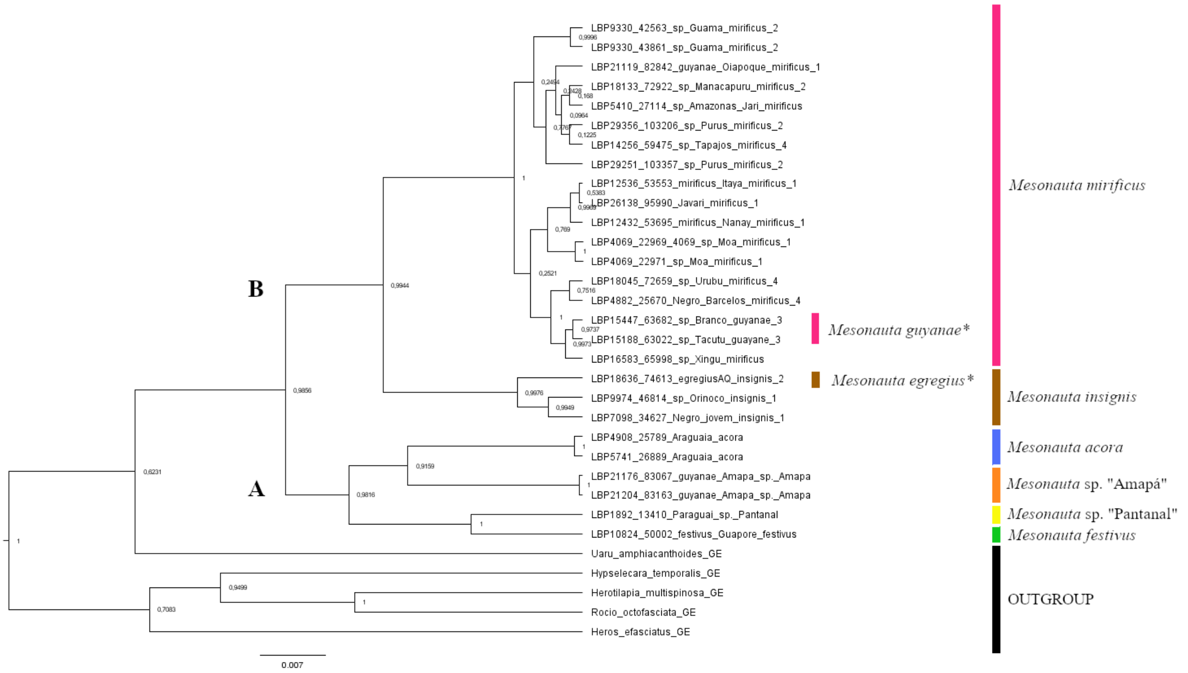

Figure 2 - Bayesian tree of *Mesonauta* species using concatenated mitochondrial COI and 16S. Node numbers are from the ultrametric tree. (*) *Mesonauta guyanae* specimens are grouped with *Mesonauta mirificus* in delimitation analysis; and *Mesonauta egregius* specimen is grouped with *Mesonauta insignis* in delimitation analysis carried out by (Oliveira *et al.*, 2024).

3.3.2.3 Parsimony analysis

Both parsimony analysis (*i.e.* EW and XIW), recovered the same topology as ML analysis, but with some differences inside *Mesonauta mirificus* and position of outgroup species.

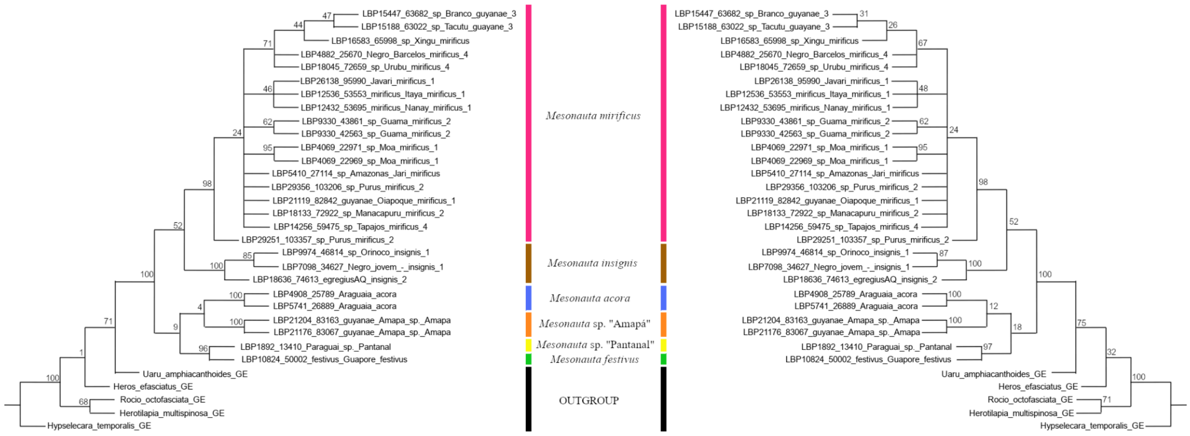

Figure 3 - Parsimony trees of *Mesonauta* species using concatenated mitochondrial COI and 16S. Node numbers are from Bootstrap method (1,000 resamplings). (*) *Mesonauta guyanae* specimens are grouped with *Mesonauta mirificus* in delimitation analysis; and *Mesonauta egregius* specimen is grouped with *Mesonauta insignis* in delimitation analysis carried out by (Oliveira *et al*., 2024). Left: Equal weighting (EW) analysis. Right: extended implied weighting (XIW) analysis.

3.4 Discussion

3.4.1 Molecular markers

Here, an accurate phylogeny of the *Mesonauta* was produced by combining mitochondrial non-coding 16S ribosomal rRNA (16S) and the mitochondrial coding genes cytochrome c oxidase subunit 1 (COI), which recovered the major lineages. Some researchers have employed the molecular sequences to delineate species and reconstruct the phylogeny of various groups (Ilves *et al*., 2018; Willis *et al*., 2012; Zhang *et al*., 2021; Zou *et al*., 2011).

3.4.2 Monophyly of *Mesonauta* Günther 1862

In all reconstructions, *Mesonauta* was recovered as a monophyletic group strongly supported. Morphological characters proposed by Kullander (1998) also corroborate the monophyly of the genus (see below). Other studies also recovered *Mesonauta* as a monophyletic group (Ilves *et al.*, 2018, López-Fernández *et al.*, 2010).

Besides, it is possible to affirm that *Mesonauta* is a monophyletic group corroborated by molecular and morphological synapomorphies, *i.e.* apomorphic conditions of characters 38, 107, 134, 137, 167, 170, 209, 248, 254, 266, 341, 408 (from COI gene) and 640, 742, 748, 749, 863, and 875 (from 16S gene) are recovered as synapomorphies of the clade of all *Mesonauta* species (see Appendix G node 36 for detailed character transformation). Further, our results agree with the monophyly of *Mesonauta* proposed by previous authors as synapomorphies listed for *Mesonauta* in Kullander (1998) hypothesis *viz.* characters Kullander's character 41 state 0 (numbers of infraorbital posterior to the lachrymal, five) and Kullander's character 71 state 0 (Expansion of anterior hemapophyses, absent).

3.4 3 Overview of the relationships among *Mesonauta* species

Mesonauta species (Node 36 in MP analysis) showed six main lineages, not differing in topology (but inside *Mesonauta mirificus*) among the three methods used, ML, BI and MP, divided in two main clades (Node 45 in parsimony analysis, clade A; and node 35 in parsimony analysis, clade B). *Mesonauta* is well supported, 100% in ML and MP analysis and 0.98 in BI analysis. Clade A and clade B have low branch support in MP analysis, however in ML they have 61 and 77%, respectively. Clades comprehending the six main lineages also have high branch supports (Figures 1 - 3).

Only a few species per genus underwent phylogenetic analysis of Neotropical cichlids to gain insight into the group's evolutionary history (López-Fernández *et al.*, 2010; Ilves et al., 2018). As these investigations solely examined *M. insignis* and *M. egregius*, the relationships between *Mesonauta* species have been unclear until now. This study represents the first attempt to categorize *Mesonauta* species.

At first, *Mesonauta insignis* and *M. egregius* were considered different species. However, after the delimitation procedure, both were included in the same MOTU (Oliveira *et al.*, 2024), but still with variation in the color pattern that clearly divides both species. Herein, we are treating both as *M. insignis*, but taking into consideration that they need to be more investigated. *Mesonauta insignis* was recovered as a sister group to *M. mirificus*, a widely distributed species recovered in delimitation analysis in the Amazonas River basin, from which the previously proposed by Schindler (1998) *M. guyanae* is considered clustered together in delimitation analysis (Oliveira *et al.*, 2024). They are part of clade B, which is sister to clade A with the remaining species (Figure 1 - 3).

Clade A is composed by *Mesonauta festivus* as sister to *Mesonauta* sp. “Pantanal”, both as the sisters to a group composed by *M. acora* as sister group to *Mesonauta* sp. “Amapá”. *Mesonauta festivus* was delimited to be in Guaporé/Madeira System, whereas a putative new species is presented in the Paraguay River basin. The relationship between *Mesonauta festivus* and *Mesonauta* sp. “Pantanal” relates to biogeographical patterns, where occurred a division of Paraguay-Paraná *vs*. Madre de Dios-upper Ucayali (Říčan *et al.*, 2023). Besides no color pattern differentiate both species, they are treated as two because of the lots of mutations in the COI gene between both, which reveals 12 molecular autapomorphies for both Paraguai and the Guaporé River species.

According to ML, BI and MP analysis, we propose the following classification of *Mesonauta*, based on our main phylogenetic hypothesis (ML tree: Figure 1; nodes based on MP analysis: Figure 3 and see Appendix G, Figure G1). New species names were proposed, *Mesonauta insignis* comprehends *M. egregius*, and *M. mirificus* comprehends *M. guyanae*.

Node 28 – Root – *Hypselecara temporalis* (Günther 1862)
- Node 53
  - Node 30 – *Rocio octofasciata* (Regan 1903)
  - Node 31 – *Heterotilapia multispinosa* (Günther, 1867)
- Node 38 – South America "Mesonautines"
  - Node 29 – *Heros efasciatus* Heckel 1840
  - Node 27 – *Uaru amphiacanthoides*
  - Node 36 – *Mesonauta* Günther 1862
    - Node 35 – Clade B
      - Node 34 – *Mesonauta insignis* (Heckel 1840)
      - Node 42 – *Mesonauta mirificus* Kullander & Silfvergrip 1991
    - Node 45 – Clade A
      - Node 44
        - Node 43 – *Mesonauta acora* (Castelnau 1855)
        - Node 49 – *Mesonauta* sp. "Amapá"
      - Node 50
        - Node 16 – *Mesonauta* sp. "Pantanal"
        - Node 26 – *Mesonauta festivus* (Heckel 1840)

3.4.4 Taxonomy in Mesonauta Günther 1862

The *Mesonauta* are riddled with taxonomic problems, and the goals of this research do not allow for a comprehensive taxonomic revision of all *Mesonauta* species. Nonetheless, this section supplies diagnoses and an estimated distribution range for each species, drawing from Kullander and Silfvergrip (1991), along with species descriptions and personal morphological observations (refer to chapter 2's morphological section in Oliveira *et al*. 2024). The intention is to facilitate taxonomic research in the future and enhance the ease of use of the proposed classification. MP analysis nodes are presented in Appendix G.

Node 36 – *Mesonauta* Günther 1862

Mesonauta Günther, 1862:300

Type species: by indication (monotypy) *Heros insignis* Heckel 1840:378

Diagnosis: All species of *Mesonauta* are distinguished from other "Mesonautines" *sensu* Ilves et al. (2018) (i.e. *Uaru*, *Symphysodon* and *Heros*) by differentiation of color pattern, presenting an oblique lateral band extending from tip of snout to ending of dorsal fin *vs*. no lateral band.

Distribution: AOG region (Amazonas-Orinoco-Guiana), Paraguai and Tocantins-Araguaia River basins.

Remarks: Six species have been described in the last century (*Mesonauta insignis*, *Mesonauta egregius*, *Mesonauta acora*, *Mesonauta festivus*, *Mesonauta mirificus* and *Mesonauta guyanae*), however, molecular analysis revealed different six lineages: *Mesonauta insignis* plus *Mesonauta egregius* representing one MOTU, *Mesonauta acora*, *Mesonauta festivus* divided into two MOTUs represented by *M. festivus* and *Mesonauta* sp. "Pantanal", *Mesonauta mirificus* plus *M. guyanae* representing one MOTU, and *Mesonauta* sp. "Amapá" (see chapter 2, for details in delimitation analysis, Oliveira *et al*., 2024). In the lines below, here presents the diagnosis of these identified lineages.

Node 34 – *Mesonauta insignis* (Heckel 1840)

Diagnosis: Distinct from all other *Mesonauta* in that the ventral portion of bar 6 is typically connected with bar 7, and the middle portion of bar 5 is sometimes combined with bar 6 and partially divided by a faint vertical stripe. Though it might not be very noticeable, the reticulate pattern on the back and nape distinguishes it from all other *Mesonauta* species. Compared to other *Mesonauta* species, *Mesonauta insignis* is also more slender and has a longer snout.

Distribution: Upper Negro and Orinoco Rivers.

Remarks: Kullander and Silfvergrip (1991) mentioned the opposite: "the middle part of bar 6 merged with bar 7, sometimes partially separated by a light vertical stripe, and the ventral part of bar 6 normally united with bar 5". Also, as molecular delimitation analysis recovered *M. egregius* with *M. insignis*, we do not propose a synonymization but treat both as one OTU. Bar 6 splitting ventrally sets *M. egregius* apart from other Mesonauta species, however unlike *M. mirificus*, which has a similar pattern, *M. egregius* lacks side horizontal stripes. See Kullander and Silfvergrip (1991) for more details

Node 42 – *Mesonauta mirificus* Kullander & Silfvergrip 1991

Diagnosis: Distinct from all other *Mesonauta* species by unique color pattern: bar 6 is made up of a light vertical stripe that typically divides the bar into two narrow parallel stripes below the middle of the side.

Distribution: Amazon River basin, Napo, Ampiyacu, Suriname, Oiapoque, Tapajós, Moa, Itaya, Javari, Ucayali, Nanay, Negro, Takutu, Branco and Xingu Rivers .

Remarks: Similar to *M. egregius* of *M. insignis*, in having bar six doubled, but with 8 or 9 instead of 6 or 7 anal fin spines. Similar to *M. guyanae* clustered together with *M. mirificus*, by also presenting dark narrow horizontal lines along the side.

Node 43 – *Mesonauta acora* (Castelnau 1855)

Diagnosis: Distinct from all *Mesonauta* species due to the preopercle's constant presence of two to four, most often three, scales *vs.* no scaled preopercle; Mottled color pattern with bar 5 interrupted.

Distribution: Tocantins-Araguaia and Xingu River basins.

Remarks: Only *M. festivus* shares the exterior microbranchiospines on all four gill arches.

Node 49 – *Mesonauta* sp. "Amapá"

Diagnosis: *Mesonauta* sp. nov., is distinguished from all of its congeners, except from *M. festivus* and *Mesonauta* sp. "Pantanal" by having bars 5 to 8 not divided or united with each other, or when divided, only near ventral portion (see juveniles) (*vs*. bars 3-4 united in the middle portion in *M. festivus*; bars 6-7 united in ventral portion in *M. insignis*; bar 5 divided in its entire length by a light stripe in *M. guyanae*; bar 6 divided in its entire length by a light stripe in *M. mirificus* and *M. egregius*). Additionally it differs from *M. insignis* and *M. guyanae* by having no reticulated pattern (*vs*. presence), and from *M. acora* by present a standard pattern of bars being inclined and not divided (*vs*. mottled pattern).

Distribution: Amapá Grande and Jeju Rivers.

Remarks: Do not present horizontal stripes.

Node 16 – *Mesonauta* sp. "Pantanal"

Diagnosis: Distinct from all *Mesonauta* species by combination of characters: bars 6 and 7 separated, bars 3 and 4 united forming and "X" except close to anal fin *vs*. bars 6 and 7 connected ventrally in *M. insignis*, bars 3 and 4 not forming an "X" in *Mesonauta* sp. "Amapá" *M. acora* and *M. mirificus*. No morphological but molecular diagnosis is found between *Mesonauta* sp. "Pantanal" and *Mesonauta festivus*, presenting transformations in 12 nucleotides (see Appendix G, node 16 for more details)

Distribution: Paraguay River basin.

Remarks: *Mesonauta* sp. "Pantanal" resembles *Mesonauta festivus* in color pattern. See morphological section in Chapter 2 for more details.

Node 26 – *Mesonauta festivus* (Heckel 1840)

Diagnosis: Distinct from all *Mesonauta* species by combination of characters: bars 6 and 7 separated, bars 3 and 4 united forming and "X" except close to anal fin *vs*. bars 6 and 7 connected ventrally in *M. insignis*, bars 3 and 4 not forming an "X" in *Mesonauta* sp.

“Amapá” *M. acora* and *M. mirificus*. No morphological but molecular diagnosis is found between *Mesonauta festivus* and *Mesonauta* sp. “Pantanal”, presenting transformations in 12 nucleotides (see Appendix G, node 26 for more details).

Distribution: Guaporé-Madeira system and Madre de Dios River.

Remarks: *Mesonauta festivus* resembles *Mesonauta* sp. “Pantanal” in color pattern, bars 3-4 forming an “X”, no See morphological section in Chapter 2 for more details Oliveira *et al*. (2024a). Specimens from Tapajós analyzed in Chapter 2 pertain to *M. mirificus* lineage.

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4 A NEW SPECIES OF *Mesonauta* (CICHLIFORMES: CICHLINAE) FROM THE AMAPÁ GRANDE RIVER BASIN, BRAZIL

ABSTRACT

The description of a new *Mesonauta* species from the Amapá Grande River basin in Brazil is supported by integrative taxonomy. The new species is distinguishable from other congeners by its pigmentation pattern in terms of bars 3 to 7 shape. Furthermore, delimitation analyses based on mitochondrial data indicate a high difference (> 6% K2P distance) between the new species and its congeners. The new species is only found in the Amapá Grande River's tributaries. Furthermore, some basins of Amapá State present mercury probably due to garimpo activities, hence this possibly endangers not only the ichthyofauna but also others and the environment as a whole, revealing a need for more research in this area.

Keywords: Amazon Coastal rivers, Cichlidae, COI, molecular data, species delimitation

4.1 Introduction

Heroini is a well-supported clade among the seven Cichlinae tribes proposed by Ilves *et al.* (2018; *viz*. Cichlini, Retroculini, Astronotini, Chaetobranchini, Geophagini, Cichlasomatini, and Heroini). It comprehends species from South and Central America, divided into nine clades of Ilves *et al.* (2018) (e.g., Amphilophines, Caquetaines, Heirichthyines, Astatheroines, Mesonautines, *Nandopsis* from Greater Antilles, the three South America subgroups *Australoheros*, *Hypselecara*+*Hoplarchus*, and *Pterophyllum*. Among them, “Mesonautines” are monophyletic deep-bodied fishes appreciated by aquarists (e.g. *Mesonauta*, *Uaru*, *Heros* and *Pterophyllum*).

Mesonauta comprises six valid species (Fricke *et al*., 2023) distributed along rivers of Amazon-Orinoco-Guiana region (AOG region of van der Sleen & Albert, 2018), Paraguay River basin, and Tocantins-Araguaia River basin. *Mesonauta* can be separated from other

“Mesonautines” by morphological traits, such as an oblique lateral band, a lateral band on the middle of the flank, and other meristic traits, such as a long peduncle with up to three vertebrae (*vs*. no complete vertebrae in *Cichlasoma*) (Kullander 1983, 1986; Kullander & Nijssen, 1989). The phenotypic characteristics used to separate species within *Mesonauta* are mainly related to coloration, such as differences in the shape of the vertical flank bars, and meristics, as presence/absence of microbranchiospines on all gill arches and opercular scales, and vertebra counts. Morphometric characteristics, on the other hand, frequently overlap and hence are ineffective diagnostic attributes.

The Amapá River is part of the Amazonas Estuary and Coastal Drainages (Abell *et al*., 2008) in the Amapá State, northern Brazil. A recent survey conducted in this region (Melo *et al*., 2016) registered 120 species from eight orders and 40 families, among of them, three species from Heroini were sampled: *Heros cf. efasciatus* Heckel 1840, *Hypselecara temporalis* (Günther 1862), and *Mesonauta guyanae* Schindler 1998. However, two samples of *Mesonauta guyanae* from Igarapé Balneário St. Bárbara and from Igarapé Balneário Raso, appeared to differ from *M. guyanae* in color pattern. Oliveira *et al*. (2024a) revealed that most *Mesonauta* specimens from Amapá State are placed alongside *M. mirificus* specimens and require additional study. The authors did, however, show that the Amapá Grande river specimens are not *M. guyanae* or any of the other species proposed thus far. The study of material obtained in the tributaries of Amapá Grande River revealed the existence of an undetermined *Mesonauta* species, which was only found in this section of the basin. Based on morphometric and genetic data, we identified it as a new species of *Mesonauta*, which we described here.

4.2 Material and methods

4.2.1 Morphological data

Measurements and counts were obtained under a stereomicroscope, in accordance with Ota *et al*. (2021, supplementary material 1) and Deprá *et al*. (2022) and Oliveira *et al*., (2024b). An asterisk denotes counts from the holotype. Unless all specimens are equal, the counts are followed by their frequency in parenthesis.

We adopted the coloration-related terminology described by Kullander & Silfvergrip (1991), with eight flank bars along the body: bar 1, at the caudal-fin base, more concentrated on the base of dorsal lobe forming a spot; bar 2, at the distal half of the caudal peduncle; bar 3, between end of dorsal and anal fins; bar 4, between dorsal fin-base and base of anal-fin ray; bar 5, between dorsal-fin base and anal-fin spines; bar 6, between dorsal-fin base and anal-fin origin; bar 7, between dorsal fin base and pelvic-fin base; bar 8, between first dorsal-fin spine and pectoral-fin insertion.

One *Mesonauta* sp. nov. specimen was cleaned and stained (c&s) for osteological examination, following Taylor & Van Dyke (1985). Counts of the vertebrae followed Ota *et al*. (2021). Fused PU1+PU1 was dealt as a single bone. The lower pharyngeal tooth plate was examined as described by Barel *et al*. (1976).

Specimens were deposited in the following institutions: Coleção Ictiológica do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Universidade Estadual de Maringá, Maringá (NUP); Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP); Coleção do Laboratório de Biologia e Genética de Peixes da Universidade Estadual Paulista, Botucatu (LBP). The Extent of Occurrence was estimated through the software GeoCAT (Geospacial Conservation Assessment Tool; http://geocat.kew.org).

4.2.2 Molecular data

4.2.2.1 Sampling, sequencing and delimitation analysis

The inquiry involved the mitochondrial coding gene cytochrome c oxidase subunit 1 (COI). The molecular dataset comprised 32 terminal taxa, with *Mesonauta* accounting for 27 of them. Outgroup species (Table 1) comprise COI sequences retrieved from Genbank whose voucher we did not analyze. Tissue samples were taken from samples that had been kept in 95º GL ethanol. The voucher specimens were fixed in 10% formalin before being kept at 70º GL ethanol.

Total DNA was extracted using the method described by Ivanova *et al.* (2006). Following that, the COI DNA barcode region was amplified using the primers FISH-F6 (5'-ACYAAYCACAAAGAYATTGGCA-3') and FISH-R7 (5'-TARACTTCTGGRTGDCCRAAGAAYCA-3') reported by Jennings *et al.* (2019). The PCR was performed on a thermocycler with a final volume of 12.5 µl containing 7.85 µl distilled water (ddH2O), 0.30 µl deoxynucleotide triphosphate (dNTP) (2 mM), 1.25 µl PCR buffer (10×), 0.4 µl MgCl2 (50 mM), 0.25 µl each primer, 2 µL DNA (200 ng) and 0.20 µl Taq DNA polymerase PHT (Phoneutria). PCR for COI was performed under the following conditions: an initial denaturation at 95º C for 5 min, followed by 30 cycles including denaturation at 95ºC for 60 s, annealing (primer hybridization) at 52º C for 45 s and nucleotide extension at 68ºC for 1 min, with a final extension at 68º C for 10 min. The PCR products were amplified and checked on a 1% agarose gel before being purified using ExoSAP-IT (USB Corporation, Cleveland, OH, USA) according to the manufacturer's protocol.

The BigDye Terminator v.3.1 Cycle Sequencing Ready Reaction kit (Applied Biosystems, Austin, TX, USA) was used to sequence both DNA strands, with a final volume of 7 µl containing 0.35 µl primer (10 mM), 1.05 µl buffer 5×, 0.7 µl BigDye mix and 3.9 µl distilled water. DNA was purified using ethanol precipitation and sequenced using the 3500-Genetic Analyzer (Applied Biosystems) at IBTEC, at the Instituto de Biociências at Universidade Estadual Paulista "Júlio de Mesquita Filho", UNESP, Botucatu, São Paulo, Brazil.

The sequences were processed with Mega-X v10.2.1 (Kumar *et al*., 2018), which includes ClustalW alignment (Thompson *et al*., 1994), translation of coding sections to adjust the reading frame and take stop codons into consideration. In cases where gaps existed between multiple taxa, alignments were confirmed visually and ends were removed to minimize the amount of missing information and non-homologous sites. Appendix I contains sequences.

Poisson Tree Process (PTP; Zhang *et al*., 2013) analysis, Automatic Barcode Gap Discovery (ABGD; Puillandre *et al*., 2012) analysis, Assemble Species by Automatic Partitioning (ASAP; Puillandre *et al*., 2021), and General Mixed Yule Coalescent Model (GMYC; Pons *et al*., 2006; Fujisawa & Barraclough, 2013) delimitation analysis were used.

In MEGA-X v10.2.1 (Kumar *et al*., 2018), a maximum likelihood (ML) analysis was done with the best nucleotide substitution model (TN93+I, lowest BIC score: 4677.759 with 67 parameters), five random searches, 1,000 bootstrap repetitions, and other settings set to default, yielding the best tree. Furthermore, genetic distances (Kimura, 1980) between and among groups were computed in MEGA-X v10.2.1 using the Kimura 2-parameter model (K2P) and 1,000 bootstrap replicates (Kumar *et al*., 2018). The generated ML tree was utilized as an input tree for PTP analysis on the PTP web server (species.h-its.org/server) with 300,000 MCMC generations and a burn-in rate of 0.

Furthermore, the ABGD analysis was carried out using the ABGD online server (bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html), with the fasta file containing the aligned sequences inserted and the Kimura (K2P; 2.0) distance model and other parameters set to default (Pmin = 0.001; Pmax = 0.1).

In addition, the ASAP analysis was carried out using the ASAP online server (https://bioinfo.mnhn.fr/abi/public/asap/), with the fasta file containing the aligned sequences being inserted using Kimura (K80; 2.0).

Using BEAUTi and BEAST v.1.8.4, a phylogenetic tree was constructed using Bayesian inference, inserting the fasta file, TN93+I nucleotide evolutionary substitution model, an uncorrelated relaxed clock, and a speciation birth-death model (Yule process), on an arbitrary timescale (Drummond *et al.*, 2012). A random tree was utilized as the starting point for the MCMC searches, with a run of 10 million generations and a tree sampled every 1,000 generations. Tracer v1.7.2 (Rambaut *et al.*, 2018) was then used to study the distribution of log-likelihood scores and the identification of the stationary phase for each search (to assess whether further runs were required to achieve convergence). The sampled topologies below the asymptote were deleted (10%) during the burn-in method, and the remaining trees were used to construct a 50% majority-rule consensus tree in TreeAnnotator v1.8.4 (included with BEAST). The resulting ultrametric tree was presented in FigTree v1.4.3 (Rambaut, 2019), and a newick archive exported was used as an input file for the GMYC analysis performed via the GMYC website (species.h-its.org/gmyc/R).

A distribution map was created using the Quantum-GIS tool v.3.18.2-Zürich, including the locations of studied specimens.

4.2.3 Data availability statement

All data generated or analyzed during this study are included in this published article [and its supplementary information files].

4.2.4 Ethical statement

The authors state no conflict of interests. The description of the new species is part of the project: “Sistemática, taxonomia e biogeografia de ciclídeos neotropicais” (#305200/2018–6 CNPq and # 4937/2020 UEM) registered in SisGen n° A954837 to WJG. The specimens were collected with under ICMBio license number 13.843-1 to Cláudio Oliveira.

4.3 Results

4.3.1 *Mesonauta* sp. nov.

Figures 1–2 and Table 1.

Mesonauta guyanae. —Melo *et al*. 2016: 135 [Brazil, Amapá, Igarapé Balneário St. Bárbara and from Igarapé Balneário Raso; first records].

4.3.1.1 Holotype

NUP 24912, 65.5 mm SL, Brazil, Amapá State, municipality of Calçoene, Igarapé Balneário Santa Bárbara, tributary of the Amapá Grande River, Amazonas Estuary and Coastal Drainages, 02°03'42.8"N 50°54'15.1"W, 02 dec 15, cols. Oliveira, C., Melo, B.F.

4.3.1.2 Paratypes

All from Brazil, Amapá Grande River basin, Amapá State municipality of Calçoene: NUP 24913, 6, 12.3-58.3 mm SL, collected with holotype. LBP 21176, 5, 17.7-61.3 mm SL, Igarapé Balneário Raso, tributary of the Amapá Grande River, 02°05'25.6"N 50°53'19.8"W, 02 dec 15, cols. Oliveira, C., Melo, B.F. MCP XXX, 4, 21.3-60.2 mm SL, collected with LBP 21176.

4.3.2 Diagnosis

Mesonauta sp. nov., is distinguished from all of its congeners, except from *M. festivus* and *Mesonauta* sp. "Pantanal" by having bars 5 to 8 not divided or united with each other, or when divided, only near ventral portion (see juveniles) (*vs*. bars 3-4 united in the middle portion in *M. festivus*; bars 6-7 united in ventral portion in *M. insignis*; bar 5 divided in its entire length by a light stripe in *M. guyanae*; bar 6 divided in its entire length by a light stripe in *M. mirificus* and *M. egregius*). Additionally it differs from *M. insignis* and *M. guyanae* by having no reticulated pattern (*vs*. presence), and from *M. acora* by present a standard pattern of bars being inclined and not divided (*vs*. mottled pattern).

4.3.3 Description

Based on holotype and paratypes. Measurements in Table 2. See also Figures 1–4 for details of shape and color pattern.

Body laterally compressed. Predorsal contour ascending straight from tip of snout to vertical through posterior margin of orbit. Convex from this point to end of dorsal fin; descending concave along caudal peduncle. Prepelvic contour descending straight from tip of snout to vertical through posterior margin of preopercle, at same angle of predorsal contour (young specimens have more obtusely angled predorsal contour than prepelvic). Abdominal contour convex and horizontal. Anal-fin base contour convex. Caudal peduncle ventral contour ascending slightly concave and horizontal.

Head short, triangular in lateral view, with dorsal margin, from tip of snout to end of supraoccipital, ascending straight and oblique, ventral contour less steep than dorsal contour. Snout long, with frontal contour elongated and continuous with dorsal and ventral contour of head. Lips thick and of “American type”, *i.e.*, lower lip fold covers upper lip. Tip of maxilla not reaching vertical through anterior margin of eye. Nostril dorsolaterally situated, above horizontal through lower margin of orbit, closer to snout than eye. Orbit large, situated on dorsal half of head, pupil ventral to level of upper lateral line. Posterior margin of preopercle, opercle, subopercle, interopercle and suprachleitrum smooth, without serrations.

E1 scales 26*(5) or 27(4). Scales between upper lateral line and dorsal-fin 4½ (9) at base of first dorsal-fin spine, 4½(9) at base of last dorsal-fin spine. Scale rows between lateral line 2*(9). Scales on lateral line 11/8(1), 15/9(1), 17/7(3), 17/8(1), 18/7*(1), 18/8(1), 19/8(1); additionally 1(4), or 2(5)* scales of lower lateral line onto caudal fin. Cheek scales in 3*(9), 3(6), or 4*(3) rows, cycloids. Opercle scales 8(1), 9*(2) or 10(5), large and cycloid, stochastically arranged. Subopercle covered with 3(7) or 4*(2) cycloid scales. Interopercle with 3(4), 4(1) or 5*(4) scales embedded in skin. Scales absent on preopercle. Infraorbital scales 6(1), 7*(5) or 8(3). Circumpeduncular scale rows 9*(9), including lateral line scales. Predorsal scales uniserial(2) or stochastic(7), cycloid, slightly smaller than flank scales. Flank scales ctenoid. Prepelvic scales 10(2), 11(4), 12(2), 13*(1), ctenoid, slightly decreasing in size towards gular region. Abdominal scales ctenoid, slightly smaller than flank scales. Pelvic fin without scales. Dorsal-fin base covered with small scales. Soft dorsal-fin covered by scales from base of rays to ⅕ of its length. Soft anal-fin covered by scales from base of rays to ⅖ of its length. Caudal-fin base covered with stochastically distributed transition scales, intermediate in size between peduncular and inter-radial scales; caudal fin with cycloid inter-radial scales from base of rays to ⅔ of its length; series increasing ontogenetically, 8–13

(11*) scales in specimens over than 40 mm SL, covering from basal ¼ to basal ⅓, without secondary series.

Dorsal-fin rays XIV.10(1), XIV.11(2), XV.11*(5) or XV.12(1); dorsal spines increasing in size up to 5th, first spine about one-fourth length of last. Dorsal-fin rays do not forming filament; lappets pointed, with posterior margin free, slightly surpassing tip of spines. Anal-fin rays VIII.10.i(4), VIII.11(3) or VIII.11.i(2); middle rays longest, pointed, in some specimens forming filament reaching caudal-fin length. Caudal-fin rounded, with 16 principal rays(9)*. Total pectoral-fin rays 11(3) or 12*(6). Pectoral fin rounded. Pelvic-fin rays I.5(9)*; second ray longest, with filamentous extension, passing anal-fin origin.

Gill rakers externally on first epibranchial 1*(8) or 2(1); 1*(9) on angle; 6*(4) or 7(5) on ceratobranchial 1.

Teeth bicuspid, decreasing gradually from symphysis. Symphysis of both jaws lacking teeth. Upper jaw series with 3 rows; lower jaw series with 3–4* rows. External hemiseries of upper jaw right/left sides with 10–19/11–14. External hemiseries of lower jaw right/left sides with 14–17/14–17.

Suture between contralateral ceratobranchial 5 not including interdigitations ventrally; posteromedial teeth large, cylindrical, with large, blunt, dorsally oriented cusp and a very small, anteriorly oriented cusps; anterolaterally, teeth gradually diminishing in size; outer teeth compressed transversally, with large cusp and a very small, upward cusps. Lower pharyngeal jaw tooth-plate (ceratobranchial 5) (Figure 5) length including posterolateral processes 67.9% of width; nine teeth along posterior margin each side; seven teeth along symphyseal margin; 14 teeth along outer margin. Pharyngobranchial 2 5 teeth stochastically arranged turned posteriad. Pharyngobranchial 3 with 46 teeth arranged in 6 rows turned backwards. Tooth plate 4 with 32 teeth arranged stochastically arranged, posteriormost ones larger, turned anteriad; three concavities in the frayed zone at the posterior margin. Right ceratobranchial 4 with 3 tooth plates, posterior with 5 teeth, anterior with 2 teeth, Left ceratobranchial 4 with 2 tooth plates, posterior with 2 teeth, anterior with 4 teeth. Two supraneurals, anterior to first neural spine. Twenty-seven total vertebrae, of which 14 abdominal and 13 caudal (first 12 and PU1+U1). Ribs 12, abdominal. Vertebrae bearing ribs, 3rd–14th. Epineurals present. Twenty-four dorsal-fin pterygiophores (one spine or ray for each pterygiophore), surrounded by vertebrae 2–22. Seventeen anal-fin proximal pterygiophores (first one bearing first two spines; last one bearing last two rays), surrounded by vertebrae 14–23 (anteriormost pterygiophore touches the anterior margin of haemal spine of 14th vertebra). Two epurals. One uroneural. Three branchiostegal rays. First branchial arch with 7 outer rakers (one on epibranchial, one on angle, and five on ceratobranchial) and 8 inner rakers (one on angle, and 7 on ceratobranchial). Second arch with 10 external rakers (one on epibranchial, eight on ceratobranchial, and one between ceratobranchial and hypobranchial) and 9 inner rakers (one on epibranchial and eight on ceratobranchial). Third arch with 9 external rakers (eight on ceratobranchial and one between ceratobranchial and hypobranchial) and 10 inner rakers (one on epibranchial, nine on ceratobranchial). Fourth arch with 11 external rakers (two on epibranchial and nine on ceratobranchial), 3 inner dentigerous plate and 12 inner micro gill rakers (all on ceratobranchial). Caudal-fin rays paired (each contralateral side of caudal-fin) present one ray). Procurrent caudal-fin rays paired. Three pairs of procurrent caudal-fin rays dorsally and two pairs ventrally. Microbranchiospines on all four branchial arches.

4.3.3.1 Color pattern in alcohol

Based on Figs. 1–2. Background light beige to yellowish-brown; ventral region below oblique lateral band yellowish-white; dorsal region above oblique lateral band dark-brown. Posterior margin of flank scales with diffuse brown pigmentation. Head brownish on neurocranial region and nape and opercle; yellowish-brown on cheek, and preopercle; and yellowish-white ventrally. One oblique, light stripes continuous across dorsal midline of head, along anterodorsal margin of lachrymal, from tip of snout to anterior margin of orbit, through nostril. Oblique lateral band pass through tip of snout to eye, preopercle and opercle. Eight bars along body (Figure 1–3): bar 1, on distal portion of caudal peduncle, with a blotch above; bar 2, on middle of caudal peduncle; bar 3, at vertical through last soft dorsal- and anal-fin rays; bar 4, at vertical through last dorsal- and anal-fin spines; bar 5, at vertical through middle dorsal-fin spine and middle anal-fin spines; bar 6, usually at vertical through 8th–10th dorsal-fin spines and 1st–3rd anal-fin spines; bar 7, usually at vertical through 4th–6th origin of dorsal-fin spines and pelvic-fin; bar 8, usually at vertical through base 1st–3rd dorsal-fin spines to pectoral-fin origin. Lateral band dark-brown origin in snout, divided into blotches at intersections with flank bars more conspicuous, mainly concentrated along E1 scale series, passing obliquely through the dorsal-fin. Beige to brown fins. Dorsal fin darker on anterior portion, lighter on distal margin; small, rounded white blotches on soft portion, in occasional specimens forming oblique stripes. Anal fin with same pattern as dorsal fin. Pelvic fin hyaline, with bar 7 surpassing mid soft portion. Caudal fin darker on distal margin; small white blotches more concentrated on anterior two thirds, forming dotted or striped pattern; one black blotch, usually ocellated, corresponding to bar 1, at base of all rays of dorsal lobe.

4.3.3.2 Color pattern in life

Based on Figure 3. Background green to yellowish; ventral region whitish. Head brownish in dorsal region, above oblique lateral band, with brownish scales on nape; lachrymal dark brown, cheek yellow, border of the scales brownish; preopercle and interopercle and subopercle silvery; opercle yellowish, border of the scales silvery brownish; ventral region light beige. Body covered by green to yellow iridescent coloration. Scales on flank yellowish, with brownish borders at posterior margin. Pattern of lateral band, blotches and bars conspicuous as in preserved specimens. Dorsal, caudal and anal fins orange in part; Dorsal fin brownish in beginning, with lateral band obliquely surpassing the base of first rays to tip of fin, with light blothches at the membranous region between rays, with distal portion orange to yellow. Anal fin orange to yellow, blotches as same pattern as preserved specimens. Pelvic fin as same pattern as preserved specimens. Caudal fin brown and yellowish at distal portion, base with blue iridescent spots/stripes.

4.3.4 Geographical distribution

Mesonauta sp. nov. is currently only known from tributaries to Amapá Grande River, from Amazonas Estuary and Coastal Drainages, in the Amapá State, Brazil (Figures 6–7).

4.3.5 Conservation status

The new species is currently known from two tributaries of the Amapá Grande River basin, which region is impacted due to garimpo activity (see Gama & Silva, 2020) causing a bioaccumulation of mercury in fish species. The Extent of Occurrence (EOO) of *Mesonauta* sp. nov. was estimated at about 10.000 km^2. The species is from a relatively small geographic area with anthropic influences; nonetheless, further knowledge about the species' distribution is needed to classify it as threatened. According to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN, 2022), *Mesonauta* sp. nov. is herein suggested to be not classified in any category, being Data Deficient (DD).

4.3.6 Common name

Mesonauta sp. nov. is popularly known in the sampled region as ‘acará bererê’.

4.3.7 Molecular analysis

COI sequences were obtained from 27 specimens (two of *Mesonauta* sp. nov., one of *M. festivus*, one of *Mesonauta* sp. "Pantanal", two of *M. acora*, two of *M. insignis*, one of *M. egregius,* 15 of *M. mirificus* and three of *M. guyanae*) and five additional sequences from GenBank, totalizing 32 sequences in the final matrix (27 *Mesonauta*, one *Uaru*, one *Hypselecara*, one *Heros*, one *Rocio*, one *Heterotilapia*).

No stop codons were observed in any of the sequences. After alignment and editing, the final matrix had 476 characters, with 337 conserved and 139 variable sites (of which 107 were parsimony-informative), with 22.4% adenine, 29.4% cytosine, 31.4% thymine and 16.8% guanine.

The calculated index of substitution saturation (Iss) in DAMBE 5.2.31 (Xia & Xie, 2001) revealed that the data was not saturated (Iss.c larger than Iss). Genetic distances (Kimura, 1980) of the COI gene between *Mesonauta* sp. nov. and other *Mesonauta* and outgroup species are presented in Table 2. All species delimitation analyses (PTP, GMYC, ABGD and ASAP) corroborate the separation of *Mesonauta* sp. nov. from the other *Mesonauta* and outgroup species included in this study (Figure 8).

The ABGD analysis resulted in nine partitions that ranged from 6 ($P = 0.021$) to 10 ($P = 0.001$) lineages, with six partitions ($P = 0.001$–0.00129) resulting in 10 lineages, and the ASAP analysis resulted in 10 partitions that ranged from 2 (score = 7.5) to 27 (6.0) lineages, with one partition with 10 lineages (lowest score = 1.0) (Figure 8). All species delimitation analyses support the distinction of the new species from other *Mesonauta* species and outgroup.

4.4 Discussion

Herein, morphological and molecular analyses supported the distinctness of *Mesonauta* sp. nov. among its congeners. Differently from other *Mesonauta*, the new species present a color pattern in adults with bars not merged, where they could be merged or somewhat divided. Further, *Mesonauta* sp. nov. do not present a reticulate color pattern (i.e. border of flank scales darker). For example, this pattern is found in *Mesonauta insignis*, which present bars 6-7 merged in its ventral portion. Some individuals of the new species present bars 3-4 almost united in two portions, above and below the lower lateral line, a pattern which differs from *Mesonauta festivus* and *Mesonauta* sp. “Pantanal”, because their specimens have strongly merged bars 3-4 in their midline. *M. mirificu*s, *M. egregius* and *M. acora* has a distinct color pattern not confusable with the new species, with bars 6 divided in its entire length in the two first species, and a mottled characteristic pattern in the latter.

Unlike *Mesonauta guyanae*, *Mesonauta* sp. nov. has straight flank bars, and bar 5 never splits over its whole length, save in certain juveniles. Furthermore, the genetic distance between both is quite large, accounting for more than 6% of the K2P distance, which is higher than 2%, a suitable threshold for this distance (de Carvalho *et al*., 2011; Pereira *et al*., 2011a; 2011b; 2013). Likewise, delimitation analysis in Oliveira *et al*. (2024a) and that performed in this study group *M. guyanae* sequences from the Branco, Takutu, Oiapoque, and Suriname Rivers together with *M. mirificus*, forming a widely distributed species on the Amazon River basin and Guiana Shield that requires further investigation.

The existence of the oblique lateral band, as well as other morphological and molecular characteristics, support the generic assignment of *Mesonauta* sp. nov. in *Mesonauta*. *Mesonauta* differentiates from other Heroini species in "Mesonautines" by Ilves *et al*. (2018) by having character 17, gill raker dentition, [0] external ceratobranchial 1 gill rakers denticulate along inner margin, with other gill rakers short, but strongly denticulate, *vs*.

[1] external ceratobranchial I gill rakers toothless, with other gill rakers toothed apically in *Symphysodon* and *Uaru*, and [2] no teeth on any of the gill rakers in *Heros*; character 40, shape of the lachrymal, [0] approximately square *vs*. [1] deeper than wide; character 71, anterior hemapophyses expansion, [0] absent *vs*. [1] present; character 76, caudal ribs continuing the pleural rib series, [1] present *vs*. [0] absent; character 79, preopercular scales [1] present (*Mesonauta acora* and some *M. festivus*) *vs*. [0] absent; and character 87, greatly elongated pelvic fin [1] present *vs*. [0] absent (see all characters in Kullander, 1998).

The holotype of *Mesonauta* sp. nov is from the Amapá Grande River brasin, which is part of the Amazonas Estuary and Coastal Drainages (Abbel, 2006). In a study, this region was delimited in the Araguari-Macari-Amapá unit, which is considered a neighboring area of the Amazonas River basin (see number 33 on the map in Dagosta & De Pinna, 2017). This area is classified as part of a monophyletic group that comprises the Suriname and Oiapoque Rivers of Guyana. Another survey (Melo *et al*., 2016) conducted in the region, showed that cichlids presented a total of 16.6% of captured species, and *Mesonauta guyanae* was the only species of the genera sampled. Even being part of similar locations, *Mesonauta guyanae*, on the other hand, is molecularly distinct from *Mesonauta* sp. nov., as previously demonstrated, and *Mesonauta guyanae* lots from Amapá Grande River basin sampled by Melo *et al*. (2016) is one representative of *Mesonauta* sp. nov. indeed.

Regarding other *Mesonauta* species, *Mesonauta festivus* and *Mesonauta* sp. “Pantanal” are morphologically similar, as pointed out by Oliveira *et al*. (2024a), however two delimitation methods (PTP and GMYC) splits both in two species herein. Although Guaporé and Paraguai are closely related River basins showing faunal interchange (Costa, 2010, Hubert & Renno 2006), and both species presenting similar morphological pattern (meristic, morphometry and coloration) further studies are needed once Oliveira *et al*. (2024a) revealed with insertion of more *Mesonauta* COI sequences that both are separated in all delimitation methods performed.

The new species is described from a small section of the Amapá Grande River basin and in a mercury-affected region (Gama & Silva, 2020), where bioaccumulation occurs according to the food chain structure. The low extent of occurrence plus the possible threat in the region could result in the new species being placed in some threatened category of IUCN. However, further information about the species' distribution is required before it can be classified. Furthermore, Amapá's coastal rivers revealed at least fifteen potential new species (Melo *et al*., 2016). As a result, it is critical to continue studying the area in order to discover and describe species, as well as to suggest conservation initiatives in this harmed region.

4.5 Material examined

4.5.1 *Mesonauta acora*

Brazil, Xingu River: BMNH 1985.6.20:1252-1261. photograph, 4, (1: 44.3 mm), Gato stream (Suiá-Missu River).

Brazil, Tocantins-Araguaia River: INPA 3529, photograph, 1, 59.3 mm, Itupiranga municipality, Tocantins River. NUP 8204, 2, 69.4-71.5, Tocantins State, Ananás municipality, unnamed lagoon. NUP 8182, 2, 33.1-64.3, Pará State, São Geraldo do Araguaia municipality, unnamed lagoon. LBP 4908, 4, 53.0-67.8, Mato Grosso State, Araguaiana municipality, Corrente Stream. MNRJ 25082, 5, 43.8-76.9, Mato Grosso State, Trinta stream.

4.5.2 *Mesonauta egregius*

ICN-MHN 1686, photograph of the holotype, young female, 57.2 mm SL. Colombia, Departamento Vichada, Rio Vichada drainage, laguna no. 1 on Finca Boca de Guarrojo at the mouth of the Rio Guarrojo. LBP 17732, 1, 53.7 mm SL, Colombia, Meta River, aquarium trade.

4.5.3 *Mesonauta insignis*

Orinoco River basin, Venezuela: LBP 2248, 2, 27.0-30.1 mm SL, Caicara del Orinoco, Bolivar, unnamed stream. LBP 2206, 1, 16.9 mm SL, Caicara del Orinoco, Bolivar, Laguna de Castilleros.

4.5.4 *Mesonauta mirificus*

Peru: LBP 23547, 4, 24.2-39.5, Peru, Maynas/Loreto, Amazonas River basin, Igarapé Nina Rumi.

4.5.5 *Mesonauta festivus*

Guaporé River basin, Brazil: UFRO-ICT 6042, 4, 22.1-44.8 ml SL, Rondônia, Corumbiara Municipality. UFRO-ICT 11166, 3, 59.7-72.5 ml SL, Rondônia, Cerejeiras Municipality, Azul Stream. UFRO-ICT 6726, 3, 16.4-62.4 ml SL, Rondônia, Pimenteiras do Oeste Municipality. MCP 38477, 3, 50.2-62.3, Mato Grosso, Nova Lacerda Municipality, Papagaio River. LBP 10824, Brazil, 5, 35.8-54.2 mm SL, Mato Grosso, Vila Bela da Santíssima Trindade

Municipality. AMNH 229313, 32.6-64.6, Bolivia, Santa Cruz, Itenez River, Bahia Piuba at mouth. UFRO-ICT 24382, 2, 65.0-64.9 ml SL, Rondônia, Guajará-Mirim Municipality.

4.5.6 *Mesonauta guyanae*

Essequibo River, Guyana: ZMB 32779, 61.5 mm SL, Rockstone, photograph of the holotype. ZMB 32780, 47.0 mm SL, Rockstone, photograph of the paratype.

Amazonas River basin, Brazil: LBP 4358, 1, 29.6 mm SL, Roraima, Boa Vista, Branco River basin, do Cajual Stream.

Takutu River basin, Brazil: LBP 15532, 4, 16.8-31.26 mm SL, Roraima, Bonfim municipality, Fazendo Romer lagoon.

4.5.7 *Mesonauta* sp. “Pantanal”

Paraguai River basin, Brazil: LBP 1982, 6, 64.0-80.1 mm SL, Mato Grosso, Taquari River basin, do Ribeirão lagoon. LBP 13638, 3, 46.2-60.8 mm SL, Mato Grosso, Poconé Municipality. LBP 14019, 1, 60.2 mm SL, Mato Grosso, Poconé municipality, Bigueirinho River. LBP 3802, 4, 34.0-58.7 mm SL, Mato Grosso do Sul, Aquidauana Municipality, Marginal Rio Negro lagoon. LBP 14000, 2, 51.5-52.9 mm SL, Mato Grosso, Poconé municipality. LBP 7594, 7, 27.5-29.6 mm SL, Mato Grosso, Barão do Melgaço Municipality, Marginal lagoon from Cuiabá River. LBP 10773, 5, 9.2-17.0 mm SL, Mato Grosso do Sul, Coxim Municipality, Veados Stream. LBP 13529, 1, 45.3 mm SL, Mato Grosso, Poconé municipality, Caracarazinho do Mono River. LBP 10135, 1, 42.5 mm SL, Mato Grosso do Sul, Coxim municipality, unnamed lagoon from dos Veados Stream. LBP 10127, 1, 42.5 mm

SL, Mato Grosso do Sul, Coxim Municipality, Buritizinho lagoon. LBP 13683, 2, 29.3-42.7 mm SL, Mato Grosso, Poconé municipality, Caracarazinho do Mono River. NUP 175, 10, 43.3-64.1, Mato Grosso do Sul, Porto Murtinho Municipality, Baía da Medalha. NUP 5999, 6, 42.2-53.3, Mato Grosso, Cáceres municipality, Baía Caiçaras.

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Tables

Table 1. Sequences of outgroup species extracted from Genbank database.

Acession number	**Genbank name**	**Current status**	**Reference**
DQ119220.1 - COI	*Uaru amphiacanthoides*	*Uaru amphiacanthoides*	Chakrabarty (2006)
DQ119219.1 - COI	*Hypselecara temporalis*	*Hypselecara temporalis*	Chakrabarty (2006)
DQ119218.1 - COI	*Heros efasciatus*	*Heros efasciatus*	Chakrabarty (2006)
DQ119197.1 - COI	*Nandopsis octofasciata*	*Rocio octofasciata*	Chakrabarty (2006)
DQ119195.1 - COI	*Herotilapia multispinosa*	*Herotilapia multispinosa*	Chakrabarty (2006)

Table 2. Morphometric data of *Mesonauta* sp. nov. Standard length in millimeters and proportional measurements as percentage of SL. N = total number of specimens examined; SD = Standard deviation.

	Holotype	Paratypes			
		N	Range	Mean	SD
Standard length (mm)	65.51	8	46.39-66.77	56.22	7.33
Body depth	59.27	8	54.76-61.29	58.15	2.21
Preanal distance	60.19	8	59.91-64.94	61.99	1.88
Prepelvic distance	43.61	8	42.79-49.69	45.13	2.24
Prepectoral distance	37.34	8	35.17-39.55	36.98	1.47
Predorsal distance	50.42	8	45.24-51.0	48.54	1.72
Distance from dorsal to caudal fin	66.39	8	62.82-68.75	66.24	1.94
Distance from dorsal to anal fin	59.47	8	54.83-61.88	58.96	2.31
Distance from dorsal to pelvic fin	53.20	8	50.09-55.77	53.53	2.00

Distance from dorsal to pectoral fin	34.67	8	31.34-35.45	34.11	1.43
Caudal peduncle depth	22.12	8	20.69-22.85	21.81	0.99
Caudal peduncle length (straight)	2.52	8	2.31-6.24	3.65	1.21
Caudal peduncle length (oblique)	11.98	8	11.27-12.89	12.04	0.55
Pectoral-fin length	30.36	8	27.50-31.95	30.01	1.91
Pelvic-fin length	60.72	8	44.90-80.91	68.82	12.13
Pelvic spine length	19.80	8	18.76-20.80	19.83	0.81
Dorsal-fin base length (spine)	46.53	8	42.90-48.61	45.37	2.18
Dorsal-fin base length (total)	62.04	8	56.11-64.38	61.09	2.54
Last dorsal-fin spine length	19.71	8	17.69-21.45	20.07	1.62
Anal-fin base length (spine)	23.31	8	26.46-25.66	24.37	0.74
Anal-fin base length (total)	44.36	8	40.55-44.93	42.68	1.62
Last anal-fin spine length	20.38	8	18.30-20.73	19.90	0.79
Head length	36.91	8	34.00-37.51	36.21	1.11
Head depth (behind the eye)	42.12	8	39.71-43.76	41.93	1.63
Head width	20.32	8	18.04-20.45	19.36	0.76
Orbital diameter	14.36	8	12.36-14.87	13.79	0.92
Postorbital head length	10.52	8	10.35-11.71	10.98	0.47
Interorbital distance	17.19	8	14.85-16.77	15.90	0.73
Snout length	14.14	8	13.06-14.83	13.79	0.59
Cheek depth	8.01	8	6.75-8.46	7.76	0.65
Lachrymal depth	7.95	8	7.10-8.79	7.84	0.61
Upper jaw length	10.07	8	7.52-10.04	9.20	0.83
Lower jaw length	11.97	8	11.05-12.73	12.07	0.51

Table 3. Interspecific Kimura 2-parameter mean distance of *Mesonauta* species. Standard errors (in blue) were obtained by a bootstrap procedure.

		Between groups									Within groups	
		1	2	3	4	5	6	7	8	9	d	S.E.
1	Mesonauta sp. nov.		0.012	0.012	0.013	0.013	0.014	0.013	0.014	0.017	0.00	0.00
2	*Mesonauta guyanae*	0.065		0.003	0.012	0.012	0.014	0.013	0.014	0.016	0.01	0.00
3	*Mesonauta mirificus*	0.063	0.011		0.012	0.012	0.014	0.012	0.013	0.016	0.01	0.00
4	*Mesonauta insignis*	0.069	0.067	0.063		0.004	0.015	0.012	0.014	0.017	0.01	0.00
5	*Mesonauta egregius*	0.072	0.061	0.057	0.010		0.015	0.012	0.014	0.016	n/c	n/c
6	*Mesonauta acora*	0.069	0.078	0.077	0.094	0.089		0.014	0.015	0.016	0.00	0.00
7	*Mesonauta festivus*	0.070	0.071	0.068	0.067	0.065	0.074		0.008	0.016	n/c	n/c
8	Mesonauta sp. "Pantanal"	0.074	0.080	0.077	0.077	0.079	0.084	0.035		0.016	n/c	n/c
9	Outgroup	0.162	0.158	0.156	0.163	0.155	0.149	0.150	0.153		0.14	0.01

Figures

Fig. 1. *Mesonauta* sp. nov., NUP 24912, 65.5mm SL, holotype, Brazil, state of Amapá, municipality of Calçoene, Igarapé Balneário Santa Bárbara, tributary of the Amapá Grande River, Amapá Grande River basin, 02°03'42.8"N 50°54'15.1"W, 02 dec 15, cols. Oliveira, C., Melo, B.F.

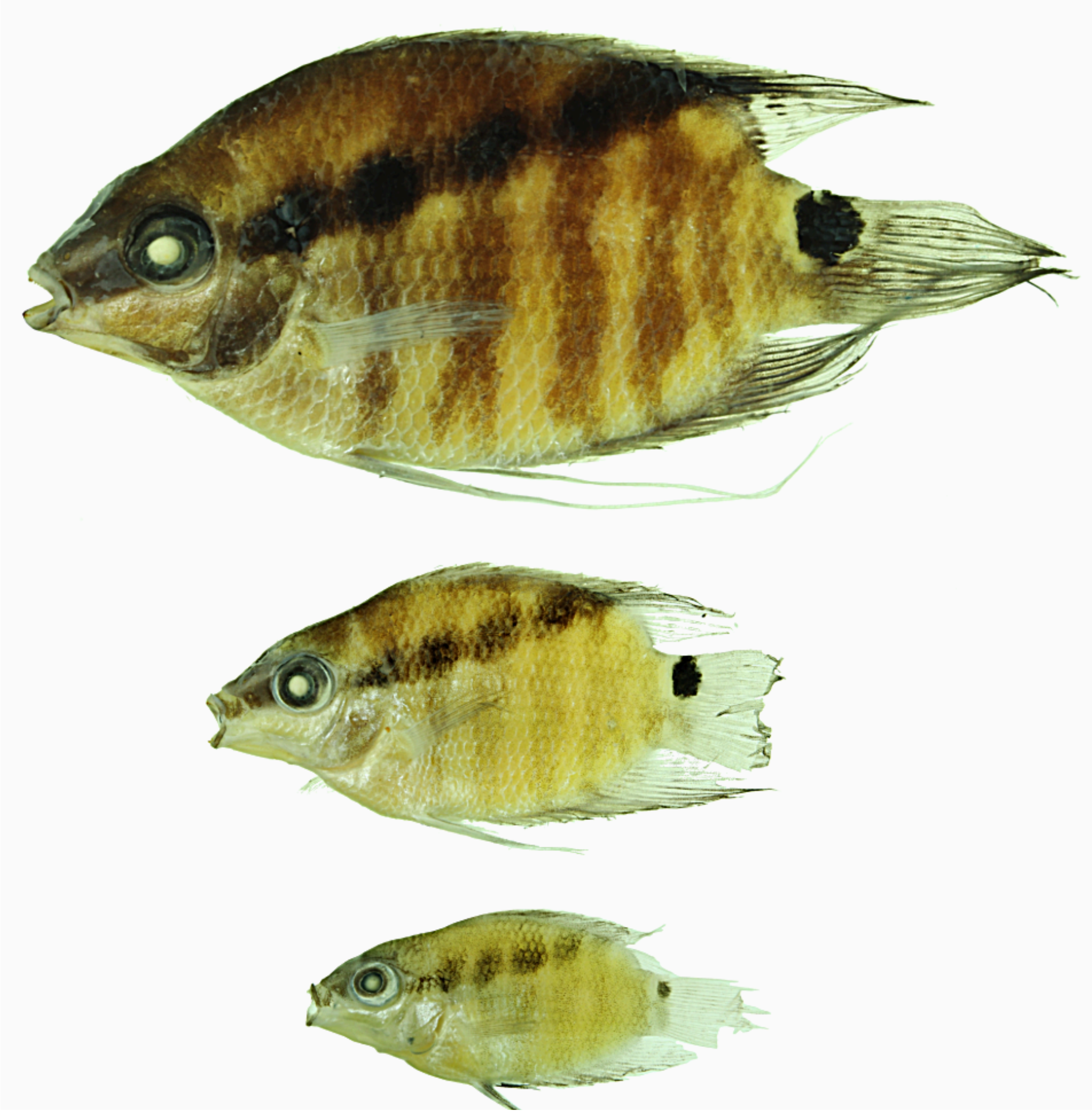
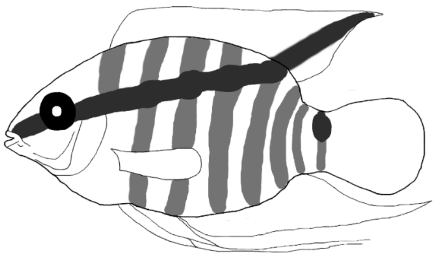
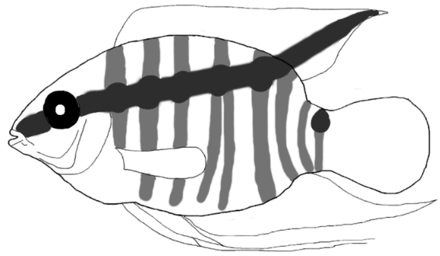


Fig. 2. Coloration and ontogenetic variation in *Mesonauta* sp. nov., (LBP 21176, 3, 17.7-57.6 paratypes).

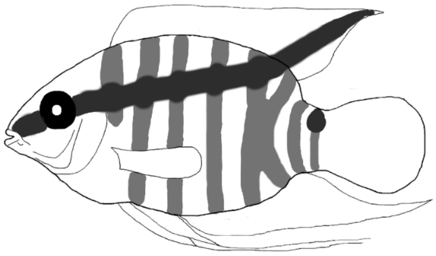
Fig. 3. *Mesonauta* sp. nov., living specimen photographed just after capture in the Amapá Grande River basin, 17°32'04.8"S 54°25'36.6"W, uncatalogued (photos by B. F. Melo).



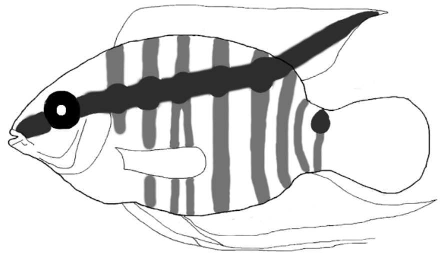
Mesonauta sp. nov.



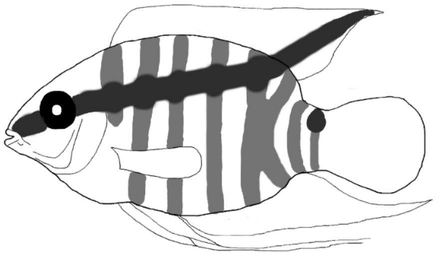
Mesonauta guyanae



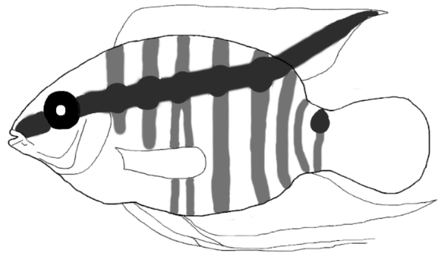
Mesonauta festivus



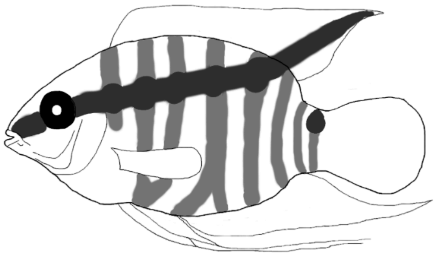
Mesonauta egregius



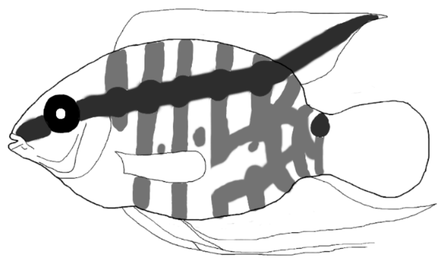
Mesonauta sp. "Pantanal"



Mesonauta mirificus



Mesonauta insignis



Mesonauta acora

Fig. 4. Schematic drawing of *Mesonauta* species showing the differences in the bars 1-8 pattern. Note that there is no difference between *Mesonauta festivus* and *Mesonauta* sp. “Pantanal”, neither between *Mesonauta egregius* and *Mesonauta mirificus*. Differences between the two latter are in counts of the anal fin spines.

Fig. 5. Lower pharyngeal tooth plate of *Mesonauta* sp. nov (LBP 21176, 54.8 mm SL) in the occlusal plane, with anterior portion upwards.

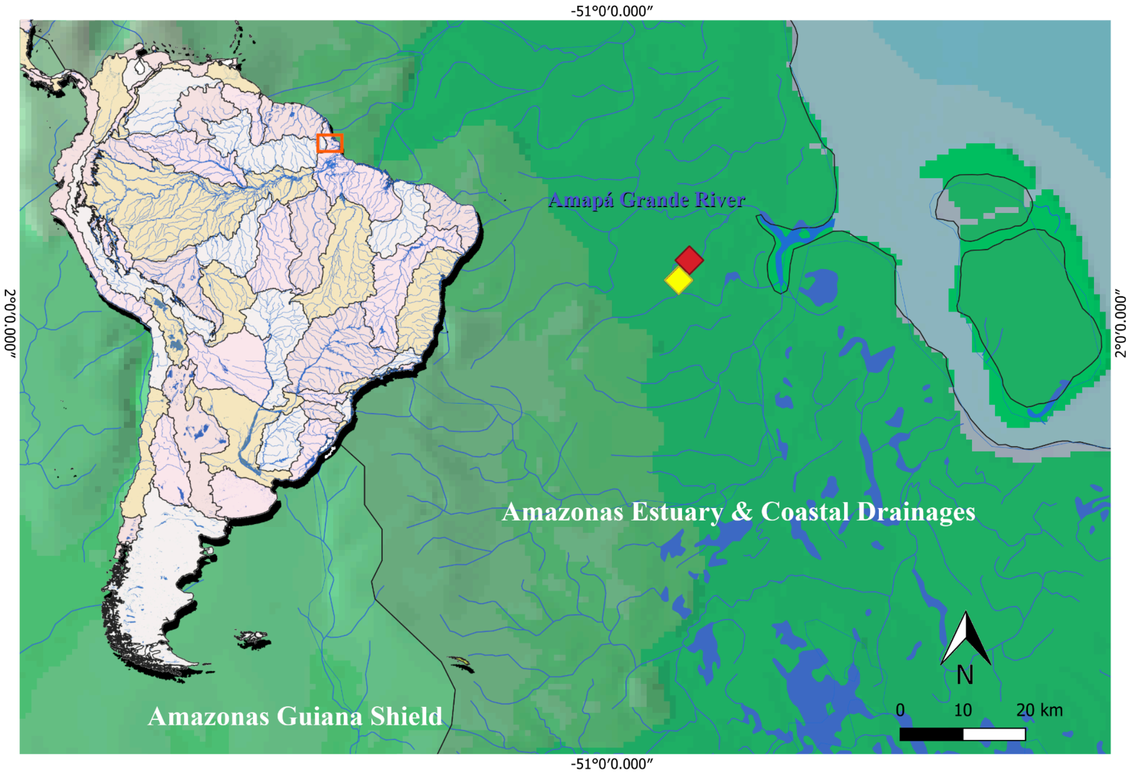


Fig. 6. Partial map of South America showing the distribution of *Mesonauta* sp. nov. in the Amapá Grande River basin, Brazil. (Yellow diamond, type locality in the Igarapé Balneário Santa Bárbara; red diamond, additional locality in the Igarapé Balneário Raso).

Fig. 6. Sample localities at A) Igarapé Balneário Santa Bárbara at 02°03'42.8"N 50°54'15.1"W and B) Igarapé Balneário Raso at 02°05'25.6"N 50°53'19.8"W. (Photos by B. F. Melo)

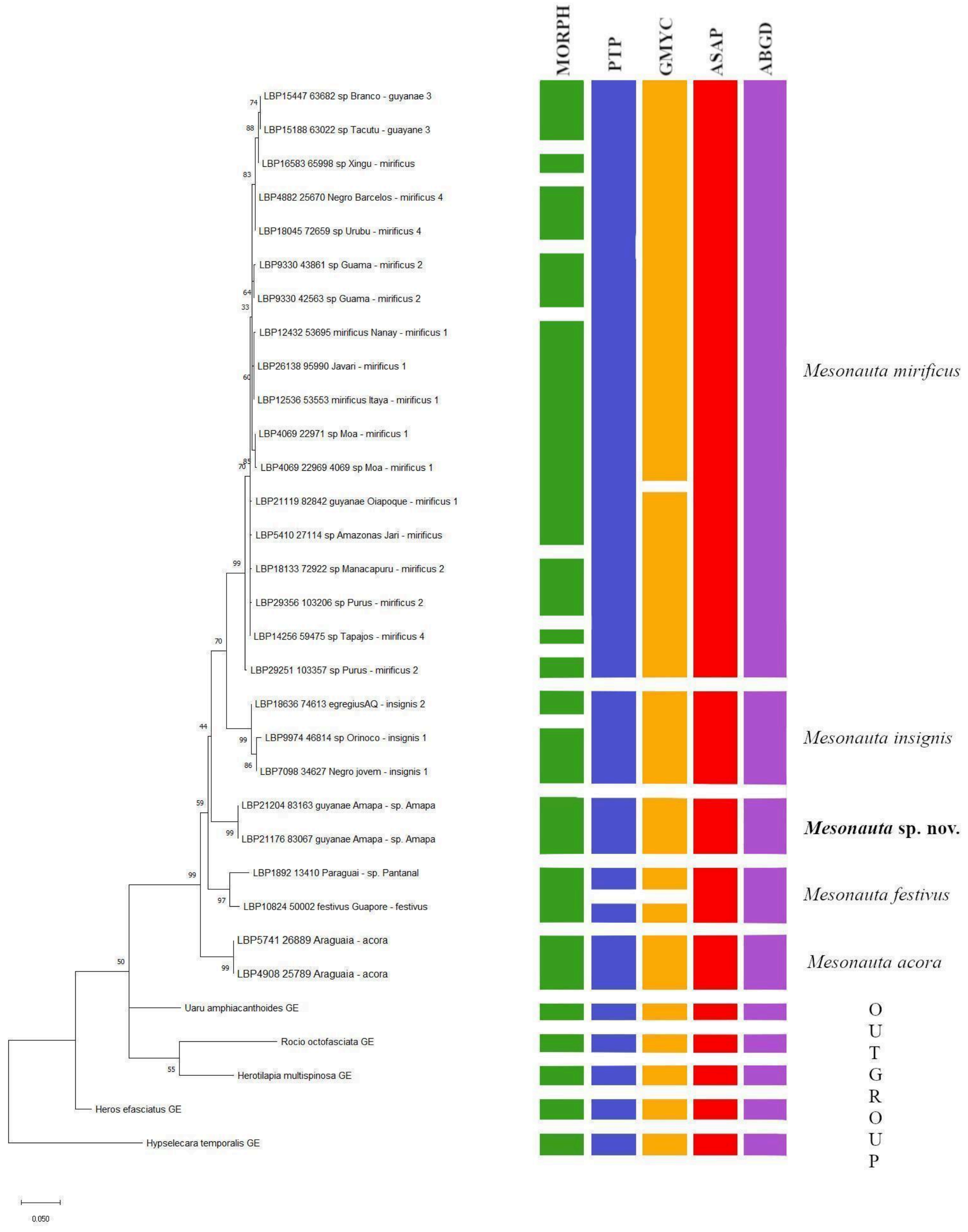


Fig. 7. Maximum-likelihood tree based on the cytochrome oxidase c subunit I gene (COI) partial sequence and the species delimitation analyses evidencing the *Mesonauta* sp. nov. clade (Amapá Grande River basin) and the presence of *Mesonauta* from Oiapoque, Branco and Takutu River basins in the *M. mirificus* clade. Morph.: morphological analysis. Nodes labeled with numbers represent bootstrap support.

5 CONCLUDING REMARKS

Mesonauta has been studied under different approaches (i.e. ecology; phylogenetics under a broader context), but this is the first draft dealing with an extensive sampling to delimit its species and seek for its intrageneric relationships. The delimitation analysis did not recover the species previously described and a new perspective is discussed where putative new species are proposed and others synonymized. Vicariant events and dispersal should be some causes of segregation and distribution of *Mesonauta* species along the entire Amazonas-Orinoco-Guiana, Tocantins-Araguaia, and Paraguay river basins. Once *Mesonauta* species delimitation is given, it was also possible to apply methods to reconstruct the molecular phylogeny of the genera. Multilocus molecular phylogeny of *Mesonauta* species is for the first time reconstructed, and relationships remain similar to delimitation analysis proposed. When three different approaches were used to analyze the phylogeny of the group, they revealed equally topologies regarding ingroup species. In general, *Mesonauta* species could be divided in two main clades: clade (A) is composed by 1) *Mesonauta festivus* from Guaporé River basin as sister to 2) *Mesonauta* sp. "Pantanal" from Paraguay River basin, both as the sisters to a group composed by 3) *M. acora* from Tocantins-Araguaia and Xingu River basins as sister group to 4) *Mesonauta* sp. "Amapá" from Amapá Grande River basin; Clade (B) is composed by 5) *Mesonauta insignis* from Orinoco and Upper Negro River basins as sister to 6) *M. mirificus* widely distributed in the Amazon River basin. Further, clade (A) is a sister group to Clade (B). Furthermore, a new species of *Mesonauta* is described from tributaries of the Amapá River basin, Amapá State, Brazil. The species is recognized from a small region, which is impacted by mercury. This marks the beginning of the investigation into the molecular phylogeny of *Mesonauta*, which has shown the intrageneric relationship based on molecular data and furnished information for a species description and for further research on the group's evolutionary history.

APPENDIX LIST

APPENDIX A - Species delimitation - list of COI sequences of *Mesonauta* species from the GenBank database

Voucher / tissue / Acession number	**Name on tree**	**Watershed**	**Species (molecular)**	**Reference**
GU804852.1	Megregius		*Mesonauta insignis*	Genbank unpublished
GU804851.1	Megregius		*Mesonauta insignis*	Genbank unpublished
GU804850.1	Megregius		*Mesonauta insignis*	Genbank unpublished
GU804848.1	Megregius		*Mesonauta insignis*	Genbank unpublished
LBP18636-74612	Megregius	Aquarium	*Mesonauta insignis*	Present study
LBP18636-74613	Megregius	Aquarium	*Mesonauta insignis*	Present study
GU804847.1	Megregius		*Mesonauta insignis*	Genbank unpublished
LBP7098-34628	Minsignis	Negro	*Mesonauta insignis*	Present study
LBP7098-34627	Minsignis	Negro	*Mesonauta insignis*	Present study
LBP3043-19178	Minsignis	Orinoco	*Mesonauta insignis*	Present study
LBP2248-15712	Minsignis	Orinoco	*Mesonauta insignis*	Present study
LBP2248-15713	Minsignis	Orinoco	*Mesonauta insignis*	Present study

LBP9994-46725	Minsignis	Pelehojo, Orinoco	*Mesonauta insignis*	Present study
LBP2192-15556	Minsignis	Orinoco	*Mesonauta insignis*	Present study
LBP9974-46814	Minsignis	Orinoco	*Mesonauta insignis*	Present study
LBP2206-15600	Minsignis	Orinoco	*Mesonauta insignis*	Present study
LBP10159-47566	Minsignis	Apure	*Mesonauta insignis*	Present study
LBP9974-46811	Minsignis	Orinoco	*Mesonauta insignis*	Present study
LBP9974-46812	Minsignis	Orinoco	*Mesonauta insignis*	Present study
LBP9974-46813	Minsignis	Orinoco	*Mesonauta insignis*	Present study
LBP29251-103357	Mesonauta sp	Purus	*Mesonauta mirificus*	Present study
LBP15188-63022	Mguyanae	Takutu	*Mesonauta mirificus*	Present study
LBP15188-63023	Mguyanae	Takutu	*Mesonauta mirificus*	Present study
LBP15447-63682	Mguyanae	Branco	*Mesonauta mirificus*	Present study
LBP15614-64266	Mguyanae	Takutu	*Mesonauta mirificus*	Present study
LBP15532-63927	Mguyanae	Takutu	*Mesonauta mirificus*	Present study
LBP15532-63926	Mguyanae	Takutu	*Mesonauta mirificus*	Present study
LBP15532-63928	Mguyanae	Takutu	*Mesonauta mirificus*	Present study

ANSP179072a	Mguyanae	Rupununi	*Mesonauta mirificus*	Present study
LBP4358-24115	Mguyanae	Branco	*Mesonauta mirificus*	Present study
LBP4882-25669	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
UFPA2358	Mesonauta sp	Xingu	*Mesonauta mirificus*	Present studyio do Sangue
LBP16583-65998	Mesonauta sp	Xingu	*Mesonauta mirificus*	Present study
UFPA11BA23	Mesonauta sp	Xingu	*Mesonauta mirificus*	Present study
LBP4408-24246	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP4292-23913	Mesonauta insignis	Negro	*Mesonauta mirificus*	Present study
LBP4882-25671	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP4292-23912	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP4408-24243	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP4477-24440	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP4882-25668	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP4882-25670	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP18045-72659	Mesonauta sp	Urubu	*Mesonauta mirificus*	Present study
LBP18045-72661	Mesonauta sp	Urubu	*Mesonauta mirificus*	Present study

LBP17959-72373	Mesonauta sp	Preto da Eva	*Mesonauta mirificus*	Present study
LBP4882-25672	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP17959-72374	Mesonauta sp	Preto da Eva	*Mesonauta mirificus*	Present study
LBP18045-72660	Mesonauta sp	Urubu	*Mesonauta mirificus*	Present study
LBP4408-24242	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP4477-24439	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
ANSP189590b	Mguyanae	Suriname	*Mesonauta mirificus*	Present study
ANSP189590a	Mguyanae	Suriname	*Mesonauta mirificus*	Present study
MHNG17280	Mguyanae	Suriname	*Mesonauta mirificus*	Present study
MHNG17281	Mguyanae	Suriname	*Mesonauta mirificus*	Present study
MHNG17282	Mguyanae	Suriname	*Mesonauta mirificus*	Present study
LBP4477-24437	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP18075-72741	Mesonauta sp	Amazonas	*Mesonauta mirificus*	Present study
LBP18045-72662	Mesonauta sp	Urubu	*Mesonauta mirificus*	Present study
LBP20992-81906	Mguyanae	Amazonas	*Mesonauta mirificus*	Present study
LBP5410-27114	Mesonauta	Jari	*Mesonauta mirificus*	Present study

LBP29342-103257	Mesonauta	Purus	*Mesonauta mirificus*	Present study
LBP4477-24438	Mesonauta	Negro	*Mesonauta mirificus*	Present study
LBP14256-59473	Mfestivus	Tapajós	*Mesonauta mirificus*	Present study
LBP14256-59474	Mfestivus	Tapajós	*Mesonauta mirificus*	Present study
LBP59478	Mfestivus	Tapajós	*Mesonauta mirificus*	Present study
LBP14256-59477	Mfestivus	Tapajós	*Mesonauta mirificus*	Present study
LBP14256-59475	Mfestivus	Tapajós	*Mesonauta mirificus*	Present study
LBP18204-74091	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP18159-72986	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP18075-72744	Mesonauta sp	Amazonas	*Mesonauta mirificus*	Present study
LBP18075-72743	Mesonauta sp	Amazonas	*Mesonauta mirificus*	Present study
LBP18133-72926	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP18075-72740	Mesonauta sp	Amazonas	*Mesonauta mirificus*	Present study
LBP18233-74186	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP18075-72742	Mesonauta sp	Amazonas	*Mesonauta mirificus*	Present study
UFPA10C59	Mesonauta sp	Amazonas (Alenquer)	*Mesonauta mirificus*	Present study

LBP18204-74092	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP18159-72985	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP18133-72924	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP18133-72923	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP18133-72925	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP18204-74093	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP21059-82651	Mguyanae	Oyapock	*Mesonauta mirificus*	Present study
LBP21087-82732	Mguyanae	Oyapock	*Mesonauta mirificus*	Present study
LBP21119-82842	Mguyanae	Oyapock	*Mesonauta mirificus*	Present study
LBP18018-72548	Mesonauta sp	Amazonas	*Mesonauta mirificus*	Present study
LBP4408-24245	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP18306-74381	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP18306-74382	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP14256-59476	Mfestivus	Tapajós	*Mesonauta mirificus*	Present study
LBP17999-72489	Mesonauta sp	Amazonas	*Mesonauta mirificus*	Present study

LBP18233-74185	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP18133-72922	Mesonauta sp	Manacapuru	*Mesonauta mirificus*	Present study
LBP25978-95579	Mmirificus	Javari	*Mesonauta mirificus*	Present study
LBP25978-95580	Mmirificus	Javari	*Mesonauta mirificus*	Present study
LBP26138-95990	Mmirificus	Javari	*Mesonauta mirificus*	Present study
LBP26138-95988	Mmirificus	Javari	*Mesonauta mirificus*	Present study
LBP26138-95989	Mmirificus	Javari	*Mesonauta mirificus*	Present study
LBP12536-53553	Mmirificus	Itaya	*Mesonauta mirificus*	Present study
ANSP179838	Mmirificus	Itaya	*Mesonauta mirificus*	Present study
ANSP191989	Mmirificus	Nanay	*Mesonauta mirificus*	Present study
LBP12536-53552	Mmirificus	Itaya	*Mesonauta mirificus*	Present study
LBP12536-53554	Mmirificus	Itaya	*Mesonauta mirificus*	Present study
MCP44245	Mmirificus	Ucayali	*Mesonauta mirificus*	Present study
LBP12432-53695	Mmirificus	Nanay	*Mesonauta mirificus*	Present study
LBP12432-53694	Mmirificus	Nanay	*Mesonauta mirificus*	Present study
LBP9330-43861	Mesonauta sp	Guamá	*Mesonauta mirificus*	Present study

LBP9330-42563	Mesonauta sp	Guamá	*Mesonauta mirificus*	Present study
LBP16767-65999	Mesonauta sp	Arapiranga	*Mesonauta mirificus*	Present study
LBP4408-24244	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP18280-74317	Mesonauta sp	Negro	*Mesonauta mirificus*	Present study
LBP4069-22969	Mesonauta sp	Moa	*Mesonauta mirificus*	Present study
LBP4069-22972	Mesonauta sp	Moa	*Mesonauta mirificus*	Present study
LBP4069-22973	Mesonauta sp	Moa	*Mesonauta mirificus*	Present study
LBP4069-22970	Mesonauta sp	Moa	*Mesonauta mirificus*	Present study
LBP4069-22971	Mesonauta sp	Moa	*Mesonauta mirificus*	Present study
UFPA11A19	Mesonauta sp	Negro (Manaus)	*Mesonauta mirificus*	Present study
LBP21176-83067	Mguyanae	Amazonas	*Mesonauta* sp. “Amapá”	Present study
LBP21204-83163	Mguyanae	Amazonas	*Mesonauta* sp. “Amapá”	Present study
UFPA11AG09	Mesonauta sp.	Jeju	*Mesonauta* sp. “Amapá”	Present study
LBP18106	Pterophyllumscalare	Aquarium	*Pterophyllum scalare*	Present study
UNIR4528	Heros efasciatus	JaciParana	*Heros efasciatus*	Present study
LBP72687	Heros sp	Amazonas	*Heros efasciatus*	Present study

LBP72688	Heros sp	Amazonas	*Heros efasciatus*	Present study
LBP74188	Heros sp	Manacapuru	*Heros efasciatus*	Present study
LBP74082	Heros sp	Manacapuru	*Heros efasciatus*	Present study
LBP74187	Heros sp	Manacapuru	*Heros efasciatus*	Present study
LBP5741-26889	Macora	Araguaia	*Mesonauta acora*	Present study
LBP4908-25789	Macora	Araguaia	*Mesonauta acora*	Present study
LBP4908-25787	Macora	Araguaia	*Mesonauta acora*	Present study
LBP4908-25788	Macora	Araguaia	*Mesonauta acora*	Present study
LBP3802-22308	Mfestivus	Paraguay	*Mesonauta* sp. "Pantanal"	Present study
LBP14019-58344	Mfestivus	Paraguay	*Mesonauta* sp. "Pantanal"	Present study
LBP13638-56645	Mfestivus	Paraguay	*Mesonauta* sp. "Pantanal"	Present study
LBP13638-56644	Mfestivus	Paraguay	*Mesonauta* sp. "Pantanal"	Present study
LBP3802-22307	Mfestivus	Paraguay	*Mesonauta* sp. "Pantanal"	Present study
LBP3802-22306	Mfestivus	Paraguay	*Mesonauta* sp. "Pantanal"	Present study
LBP7594-36254	Mesonauta sp	Cuiabá	*Mesonauta* sp. "Pantanal"	Present study

LBP7594-36252	Mfestivus	Cuiabá	*Mesonauta* sp. “Pantanal”	Present study
LBP7594-36253	Mfestivus	Cuiabá	*Mesonauta* sp. “Pantanal”	Present study
LBP1892-13439	Mfestivus	Taquari	*Mesonauta* sp. “Pantanal”	Present study
LBP1892-13411	Mfestivus	Taquari	*Mesonauta* sp. “Pantanal”	Present study
LBP1892-13410	Mfestivus	Taquari	*Mesonauta* sp. “Pantanal”	Present study
LBP1892-13412	Mfestivus	Taquari	*Mesonauta* sp. “Pantanal”	Present study
UFPA10A42	Mesonauta sp	Jauru	*Mesonauta festivus* (Guaporé)	Present study
UFPA10B95	Mesonauta sp	Curucamba	*Mesonauta festivus* (Guaporé)	Present study
UNIR4835	Mfestivus	Madeira	*Mesonauta festivus* (Guaporé)	Present study
UNIR1871	Mfestivus	Madeira	*Mesonauta festivus* (Guaporé)	Present study
LBP18018-72549	Mesonauta	Amazonas	*Mesonauta festivus* (Guaporé)	Present study
UFPA10B94	Mesonauta	Curucamba	*Mesonauta festivus* (Guaporé)	Present study

UNIR7349	Mfestivus	Pacaás	*Mesonauta festivus* (Guaporé)	Present study
LBP10824-50001	Mfestivus	Guaporé	*Mesonauta festivus* (Guaporé)	Present study
LBP10824-50004	Mfestivus	Guaporé	*Mesonauta festivus* (Guaporé)	Present study
LBP10824-50005	Mfestivus	Guaporé	*Mesonauta festivus* (Guaporé)	Present study
UFPA10A41	Mesonauta sp	Jauru	*Mesonauta festivus* (Guaporé)	Present study
UFPA10H16	Mesonauta sp	Jauru	*Mesonauta festivus* (Guaporé)	Present study
UFPA10H18	Mesonauta sp	Jauru	*Mesonauta festivus* (Guaporé)	Present study
LBP11027-50587	Mfestivus	Pacaás	*Mesonauta festivus* (Guaporé)	Present study
LBP10824-50003	Mfestivus	Guaporé	*Mesonauta festivus* (Guaporé)	Present study
LBP10824-50002	Mfestivus	Guaporé	*Mesonauta festivus* (Guaporé)	Present study

APPENDIX B - Species delimitation - morphometric data of *Mesonauta* species used in PCA analysis.

Species (molecular)	roups	ody depth	nout-anal	nout-pelvic (pre pelvic)	nout-pectoral (pre pectoral)	nout-dorsal (pre dorsal)	orsal-caudal	orsal-anal	orsal-pelvic	orsal-pectoral	eduncle depth	eduncle length (straight)	eduncle length (oblique)	ectoral length	elvic spine length	orsal base length (spine)	orsal base length (spine+ray)	nal base length (spine)	nal base length (spine+ray)	ast A spine length	L	ead width	rbital width	ostorbital	nterorbital width	nout length	heek depth	acrimal depth	pper jaw length	ower jaw length	red/prepel
Mesonauta festivus (Guaporé)		1.83	1.15	4.54	6.42	8.78	6.11	0.28	6.58	4.76	3.77	.25	2.37	8.25	1.50	5.24	8.45	1.50	4.80	2.74	5.90	3.38	6.80	9.41	0.54	7.97	0.76	1.29	5.13	4.52	6.21
Mesonauta festivus (Guaporé)		1.84	2.83	4.99	5.56	8.22	7.80	1.16	6.85	5.41	2.76	.95	1.62	0.02	2.77	8.35	1.82	4.14	3.45	3.22	5.41	4.19	6.77	9.81	6.28	8.37	3.51	2.64	6.60	3.90	4.82
Mesonauta festivus (Guaporé)		8.62	0.98	4.38	5.50	5.71	7.51	9.14	3.15	2.63	1.79	.70	1.42	6.69	1.81	0.70	2.34	5.48	4.38	0.52	4.30	4.31	7.16	1.92	2.51	4.94	2.08	1.07	5.36	3.67	5.99
Mesonauta festivus (Guaporé)		8.65	9.43	3.82	4.93	5.83	8.25	8.49	3.35	2.91	0.90	.63	1.38	6.27	9.49	9.59	2.62	5.32	3.91	1.35	4.11	2.59	4.83	3.09	2.60	5.68	0.98	2.04	4.10	6.73	5.91
Mesonauta festivus (Guaporé)		3.44	0.04	4.88	8.28	9.89	6.55	1.20	6.48	4.47	4.28	.07	3.13	0.59	0.80	5.91	0.22	6.09	7.43	2.78	6.70	4.27	9.63	3.91	3.28	5.17	2.59	0.09	4.88	3.81	8.33
Mesonauta festivus (Guaporé)		1.90	9.78	4.61	6.40	7.40	5.87	9.69	4.16	3.78	5.24	.73	3.56	0.66	2.08	6.40	9.63	3.27	7.04	3.18	6.18	3.54	7.38	0.02	3.51	6.15	0.66	1.30	4.70	1.56	7.53
Mesonauta festivus (Guaporé)		0.13	9.08	4.00	7.08	9.03	6.23	9.13	3.63	2.23	4.66	.03	2.79	7.82	9.85	5.13	0.10	4.94	5.13	3.64	6.22	4.59	5.66	1.58	7.39	7.07	8.75	9.72	6.57	4.26	1.43
Mesonauta festivus (Guaporé)		0.57	2.91	6.41	7.60	8.58	5.45	9.37	3.59	4.06	1.67	.16	0.84	6.84	9.99	4.29	7.85	1.65	3.54	0.07	5.85	3.16	2.68	9.77	4.20	9.83	9.71	8.48	7.17	8.87	0.65
Mesonauta festivus (Guaporé)		4.01	2.19	5.33	5.94	0.19	6.28	4.38	7.96	8.09	3.89	.59	2.31	9.85	1.93	6.83	8.66	6.05	6.03	9.05	6.14	5.31	3.32	9.71	5.01	0.95	4.37	4.05	7.86	2.62	6.60
Mesonauta festivus (Guaporé)		3.67	2.23	4.72	6.11	9.08	8.69	2.86	6.97	5.11	4.61	.45	2.73	9.10	4.05	7.38	1.89	5.27	4.44	2.60	5.90	4.42	0.35	1.75	3.12	4.25	3.41	4.78	7.74	3.11	6.16
Mesonauta festivus (Guaporé)		2.14	2.01	4.10	5.69	7.62	8.68	1.60	6.02	6.27	3.02	.95	2.64	0.75	1.17	6.90	2.49	4.01	6.64	1.14	5.48	4.84	1.37	1.49	2.12	1.25	5.11	3.22	8.04	3.26	5.01

Mesonauta festivus (Guaporé)		8.53	1.79	5.53	6.20	5.93	6.16	8.06	2.73	4.84	0.03	.61	0.24	8.28	1.30	0.14	0.63	6.72	3.59	7.62	5.67	3.28	4.21	2.96	0.28	4.58	6.76	8.95	6.95	4.40	7.10
Mesonauta festivus (Guaporé)		9.98	2.07	5.13	6.11	7.71	7.14	0.59	5.89	6.80	1.88	.75	1.64	9.79	1.19	4.77	0.26	7.87	5.81	1.30	6.53	4.90	4.41	1.62	1.02	6.73	1.26	1.22	7.23	4.71	5.37
Mesonauta sp. Pantanal (Paraguay)		7.70	5.89	9.63	9.68	1.59	5.92	7.17	1.10	6.87	4.98	.95	3.49	1.99	3.81	6.21	0.35	8.94	4.33	6.16	8.85	4.80	5.19	9.37	5.64	9.98	3.62	2.54	5.39	4.19	4.44
Mesonauta sp. Pantanal (Paraguay)		5.30	3.79	7.17	7.38	0.33	7.48	5.15	9.16	6.57	5.20	.70	3.65	0.02	1.64	9.21	3.65	5.31	7.53	2.73	7.54	3.65	6.83	1.98	4.54	8.47	3.14	1.28	5.16	2.66	5.08
Mesonauta sp. Pantanal (Paraguay)		8.37	6.47	7.96	8.43	0.44	6.60	8.17	0.94	7.41	4.34	.01	2.63	8.96	3.36	7.31	2.40	4.63	5.61	9.82	8.03	5.35	7.23	9.30	5.87	9.04	2.05	0.70	6.64	3.64	2.77
Mesonauta sp. Pantanal (Paraguay)		4.20	2.13	7.59	7.82	0.95	8.66	5.03	9.51	5.51	3.49	.38	3.39	1.24	2.71	7.94	1.94	1.98	5.41	2.14	7.28	4.19	6.55	2.16	1.96	6.21	0.66	0.03	7.34	4.84	5.62
Mesonauta sp. Pantanal (Paraguay)		3.79	4.38	7.54	8.94	0.41	5.86	3.92	6.64	4.85	3.97	.27	3.43	3.23	3.12	4.51	1.06	4.46	2.89	3.97	8.21	2.39	6.96	0.86	2.04	6.82	9.14	9.58	6.27	6.04	9.00
Mesonauta sp. Pantanal (Paraguay)		4.58	4.26	7.45	9.12	1.99	6.77	4.84	8.76	5.60	2.13	.35	1.87	0.72	2.49	7.95	2.05	3.41	5.60	4.56	7.27	2.22	8.16	0.79	1.42	6.93	1.06	8.12	5.44	3.08	8.47
Mesonauta sp. Pantanal (Paraguay)		5.24	7.17	8.82	9.66	1.97	5.36	4.01	8.11	4.60	3.17	.63	2.82	1.58	2.91	5.82	1.49	7.84	3.95	3.23	8.08	3.03	8.46	2.34	2.66	6.70	0.37	7.61	5.85	3.72	9.44
Mesonauta sp. Pantanal (Paraguay)		4.39	6.19	7.05	8.51	2.53	6.72	5.09	9.78	6.94	4.74	.41	3.73	2.32	5.82	4.14	1.41	4.68	7.45	3.98	7.34	5.76	3.45	8.08	2.37	7.04	9.91	7.92	5.64	3.75	7.88
Mesonauta sp. Pantanal (Paraguay)		1.70	2.71	7.94	8.70	1.11	3.52	3.29	6.31	4.93	1.36	.61	1.26	1.21	1.38	3.76	0.01	1.98	3.27	4.48	7.45	1.91	8.52	1.11	9.88	3.77	9.69	7.16	3.95	8.95	0.76
Mesonauta sp. Pantanal (Paraguay)		2.54	8.54	1.92	1.78	2.16	1.77	2.05	6.08	3.52	2.90	.37	1.91	9.38	1.44	2.99	8.25	8.93	3.56	3.69	7.61	0.23	6.00	7.55	3.34	0.82	8.40	7.80	6.04	1.83	3.02
Mesonauta sp. Pantanal (Paraguay)		1.08	4.33	6.83	6.66	7.67	6.79	1.54	4.55	3.28	2.12	.48	1.79	9.12	1.86	4.33	9.88	1.13	3.18	3.24	4.85	3.30	5.06	9.39	2.20	9.41	2.49	1.37	6.89	4.91	7.38
Mesonauta sp. Pantanal (Paraguay)		1.24	2.94	6.96	8.09	9.28	5.92	0.78	5.13	3.96	2.29	.45	2.53	8.34	1.21	4.60	9.75	1.65	2.00	0.30	6.37	9.22	3.63	9.36	1.18	9.57	0.06	0.11	5.89	4.04	9.39
Mesonauta sp. Pantanal (Paraguay)		3.08	4.14	6.32	6.98	8.33	6.60	1.91	4.69	3.20	3.10	.53	2.68	7.53	1.62	9.65	6.91	0.80	4.68	1.78	6.06	3.52	7.58	0.31	2.38	7.90	1.03	8.73	6.82	5.34	8.37

Mesonauta sp. Pantanal (Paraguay)		5.90	3.15	5.73	5.37	8.13	7.69	4.46	8.74	5.88	4.94	.60	2.99	2.61	3.29	5.22	0.86	3.14	6.37	3.79	5.18	7.23	7.49	1.52	4.64	3.49	1.65	9.15	5.97	3.92	1.95
Mesonauta sp. Pantanal (Paraguay)		5.61	4.20	7.70	7.15	9.84	5.82	4.01	8.94	5.38	3.52	.43	2.28	0.85	4.14	5.85	1.79	4.75	6.17	2.36	6.17	4.05	7.28	0.27	4.92	6.24	9.59	8.21	2.98	5.32	4.56
Mesonauta sp. Pantanal (Paraguay)		5.25	6.13	9.40	8.05	8.99	6.67	4.08	9.88	6.15	3.77	.57	2.65	0.44	4.80	8.05	1.84	6.87	5.83	3.71	6.73	3.67	7.73	2.95	5.19	2.90	0.55	8.61	6.29	4.32	1.81
Mesonauta sp. Pantanal (Paraguay)		6.74	5.91	7.61	7.73	0.80	6.33	6.04	0.57	6.63	2.93	.60	2.83	0.83	4.55	8.42	0.75	0.21	5.14	4.23	7.02	4.78	7.95	2.90	4.40	3.84	0.47	8.53	5.81	5.78	3.87
Mesonauta sp. Pantanal (Paraguay)		7.42	1.94	5.48	7.34	1.22	6.67	5.32	0.80	6.73	4.27	.38	3.29	2.17	4.09	6.53	1.74	5.80	7.03	4.01	7.25	3.54	8.25	1.40	3.70	3.92	0.68	8.28	1.50	4.92	4.24
Mesonauta sp. Pantanal (Paraguay)		5.27	4.82	8.99	9.37	0.51	5.20	4.34	9.80	6.08	3.95	.24	2.91	0.68	1.77	7.33	0.60	4.50	6.15	3.88	7.69	4.93	9.03	2.12	3.49	1.49	7.54	8.54	6.65	5.89	4.47
Mesonauta sp. Pantanal (Paraguay)		9.53	6.52	5.50	5.45	0.67	5.77	1.97	4.08	4.08	1.40	.38	1.52	6.45	2.01	4.43	7.98	0.50	0.87	3.23	6.06	0.70	0.42	0.09	1.88	7.35	1.22	1.78	5.18	5.23	3.71
Mesonauta sp. Pantanal (Paraguay)		0.89	6.97	6.72	8.61	0.65	4.49	2.35	5.61	4.66	2.26	.81	1.80	4.35	1.87	2.12	8.22	0.65	2.06	5.66	7.05	0.38	0.80	9.43	1.89	6.99	1.93	8.64	5.85	5.49	1.08
Mesonauta sp. Pantanal (Paraguay)		8.42	4.39	3.55	5.35	9.45	5.96	0.12	2.91	3.72	0.71	.91	0.95	7.19	1.79	3.64	0.51	1.25	1.12	2.60	5.57	9.91	8.02	0.78	0.19	5.00	0.64	7.86	4.38	7.05	3.47
Mesonauta sp. Pantanal (Paraguay)		0.48	6.46	5.60	6.22	8.31	4.96	1.93	6.07	5.41	1.02	.33	1.53	6.54	0.71	5.36	8.52	2.93	2.08	2.87	5.61	2.53	0.17	0.04	1.29	3.87	1.32	7.12	5.34	6.34	6.15
Mesonauta sp. Pantanal (Paraguay)		0.16	4.30	8.34	7.01	9.35	5.43	0.18	5.24	3.08	0.91	.70	0.83	5.24	9.73	4.36	9.45	9.73	4.05	3.36	5.51	4.24	0.98	3.22	4.69	0.04	6.98	7.37	5.86	2.10	9.34
Mesonauta sp. Pantanal (Paraguay)		0.41	2.79	8.64	6.98	8.66	6.06	9.97	5.05	3.62	0.73	.85	0.63	7.20	9.75	3.58	0.23	1.72	5.37	3.91	5.73	3.95	2.70	1.64	4.54	8.68	6.84	7.17	7.43	4.01	8.39
Mesonauta sp. Pantanal (Paraguay)		2.14	5.67	5.55	5.66	9.48	5.56	2.70	5.04	4.27	1.52	.21	1.80	6.98	2.70	2.04	8.53	8.96	2.23	2.20	4.50	5.87	1.14	9.70	6.56	2.74	7.35	7.22	7.08	5.61	9.89
Mesonauta sp. Pantanal (Paraguay)		9.29	8.41	4.26	0.88	7.62	5.43	8.19	4.39	2.85	1.37	.75	1.57	8.59	3.64	2.41	9.12	4.24	3.31	3.91	8.12	9.74	5.84	2.02	2.27	5.44	8.24	7.43	4.44	2.37	7.54
Mesonauta sp. Pantanal (Paraguay)		4.73	4.78	7.37	7.92	8.16	5.84	3.28	5.80	4.39	4.28	.61	2.38	0.18	2.47	7.07	2.21	4.79	5.45	2.88	6.36	1.94	2.37	1.51	6.61	8.47	1.20	1.56	5.36	4.58	6.30

Mesonauta sp. Pantanal (Paraguay)		0.08	5.87	1.23	0.49	7.12	3.91	8.45	3.96	1.91	1.74	.67	1.31	9.06	2.32	6.91	9.89	1.30	0.95	0.86	7.88	7.58	5.68	0.45	1.24	7.33	5.80	7.24	3.13	1.39	7.32
Mesonauta sp. Pantanal (Paraguay)		0.28	8.04	1.94	0.89	8.60	2.71	0.54	5.67	3.63	1.84	.75	2.03	6.93	1.17	4.03	6.53	2.97	2.10	1.02	8.05	8.97	5.54	1.38	0.89	4.28	6.17	7.60	4.15	4.40	7.31
Mesonauta sp. Pantanal (Paraguay)		2.51	8.86	2.56	0.34	1.08	4.87	3.18	8.69	5.16	2.99	.76	2.48	8.50	2.20	2.19	9.52	3.29	3.36	2.53	7.20	3.93	0.32	1.37	5.24	1.37	1.60	8.34	6.26	5.14	7.04
Mesonauta sp. Pantanal (Paraguay)		8.80	9.12	1.96	0.12	5.62	4.98	9.80	3.48	1.89	1.53	.02	1.37	8.24	1.85	4.64	8.31	3.54	2.12	2.70	7.36	1.16	5.74	1.19	2.92	4.28	0.78	8.60	4.67	2.46	5.31
Mesonauta sp. Pantanal (Paraguay)		2.94	0.10	2.90	1.25	8.28	3.58	3.29	6.49	3.88	1.86	.86	1.20	8.46	2.17	3.35	9.02	2.62	1.78	1.90	8.26	1.60	4.09	1.46	0.69	3.79	9.08	8.47	3.49	2.17	5.46
Mesonauta sp. Pantanal (Paraguay)		9.03	5.71	0.27	0.47	0.14	1.94	8.30	3.66	2.23	2.17	.69	1.80	7.17	0.58	3.01	5.58	3.62	1.70	2.95	7.43	8.93	4.90	8.82	1.52	1.25	8.21	9.85	5.80	1.75	3.43
Mesonauta sp. Pantanal (Paraguay)		0.80	3.87	8.38	6.31	9.98	8.77	1.42	6.88	3.68	1.99	.48	1.35	9.09	0.55	4.95	0.55	1.25	3.04	0.63	5.05	4.31	5.54	0.24	8.36	0.74	6.18	4.47	7.88	4.26	7.86
Mesonauta sp. Pantanal (Paraguay)		1.23	4.38	6.85	7.31	9.48	6.30	1.72	4.59	4.04	2.06	.18	1.44	7.32	0.36	3.22	9.83	3.03	3.03	2.93	5.36	3.06	4.73	0.25	7.40	1.46	7.22	3.88	8.26	3.91	0.64
Mesonauta sp. Pantanal (Paraguay)		1.45	7.07	7.93	6.59	0.22	4.44	2.88	4.48	5.11	1.97	.81	1.47	7.33	1.24	3.45	7.30	9.59	1.89	3.08	5.50	2.83	6.03	9.74	4.71	0.33	7.72	2.76	9.71	5.63	2.17
Mesonauta sp. Pantanal (Paraguay)		4.60	6.56	9.13	8.40	9.60	6.96	4.88	7.21	5.82	1.87	.15	1.13	7.15	3.21	5.07	0.70	0.38	5.26	3.61	6.51	1.30	4.04	9.85	4.84	9.74	4.91	1.60	7.38	4.08	6.70
Mesonauta sp. Pantanal (Paraguay)		2.38	4.74	7.80	7.61	8.90	5.93	2.23	4.43	4.74	2.03	.35	2.42	8.87	0.43	6.67	8.74	1.54	4.61	1.97	5.11	2.07	5.30	1.41	5.67	7.81	2.17	2.17	6.35	3.79	9.83
Mesonauta sp. Pantanal (Paraguay)		1.66	4.49	1.23	9.73	0.27	5.04	1.95	6.50	4.43	1.27	.42	1.41	6.36	0.02	6.06	8.70	1.88	2.90	0.38	6.40	1.78	6.59	8.79	6.59	0.15	3.17	1.15	7.28	3.89	8.97
Mesonauta acora (Araguaia)		2.93	1.30	4.08	6.94	9.80	4.67	3.36	9.45	0.98	0.49	.77	0.65	9.65	0.49	4.72	9.95	2.16	5.15	2.91	7.40	1.63	4.50	7.14	9.93	4.26	0.19	4.49	7.51	4.24	00.71
Mesonauta acora (Araguaia)		5.53	2.28	5.31	7.96	8.83	3.85	5.52	1.12	2.49	2.24	.84	1.45	0.16	2.02	5.82	0.96	2.58	3.42	5.82	8.45	1.91	5.02	7.83	0.97	2.02	1.27	3.18	6.63	3.30	5.52
Mesonauta acora (Araguaia)		3.90	3.36	5.62	8.45	9.84	4.72	3.92	0.20	0.92	1.38	.53	1.69	0.55	1.81	6.67	0.00	2.59	1.90	3.65	7.97	9.34	1.61	7.85	8.00	2.87	1.58	2.69	6.82	4.81	9.29

Mesonauta acora (Araguaia)		7.25	1.80	6.91	7.83	8.57	6.88	8.77	3.25	3.08	1.43	.05	1.79	4.06	0.55	7.96	2.10	6.09	3.95	0.03	5.38	2.80	4.37	9.97	2.45	7.99	2.73	0.46	5.95	6.16	1.21
Mesonauta acora (Araguaia)		4.25	3.79	9.90	9.33	7.23	3.27	5.15	9.66	0.19	0.48	.37	1.45	7.60	2.22	4.11	8.26	2.61	2.55	1.41	5.39	0.29	6.17	7.91	9.62	7.85	9.08	0.60	5.35	3.51	5.12
Mesonauta acora (Araguaia)		8.23	2.24	4.94	6.40	7.87	7.86	8.61	3.85	3.19	2.15	.02	3.01	0.36	0.79	8.15	2.41	1.66	2.98	3.19	4.67	5.99	2.76	0.34	1.94	6.71	0.15	0.10	7.45	7.20	8.88
Mesonauta acora (Xingu)		7.01	1.08	3.88	5.28	7.66	6.18	6.41	1.44	2.59	0.47	.86	0.00	6.63	0.66	6.19	9.05	2.76	2.89	4.37	4.17	3.69	4.67	7.09	2.66	2.05	4.73	3.06	6.64	3.60	2.64
Mesonauta acora (Xingu)		0.82	3.28	5.29	6.67	0.50	8.23	0.45	4.38	4.79	2.50	.61	1.64	8.22	2.04	8.07	0.64	1.79	2.83	6.06	5.44	3.72	4.68	7.35	5.85	3.03	3.92	3.59	6.91	3.89	2.87
Mesonauta acora (Xingu)		8.75	3.92	5.33	8.50	1.57	4.79	9.86	4.64	4.74	9.53	.47	1.13	6.65	3.38	5.09	8.30	0.41	0.71	6.31	6.75	2.47	7.81	8.86	0.23	9.09	1.69	0.55	6.44	3.29	4.38
Mesonauta acora (Xingu)		0.47	5.20	5.99	8.13	0.72	2.29	9.65	4.88	4.71	9.68	.17	1.09	5.76	0.12	4.00	7.73	1.79	1.41	3.86	7.16	1.42	1.19	7.56	8.69	4.77	7.44	7.67	4.66	5.11	2.42
Mesonauta acora (Xingu)		3.89	1.91	6.63	8.09	8.89	4.88	4.10	0.40	0.53	0.16	.45	0.62	3.41	9.53	2.36	8.73	2.52	2.66	2.20	6.26	0.57	6.84	8.97	7.41	4.63	8.51	7.76	4.81	6.15	7.01

APPENDIX C - Species delimitation - COI sequences of *Mesonauta* species and outgroup used to the PTP, ABGD and ASAP delimitation analyzes, and haplotypes used to the GMYC analysis.

>ANSP179072a_Mguyanae_Rio_Rupununi

GGAGACGACCAAATTTATAATGTAATCGTAACTGCACATGCCTTTGTAATAATTTTCTTTATAGTTATACCCATCATAATTGGAGGCTTTGG
CAACTGACTTATTCCGCTTATAATTGGTGCCCCAGACATGGCTTTTCCACGAATAAACAATATAAGCTTCTGACTTTTACCCCCCTCATTTCTCCTTCT
CCTCGCTTCGTCTGGGGTCGAAGCCGGTGCTGGGACAGGATGAACCGTCTACCCCCCTTTAGCTGGTAACCTGGCGCACGCTGGCCCTTCAGTCGA
CCTAACCATCTTTTCCCTCCACCTAGCCGGGGTTTCATCTATTCTTGGGGCAATCAACTTTATTACTACAATTATCAATATGAAACCTCCAGCAATCTC
CCAGTATCAAACTCCCCTGTTTGTCTGAGCCCTCTTAATTACCGCCGTCCTACTCCTCCTGTCCTTACCAGTTCTTGCCGCCGGCATTAC

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Haplotypes

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Hap_4: 1 [GU804847.1]

Hap_5: 6 [GU804848.1 GU804850.1 GU804851.1 GU804852.1 LBP18636-74612 LBP18636-74613]

Hap_6: 8 [LBP10159-47566 LBP2192-15556 LBP2206-15600 LBP9974-46811 LBP9974-46812 LBP9974-46813 LBP9974-46814 LBP9994-46725]

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Hap_8: 1 [LBP10824-50002]

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Hap_10: 1 [LBP11027-50587]

Hap_11: 2 [LBP12432-53694 LBP12432-53695]

Hap_12: 9 [LBP13638-56644 LBP13638-56645 LBP14019-58344 LBP3802-22306 LBP3802-22307 LBP3802-22308 LBP7594-36252 LBP7594-36253 LBP7594-36254]

Hap_13: 22 [LBP14256-59473 LBP14256-59474 LBP14256-59475 LBP14256-59477 LBP18075-72740 LBP18075-72742 LBP18075-72743 LBP18075-72744 LBP18133-72923 LBP18133-72924 LBP18133-72925 LBP18133-72926 LBP18159-72985 LBP18159-72986 LBP18204-74091 LBP18204-74092 LBP18204-74093 LBP18233-74186 LBP29342-103257 LBP4477-24438 LBP59478 UFPA10C59]

Hap_14: 2 [LBP14256-59476 LBP17999-72489]

Hap_15: 4 [LBP16583-65998 LBP4882-25669 UFPA11BA23 UFPA2358]

Hap_16: 1 [LBP16767-65999]

Hap_17: 14 [LBP17959-72373 LBP17959-72374 LBP18045-72659 LBP18045-72660 LBP18045-72661 LBP4292-23912 LBP4292-23913 LBP4408-24243 LBP4408-24246 LBP4477-24440 LBP4882-25668 LBP4882-25670 LBP4882-25671 LBP4882-25672]

Hap_18: 1 [LBP18018-72548]

Hap_19: 1 [LBP18045-72662]

Hap_20: 1 [LBP18075-72741]

Hap_21: 1 [LBP18106]

Hap_22: 1 [LBP18133-72922]

Hap_23: 1 [LBP18233-74185]

Hap_24: 1 [LBP18280-74317]

Hap_25: 3 [LBP18306-74381 LBP18306-74382 LBP4408-24245]

Hap_26: 4 [LBP1892-13410 LBP1892-13411 LBP1892-13412 LBP1892-13439]

Hap_27: 2 [LBP20992-81906 LBP5410-27114]

Hap_28: 3 [LBP21059-82651 LBP21087-82732 LBP21119-82842]

Hap_29: 3 [LBP21176-83067 LBP21204-83163 UFPA11AG09]

Hap_30: 3 [LBP2248-15712 LBP2248-15713 LBP3043-19178]

Hap_31: 1 [LBP29251-103357]

Hap_32: 3 [LBP4069-22969 LBP4069-22972 LBP4069-22973]

Hap_33: 2 [LBP4069-22970 LBP4069-22971]

Hap_34: 2 [LBP4408-24242 LBP4477-24439]

Hap_35: 1 [LBP4408-24244]

Hap_36: 1 [LBP4477-24437]

Hap_37: 4 [LBP4908-25787 LBP4908-25788 LBP4908-25789 LBP5741-26889]

Hap_38: 2 [LBP7098-34627 LBP7098-34628]

Hap_39: 2 [LBP72687 LBP72688]

Hap_40: 2 [LBP74082 LBP74188]

Hap_41: 1 [LBP74187]

Hap_42: 1 [LBP9330-42563]

Hap_43: 1 [LBP9330-43861]

Hap_44: 3 [UFPA10A41 UFPA10H16 UFPA10H18]

Hap_45: 1 [UFPA10A42]

Hap_46: 1 [UFPA11A19]

Hap_47: 1 [UNIR4528]

APPENDIX D - Species delimitation - delimitation analyzes results

Figure D1. Maximum-likelihood tree based on the cytochrome oxidase c subunit I gene (COI). Each color represents one morphospecies.

Figure D2. PTP delimitation tree.

Poisson Tree Process (PTP) delimitation results

```
# Max likilhood partition
Species 1 (support = 0.250)

LBP4908-25787_Macora_Rio_Araguaia,LBP4908-25788_Macora_Rio_Araguaia,LBP4908-25789_Macora_Rio_Araguaia,LBP5741-26889_Macora_Rio_Araguaia

Species 2 (support = 0.325)

LBP21176-83067_Mguyanae_AMAZONAS_AP_-_sp._7,LBP21204-83163_Mguyanae_AMAZONAS_AP_-_sp._7,UFPA11AG09_Mesonauta_sp_Jeju

Species 3 (support = 0.000)

LBP15614-64266_Mguyanae_TACUTU_sp.,LBP4358-24115_Mguyanae_Rio_Branco,LBP15532-63928_M_guyanae_Rio_Tacutu,LBP15532-63927_Mguyanae_Rio_Tacutu,LBP15532-63926_Mguyanae_Rio_Tacutu,LBP15447-63682_Mguyanae_BRANCO_sp.,LBP15188-63023_Mguyanae_TACUTU,LBP15188-63022_Mguyanae_TACUTU,ANSP179072a_Mguyanae_Rio_Rupununi,ANSP179072b_Mguyanae_Rio_Rupununi,LBP16583-65998_Mesonauta_sp_Rio_Xingu,LBP4882-25669_Mesonauta_sp_Rio_Negro,UFPA11BA23_Mesonauta_sp_Rio_Xingu,UFPA2358_Mesonauta_sp_Rio_Xingu,LBP4477-24437_Mesonauta_sp_Rio_Negro,ANSP189590a_Mguyanae_Rio_Suriname,ANSP189590b_Mguyanae_Rio_Suriname,MHNG17280_Mguyanae_Rio_Suriname,MHNG17281_Mguyanae_Rio_Suriname,MHNG17282_Mguyanae_Rio_Suriname,LBP18075-72741_Mesonauta_sp_Rio_Amazonas,LBP4408-24242_Mesonauta_sp_Rio_Negro,LBP4477-24439_Mesonauta_sp_Rio_Negro,LBP18045-72662_Mesonauta_sp_Rio_Urubu,LBP4882-25672_Mesonauta_sp_Rio_Negro,LBP17959-72373_Mesonauta_sp_Rio_Preto_Eva,LBP17959-72374_Mesonauta_sp_Rio_Preto_Eva,LBP18045-72659_Mesonauta_sp_Rio_Urubu,LBP18045-72660_Mesonauta_sp_Rio_Urubu,LBP18045-72661_Mesonauta_sp_Rio_Urubu,LBP4292-23912_Mesonauta_sp_Rio_Negro,LBP4292-23913_Mesonauta_insignis_Rio_Negro,LBP4408-24243_Mesonauta_sp_Rio_Negro,LBP4408-24246_Mesonauta_sp_Rio_Negro,LBP4477-24440_Mesonauta_sp_Rio_Negro,LBP4882-25668_Mesonauta_sp_Rio_Negro,LBP4882-25670_Mesonauta_sp_Rio_Negro,LBP4882-25671_Mesonauta_sp_Rio_Negro,LBP4069-22970_Mesonauta_sp_Rio_Moa,LBP4069-22971_Mesonauta_sp_Rio_Moa,LBP4069-22969_Mesonauta_sp_Rio_Moa,LBP4069-22972_Mesonauta_sp_Rio_Moa,LBP4069-22973_Mesonauta_sp_Rio_Moa,LBP18280-74317_Mesonauta_sp_Rio_Negro,UFPA11A19_Mesonauta_so_Manaus,LBP9330-43861_Mesonauta_sp_Rio_Guama,LBP16767-65999_Mesonauta_sp_Rio_Arapiranga,LBP9330-42563_Mesonauta_sp_Rio_Guama,LBP12432-53694_Mmirificus_Rio_Nanay,LBP12432-53695_Mmirificus_Rio_Nanay,ANSP179838_Mmirificus_Rio_Itaya,ANSP191989_Mmirificus_Rio_Nanay,LBP12536-53552_Mmirificus_Rio_Itaya,LBP12536-53553_Mmirificus_Rio_Itaya,LBP12536-53554_Mmirificus_Rio_Itaya,LBP25978-95579_Mmirificus_JAVARI,LBP25978-95580_Mmirificus_JAVARI,LBP26138-95988_Mmirificus_JAVARI,LBP26138-95989_Mmirificus_JAVARI,LBP26138-95990_Mmirificus_JAVARI,MCP44245_Mmirificus_Rio_Ucayali,LBP21087-82732_Mguyanae_OIAPOQUE,LBP21119-82842_Mguyanae_OIAPOQUE,LBP21059-82651_Mguyanae_OIAPOQUE,LBP18018-72548_Mesonauta_sp_Rio_Amazonas,LBP18133-72922_Mesonauta_sp_Manacapuru,LBP18306-74382_Mesonauta_sp_Rio_Negro,LBP4408-24245_Mesonauta_sp_Rio_Negro,LBP18306-74381_Mesonauta_sp_Rio_Negro,LBP17999-72489_Mesonauta_sp_Rio_Amazonas,LBP29356-103206_Mesonauta_sp_PURUS,LBP14256-59476_Mfestivus_Rio_Tapajos,LBP18233-74185_Mesonauta_sp_Manacapuru,UFPA10C59_Mesonauta_sp_Alenquer,LBP20992-81906_Mguyanae_AMAZONAS_AP,LBP5410-27114_Mesonauta_sp_Rio_Jari,LBP14256-59473_Mfestivus_Rio_Tapajos,LBP14256-59474_Mfestivus_Rio_Tapajos,LBP14256-59475_Mfestivus_Rio_Tapajos,LBP14256-59477_Mfestivus_Rio_Tapajos,LBP18075-72740_Mesonauta_sp_Rio_Amazonas,LBP18075-72742_Mesonauta_sp_Rio_Amazonas,LBP18075-72743_Mesonauta_sp_Rio_Amazonas,LBP18075-72744_Mesonauta_sp_Rio_Amazonas,LBP18133-72923_Mesonauta_sp_Manacapuru,LBP18133-72924_Mesonauta_sp_Manacapuru,LBP18133-72925_Mesonauta_sp_Manacapuru,LBP18133-72926_Mesonauta_sp_Manacapuru,LBP18159-72985_Mesonauta_sp_Manacapuru,LBP18159-72986_Mesonauta_sp_Manacapuru,LBP18204-74091_Mesonauta_sp_Manacapuru,LBP18204-74092_Mesonauta_sp_Manacapuru,LBP18204-74093_Mesonauta_sp_Manacapuru,LBP18233-74186_Mesonauta_sp_Manacapuru,LBP29342-103257_Mesonauta_sp_PURUS,LBP4477-24438_Mesonauta_sp_Rio_Negro,LBP59478_Mfestivus_Rio_Tapajos,LBP4408-24244_Mesonauta_sp_Rio_Negro,LBP29251-103357_Mesonauta_sp_PURUS

Species 4 (support = 0.001)
```

LBP18636-74612_Megregius_AQUARIO,LBP18636-74613_Megregius_AQUARIO,GU804852.1_Megregius_OL-0269,GU804851.1_Megregius_OL-0267,GU804850.1_Megregius_OL-0268,GU804848.1_Megregius_OL-0272,GU804847.1_Megregius_OL-0264,LBP7098-34627_Minsignis_Rio_Negro,LBP7098-34628_Minsignis_Rio_Negro,LBP2248-15713_Minsignis_Rio_Orinoco,LBP3043-19178_Minsignis_Rio_Orinoco,LBP2248-15712_Minsignis_Rio_Orinoco,LBP10159-47566_Minsignis_Rio_Apure,LBP2192-15556_Minsignis_Rio_Orinoco,LBP2206-15600_Minsignis_Rio_Orinoco,LBP9974-46811_Minsignis_Rio_Orinoco,LBP9974-46812_Minsignis_Rio_Orinoco,LBP9974-46813_Minsignis_Rio_Orinoco,LBP9974-46814_Minsignis_Rio_Orinoco,LBP9994-46725_Minsignis_Rio_Pelehojo

Species 5 (support = 0.040)

LBP7594-36253_Mfestivus_Rio_Cuiaba,LBP7594-36254_Mesonauta_festivus_Rio_Cuiaba,LBP7594-36252_Mfestivus_Rio_Cuiaba,LBP3802-22308_Mfestivus_Rio_Paraguai,LBP3802-22307_Mfestivus_Rio_Paraguai,LBP3802-22306_Mfestivus_Rio_Paraguai,LBP14019-58344_Mfestivus_Rio_Paraguai,LBP13638-56645_Mfestivus_Rio_Paraguai,LBP13638-56644_Mfestivus_Rio_Paraguai,LBP1892-13410_Mfestivus_Rio_Taquari,LBP1892-13411_Mfestivus_Rio_Taquari,LBP1892-13412_Mfestivus_Rio_Taquari,LBP1892-13439_Mfestivus_Rio_Taquari

Species 6 (support = 0.186)

LBP10824-50002_Mfestivus_Rio_Guapore,LBP10824-50003_Mfestivus_Rio_Guapore,UFPA10A41_Mesonauta_sp_Jauaru,UFPA10H16_Mesonauta_sp_Jauaru,UFPA10A42_Mesonauta_sp_Jauaru,UFPA10H18_Mesonauta_sp_Jauaru,LBP11027-50587_Mfestivus_Rio_Pacaas,LBP10824-50001_Mfestivus_Rio_Guapore,LBP10824-50004_Mfestivus_Rio_Guapore,LBP10824-50005_Mfestivus_Rio_Guapore,UFPA10B94_Mesonauta_sp_Curucamba,UFPA10B95_Mesonauta_sp_Curucamba,UNIR1871_Mfestivus_Rio_Madeira,UNIR4835_M_festivus_Rio_Madeira,UNIR7349_Mfestivus_Rio_Pacaas

Automatic Barcode Gap Discovery (ABGD) analysis

```
/*
/* ABGD (Automatic Barcod Gap Discovery)
/* web version 05/22/23 - 10:13AM

Fasta Format detected
Nb seq:159 */
Partition 1 : found 45 groups (prior maximal distance P= 0.001000)
Partition 2 : found 45 groups (prior maximal distance P= 0.001668)
Partition 3 : found 13 groups (prior maximal distance P= 0.002783)
Partition 4 : found 8 groups (prior maximal distance P= 0.004642)
Partition 5 : found 8 groups (prior maximal distance P= 0.007743)
Partition 6 : found 8 groups (prior maximal distance P= 0.012915)
Partition 7 : found 8 groups (prior maximal distance P= 0.021544)
Partition 8 : found 7 groups (prior maximal distance P= 0.035938)
Partition 9 : found 3 groups (prior maximal distance P= 0.059948)
```

Partition 4

Partition with prior maximal distance P=4.64e-03

Distance K80 Kimura MinSlope=1.500000

Group[1] n: 97 ;id: ANSP179072a Mguyanae Rio Rupununi ANSP179838 Mmirificus Rio Itaya ANSP189590a Mguyanae Rio Suriname ANSP189590b Mguyanae Rio Suriname ANSP191989 Mmirificus Rio anay LBP12432-53694 Mmirificus Rio anay LBP12432-53695 Mmirificus Rio anay LBP12536-53552 Mmirificus Rio Itaya LBP12536-53553 Mmirificus Rio Itaya LBP12536-53554 Mmirificus Rio Itaya LBP14256-59473 Mfestivus Rio Tapajos LBP14256-59474 Mfestivus Rio Tapajos LBP14256-59475 Mfestivus Rio Tapajos LBP14256-59476 Mfestivus Rio Tapajos LBP14256-59477 Mfestivus Rio Tapajos LBP15188-63022 Mguyanae TACUTU LBP15188-63023 Mguyanae TACUTU LBP15447-63682 Mguyanae BRA CO sp. LBP15532-63926 Mguyanae Rio Tacutu LBP15532-63927 Mguyanae Rio Tacutu LBP15532-63928 M guyanae Rio Tacutu LBP15614-64266 Mguyanae TACUTU sp. LBP16583-65998 Mesonauta sp Rio Xingu LBP16767-65999 Mesonauta sp Rio Arapiranga LBP17959-72373 Mesonauta sp Rio Preto Eva LBP17959-72374 Mesonauta sp Rio Preto Eva LBP17999-72489 Mesonauta sp Rio Amazonas LBP18018-72548 Mesonauta sp Rio Amazonas LBP18045-72659 Mesonauta sp Rio Urubu LBP18045-72660 Mesonauta sp Rio Urubu LBP18045-72661 Mesonauta sp Rio Urubu LBP18045-72662 Mesonauta sp Rio Urubu LBP18075-72740 Mesonauta sp Rio Amazonas LBP18075-72741 Mesonauta sp Rio Amazonas LBP18075-72742 Mesonauta sp Rio Amazonas LBP18075-72743 Mesonauta sp Rio Amazonas LBP18075-72744 Mesonauta sp Rio Amazonas LBP18133-72922 Mesonauta sp Manacapuru LBP18133-72923 Mesonauta sp Manacapuru LBP18133-72924 Mesonauta sp Manacapuru LBP18133-72925 Mesonauta sp Manacapuru LBP18133-72926 Mesonauta sp Manacapuru LBP18159-72985 Mesonauta sp Manacapuru LBP18159-72986 Mesonauta sp Manacapuru LBP18204-74091 Mesonauta sp Manacapuru LBP18204-74092 Mesonauta sp Manacapuru LBP18204-74093 Mesonauta sp Manacapuru LBP18233-74185 Mesonauta sp Manacapuru LBP18233-74186 Mesonauta sp Manacapuru LBP18280-74317 Mesonauta sp Rio egro LBP18306-74381 Mesonauta sp Rio egro LBP18306-74382 Mesonauta sp Rio egro LBP20992-81906 Mguyanae AMAZO AS AP LBP21059-82651 Mguyanae OIAPOQUE LBP21087-82732 Mguyanae OIAPOQUE LBP21119-82842 Mguyanae OIAPOQUE LBP25978-95579 Mmirificus JAVARI LBP25978-95580 Mmirificus JAVARI LBP26138-95988 Mmirificus JAVARI LBP26138-95989 Mmirificus JAVARI LBP26138-95990 Mmirificus JAVARI LBP29251-103357 Mesonauta sp PURUS LBP29342-103257 Mesonauta sp PURUS LBP4069-22969 Mesonauta sp Rio Moa LBP4069-22970 Mesonauta sp Rio Moa LBP4069-22971 Mesonauta sp Rio Moa LBP4069-22972 Mesonauta sp Rio Moa LBP4069-22973 Mesonauta sp Rio Moa LBP4292-23912 Mesonauta sp Rio egro LBP4292-23913 Mesonauta insignis Rio egro LBP4358-24115 Mguyanae Rio Branco LBP4408-24242 Mesonauta sp Rio egro LBP4408-24243 Mesonauta sp Rio egro LBP4408-24244 Mesonauta sp Rio egro LBP4408-24245 Mesonauta sp Rio egro LBP4408-24246 Mesonauta sp Rio egro LBP4477-24437 Mesonauta sp Rio egro LBP4477-24438 Mesonauta sp Rio egro LBP4477-24439 Mesonauta sp Rio egro LBP4477-24440 Mesonauta sp Rio egro LBP4882-25668 Mesonauta sp Rio egro LBP4882-25669 Mesonauta sp Rio egro LBP4882-25670 Mesonauta sp Rio egro LBP4882-25671 Mesonauta sp Rio egro LBP4882-25672 Mesonauta sp Rio egro LBP5410-27114 Mesonauta sp Rio Jari LBP59478 Mfestivus Rio Tapajos LBP9330-42563 Mesonauta sp Rio Guama LBP9330-43861 Mesonauta sp Rio Guama MCP44245 Mmirificus Rio Ucayali MHNG17280 Mguyanae Rio Suriname MHNG17281 Mguyanae Rio Suriname MHNG17282 Mguyanae Rio Suriname UFPA10C59 Mesonauta sp Alenquer UFPA11A19 Mesonauta so Manaus UFPA11BA23 Mesonauta sp Rio Xingu UFPA2358 Mesonauta sp Rio Xingu

Group[2] n: 20 ;id: GU804847.1 Megregius OL-0264 GU804848.1 Megregius OL-0272 GU804850.1 Megregius OL-0268 GU804851.1 Megregius OL-0267 GU804852.1 Megregius OL-0269 LBP10159-47566 Minsignis Rio Apure LBP18636-74612 Megregius AQUARIO LBP18636-74613 Megregius AQUARIO LBP2192-15556 Minsignis Rio Orinoco LBP2206-15600 Minsignis Rio Orinoco LBP2248-15712 Minsignis Rio Orinoco LBP2248-15713 Minsignis Rio Orinoco LBP3043-19178 Minsignis Rio Orinoco LBP7098-34627 Minsignis Rio egro LBP7098-34628 Minsignis Rio egro LBP9974-46811 Minsignis Rio Orinoco LBP9974-46812 Minsignis Rio Orinoco LBP9974-46813 Minsignis Rio Orinoco LBP9974-46814 Minsignis Rio Orinoco LBP9994-46725 Minsignis Rio Pelehojo

Group[3] n: 15 ;id: LBP10824-50001 Mfestivus Rio Guapore LBP10824-50002 Mfestivus Rio Guapore LBP10824-50003 Mfestivus Rio Guapore LBP10824-50004 Mfestivus Rio Guapore LBP10824-50005 Mfestivus Rio Guapore LBP11027-50587 Mfestivus Rio Pacaas UFPA10A41 Mesonauta sp Jauaru UFPA10A42 Mesonauta sp Jauaru UFPA10B94 Mesonauta sp Curucamba UFPA10B95 Mesonauta sp Curucamba UFPA10H16 Mesonauta sp Jauaru UFPA10H18 Mesonauta sp Jauaru UNIR1871 Mfestivus Rio Madeira UNIR4835 M festivus Rio Madeira UNIR7349 Mfestivus Rio Pacaas

Group[4] n: 1 ;id: LBP18106 Pterophyllum scalare Aqua

Group[5] n: 3 ;id: LBP21176-83067 Mguyanae AMAZO AS AP - sp. 7 LBP21204-83163 Mguyanae AMAZO AS AP - sp. 7 UFPA11AG09 Mesonauta sp Jeju

Group[6] n: 4 ;id: LBP4908-25787 Macora Rio Araguaia LBP4908-25788 Macora Rio Araguaia LBP4908-25789 Macora Rio Araguaia LBP5741-26889 Macora Rio Araguaia

Group[7] n: 6 ;id: LBP72687 Heros sp Rio Amazonas LBP72688 Heros sp Rio Amazonas LBP74082 Heros sp Manacapuru LBP74187 Heros sp Manacapuru LBP74188 Heros sp Manacapuru UNIR4528 Heros efasciatus Rio JaciParana Madeira RO

Group[8] n: 13 ;id: LBP13638-56644 Mfestivus Rio Paraguai LBP13638-56645 Mfestivus Rio Paraguai LBP14019-58344 Mfestivus Rio Paraguai LBP1892-13410 Mfestivus Rio Taquari LBP1892-13411 Mfestivus Rio Taquari LBP1892-13412 Mfestivus Rio Taquari LBP1892-13439 Mfestivus Rio Taquari LBP3802-22306 Mfestivus Rio Paraguai LBP3802-22307 Mfestivus Rio Paraguai LBP3802-22308 Mfestivus Rio Paraguai LBP7594-36252 Mfestivus Rio Cuiaba LBP7594-36253 Mfestivus Rio Cuiaba LBP7594-36254 Mesonauta festivus Rio Cuiaba

Tree file of partition 4

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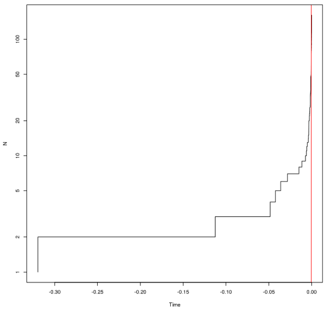
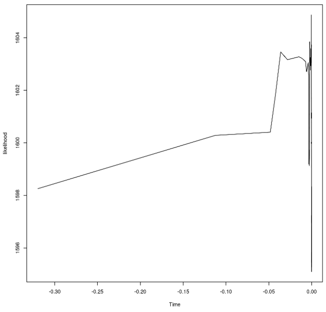
:0.000000,(LBP25978-95579 Mmirificus JAVARI _group 1 :0.000000,(LBP12536-53554 Mmirificus Rio Itaya _group 1 :0.000000,(LBP12536-53553 Mmirificus Rio Itaya _group 1 :0.000000,(LBP12536-53552 Mmirificus Rio Itaya _group 1 :0.000000,(ANSP191989 Mmirificus Rio anay _group 1 :0.000000,ANSP179838 Mmirificus Rio Itaya _group 1 :0.000000) :0.000000) :0.000000) :0.000000) :0.000000) :0.000000) :0.000000) :0.000000) :0.000000) :0.000000) :0.000048,(LBP12432-53695 Mmirificus Rio anay _group 1 :0.000000,LBP12432-53694 Mmirificus Rio anay _group 1 :0.000000) :0.002058) :0.002053) :0.002015) :0.000067,(LBP21119-82842 Mguyanae OIAPOQUE _group 1 :0.000000,(LBP21087-82732 Mguyanae OIAPOQUE _group 1 :0.000000,LBP21059-82651 Mguyanae OIAPOQUE _group 1 :0.000000) :0.000000) :0.002080) :0.000023,LBP18018-72548 Mesonauta sp Rio Amazonas _group 1 :0.002102) :0.000001,LBP14256-59473 Mfestivus Rio Tapajos _group 1 :-0.000001) :0.000001);

General Mixed Yule Coalescent Model (GMYC) analysis.





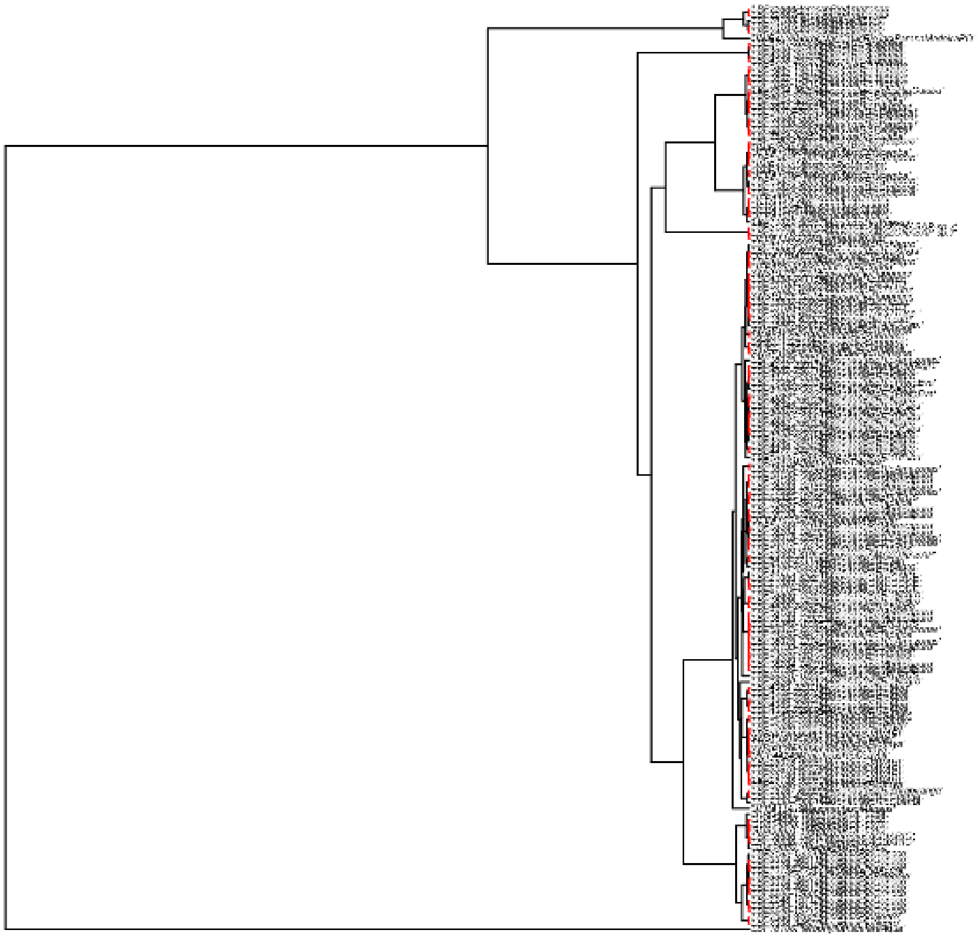


Figure D3. GMYC delimitation tree.

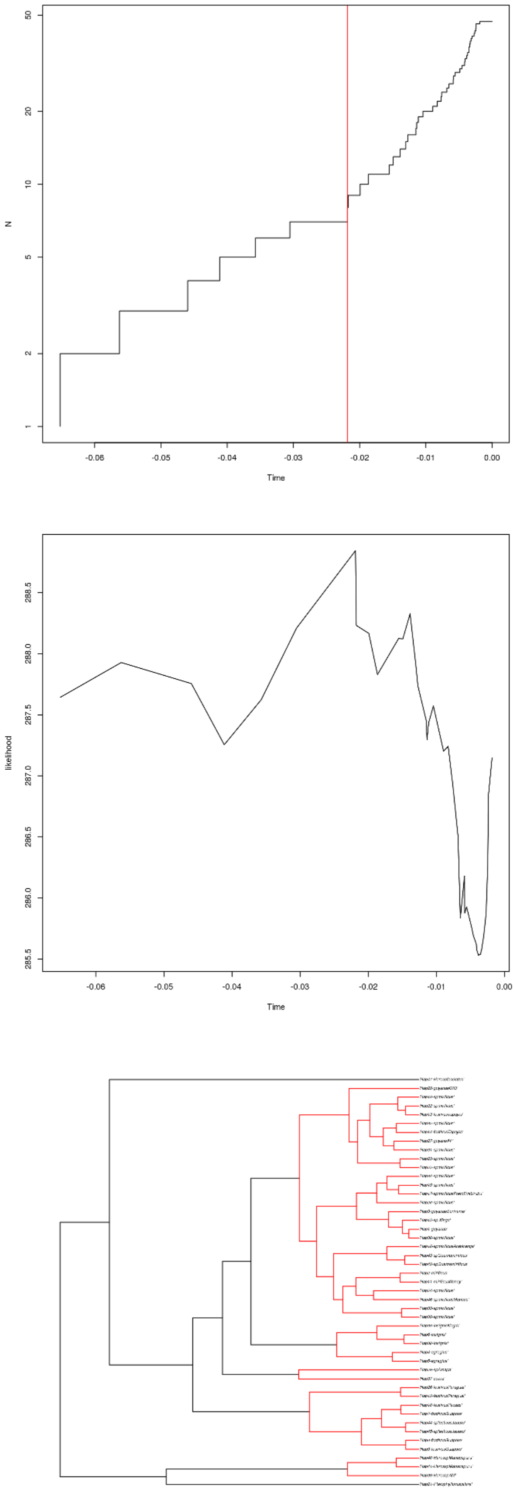


Figure D4. GMYC delimitation tree using unique haplotypes.

Assemble Species by Automatic Partitioning (ASAP) analysis

Nb of subsets	asap-score	P-val (rank)	W (rank)	Treshold dist.
* 8	2.50	4.56e-02 (3)	3.11e-04 (2)	0.037630

* 9	3.00	4.17e-01 (5)	4.84e-04 (1)	0.014866
* 8	3.50	7.84e-03 (2)	6.69e-05 (5)	0.024500
2	4.00	2.28e-01 (4)	9.12e-05 (4)	0.162935
3	5.00	6.01e-01 (7)	1.46e-04 (3)	0.096040
7	7.50	7.62e-01 (9)	1.00e-05 (6)	0.051992
47	8.00	7.48e-04 (1)	3.67e-06 (15)	0.001052
* 12	9.50	5.39e-01 (6)	3.95e-06 (13)	0.006328
24	9.50	6.21e-01 (8)	5.50e-06 (11)	0.003159
6	10.00	8.38e-01 (10)	6.27e-06 (10)	0.057567

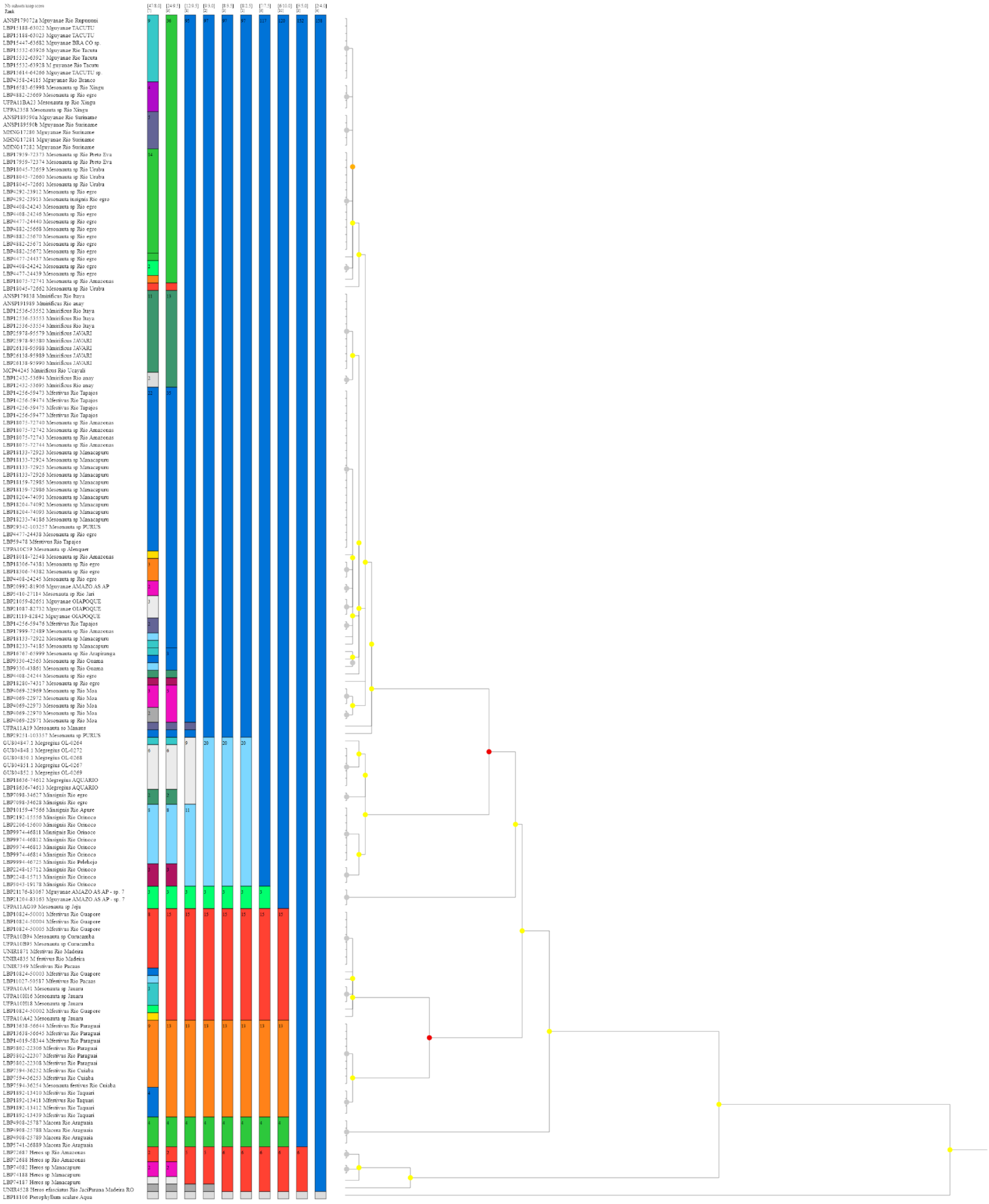


Figure D5. ASAP delimitation tree.

APPENDIX E - Species delimitation - *Mesonauta mirificus* morphological groups

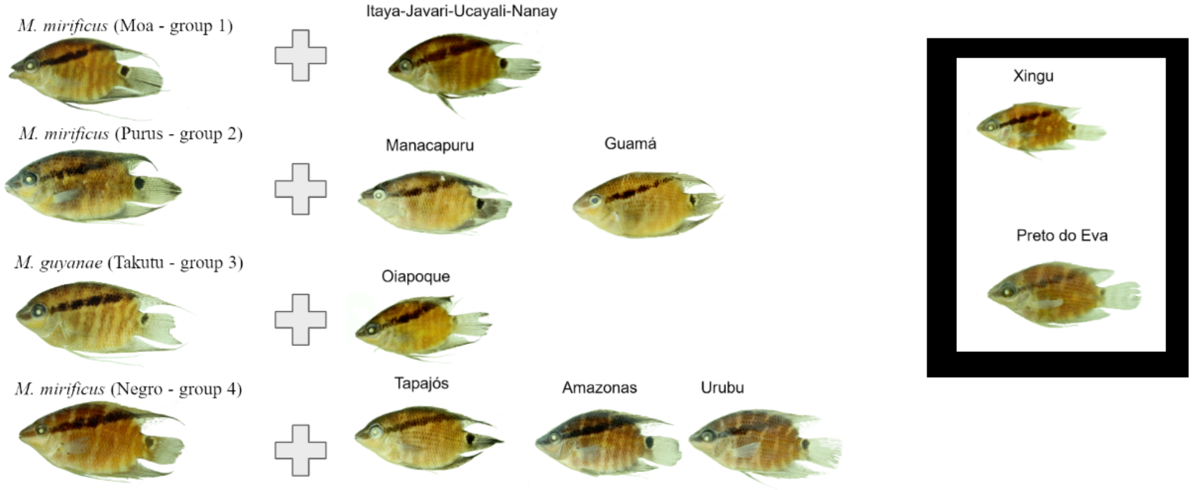


Figure E1. *Mesonauta mirificus* morphological groups. Xingu and Preto do Eva rivers' specimens are too young to verify the color pattern.

APPENDIX F - Molecular phylogeny - Input files with two partitions (COI, 16S) with XIW (command “piwe=”).

```
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        piwe=;
        xread
        1064 32
        &[dna]
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```

LBP5741_26889_Araguaia_-_acora

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LBP5410_27114_sp_Amazonas_Jari_-_mirificus

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LBP4908_25789_Araguaia_-_acora

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LBP4882_25670_Negro_Barcelos_-_mirificus_4

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LBP4069_22971_sp_Moa_-_mirificus_1

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LBP4069_22971_sp_Moa_-_mirificus_1

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LBP4069_22969_4069_sp_Moa_-_mirificus_1

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LBP29356_103206_sp_Purus_-_mirificus_2

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LBP29251_103357_sp_Purus_-_mirificus_2

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LBP26138_95990_Javari_-_mirificus_1

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LBP21204_83163_guyanae_Amapa_-_sp._Amapa

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ACCGATCAACGAACCGAGTTACCCTAGGGATAACAGCGCAATCCCCTTCTAGAGTCCATATCGACAAGGGGGTTTACGACCTCG
ATGTTGGATCA??

LBP21176_83067_guyanae_Amapa_-_sp._Amapa

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ATGTTGGAT??

LBP21119_82842_guyanae_Oiapoque_-_mirificus_1

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TGTTGGATCAGGACATCCTACTGGTGCAGCCGCTATTAA?????????????????????????????

LBP1892_13410_Paraguai_-_sp._Pantanal

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CGTGCAGAAGCGGGGATTATCTCATAAGACGAGAAGACCCTATGGAGCTTTAGGCACCAGAACAGACTATGTTAAACATCCCAA
--AACAAAGATA-AAACCAATTAGACCCTGTTCCA-ATGCCTTTGGTTGGGGCGACCGCGGGGTAATAAAAACCCCCCACGTGGAT
TAGGAGCACCCTT-ACTCCCACAACCCAGGGCCACAGCCCTAAGCAACAGAAATTCTGACCAACTAATGATCCGGTAATA-CCGA
TCAACGAACCGAGTTACCCTAGGGATAACAGCGCAATCCCCTTCTAGAGTCCATATCGACAAGGGGGTTTACGACCTCGATGTT
GGATCAGGACATCCTATTGGTGCAGCCGCTA?????????????????????????????????

LBP18636_74613_egregiusAQ_-_insignis_2

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CCGATCAACGAACCGAGTTACCCTAGGGATAACAGCGCAATCCCCTTCTAGAGTCCATATCGACAAGGGGGTTTACGACCT?????
???

LBP18133_72922_sp_Manacapuru_-_mirificus_2

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GACTAGGAGTACCCTC-ACTCCCACAACCCAGGGCCACAGCCCTAAGCAACAGAATTTCTGACCAGCTAATGATCCGGTGTTAA
CCGATCAACGAACCGAGTTACCCTAGGGATAACAGCGCAATCCCCTTCTAGAGCCCATATCGACAAGGGGGTTTACGACCTCGA
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LBP18045_72659_sp_Urubu_-_mirificus_4

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GACA-AAACCAATTAGACCCTGTCCAA-ATGCCTTTGGTTGGGGCGACCGCGGGGAAATAAAAAACCCCCATGTGGACTAGGAG
TACCCTC-ACTCCCACAACCCAGGGCCACAGCCCTAAGCAACAGAATTTCTGACCAGCTAATGATCCGGTGTTAACCGATCAAC
GAACCGAGTTACCCTAGGGATAACAGCGCAATCCCCTTCTAGAGCCCATATCGACAAGGGGGTTTACGACCTCGATGTTGGATC
A???

LBP16583_65998_sp_Xingu_-_mirificus

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GTTACCCTAGGGATAACAGCGCAATCCCCTTCTAGAGCCCATATCGACAAGGGGGTTTACGACCTCGATGTTGGATCAGGACATC
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LBP15447_63682_sp_Branco_-_guyanae_3

??????????????????TAAAAACATAAGAGGTCCCGCCTGCCCGGTGACTATAAGTTTAACGGCCGCGGTATTTTGACCGTGCAAAGG
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GACCTCGATGTTGGATCA???

LBP15188_63022_sp_Tacutu_-_guayane_3

???????????????AAATAAAAACATAAGAGGTCCCGCCTGCCCAGTGACTATAAGTTTAACGGCCGCGGTATTTTGACCGTGCAAAG

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ATTGATCTCCCCGTGCAGAAGCGGGGATTATTACATAAGACGAGAAGACCCTATGGAGCTTTAGGCACCAGAACAGACTATGTT

AAATATCCCAA--AACAAAGACA-AAACCAATTAGACCCTGTCCAA-ATGCCTTTGGTTGGGGCGACCGCGGGGAAATAAAAAAC

CCCCATGTGGACTAGGAGTACCCTC-ACTCCCACAACCCAGGGCCACAGCCCTAAGCAACAGAATTTCTGACCAGCTAATGATC

CGGTATTAACCGATCAACGAACCGAGTTACCCTAGGGATAACAGCGCAATCCCCTTCTAGAGCCCATATCGACAAGGGGGTTTA

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LBP14256_59475_sp_Tapajos_-_mirificus_4

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TTACGACCTCGATGTTGGATCAGGACATCCTACTGGTGCAGCCGCTATTAAGGGTTCGTTTGTTCAA?????????????

LBP12536_53553_mirificus_Itaya_-_mirificus_1

?????????????????????????????GAGGTCCCGCCTGCCCGGTGACTATAAGTTTAACGGCCGCGGTATTTTGACCGTGCAAAGGTAGC

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TCCCAA--AACAAAGACA-AAACCAATTAGACCCTGTCCCA-ATGCCTTTGGTTGGGGCGACCGCGGGGAAATAAAAAACCCCCA

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LBP12432_53695_mirificus_Nanay_-_mirificus_1

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TGTTGGATCAGGACATCCTACTGGTGCAGCCGCTATTAAGGGTTCGTTTGTTCAACGA??????????

LBP10824_50002_festivus_Guapore_-_festivus

????TCGCCTCTTGAA-GTATAAACATAAGAGGTCCCGCCTGCCCGGTGACTATAAGTTTAACGGCCGCGGTATTTTGACCGTGCA

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GAAATTGATCTCCCCGTGCAGAAGCGGGGATAATATCATAAGACGAGAAGACCCTATGGAGCTTTAGGCACCAGAACAGACTAT

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ACCCCCACGTGGACTAGGAGCACCCTT-ACTCCCACAACCCAGGGCCACAGCCCTAAGCAACAGAAATTCTGACCAAATAATGA

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ACGACCTCGATGTTGGATCAGGACATCCTATTGGTGCAGCCGCTATTAAGGGTTCGTTTGTTCAACGA??????????

Uaru_amphiacanthoides_GE

?????CGCCTCTTGAA-CTAAAAACATAAGAGGTCCCGCCTGCCCAGTGACTATAAGTTTAACGGCCGCGGTATTCTGACCGTGCA
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Hypselecara_temporalis_GE

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Heros_efasciatus_GE

?????CGCCTCTTGAA-ACAAAAACATAAGAGGTCCCGCCTGCCCGGTGACTA--AGTTTAACGGCCGCGGTATTTTGACCGTGCAA
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Rocio_octofasciata_GE

?????CGCCTCTTGAA-GCAAAAACATAAGAGGTCCCGCCTGCCCAGTGACTATTAGTTCAACGGCCGCGGTATTTTGACCGTGCA
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Herotilapia_multispinosa_GE

?????CGCCTCCTGAA-ACAAAAACATAGGAGGTCCCGCCTGCCCAGTGACTATAAGTTTAACGGCCGCGGTATTTTGACCGTGCA
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GATCCGGCAC-AGCCGATCAACGAACCGAGTTACCCTAGGGATAACAGCGCAATCCCCTTCTAGAGTCCATATCGACAAGGGGG
TTTACGACCTCGATGTTGGATCAGGACATCCTATTGGTGCAGCCGCTATTAAGGGTTCGTTTGTTCAACGATTAAAGTCCT;
        proc /;
        comments 0;
```

Appendix G - Molecular phylogeny - lists of synapomorphies and character transformations across the topology plus the tree with nodes

Figure G1 - Parsimony tree with number of nodes.

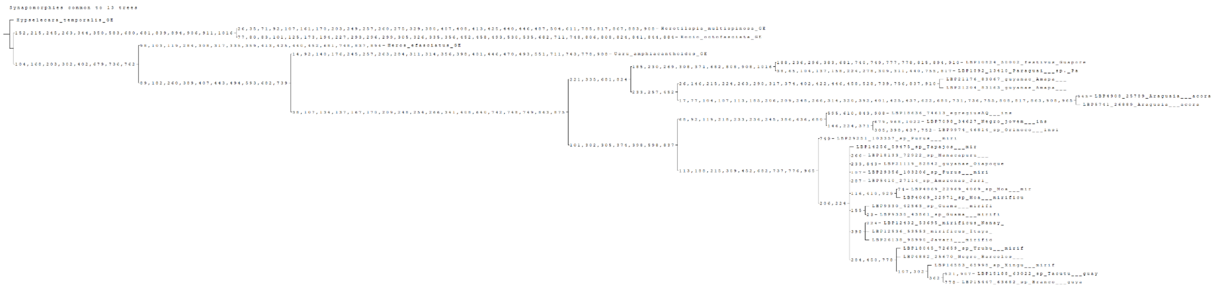

Figure G2 - Parsimony tree with mapped synapomorphies.

List of Synapomorphies common to 13 trees (XIW analysis). Divided into two columns.

(Node numbers refer to nodes in consensus)

LBP9974_46814_sp_Orinoco___insi :
All trees:
Char. 305: C --> T
Char. 398: T --> A
Char. 437: A --> G
Char. 752: A --> G

LBP9330_43861_sp_Guama___mirifi :
All trees:
Char. 23: A --> G

LBP9330_42563_sp_Guama___mirifi :
All trees:
No autapomorphies:

LBP7098_34627_Negro_jovem___ins :
All trees:
Char. 679: A --> C
Char. 968: A --> C
Char. 1022: C --> T

LBP5741_26889_Araguaia___acora :
All trees:
No autapomorphies:

LBP5410_27114_sp_Amazonas_Jari_ :
All trees:
Char. 287: C --> T

LBP4908_25789_Araguaia___acora :
All trees:
Char. 945: A --> C

LBP4882_25670_Negro_Barcelos___ :
All trees:
No autapomorphies:

LBP4069_22971_sp_Moa___mirificu :
All trees:
No autapomorphies:

LBP4069_22969_4069_sp_Moa___mir :
All trees:
Char. 74: C --> T

LBP29356_103206_sp_Purus___miri :
All trees:
Char. 107: A --> C

LBP29251_103357_sp_Purus___miri :
All trees:
Char. 749: C --> T
Some trees:
Char. 311: A --> G

LBP26138_95990_Javari___mirific :
All trees:
No autapomorphies:

LBP21204_83163_guyanae_Amapa___ :
All trees:
No autapomorphies:

LBP21176_83067_guyanae_Amapa___ :
All trees:
No autapomorphies:

LBP21119_82842_guyanae_Oiapoque :
All trees:
Char. 233: A --> G
Char. 843: C --> A

LBP1892_13410_Paraguai___sp._Pa :
All trees:
Char. 38: T --> C
Char. 65: T --> C
Char. 104: T --> C
Char. 137: T --> C
Char. 158: C --> T
Char. 224: A --> G
Char. 278: T --> C
Char. 309: T --> C
Char. 311: A --> G
Char. 440: C --> T
Char. 755: C --> T
Char. 817: A --> C

LBP18636_74613_egregiusAQ___ins :
All trees:
Char. 595: A --> G
Char. 610: A --> T
Char. 843: C --> T
Char. 908: T --> C

LBP18133_72922_sp_Manacapuru___ :
All trees:
Char. 266: G --> C

LBP18045_72659_sp_Urubu___mirif :
Some trees:
Char. 595: G --> A

LBP16583_65998_sp_Xingu___mirif :
Some trees:
Char. 595: G --> A

LBP15447_63682_sp_Branco___guya :
All trees:
Char. 778: A --> C

```
LBP15188_63022_sp_Tacutu___guay :
  All trees:
    Char. 521: G --> A
    Char. 907: G --> A

  LBP14256_59475_sp_Tapajos___mir
:
  Some trees:
    Char. 311: A --> G

  LBP12536_53553_mirificus_Itaya_ :
  All trees:
    No autapomorphies:

  LBP12432_53695_mirificus_Nanay_
:
  All trees:
    Char. 224: G --> C

  LBP10824_50002_festivus_Guapore
:
  All trees:
    Char. 188: C --> T
    Char. 236: C --> T
    Char. 296: C --> T
    Char. 383: C --> T
    Char. 681: C --> A
    Char. 740: C --> T
    Char. 749: C --> T
    Char. 777: C --> T
    Char. 778: C --> T
    Char. 815: A --> G
    Char. 894: C --> A
    Char. 910: A --> T

  Uaru_amphiacanthoides_GE :
  All trees:
    Char. 14: T --> C
    Char. 92: C --> T
    Char. 140: A --> G
    Char. 176: C --> T
    Char. 245: C --> T
    Char. 257: T --> C
    Char. 263: G --> A
    Char. 284: T --> C
    Char. 311: A --> G
    Char. 314: C --> T
    Char. 356: A --> G
    Char. 398: C --> G
    Char. 401: C --> A
    Char. 446: G --> A
    Char. 470: C --> T
    Char. 493: A --> C
    Char. 551: T --> C
    Char. 711: T --> C
    Char. 743: A --> G
    Char. 778: C --> A
    Char. 908: T --> A

  Hypselecara_temporalis_GE :
  All trees:
    No autapomorphies:

  Heros_efasciatus_GE :
  All trees:
    Char. 98: A --> G
    Char. 103: T --> C
    Char. 119: T --> C
    Char. 284: T --> A
    Char. 308: C --> T
    Char. 317: G --> A
    Char. 335: G --> A
    Char. 359: T --> C
    Char. 413: A --> G
    Char. 425: T --> C
    Char. 440: C --> T
    Char. 452: G --> A
    Char. 681: T --> A
    Char. 748: T --> C
    Char. 837: C --> T
    Char. 894: C --> A

Rocio_octofasciata_GE :
  All trees:
    Char. 77: A --> G
    Char. 80: T --> C
    Char. 83: A --> G
    Char. 101: A --> C
    Char. 125: A --> C
    Char. 173: C --> T
    Char. 194: C --> T
    Char. 227: A --> G
    Char. 293: C --> T
    Char. 296: C --> T
    Char. 299: T --> C
    Char. 305: T --> C
    Char. 326: T --> C
    Char. 335: G --> A
    Char. 356: A --> T
    Char. 452: G --> T
    Char. 458: T --> C
    Char. 493: A --> G
    Char. 530: A --> T
    Char. 535: T --> C
    Char. 682: A --> C
    Char. 711: T --> C
    Char. 748: T --> C
    Char. 806: G --> A
    Char. 808: A --> T
    Char. 824: T --> C
    Char. 841: C --> A
    Char. 844: T --> C
    Char. 884: T --> C

Herotilapia_multispinosa_GE :
  All trees:
    Char. 26: C --> T
    Char. 35: A --> G
    Char. 71: T --> C
    Char. 92: C --> T
    Char. 107: G --> T
    Char. 161: T --> C
    Char. 170: G --> A
    Char. 203: A --> C
    Char. 249: C --> T
    Char. 257: T --> C
    Char. 260: T --> C
    Char. 275: C --> T
    Char. 329: T --> C
    Char. 380: A --> G
    Char. 407: C --> T
    Char. 408: A --> G
    Char. 413: A --> G
    Char. 425: T --> C
    Char. 440: C --> T
    Char. 446: G --> A
    Char. 487: T --> C
    Char. 504: A --> G
    Char. 611: C --> T
    Char. 785: C --> T
    Char. 817: A --> C
    Char. 867: G --> A
    Char. 883: C --> T
    Char. 908: T --> C

Node 33 :
  All trees:
    Char. 146: A --> G
    Char. 224: A --> G
    Char. 371: A --> G

Node 34 :
  All trees:
    Char. 68: A --> G
    Char. 92: C --> T
    Char. 119: T --> A
    Char. 218: T --> C
    Char. 233: A --> G
    Char. 236: C --> T
    Char. 245: C --> T
    Char. 386: C --> T
    Char. 636: T --> C
    Char. 680: T --> C

Node 35 :
  All trees:
    Char. 101: A --> T
    Char. 302: C --> T
    Char. 305: T --> C
    Char. 374: C --> T
    Char. 398: C --> T
    Char. 598: T --> C
    Char. 837: C --> T

Node 36 :
  All trees:
    Char. 38: C --> T
    Char. 107: G --> A
    Char. 134: C --> T
    Char. 137: C --> T
    Char. 167: C --> T
    Char. 170: G --> A
    Char. 209: T --> C
    Char. 248: A --> T
    Char. 254: A --> T
    Char. 266: A --> G
    Char. 341: T --> C
    Char. 408: A --> G
    Char. 640: T --> C
    Char. 742: T --> C
    Char. 748: T --> A
    Char. 749: A --> C
    Char. 863: T --> C
    Char. 875: T --> C

Node 37 :
  All trees:
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    Char. 89: C --> T
    Char. 182: C --> T
    Char. 260: T --> C
    Char. 389: A --> G
    Char. 407: C --> T
    Char. 443: T --> C
    Char. 494: C --> T
    Char. 593: A --> G
    Char. 682: A --> C
    Char. 739: C --> T

Node 38 :
  All trees:
    Char. 104: C --> T
    Char. 168: C --> T
    Char. 203: A --> T
    Char. 302: T --> C
    Char. 402: T --> C
    Char. 679: C --> A
    Char. 736: G --> A
    Char. 762: T --> C

Node 39 :
  All trees:
    No synapomorphies

Node 40 :
  All trees:
    Char. 155: A --> G

Node 41 :
  All trees:
    Char. 206: A --> G
    Char. 224: A --> G

Node 42 :
  All trees:
    Char. 113: G --> A
    Char. 188: C --> T
    Char. 215: T --> C
    Char. 309: T --> C
    Char. 452: G --> A
    Char. 682: C --> A
    Char. 737: C --> T
    Char. 776: T --> C
    Char. 965: T --> C
  Some trees:
    Char. 311: A --> AG

Node 43 :
  All trees:
    Char. 17: T --> C
    Char. 77: A --> G
    Char. 104: T --> C
    Char. 107: A --> T
    Char. 113: G --> A
    Char. 185: C --> A
    Char. 206: A --> G
    Char. 209: C --> T
    Char. 248: T --> C
    Char. 266: G --> A
    Char. 314: C --> T
    Char. 320: T --> C
    Char. 392: T --> C
    Char. 401: C --> T
    Char. 425: T --> C
    Char. 437: A --> G
    Char. 622: C --> T
    Char. 680: T --> A
    Char. 731: G --> A
    Char. 736: A --> G
    Char. 755: C --> T
    Char. 808: A --> C
    Char. 817: A --> C
    Char. 863: C --> T
    Char. 908: T --> C
    Char. 965: T --> C

Node 44 :
  All trees:
    Char. 233: A --> G
    Char. 257: T --> C
    Char. 452: G --> A

Node 45 :
  All trees:
    Char. 221: T --> C
    Char. 335: G --> A
    Char. 681: T --> C
    Char. 824: T --> C

Node 46 :
  All trees:
    Char. 284: T --> C
    Char. 450: C --> T
    Char. 778: C --> A

Node 47 :
  All trees:
    Char. 116: T --> C
    Char. 410: C --> T
    Char. 929: T --> C

Node 48 :
  All trees:
    Char. 398: T --> C

Node 49 :
  All trees:
    Char. 26: C --> T
    Char. 146: A --> G
    Char. 215: T --> G
    Char. 224: A --> G
    Char. 263: G --> A
    Char. 290: A --> G
    Char. 317: G --> A
    Char. 374: C --> T
    Char. 402: C --> T
    Char. 422: A --> G
    Char. 446: G --> A
    Char. 458: T --> C
    Char. 528: A --> G
    Char. 739: T --> C
    Char. 756: A --> G
    Char. 837: C --> T
    Char. 910: A --> G

Node 50 :
  All trees:
    Char. 185: C --> T
    Char. 230: A --> G
    Char. 269: C --> T
    Char. 308: C --> T
    Char. 371: A --> G
    Char. 682: C --> T
    Char. 808: A --> T
    Char. 908: T --> A
    Char. 1016: C --> T

Node 51 :
  All trees:
    Char. 107: A --> G
    Char. 302: T --> C

Node 52 :
  All trees:
    Char. 362: T --> C

Node 53 :
  All trees:
    Char. 152: T --> C
    Char. 215: T --> C
    Char. 245: C --> T
    Char. 263: G --> A
    Char. 344: C --> T
    Char. 350: T --> C
    Char. 583: C --> T
    Char. 680: T --> C
    Char. 681: T --> C
    Char. 839: C --> A
    Char. 894: C --> T
    Char. 906: T --> C
    Char. 911: A --> G
    Char. 1016: C --> T
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APPENDIX H - Molecular phylogeny - alignments from COI and 16S

>LBP9974 46814 sp Orinoco - insignis 1

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>LBP9330 43861 sp Guama - mirificus 2

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>LBP9330 42563 sp Guama - mirificus 2

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>LBP7098 34627 Negro jovem - insignis 1

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>LBP5741 26889 Araguaia - acora

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>LBP5410 27114 sp Amazonas Jari - mirificus

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>LBP4908 25789 Araguaia - acora

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>LBP4882 25670 Negro Barcelos - mirificus 4

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>LBP4069 22971 sp Moa - mirificus 1

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>LBP29356 103206 sp Purus - mirificus 2

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>LBP21204 83163 guyanae Amapa - sp. Amapa

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>LBP21176 83067 guyanae Amapa - sp. Amapa

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>LBP21119 82842 guyanae Oiapoque - mirificus 1

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>LBP1892 13410 Paraguai - sp. Pantanal

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>LBP18045 72659 sp Urubu - mirificus 4

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>LBP16583 65998 sp Xingu - mirificus

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>LBP15447 63682 sp Branco - guyanae 3

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>LBP14256 59475 sp Tapajos - mirificus 4

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>LBP12432 53695 mirificus Nanay - mirificus 1

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>LBP10824 50002 festivus Guapore - festivus

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>Heros efasciatus GE

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APPENDIX I - New species - COI sequences of Mesonauta species and outgroup used to the delimitation analyzes.

>LBP9974 46814 sp Orinoco - insignis 1

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>LBP7098 34627 Negro jovem - insignis 1

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>LBP5741 26889 Araguaia - acora

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>LBP5410 27114 sp Amazonas Jari - mirificus

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>LBP4908 25789 Araguaia - acora

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>LBP4069 22971 sp Moa - mirificus 1

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>LBP29356 103206 sp Purus - mirificus 2

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>LBP29251 103357 sp Purus - mirificus 2

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>LBP21204 83163 guyanae Amapa - sp. Amapa

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>LBP21176 83067 guyanae Amapa - sp. Amapa

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>LBP18636 74613 egregiusAQ - insignis 2

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>LBP18133 72922 sp Manacapuru - mirificus 2

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>LBP18045 72659 sp Urubu - mirificus 4

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>LBP16583 65998 sp Xingu - mirificus

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>LBP15447 63682 sp Branco - guyanae 3

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>LBP15188 63022 sp Tacutu - guayane 3

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>LBP14256 59475 sp Tapajos - mirificus 4

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>LBP12536 53553 mirificus Itaya - mirificus 1

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>LBP12432 53695 mirificus Nanay - mirificus 1

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>LBP10824 50002 festivus Guapore - festivus

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>Uaru amphiacanthoides GE

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>Hypselecara temporalis GE

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>Heros efasciatus GE

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>Rocio octofasciata GE

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>Herotilapia multispinosa GE

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APPENDIX J - New species - Delimitation analyzes results.

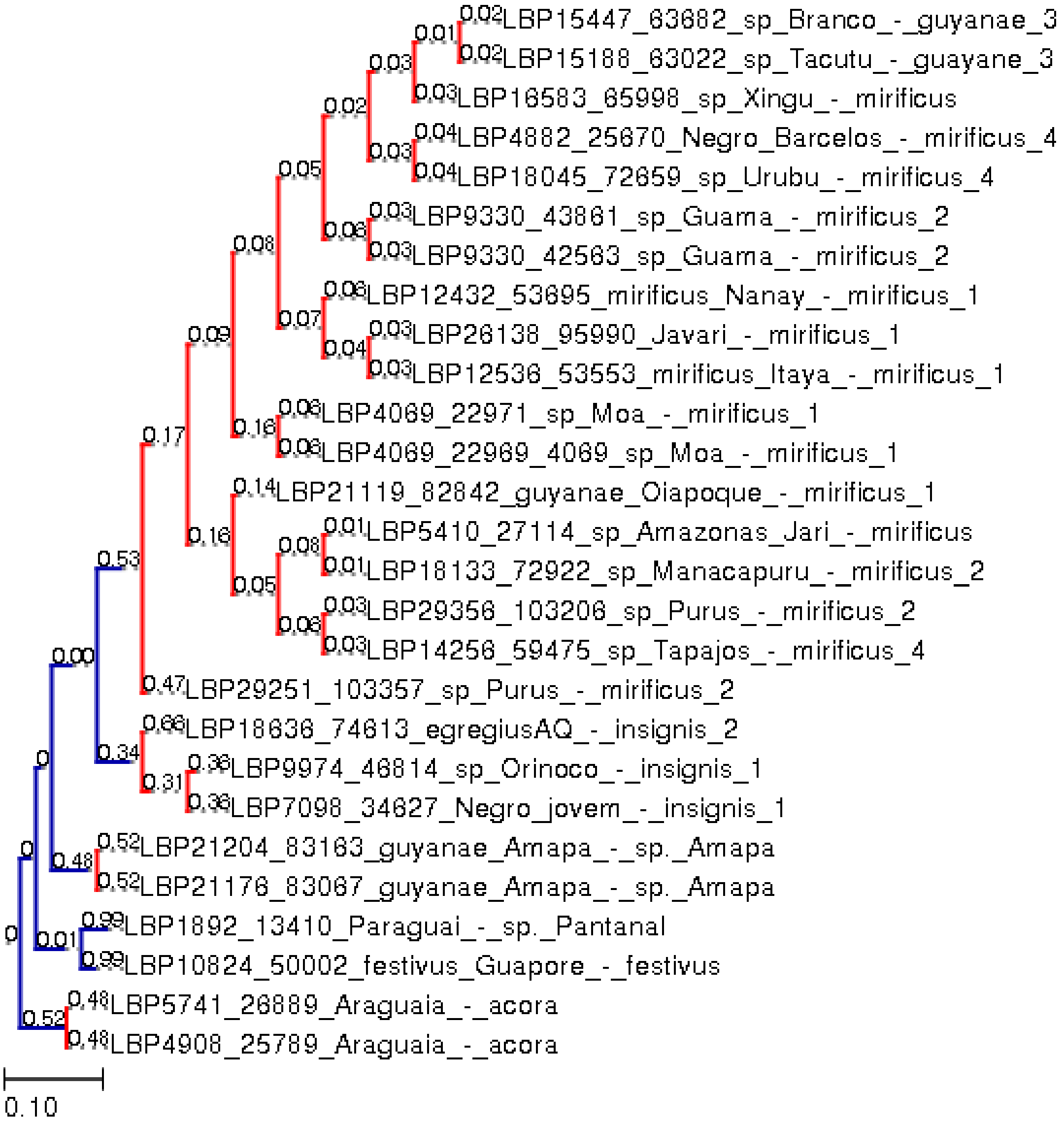

Figure J1. PTP delimitation tree.

Poisson Tree Process (PTP) delimitation results

Max likilhood partition

Species 1 (support = 0.517)

LBP5741_26889_Araguaia_-_acora,LBP4908_25789_Araguaia_-_acora

Species 2 (support = 0.483)

LBP21204_83163_guyanae_Amapa_-_sp._Amapa,LBP21176_83067_guyanae_Amapa_-_sp._Amapa

Species 3 (support = 0.533)

LBP15447_63682_sp_Branco_-_guyanae_3,LBP15188_63022_sp_Tacutu_-_guayane_3,LBP16583_65998_sp_Xingu_-_mirificus,LBP4882_25670_Negro_Barcelos_-_mirificus_4,LBP18045_72659_sp_Urubu_-_mirificus_4,LBP9330_43861_sp_Guama_-_mirificus_2,LBP9330_42563_sp_Guama_-_mirificus_2,LBP12432_53695_mirificus_Nanay_-_mirificus_1,LBP26138_95990_Javari_-_mirificus_1,LBP12536_53553_mirificus_Itaya_-_mirificus_1,LBP4069_22971_sp_Moa_-_mirificus_1,LBP4069_22969_4069_sp_Moa_-_mirificus_1,LBP21119_82842_guyanae_Oiapoque_-_mirificus_1,LBP5410_27114_sp_Amazonas_Jari_-_mirificus,LBP18133_72922_sp_Manacapuru_-_mirificus_2,LBP29356_103206_sp_Purus_-_mirificus_2,LBP14256_59475_sp_Tapajos_-_mirificus_4,LBP29251_103357_sp_Purus_-_mirificus_2

Species 4 (support = 0.335)

LBP18636_74613_egregiusAQ_-_insignis_2,LBP9974_46814_sp_Orinoco_-_insignis_1,LBP7098_34627_Negro_jovem_-_insignis_1

Species 5 (support = 0.992)
LBP1892_13410_Paraguai_-_sp._Pantanal

Species 6 (support = 0.992)
LBP10824_50002_festivus_Guapore_-_festivus

Automatic Barcode Gap Discovery (ABGD) analysis

/* ABGD (Automatic Barcod Gap Discovery)
/* web version 05/22/23 - 10:13AM

Fasta Format detected
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Partition 1 : found 10 groups (prior maximal distance P= 0.001000)
Partition 2 : found 10 groups (prior maximal distance P= 0.001668)
Partition 3 : found 10 groups (prior maximal distance P= 0.002783)
Partition 4 : found 10 groups (prior maximal distance P= 0.004642)
Partition 5 : found 10 groups (prior maximal distance P= 0.007743)
Partition 6 : found 10 groups (prior maximal distance P= 0.012915)
Partition 7 : found 6 groups (prior maximal distance P= 0.021544)
Partition 8 : found 6 groups (prior maximal distance P= 0.035938)
Partition 9 : found 6 groups (prior maximal distance P= 0.059948)

Partition 1:

Group[1] n: 3 ;id: LBP9974 46814 sp Orinoco - insignis 1 LBP7098 34627 Negro jovem - insignis 1 LBP18636 74613 egregiusAQ - insignis 2

Group[2] n: 18 ;id: LBP9330 43861 sp Guama - mirificus 2 LBP9330 42563 sp Guama - mirificus 2 LBP5410 27114 sp Amazonas Jari - mirificus LBP4882 25670 Negro Barcelos - mirificus 4 LBP4069 22971 sp Moa - mirificus 1 LBP4069 22969 4069 sp Moa - mirificus 1 LBP29356 103206 sp Purus - mirificus 2 LBP29251 103357 sp Purus - mirificus 2 LBP26138 95990 Javari - mirificus 1 LBP21119 82842 guyanae Oiapoque - mirificus 1 LBP18133 72922 sp Manacapuru - mirificus 2 LBP18045 72659 sp Urubu - mirificus 4 LBP16583 65998 sp Xingu - mirificus LBP15447 63682 sp Branco - guyanae 3 LBP15188 63022 sp Tacutu - guayane 3 LBP14256 59475 sp Tapajos - mirificus 4 LBP12536 53553 mirificus Itaya - mirificus 1 LBP12432 53695 mirificus Nanay - mirificus 1

Group[3] n: 2 ;id: LBP5741 26889 Araguaia - acora LBP4908 25789 Araguaia - acora

Group[4] n: 2 ;id: LBP21204 83163 guyanae Amapa - sp. Amapa LBP21176 83067 guyanae Amapa - sp. Amapa

Group[5] n: 2 ;id: LBP1892 13410 Paraguai - sp. Pantanal LBP10824 50002 festivus Guapore - festivus

Group[6] n: 1 ;id: Uaru amphiacanthoides GE

Group[7] n: 1 ;id: Hypselecara temporalis GE

Group[8] n: 1 ;id: Heros efasciatus GE

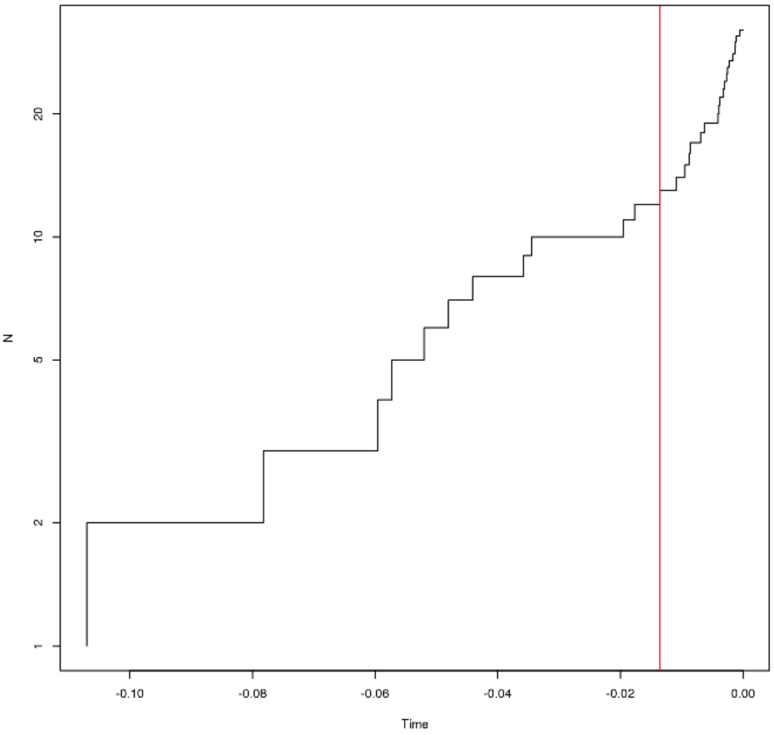
Group[9] n: 1 ;id: Rocio octofasciata GE

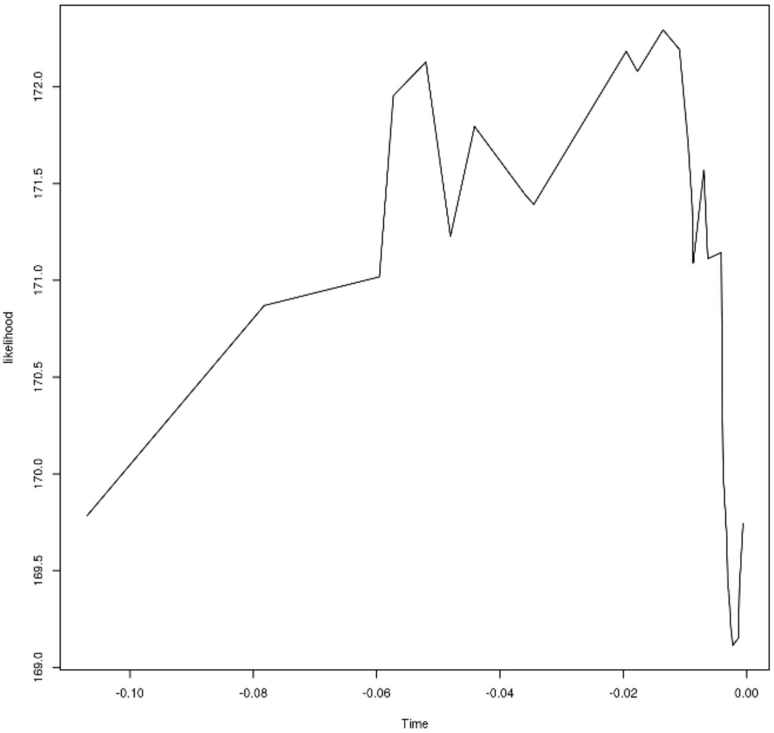
Group[10] n: 1 ;id: Herotilapia multispinosa GE

<u>Tree file:</u>

((LBP18133 72922 sp Manacapuru - mirificus 2 _group 2 :0.002110,LBP5410 27114 sp Amazonas Jari - mirificus _group 2 :0.002107) :0.000001,LBP14256 59475 sp Tapajos - mirificus 4 _group 2 :-0.000005,(((((((((((Herotilapia multispinosa GE _group 10 :0.052182,Rocio octofasciata GE _group 9 :0.073111) :0.011397,(Heros efasciatus GE _group 8 :0.052975,Hypselecara temporalis GE _group 7 :0.088300) :0.009424) :0.007073,Uaru amphiacanthoides GE _group 6 :0.049136) :0.032897,(LBP4908 25789 Araguaia - acora _group 3 :0.000000,LBP5741 26889 Araguaia - acora _group 3 :0.000000) :0.034237) :0.005769,(LBP10824 50002 festivus Guapore - festivus _group 5 :0.013209,LBP1892 13410 Paraguai - sp. Pantanal _group 5 :0.021028) :0.017887) :0.003456,(LBP21176 83067 guyanae Amapa - sp. Amapa _group 4 :0.000000,LBP21204 83163 guyanae Amapa - sp. Amapa _group 4 :0.000000) :0.030323) :0.005573,(LBP18636 74613 egregiusAQ - insignis 2 _group 1 :0.001974,(LBP7098 34627 Negro jovem - insignis 1 _group 1 :0.000727,LBP9974 46814 sp Orinoco - insignis 1 _group 1 :0.005605) :0.003796) :0.028312) :0.017353,LBP29251 103357 sp Purus - mirificus 2 _group 2 :0.004910) :0.003708,(((LBP12432 53695 mirificus Nanay - mirificus 1 _group 2 :0.002008,(LBP12536 53553 mirificus Itaya - mirificus 1 _group 2 :0.000000,LBP26138 95990 Javari - mirificus 1 _group 2 :0.000000) :0.000098) :0.001988,((((LBP15188 63022 sp Tacutu - guayane 3 _group 2 :0.000000,LBP15447 63682 sp Branco - guyanae 3 _group 2 :0.000000) :0.002121,LBP16583 65998 sp Xingu - mirificus _group 2 :-0.000018) :0.004141,(LBP18045 72659 sp Urubu - mirificus 4 _group 2 :0.000000,LBP4882 25670 Negro Barcelos - mirificus 4 _group 2 :0.000000) :0.000088) :0.004140,(LBP9330 42563 sp Guama - mirificus 2 _group 2 :0.000088,LBP9330 43861 sp Guama - mirificus 2 _group 2 :0.002016) :0.002021) :0.000031) :0.000145,(LBP4069 22969 4069 sp Moa - mirificus 1 _group 2 :0.002118,LBP4069 22971 sp Moa - mirificus 1 _group 2 :-0.000015) :0.004084) :0.001701) :0.000115,LBP29356 103206 sp Purus - mirificus 2 _group 2 :0.001915) :0.000183,LBP21119 82842 guyanae Oiapoque - mirificus 1 _group 2 :0.002080) :0.000026);

General Mixed Yule Coalescent Model (GMYC) analysis.





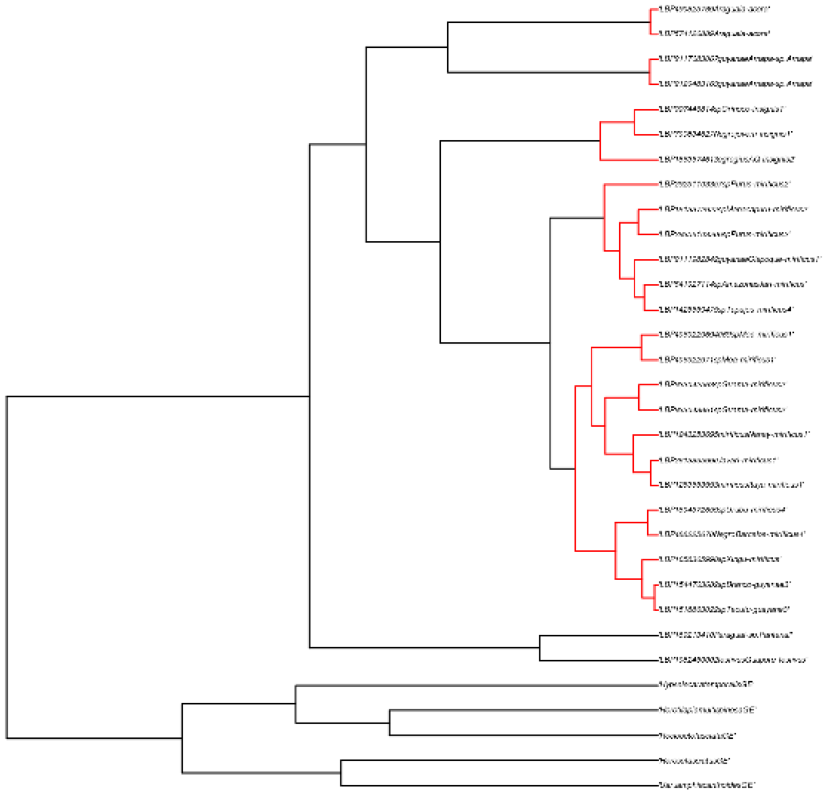


Figure J2. GMYC delimitation tree.

Assemble Species by Automatic Partitioning (ASAP) analysis

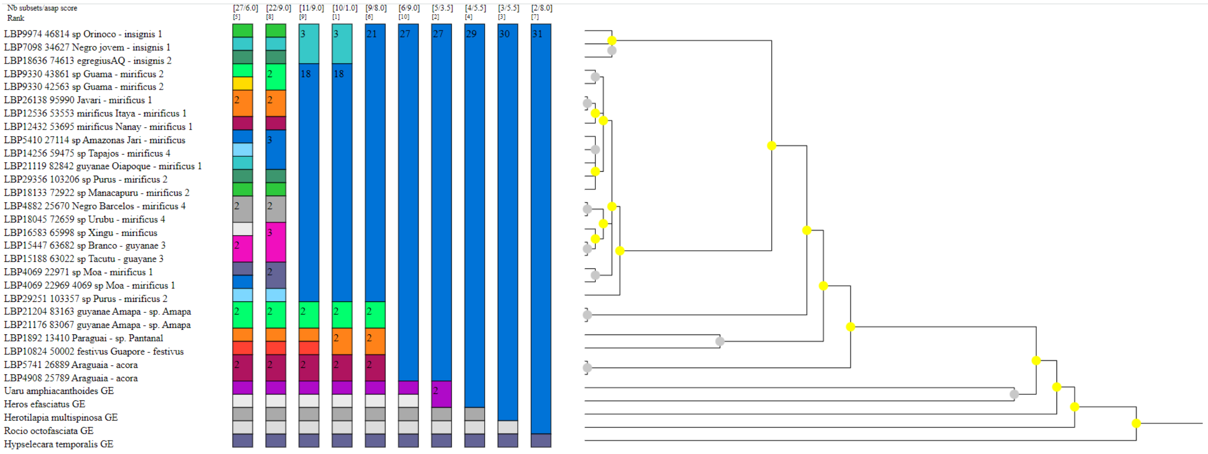


Figure J3. ASAP delimitation tree.