Molecular Phylogenetics and Evolution 95 (2016) 20-33

Contents lists available at ScienceDirect





journal homepage: www.elsevier.com/locate/ympev

Model-based total evidence phylogeny of Neotropical electric knifefishes (Teleostei, Gymnotiformes) $\stackrel{\circ}{\sim}$



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ARTICLE INFO

Article history: Received 16 December 2014 Revised 26 October 2015 Accepted 8 November 2015 Available online 23 November 2015

Keywords: Freshwater fishes Electric fishes Morphological characters Molecular systematics Tropical biodiversity South America

ABSTRACT

This study provides the most comprehensive Model-Based Total Evidence (MBTE) phylogenetic analyses of the clade Gymnotiformes to date, reappraising relationships using a dataset comprised of six genes (5277 bp) and 223 morphological characters, and an ingroup taxon sample including 120 of 212 valid species representing 34 of the 35 extant genera. Our MBTE analyses indicate the two main gymnotiform clades are Gymnotidae and Sternopygoidei, the latter comprised of Rhamphichthyoidea (Rhamphichthyidae + Hypopomidae) and Sinusoidea (Sternopygidae + Apteronotidae). Within Gymnotidae. *Electrophorus* and *Gymnotus* are sister taxa, and *Gymnotus* includes the following six clades: (i) G. pantherinus clade, (ii) G. coatesi clade, (iii) G. anguillaris clade, (iv) G. tigre clade, (v) G. cylindricus clade, and (vi) G. carapo clade. Within Rhamphichthyoidea, Steatogenae (Steatogenys + Hypopygus) is a member of Rhamphichthyidae, and Hypopomidae includes the following clades: (i) Akawaio, (ii) Hypopomus, (iii) Microsternarchini, and (iv) Brachyhypopomus. Within Sternopygidae, Sternopygus and Eigenmanninae are sister groups, Rhabdolichops is the sister to other Eigenmanninae, Archolaemus + Distocyclus is the sister to Eigenmannia, and Japigny is nested within Eigenmannia. Within Apteronotidae, Sternarchorhamphinae (Sternarchorhamphus + Orthosternarchus) is the sister to Apteronotinae, Adontosternarchus is the sister group to other Apteronotinae, Sternarchorhynchini (Sternarchorhynchus + Platyurosternarchus) is the sister to Navajini, and species assigned to Apteronotus are members of two separate clades: (i) A. sensu stricto in the Apteronotini, and (ii) the "A." bonapartii clade in the Navajini.

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1. Introduction

1.1. Overview of Gymnotiformes

Gymnotiformes is a clade of obligate freshwater fishes composed of 219 valid species ranging from the Río Salado in the Pampas of Argentina to the Río San Nicolas of southwestern Chiapas in Mexico. Among Neotropical fishes, gymnotiforms are readily recognized by their elongate eel-shaped body, the absence of dorsal, pelvic, and adipose fins, and a caudal fin that is either highly reduced (Apteronotidae and *Electrophorus*) or entirely absent (Albert, 2001; de Santana et al., 2013; Mago-Leccia, 1994). Gymnotiform species typically move by contractions of the anal-fin pterygiophore muscles, which causes undulations of the elongate anal-fin membrane. The electric eel *Electrophorus electricus* is the largest and most widely known gymnotiform growing to more than 7 feet (2.2 m) and producing electric discharges of up to 600 V (Ellis, 1913).

All gymnotiform fish are capable of producing and detecting weak electric signals (less than 1 V) in the water around their body (Bennett, 1971; Von der Emde, 1999). This weak electric field is generated by specialized muscle or nerve cells that produce rhythmic electric organ discharges (EODs) used as social signals in territorial and sexual behaviors, and in object location and navigation (Albert and Crampton, 2005b; von der Emde, 2013). Gymnotiforms also possess specialized laterosensory organs called electroreceptor organs, which detect voltage changes across their body surface (Zakon, 1986). Active electroreception is a specialized sensory modality that generates high-resolution sensory percepts of the external environment (Caputi et al., 2008). Depending on the gymnotiform species, EODs may be produced as low frequency (1–120 Hz) discrete non-overlapping pulses, or at high frequencies (60–2000 Hz) with individual pulses overlapping to form a

 $^{^{\}star}$ This paper was edited by the Associate Editor G. Orti.

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quasi-sinusoidal discharge pattern (Crampton, 1998; Crampton and Albert, 2006; Franchina et al., 2001).

Gymnotiform fishes inhabit most lowland Neotropical aquatic habitats, including rainforest streams and swamps, xeric coastal rivers and estuaries, caves, flooded forests, grassland streams, large river channels and cataracts (Albert and Crampton, 2001; Crampton, 1996, 1998). Two genera with pulse-type EODs (*Gymnotus* and *Brachyhypopomus*) are especially diverse and abundant in the floating meadows of floodplains. Gymnotiforms with wavetype EODs, notably species of the clades Eigenmannini (*Distocyclus, Eigenmannia, Rhabdolichops*) and Navajini (a species-rich suprageneric taxon within the Apteronotinae), dominate the benthos of deep river channels, with more than 75% of the biomass in trawl samples from both blackwater and whitewater rivers (Cox-Fernandes et al., 2004; Crampton, 2008; Lundberg et al., 1987).

1.2. Phylogenetic studies among Gymnotiformes

There have been six published studies of gymnotiform systematics using formal phylogenetic methods to elucidate higher-level (interfamily) relationships. Three of these studies used morphological data only (Albert and Campos-da-Paz, 1998; Gayet et al., 1994; Triques, 1993), one study used two mitochondrial genes (Alves-Gomes et al., 1995), and two studies analyzed both morphological and molecular data under a parsimony-based methodology to infer relationships (Albert, 2001; Albert and Crampton, 2005a).

The morphology-based phylogenies by Triques (1993) and Gayet et al. (1994) followed Mago-Leccia (1994) in recognizing six gymnotiform families: Apteronotidae, Gymnotidae, Electrophoridae, Hypopomidae, Rhamphichthyidae and Sternopygidae. In their studies, Triques (1993) and Gayet et al. (1994) proposed that Apteronotidae is the sister-group to all other gymnotiform families. Triques (1993) and Gayet et al. (1994) also proposed that Hypopomidae + Rhamphichthyidae (Rhamphichthyoidea) form a monophyletic group, and that this clade is more closely related to Sternopygidae than to the clade Electrophoridae + Gymnotidae.

The molecular phylogeny of Alves-Gomes et al. (1995) recognized seven family-level taxa, including those of Mago-Leccia (1994) with the additional division of Sternopygidae (*sensu* Mago-Leccia, 1994) into two clades: Eigenmanniidae (all sternopygids except *Sternopygus*) and Sternopygidae (*Sternopygus* only). Alves-Gomes et al. (1995) placed *Sternopygus* (and thus the Sternopygidae) as the sister group to all other Gymnotiformes. Alves-Gomes et al. (1995) concluded that Hypopomidae + Rhamphichthyidae (Rhamphichthyoidea) form the sister-group to Electrophoridae + Gymnotidae, and that these four families together comprise the sister-group to Apteronotidae + Eigenmanniidae. The main conclusions of this molecular study were that taxa with a wave-type (quasi-sinusoidal) EOD are not monophyletic whereas taxa with a pulse-type EOD are monophyletic, and that the wavetype EOD gave rise to the pulse-type EOD.

In a series of papers, Albert and colleagues (Albert and Camposda-Paz, 1998; Albert, 2001; Albert and Crampton, 2005a) proposed new hypotheses of relationships for Gymnotiformes using all data then available. Their cladograms recognized five gymnotiform families including those originally proposed of Mago-Leccia (1994) with the exception of Electrophoridae, which was subsumed within Gymnotidae (Gymnotinae *sensu* Ellis, 1913). Albert and colleagues concluded that Gymnotidae is the sister-group to other Gymnotiformes, and that *Sternopygus* + Eigenmanninae form a monophyletic group (Sternopygidae *sensu* Mago-Leccia, 1994). Albert and colleagues concluded that Hypopomidae is the closest relative to Rhamphichthyidae (Rhamphichthyoidea), and introduced a new hypothesis of relationships that species with a wave-type EOD (Apteronotidae + Sternopygidae) are monophyletic, constituting the clade Sinusoidea (Albert, 2001).

These six phylogenetic hypotheses of Gymnotiformes (Triques, 1993; Gayet et al., 1994; Alves-Gomes et al., 1995; Albert and Campos-da-Paz, 1998; Albert, 2001; Albert and Crampton, 2005a, 2005b) differ in various aspects, especially in some of the generic relationships. However, these studies agree that Gymnotus + Electrophorus (Gymnotidae) and Apteronotidae form monophyletic groups. Interrelationships among Gymnotidae, Rhamphichthyoidea (Hypopomidae + Rhamphichthyidae), and Sinusoidea (Sternopygidae + Apteronotidae) remain incompletely understood, either using molecular (Alves-Gomes et al., 1995), morphological (Albert and Campos-da-Paz, 1998; Gayet et al., 1994; Triques, 1993) or morphological + molecular dataset combined under parsimony (Albert, 2001; Albert and Crampton, 2005a). Here, we provide the most comprehensive Model-Based Total Evidence (MBTE) phylogeny of Gymnotiformes to date using a dataset comprised of six genes (5277 bp) and 223 morphological characters within an ingroup taxon sample of 120 species, representing 34 out of the 35 extant genera.

2. Material and methods

2.1. Taxon sampling

Outgroups were chosen to cover a broad spectrum of phylogenetic diversity in Otophysi. Outgroup species represented nine major lineages of Otophysi including: (i) one exemplar of Cypriniformes (*Carassius auratus*), (ii) four exemplars of Characiformes (*Erythrinus erythrinus* – Erythrinidae, *Serrasalmus rhombeus* – Serrasalmidae, *Cyphocharax festivus* – Curimatidae, *Charax tectifer* – Characidae), and (iii) four exemplars of Siluriformes (*Pseudostegophilus nemurus* – Trichomycteridae, *Brachyplatystoma juruense* – Pimelodidae, *Dianema longibarbis* – Callichthyidae, *Pterygoplichthys multiradiatus* – Loricariidae).

Ingroups were selected with a clade-based approach to maximize the phylogenetic diversity in Gymnotiformes. Ingroup species included representatives of all major gymnotiform lineages containing molecular sequences for 149 specimens (115 ssp.) and morphological data for 166 specimens (120 ssp.) This study comprises the most comprehensive ingroup sampling to date, with 33 of 35 (94%) recognized gymnotiform genera (except *Tembeassu* from the Rio Parana, and *Humboldtichthys* known only from fossils), and 120 of 219 (55%) of all currently recognized species. For information about molecular vouchers and museum lots see Table 1 in Tagliacollo et al. (in press – Data in Brief).

Most tissue samples were collected by the authors or provided by the following institutions: ANSP, MUSM, and MCP – see Sabaj Pérez (2014) for institution abbreviations. Voucher specimens for tissue samples were identified either directly by the authors, by curators and collection managers at contributing institutions, or by exchange of photographs. Species identifications of Genbank sequences were not reevaluated.

2.2. DNA extraction, PCR amplification, and gene sequencing

Genomic DNA was extracted from tissues, fins or livers of specimens preserved in pure ethanol with the NucleoSpin[®] 96 Tissue kit (Macherey-Nagel). Fragments of the mitochondrial genes 16S rRNA (16S-mit), Cytochrome Oxidase subunit I (COI-mit), Cytochrome B (CytB-mit), and the nuclear gene Zic family member 1 (ZIC-nuc) were amplified by one round of polymerase chain reaction (PCR), which was carried out in a volume of 25.0 μ l consisting of: 2.5 μ l of 10× Taq Buffer, 2.0 μ l of dNTP mixture at 10 mM each, 1.5 μ l of 50 mM MgCl₂, 1.0 μ l of each primer at 5 μ M, 0.2 μ l of Platinum[®] Taq DNA Polymerase, 2.0 μ l of template DNA (~50 ng), and 15.8 μ l of double-distilled H₂O. Fragments of the nuclear gene Recombination-Activating gene 2 (RAG2-nuc) and Recombination-Activating gene 1 (RAG1-nuc) were amplified by nested-PCRs. Each round of the two PCR was carried out in a volume of 25.0 µl consisting of: 2.5 μ l of 10× Taq Buffer, 2.0 μ l of dNTP mixture at 10 mM each, 2.0 µl of 50 mM MgCl₂, 1.5 µl of each primer at 5 μM, 0.2 μl of Platinum[®] Taq DNA Polymerase, 2.0 μl of template DNA (\sim 50 ng), and 14.8 µl of double-distilled H₂O. Cycles of PCR for the mitochondrial genes consisted of five steps: (1) 60 s for enzyme activation at 94 °C, (2) 30 s of denaturation at 94 °C, (3) 60 s of annealing at 56 °C (16S-mit), 54-58 °C (COI-mit), or 50-52 °C (CytB-mit), (4) 80 s of extension at 72 °C, and (5) 300 s of extension at 72 °C. The steps 2–4 were repeated 35 times. Cycles of PCR for the nuclear genes consisted of six steps: (1) 60 s for enzyme activation at 94 °C, (2) 30 s of denaturation at 94 °C, (3) two start cycles of 60 s each at 56 °C, 50 °C, 52 °C, 54 °C (RAG2nuc, RAG1-nuc) and 54 °C, 50 °C 52 °C, 56 °C (ZIC-nuc), (4) 60 s of annealing at 50 °C (RAG2-nuc, RAG1-nuc) and 52 °C (ZIC-nuc) and (5) 80 s of extension at 72 °C, and (6) 300 s of extension at 72 °C. The steps 2, 4 and 5 were repeated 35 times. PCR products were visually identified on a 1% agarose gel. Sequencing was held at Beckman Coulter Genomics Facility. For information about primers used in this study see Table 2 in Tagliacollo et al. (in press - Data in Brief).

2.3. Contigs, sequence alignments, and molecular analyses

Forward and reverse sequences were assembled in Geneious 5.5.6 (Drummond et al., 2011). The IUPAC ambiguity code was applied in cases where nucleotide identity was dubious. We combined newly generated data with available sequences from previous studies (Alves-Gomes et al., 1995; Sullivan, 1997; Brochu, 2011; Cox-Fernandes et al., 2009; Lovejoy et al., 2010; Maldonado-Ocampo et al., 2014; Picq et al., 2014). For information about GenBank accession numbers see Table 1 in Tagliacollo et al. (in press - Data in Brief). Each gene was independently aligned using MAFFT 5.3 (Katoh et al., 2005) under default parameters. To detect potential errors such as amplification of pseudogenes. paralogous copies or potential laboratory cross-contamination. each gene alignment was analyzed in PhyML 3.0 (Guindon et al., 2010). Sequences suspiciously misplaced in the resulting gene trees were then re-amplified. The Index of Substitution Saturation (Iss) was estimated in DAMBE 5.0 (Xia, 2013) with 60 replicates. Overall genetic distances among sequences were calculated in Mega 6.0 (Tamura et al., 2013) under Tamura-3-parameter model. Individual gene alignments were concatenated in Geneious 5.5.6 (Drummond et al., 2011). The matrix used in this study is available in Tagliacollo et al. (in press – Data in Brief).

2.4. Morphological characters

The morphological dataset consisted of 223 characters including multiple aspects of osteology, musculature, neurology, meristics, morphometrics, and color patterns (see in Tagliacollo et al., in press – Data in Brief). Characters and states were acquired from Albert (2001), and from examination of museum specimens and published species descriptions (Albert and Crampton, 2001, 2003, 2005a, 2006, 2009; Albert et al., 2005; Carvalho and Albert, 2011, 2013, 2015; Carvalho et al., 2011; Correa et al., 2006; Cox-Fernandes et al., 2014; Hulen et al., 2005; Ivanyisky and Albert, 2014; Maldonado-Ocampo et al., 2014; Maxime, 2013; Maxime and Albert, 2014; Maxime et al., 2011; Richer-de-Forges et al., 2009). Osteological terminology followed descriptions by Albert (2001) with some additions from Maxime (2013) for Gymnotidae, Carvalho and Albert (2013) for Rhamphichthyoidea, Hulen et al. (2005) and Correa et al. (2006) for Sternopygidae, and Albert and Crampton (2006, 2009) and Ivanyisky and Albert (2014) for Apteronotidae. The number of vertebrae and Displaced Hemal Spines (DHS) were counted from radiographs and cleared-andstained specimens. Myological nomenclature followed Winterbottom (1974). Cleared and stained specimens (cs) were prepared according to the method of Taylor and Van Dyke (1985). The morphological matrix is available in Tagliacollo et al. (in press – Data in Brief).

2.5. Nucleotide substitution model selection

For the molecular dataset, optimum partitioning schemes and nucleotide substitution models were estimated in PartitionFinder v.1.1.1 (Lanfear et al., 2012). Two independent analyses were conducted to estimate the best partitioning schemes including substitution models implemented in Garli 2.01 (Bazinet et al., 2014) and MrBayes 3.2 (Ronquist et al., 2012). Each analysis assumed a fully partitioned dataset (by gene and by codon position in proteincoding genes) and the best-fit partitioning scheme with its respective substitution models was selected according to the Akaike Information Criterion with correction (AICc). Substitution models with a proportion of invariant sites (+I) were excluded because the rate of heterogeneity is already accounted by the gamma shape parameters (+ Γ).

For the morphological dataset, the *Mkv* model was applied for discrete character evolution. In the Mkv model, M refers to Markov chain, *k* refers to the number of discrete character states (with $k \ge 2$), and v refers to the number of variable characters (Lewis, 2001). The Mkv model is a generalized Jukes–Cantor (JC69) model, where JC69 is a special case of Mk models with k = 4 discrete character states and symmetrical $k \times k$ instantaneous rate matrix. The Mkv model assumes only variable characters, while the Mk model resembles the JC69 model by considering constant characters; i.e. Mkv model brings step-counting parsimony into a likelihood framework, in which independent partitions (molecular vs. morphology) can be modeled separately by appropriate evolutionary models. The *Mkv* model is becoming widely applied for inferring phylogenies using discrete morphological characters (Castaneda and de Oueiroz. 2013: di Domenico et al., 2014: Norlinder et al., 2012; Wright and Hillis, 2014). The Mkv model of morphological evolution is readily implemented in the packages Garli 2.01 (Bazinet et al., 2014) and MrBayes 3.2 (Ronquist et al., 2012).

2.6. Phylogenetic reconstructions

2.6.1. Maximum-likelihood (ML)

ML analyses of molecular, morphological, and combined morphological + molecular (hereafter supermatrix) datasets were conducted in Garli 2.01 (Bazinet et al., 2014). Models of nucleotide evolution were estimated in PartitionFinder v.1.1.1 (Lanfear et al., 2012). *Mkv* model (Lewis, 2001) was used for the morphological dataset. ML analyses consisted of two independent runs, each one starting from a BioNJ starting tree and using the Subtree Pruning and Regrafting (SPR) algorithm to search for tree improvement in terms of likelihood scores. All other parameters were set as default. To assess node support, 100 non-parametric bootstrap replications were performed for each independent tree search resulting in a total of 200 pseudo-replicates. A consensus tree with bootstraps was computed using the function SumTrees from DendroPy 3.7.0 (Sukumaran and Holder, 2010).

2.6.2. Bayesian inference (BI)

BI analyses of molecular, morphological, and supermatrix datasets were conducted in MrBayes 3.2 (Ronquist et al., 2012). Models of nucleotide evolution were estimated in PartitionFinder v.1.1.1 (Lanfear et al., 2012). *Mkv* model (Lewis, 2001) was used for the morphological dataset. BI analysis consisted of two runs (four chains each) of the Metropolis-Coupled Markov Chain Monte Carlo (MC³). Each run was comprised of 5.0×10^7 generations with model parameter values and a single tree sampled every 5×10^3 generation. All other parameters were set as default. To ensure adequate mixing of the MCMC, effective sample size values (ESS > 200) were inspected for parameter estimates in Tracer 1.5. The two independent runs were summarized with "sump" and "sumt" commands in MrBayes 3.2 (Ronquist et al., 2012). The initial 25% of sampled topologies were used to construct a 50% majority-rule consensus tree. Posterior probabilities were visualized in FigTree 1.4.0.

3. Results

3.1. Molecular dataset

The molecular dataset was comprised of three mitochondrial (16-mit, COI-mit, CytB-mit) and three nuclear genes (ZIC-nuc, RAG2-nuc, RAG1-nuc) resulting in an alignment of 5277 base pairs. Information content and gene characteristics are summarized in Table 1. The overall means of genetic distances ranged from 0.07 ± 0.01 (ZIC1-nuc) to 0.32 ± 0.01 (CytB-mit) indicating the

makers used in this study had sufficient genetic variation to conduct phylogenetic analyses (Fig. 1). The Iss index did not indicate substitution saturation, except for the 3rd codon position of the mitochondrial gene COI-mit, in which saturation was found under both asymmetrical (Iss.cA) and symmetrical (Iss.cS) tree topologies (Table 1). Exploratory phylogenetic analyses were performed in Garli 2.01 and MrBayes 3.2 to evaluate the effect of excluding the 3rd codon position of the gene COI-mit from the concatenated matrix. The results did not show changes in branching order; slight changes were observed in branch lengths, especially in the clade Apteronotidae (data not shown).

3.2. Models of nucleotide substitution

Partition Finder v.1.1.1 estimated two similar, but not identical, optimum partitioning schemes for ML analyses in Garli 2.01 and BI in MrBayes 3.2 (Table 2). These two phylogenetic programs have alternative sets of implemented models of nucleotide substitution, and therefore alternative models might be expected for different portions of a single matrix. Estimated optimum partitioning schemes were composed of 16 subsets, and all genes (codon position in protein-coding genes) required the Γ parameter. Table 2 summarizes best-partition schemes and models of nucleotide

Table 1

General content information for the molecular and morphological partitions. GenBank accession numbers are available in Tagliacollo et al. (in press - Data in Brief).

	Molecular dataset						
	16S-mit	COI-mit	CytB-mit	RAG2-nuc	RAG1-nuc	ZIC1-nuc	
Number of sequences	130 (87%)	137 (92%)	117 (79%)	124 (83%)	7 (%5)	89 (60%)	
Bp after alignment	543	658	1029	972	1337	738	
Number of variable sites	249	318	596	551	756	312	
Π _A	0.37	0.32	0.29	0.26	0.26	0.21	
П _с	0.24	0.31	0.43	0.24	0.23	0.27	
Π_{G}	0.18	0.12	0.05	0.27	0.28	0.31	
Π _T	0.21	0.25	0.23	0.24	0.24	0.21	
Overall mean genetic distance	0.17 ± 0.01	0.28 ± 0.02	0.32 ± 0.01	0.13 ± 0.01	0.10 ± 0.01	0.07 ± 0.01	
Substitution saturation index	Iss < Iss.c	Iss > Iss.c*	Iss < Iss.c	Iss < Iss.c	Iss < Iss.c	Iss < Iss.c	
	Morphological dataset						
	Total	Constant	Variable	Proportion of missing data			
Characters	223	0	223		0.083 (8%)		

Indicates significance of p < 0.05.



Fig. 1. Boxplots summarizing overall means of genetic distances among three mitochondrial (mit-16S; mit-COI; mit-CYTB) and three nuclear (nuc-RAG1; nuc-RAG2; nuc-ZIC1) genes used in this study to infer relationships of Gymnotiformes. This dataset comprised of six genes (5277 bp) for at least 120 species includes suitable nucleotide variation to infer relationships at multiple taxonomic levels.

Table 2

Best-fit partitioning schemes of nucleotide substitution models under AICc criteria used to conduct phylogenetic analyses in the Garli 2.01 (MBTE-ML) and MrBayes 3.2 (MBTE-BI).

PartitionFinder	MrBayes	Garli
Optimum partitioning Schemes (lnL)	-79311.503	-79295.929
Best scheme under AICc	159580.873	159566.409
Number of parameters	439	446
Number of subsets	16	16
Best-fitting models		
16S-mit	GTR + Γ	GTR + Γ
COI-mit_1	GTR + Γ	GTR + Γ
COI-mit_2	GTR + Γ	TVM + Γ
COI-mit_3	GTR + Γ	TIM + Γ
CYTB-mit_1	GTR + Γ	GTR + Γ
CYTB-mit_2	GTR + Γ	GTR + Γ
CYTB-mit_3	SYM + Γ	SYM + Γ
RAG2-nuc_1	SYM + Γ	TVMef + Γ
RAG2-nuc_2	GTR + Γ	TVM + Γ
RAG2-nuc_3	SYM + Γ	SYM + Γ
RAG1-nuc_1	HKY + Γ	TVM + Γ
RAG1-nuc_2	SYM + Γ	TVM + Γ
RAG1-nuc_3	GTR + Γ	GTR + Γ
ZIC-nuc_1	GTR + Γ	TVM + Γ
ZIC-nuc_2	НКҮ + Γ	НКҮ + Γ
ZIC-nuc_3	НКҮ + Γ	TrN + Γ
morph_data	Mkv	Mkv

substitution. The implementations of these models in Garli 2.01 and MrBayes 3.2 are provided in Tagliacollo et al. (in press – Data in Brief).

3.3. Phylogenetic relationships: molecular vs. morphological datasets

ML and BI analyses inferred for independent dataset partition (molecular vs. morphology) obtained more congruent relationships at the genus level, however results were notably much less consistent at interfamily relationships (Fig. 2A and B). While molecular analyses (Fig. 2A) obtained a poor resolution of interfamilial relationships with a polytomy among Apteronotidae, Gymnotidae, Sternopygidae and Rhamphichthyoidea (Hypopomidae + Rhamphichthyidae), morphological analyses (Fig. 2B) obtained Gymnotidae as the sister group to all other Gymnotiformes; i.e., Rhamphichthyoidea plus Sinusoidea (Sternopygidae + Apteronotidae) (Fig. 2B). The nodal supports for major clades of Gymnotiformes are shown in Table 3.

Within Gymnotidae, molecular and morphological datasets obtained similar results indicating a close relationship between *Gymnotus* and *Electrophorus* (Fig. 2A and B). However, the taxonomic compositions of the *Gymnotus* clades varied substantially with two (out of six) recognized species-clades (*sensu* Crampton et al., 2013) being similar between the analyses: *G. tigre* clade and *G. pantherinus* clade (Fig. 2A and B). Relationship among these clades of *Gymnotus* also depended on the dataset; molecular results placed, albeit with low statistical support (ML: 61 and BI: 0.65), the *G. pantherinus* clade as the sister group to all groups of *Gymnotus* (Fig. 2A), while morphological results placed representatives of the *G. cylindricus* clade as the sister group to all *Gymnotus* (Fig. 2B).

Within Rhamphichthyoidea (Hypopomidae and Rhamphichthyidae), molecular and morphological analyses obtained similar results suggesting the monophyly of the Hypopomidae, with the exclusion of Steatogenae, and the monophyly of *Brachyhypopomus* (Fig. 2A and B). The major divergence between the analyses was the placement of the clade Steatogenae (*Hypopygus* + *Steatogenys*) as either sister to the Rhamphichthyinae (Fig. 2A) or within a polytomy with Hypopomidae and Rhamphichthyinae (Fig. 2B). Additionally, molecular analyses placed *Akawaio* as sister group to all other hypopomids and indicated a sister relationship between *Hypopomus* and Microsternarchini but with low statistical support (Fig. 2A, Table 3). Morphological analyses, however, obtained *Akawaio* and *Hypopomus* as sister taxa, and found a close relationship between Microsternarchini and *Brachyhypopomus* but with low statistical support (ML: 0.51, BI: 0.63) (Fig. 2B). For the taxa *Procerusternarchus* and *Iracema* only morphological characters were available and their relationships were inferred based exclusively on synapomorphies (Fig. 2B) therefore node supports are statistically low (Table 3, Fig. 2).

Within Apteronotidae, the molecular (Fig. 2A) and morphological (Fig. 2B) analyses indicate with high statistical support (Table 3) a sister-group relationship between Orthosternarchus and Sternarchorhamphus (clade Sternarchorhamphinae), the monophyly of the Navajini and its two subclades, the exclusion of Adontosternarchus from the Navajini, and the non-monophyly of the Apteronotus. Morphological analyses placed the Sternarchorhamphinae as sister to Sternarchorhynchini (Sternarchorhynchus + Platyurosternarchus); i.e. part of an early-branching lineage within Apteronotidae sister group to all other apteronotids (Fig. 2B, see also Albert, 2001). On the other hand, molecular analyses failed to obtain this relationship, instead placing Sternarchorhynchus as sister to the Navajini together forming the sister clade to Platyurosternarchus (Fig. 2A). Within Navajini, the molecular (Fig. 2A) and morphological (Fig. 2B) analyses showed little agreement in the placement of genera within the clade comprised of Sternarchogiton, Compsaraia, Porotergus, and the "Apteronotus" bonapartii clade. The molecular analyses placed, Sternarchogiton porcinum as the sister to Compsaraia + Sternarchogiton, and this clade as the sister group to a clade comprised of the "Apteronotus" bonapartii clade + Porotergus (Fig. 2A). The morphological analyses (Fig. 2B) obtained a monophyletic Sternarchogiton as the sister group to Porotergus, and this clade as sister to the "Apteronotus" bonapartii group + Compsaraia. This latter relationship between Sternarchogiton + Porotergus and "A." bonapartii + Compsaraia was poorly supported by statistical indices (ML: 0.54, BI: 0.79). Finally, molecular and morphological analyses were incongruent with regard to the position of Parapteronotus, placing it as either the sister group to Megadontognathus and Apteronotus sensu stricto forming a clade herein named Apteronotini (Fig. 2A), or as the sister group to a clade comprised of Megadontognathus and Apteronotus sensu stricto + Navaiini (Fig. 2B).

For Sternopygidae, the molecular and morphology analyses both found a sister-group relationship between *Sternopygus* and Eigenmanninae, a clade comprised of *Archolaemus*, *Distocyclus*, *Eigenmannia*, and *Rhabdolichops*, but different relationships among the genera of Eigenmanninae (Fig. 2A and B). In the molecular analysis (Fig. 2A), *Rhabdolichops* was found to be the sister taxon to Eigenmannini, a group comprised of *Archolaemus*, *Distocyclus* and *Eigenmannia*. In morphology analyses (Fig. 2B), *Archolaemus* was found to be the sister group to all other Eigenmannina. The phylogenetic position of *Japigny* nested within *Eigenmannia* was inferred based exclusively on morphological traits (Fig. 2B).

3.4. Phylogenetic relationships: Model-based total evidence

Phylogenetic analyses performed using MBTE-ML and MBTE-BI (hereafter MBTE) obtained similar evolutionary relationships, closely matching interfamily hypotheses proposed in a series of papers by Albert and colleagues (Albert, 2001; Albert and Campos-da-Paz, 1998; Albert and Crampton, 2005a). The main difference in our results from those of earlier studies by Albert and colleagues is the inclusion of *Steatogenys* + *Hypopygus* (Steatogenae) in the clade Rhamphichthyidae (Alves-Gomes et al., 1995; Maldonado-Ocampo et al., 2014; Carvalho and Albert, 2013).



Fig. 2. Majority rule consensus trees of (A) molecular and (B) morphological datsets inferred in MrBayes using best-fit partitioning schemes of substitution models described in Table 2. Individual partitions are congrue hh nt with one another regarding the monophyly of Gymnotidae, Rhamphichthyoidea, Sternopygidae, and Apteronotidae. The main differences between these analyses include: (i) the phylogenetic position of *Gymnotus pantherinus and G. cylindricus* clades within Gymnotidae, (ii) the number of subclades within Gymnotidae and its relationships, (iii) the relationship of *Hypopomus* within the Hypopomidae, (iv) inter-generic relationships within Eigenmanniae, (v) the position of the Sternarchorhynchini (*Platyurosternarchus* + *Sternarchorhynchus*), and (vi) the sister group of *Parapteronotus*. PP = posterior probabilities. Node supports in Table 3.

Within Gymnotidae, MBTE analyses (Figs. 3 and 4) obtained with high statistical support (Table 3) a sister-group relationship between the *Electrophorus* and *Gymnotus* and six subclades in *Gymnotus*: (i) *G. pantherinus* clade, (ii) *G. coatesi* clade, (iii) *G.*

anguillaris clade, (iv) *G. tigre* clade, (v) *G. cylindricus* clade, and (vi) *G. carapo* clade. The sister-group relationship between the *G. tigre* and *G. cylindricus* + *G. carapo* clades has low statistical support (ML: 65, BI: 0.89). The phylogenetic position of the *G. pantherinus*

Table 3

Node support values (bootstraps and posterior probabilities) for major clades of Gymnotiformes obtained by phylogenetic inferences using either molecular-only, morphologicalonly, or combined molecular + morphological dataset partitions. In bold is shown clades with low statistical values. The symbol "*" indicates incongruence between the datasets.

Clades	Node	ML – Bootstraps (Mol/Mor/Mol + Mor)	BI – Posterior probabilities (Mol/Mor/Mol + Mor)
Gymnotiformes	175	99/100/100	1.00/1.00/0.99
Gymnotidae	176	72/75/73	0.96/0.95/0.95
G. pantherinus clade	178	100/90/96	1.00/0.96/0.96
G. coatesi clade	181	100/*/89	1.00/*/0.95
G. anguillaris clade	188	100/*/97	1.00/*/0.99
G. tigre clade	191	88/96/95	0.96/1.00/0.99
G. cylindricus clade	193	70/*/70	1.00/*/0.99
G. carapo clade	196	64 /*/75	1.00/*/0.97
Sternopygoidei	216	*/89/76	*/1.00/0.95
Rhamphichthyoidea	217	100/73/80	1.00/0.99/1.00
Hypopomidae	218	100/*/77	0.98/*/0.96
Hypopomus + Microsternarchini	220	64 /*/ 58	0.83/*/0.69
Microsternarchini	221	100/73/87	0.99/0.98/0.99
Rhamphichthyidae	234	100/*/95	1.00/*/0.92
Steatogenae	235	100/98/98	1.00/1.00/0.99
Rhamphichthyinae	240	100/93/96	0.96/0.99/0.97
Rhamphichthyini	249	*/60/56	*/ 0.68/0.78
Sinusoidea	259	*/89/72	*/0.97/0.96
Sternopygidae	260	65 /91/77	0.93 /1.00/0.95
Eigenmanninae	265	100/*/89	0.99/0.99/0.99
Eigenmannini	270	97/*/79	1.00/*/ 0.82
Eigenmannia (incl. Japigny)	272	*/*/56	*/ 0.80/0.74
Apteronotidae	279	100/89/95	1.00/0.99/1.00
Sternarchorhamphinae	280	97/98/98	0.97/1.00/1.00
Apteronotinae	281	100/*/81	1.00/*/0.95
Apteronotini	287	100/*/79	0.99/*/0.96
Megadontognathus + Apteronotus	289	*/70/ 68	*/0.99/ 0.93
Sternarchorhynchini	299	*/60/54	*/0.90/ 0.79
Navajini	316	100/ 54 /70	0.96/ 0.87 /0.90
Porotergus + "A." bonapartii	324	100/*/89	1.00/*/99
Sternarchellini	313	97/95/97	0.99/1.00/1.00

clade followed molecular analyses (Fig. 2A), as the sister group to all other subclades of *Gymnotus* (Figs. 3 and 4).

Within Rhamphichthyoidea, MBTE analyses (Figs. 3 and 5) obtained the monophyly of the two clades Hypopomidae and Rhamphichthvidae (sensu Carvalho and Albert, 2013) with high statistical support (Table 3). For the Hypopomidae, MBTE analyses placed Akawaio as the sister group to other hypopomids, and obtained the monophyly of the clades Brachyhypopomus and Microsternarchini (Figs. 3 and 5). MBTE analyses found similar results to that of molecular analyses (Fig. 2A) suggesting a close relationship between Hypopomus and Microsternarchini, albeit with low statistical support (Table 3). For the Rhamphichthyidae, MBTE analyses obtained a sister relationship between the Steatogenae (Hypopygus + Steatogenys) and Rhamphichthyinae, a clade comprised of Rhamphichthys, Iracema, and Gymnorhamphichthys (Figs. 3 and 5). The relationship between Iracema, for which only morphological characters were available, and Rhamphichthys had low statistical support (Table 3).

Within Sinusoidea, MBTE analyses obtained the monophyly of the clades Apteronotidae and Sternopygidae, the latter including *Sternopygus* as the sister group to Eigenmanninae (Figs. 3 and 6) with high statistical support (Table 3). For the Apteronotidae, MBTE analyses obtained several novel relationships including: the species composition and relationships of Apteronotini (*sensu* present study) comprised of *Parapteronotus, Megadontognathus*, and *Apteronotus sensu stricto* (i.e. the *A. magdalenensis, A. leptorhynchus*, and *A. albifrons* clades) (Figs. 3 and 6); a sister relationship between Sternarchorhynchini and Navajini (Figs. 3 and 6); the exclusion of *Adontosternarchus* from the Navajini and the relationship of *Adontosternarchus* as the sister group to all other apteronotids except Sternarchorhamphinae (Figs. 3 and 6); and some novel relationships within Navajini, especially a clade comprised of *Sternarchogiton, Compsaraia, Porotergus*, and the "*A*." bonapartii clade. Among these newly proposed relationships, the clade comprised of *Megadontognathus* and *Apteronotus sensu stricto* is poorly supported (Table 3). The remaining relationships have been previously proposed by other studies including: the monophyly of Sternarchorhamphinae (*Orthosternarchus* + *Sternarchorhamphus*) and the relationship of Sternarchorhamphinae as the sister group to Apteronotinae (Triques, 2005; de Santana, 2007; Figs. 3 and 6), the monophyly of Sternarchorhynchini (*Platyurosternarchus* + *Sternarchorhynchus*) (Albert and Crampton, 2005a), the monophyly of Sternarchellini (Ivanyisky and Albert, 2014; Figs. 3 and 6), and the non-monophyly of *Apteronotus* (Albert and Crampton, 2005a, Figs. 3 and 6).

For the Sternopygidae, MBTE analyses obtained well-supported relationships (Table 3) similar to those proposed by Triques (1993) and previous molecular studies (Alves-Gomes, 1999; Alves-Gomes et al., 1995) with *Rhabdolichops* as the sister group to Eigenmannini (Figs. 3 and 5). Relationships within the Eigenmannini closely match those obtained by molecular analyses (Fig. 2A), except for the position of the monotypic *Japigny* nested within *Eigenmannia*, for which only morphological characters were available (Figs. 3 and 5). Unlike molecular topologies (Fig. 2A), relationships within Eigenmannini were poorly supported by statistical indices (Table 3).

4. Discussion

4.1. Phylogenetic relationships of Gymnotidae

Previous studies of Gymnotidae indicate alternative hypotheses of relationships depending on data type (molecular vs. morphological) and methodology (parsimony vs. model-based) (Albert et al., 2005; Brochu, 2011; Lovejoy et al., 2010; Maxime, 2013). All these



Fig. 3. MBTE analyses showing results of ML and BI analyses of gymnotiform interrelationships. These results are congruent with some aspects of previous morphology-based studies, including the monophyly of Sternopygidae (*sensu* Mago-Leccia, 1978, 1994), and aspects of previous molecular-based studies, including a close relationship between Steatogenae (*Hypopygus, Steatogenys*) and Rhamphichthyinae (*Gymnorhamphichthys, Iracema, Rhamphichthys*) forming the clade Rhamphichthyidae. These results also support several newly-proposed relationships within Apteronotidae (node 281) including sister group relationships between: (i) *Adontosternarchus* and other Apteronotiae, (ii) Sternarchorhynchini (node 299) and Navajini (node 312), and (iii) *Porotergus* and the "Apteronotus" bonapartii clade. Node supports in Table 3. PP = posterior probabilities. GQ = GenBank sequences, * = published sequences, m* = morphology-only characters. For information about GenBank accession numbers see Table 1 in Tagliacollo et al. (in press – Data in Brief).

studies corroborate the monophyly of Gymnotidae and a sister group relationship between *Gymnotus* and *Electrophorus*. Our analyses obtained the monophyly of Gymnotidae (Figs. 2A and B and 4), and both molecular (Fig. 2A) and MBTE (Fig. 4) topologies recognized six clades within *Gymnotus*: (i) *G. pantherinus* clade, (ii) *G. coatesi* clade, (iii) *G. anguillaris* clade (=*G. cataniapo* species group *sensu* Crampton et al., 2013), (iv) *G. tigre* clade (=*G. henni* species group *sensu* Crampton et al., 2013), (v) *G. cylindricus* clade, and



Fig. 4. MBTE-BI analysis showing interrelationships among Gymnotidae. This topology supports a close relationship between *Electrophorus* and *Gymnotus*, and corroborate six subclades of *Gymnotus*. Relationships among these subclades are similar to previous molecular studies, except for the position of the *G. pantherinus* clade, which is proposed here as the sister group to all other *Gymnotus* clades. Node supports in Table 3. PP = posterior probabilities. GQ = GenBank sequences, * = published sequences, m* = morphology-only characters. For information about GenBank accession numbers see Table 1 in Tagliacollo et al. (in press – Data in Brief).

(vi) G. carapo clade. These clades are summarized in Crampton et al. (2013).

Our molecular (Fig. 2A) and MBTE (Figs. 3 and 4) analyses supported relationships among Gymnotus species groups closely matching results of molecular studies by Lovejoy et al. (2010), except for the placement of the *G. pantherinus* clade. Our results suggest the G. pantherinus clade is the sister group to all other *Gymnotus* clades (Figs. 3 and 4), rather than a sister group to a clade composed of the G. cylindricus + G. carapo species groups (Lovejoy et al., 2010). The position of *G. pantherinus* clade has been an unresolved issue in evolutionary studies of Gymnotidae. Morphology-based studies have placed the *G. pantherinus* clade as the sister group to the G. coatesi clade + G. anguillaris clade (Albert and Crampton, 2005a, 2005b; Maxime, 2013, Fig. 2B). The phylogenetic placement of the G. pantherinus clade is less consistent among molecular phylogenies, sometimes being placed as the sister-group to the G. cylindricus clade + G. carapo clade (Lovejoy et al., 2010), or as the sister group to all Gymnotus except the G. coatesi clade (Brochu, 2011).

All six recognized groups of *Gymnotus* obtained by molecular (Fig. 2A) and MBTE (Figs. 3 and 4) inferences are statistically supported (Table 3, but see bootstrap for the *G. carapo* clade), however some of these clades (e.g. *G. cylindricus, G. anguillaris,* and *G. carapo* clades) were not obtained by the morphological dataset (Fig. 2B). Furthermore, some of these recognized clades (e.g. *G. anguillaris* and *G. coatesi* clades) do not possess unambiguous diagnostic morphological traits (see in Tagliacollo et al., in press – Data in Brief), suggesting that most of the relationships in the MBTE analyses are supported by evidence present in the molecular dataset. This absence of morphological traits results mainly from the high degree of homoplasy in salient morphological characters previously used to diagnose clades in *Gymnotus* (Albert and Crampton,

2003; Albert et al., 2005; Nagamachi et al., 2010; Casciotta et al., 2013; Maxime, 2013).

4.2. Rhamphichthyoidea

4.2.1. Phylogenetic relationships of Hypopomidae

Alternative data sources (morphology vs. molecules) and methodologies used to infer relationships (parsimony vs. modelbased) have obtained similar hypotheses for the relationships within Hypopomidae (Sullivan, 1997; Carvalho and Albert, 2013; Maldonado-Ocampo et al., 2014). These studies concluded that Hypopomidae, excluding Steatogenae (*Steatogenys* + *Hypopygus*), is monophyletic. Our molecular (Fig. 2A) and MBTE (Figs. 3 and 5) topologies corroborate these results, supporting the monophyly of the Hypopomidae (excluding Steatogenae) with a taxonomic composition of six genera: *Akawaio, Brachyhypopomus, Hypopomus, Microsternarchus, Procerusternarchus*, and *Racenisia* (Fig. 4).

Our molecular (Fig. 2A) and MBTE (Figs. 3 and 5) analyses indicate similar hypotheses of relationships for hypopomids; the only difference is the lack of *Procerusternarchus* in the molecular topologies because its sequence data were unavailable. The resulting MBTE analyses obtained two new hypotheses in the Hypopomidae: a sister relationship between *Hypopomus* and Microsternarchini, and the phylogenetic position of *Procerusternarchus* within Microsternarchini (Figs. 3 and 5). The sister group relationship between *Hypopomus* and Microsternarchini is not statistically well supported (Table 3).

A mitochondrial DNA-based study by Sullivan (1997) and morphological studies by Albert and Campos-da-Paz (1998), Albert and Crampton (2005a) and Carvalho and Albert (2013) consistently placed *Hypopomus* as more closely related to *Brachyhypopomus* + Microsternarchini. Our morphological (Fig. 2B) topology is



Fig. 5. MBTE-BI analysis showing relationships among Rhamphichthyoidea. This topology supports a close relationship between Hypopomidae and Rhamphichthyidae, with the inclusion of the Steatogenae in Rhamphichthyidae. Within Hypopomidae, our results obtain a novel sister group relationship between *Hypopomus* and Microsternarchini; in Microsternarchini, *Procerusternarchus* and *Microsternarchus* are proposed as sister taxa based on branchiostegal ray counts (see in Tagliacollo et al., in press – Data in Brief). Within Rhamphichthyidae, our results support a close relationship between *Iracema* and *Rhamphichthys*. Node supports in Table 3. PP = posterior probabilities. GQ = GenBank sequences, * = published sequences, m* = morphology-only characters. For information about GenBank accession numbers see Table 1 in Tagliacollo et al. (in press – Data in Brief).

similar to those of previous studies, obtaining *Hypopomus* as the sister group to *Akawaio*, and both genera together the sister group to *Brachyhypopomus* + Microsternarchini. *Akawaio* was not known and therefore not used in the studies by Sullivan (1997) and Albert and colleagues. Because of incongruence and low statistical support values, the relationship between *Hypopomus* + Microsternarchini is best viewed as an unresolved polytomy at this time (e.g. Maldonado-Ocampo et al., 2014).

4.2.2. Phylogenetic relationships of Rhamphichthyidae

Relationships among rhamphichthyids using molecular (Alves-Gomes et al., 1995; Sullivan, 1997) and morphological (Carvalho and Albert, 2013) data sets are largely congruent. Our molecular (Fig. 2A) and MBTE (Figs. 3 and 5) analyses corroborate with high statistical support (Table 3) the monophyly of Rhamphichthyidae and its two subfamilies: Steatogenae, comprised of *Steatogenys* and *Hypopygus*, and Rhamphichthyinae comprised of *Gymnorhamphichthys*, *Iracema*, and *Rhamphichthys*. The monophyly of the Rhamphichthyidae including Steatogenae had been proposed by previous molecular studies (Alves-Gomes et al., 1995; Maldonado-Ocampo et al., 2014; Sullivan, 1997) and recently by a morphological-based study focusing on the Rhamphichthyidae (Carvalho and Albert, 2013).

A systematic issue in the Rhamphichthyinae regards the phylogenetic position of the enigmatic *Iracema*, a monotypic and rare taxon known only from its holotype and three paratypes. Albert (2001) used characters of external morphology to conclude that *Iracema* and *Gymnorhamphichthys* were closely related taxa. Later, Carvalho and Albert (2011) used images from CT to code skeletal characters and concluded that *Iracema* and *Rhamphichthys* were sister groups. Tissue samples from *Iracema* are not available and results reported here for this genus are based exclusively on morphological information. Our morphology (Fig. 2B) and MBTE (Figs. 3 and 5) analyses obtained similar relationships to those proposed by Carvalho and Albert (2011, 2013) proposing *Iracema* as the sister group to *Rhamphichthys*. This relationship is not well supported by statistical indices (Table 3) due to the limited number of characters used to infer its phylogenetic relationship.

4.3. Sinusoidea

4.3.1. Phylogenetic relationships of Apteronotidae

Previous studies of Apteronotidae were based largely on morphological characters, focusing especially on the many osteological specializations of head and snout morphology (Triques, 1993; Gayet et al., 1994; Lundberg and Mago-Leccia, 1996; Albert and Campos-da-Paz, 1998; Albert, 2001; Albert and Crampton, 2005a, 2005b; Triques, 2005; de Santana, 2007; Ivanyisky and Albert, 2014). Previous molecular information on Apteronotidae were limited to sequence data on two mitochondrial markers from a limited taxon sampling (Alves-Gomes et al., 1995). Similar to all these broad-scale phylogenetic studies of Gymnotiformes (Triques, 1993; Gayet et al., 1994; Alves-Gomes et al., 1995; Albert and Campos-da-Paz, 1998; Albert, 2001; Albert and Crampton, 2005a,



Fig. 6. MBTE-BI analysis showing interrelationships within Sinusoidea. This topology supports the monophyly of Sternopygidae (*sensu* Mago-Leccia, 1994), and a close relationship between *Sternopygus* and Eigenmanniae. Within the Eigenmanniae, *Rhabdolichops* is the sister to other eigenmannins, *Archolaemus* and *Distocyclus* are sister groups, and *Japigny* is nested within *Eigenmannia*. In Apteronotidae, this topology supports two subfamilies: Sternarchorhamphinae and Apteronotinae. Within Apteronotiae, this topology supports two subfamilies: Sternarchorhamphinae and Apteronotinae. Within Apteronotiae, this topology supports two subfamilies: Sternarchorhamphinae and Apteronotinae. Within Apteronotiae, this topology supports two subfamilies: Sternarchorhamphinae and Apteronotinae. Within Apteronotiae, this topology supports two subfamilies: Sternarchorhamphinae and Apteronotinae. Within Apteronotiae, this topology supports two subfamilies: Sternarchorhamphinae and Apteronotinae. Within Apteronotiae, this topology supports two subfamilies: Sternarchorhamphinae and Apteronotinae. Within Apteronotiae, this topology supports two subfamilies: Sternarchorhamphinae and Apteronotinae. Within Apteronotiae, this topology supports the advected to a sternarchorhamphinae and Apteronotiae. Within Apteronotus as the sister group to all other Apteronotiae, (ii) Sternarchorhynchini and Navajini as sister clades, and (iii) *Apteronotus* in two separate, non-monophyletic groups: Apteronotus sensu stricto and "A." *bonapartii* clades, the latter of which is more closely related to *Porotergus*. Node supports in Table 3. PP = posterior probabilities. GQ = GenBank sequences, * = published sequences, m* = morphology-only characters. For information about GenBank accession numbers see Table 1 in Tagliacollo et al. (in press – Data in Brief).

2005b), all our analyses obtained the monophyly of Apteronotidae (Figs. 2A and B and 3).

Triques (1993) and Gayet et al. (1994) interpreted the dorsal organ as an adipose fin and used this character along with the presence of a caudal fin (both plesiomorphic states) to discuss the relationship of Apteronotidae as the sister group to all other Gymnotiformes. Our molecular analyses placed Apteronotidae within a polytomy (Fig. 2A), while morphology (Fig. 2B) and MBTE (Fig. 3) analyses suggest Apteronotidae as the sister group to Sternopygidae, which together form the clade Sinusoidea (Albert, 2001). Sinusoidea is characterized by, among other traits, a

wave-type EOD, despite the fact that the electric organs of adult sternopygids and apteronotids are not derived from the same embryological tissues, and produce wave-type EODs using different (although similar) physiological mechanisms (Albert, 2001).

Our molecular (Fig. 2A) and MBTE (Figs. 3 and 6) analyses obtained similar phylogenetic results to those of previous studies regarding the monophyly of the Sternarchorhamphinae (*Orthosternarchus* + *Sternarchorhamphus*) and its sister relationship to all other apteronotids. Sternarchorhamphinae is the only apteronotid clade to retain a monophasic EOD into maturity, characterized by an exclusively head-positive depolarization (Hilton et al., 2007). In our molecular (Fig. 2A) and MBTE (Figs. 3 and 6) analyses, Sternarchorhamphinae is found to be the sister group to Apteronotinae, a clade comprised of *Adontosternarchus*, Apteronotini (newly recognized herein), Sternarchorhynchini, and Navajini.

Our analyses found *Adontosternarchus* as the sister group to all other Apteronotinae (Figs. 2 and 6), a finding qualitatively similar to the classification schemes of Mago-Leccia (1978, 1994). Other previous morphological studies had placed *Adontosternarchus* within the Navajini, but several characters in these studies were optimized as derived reversals (Albert, 2001; de Santana, 2007). These derived reversal traits are associated with oral jaws, which are known to be variable in the Navajini especially due to phenotypic changes associated with sexual dimorphisms (Albert and Crampton, 2009; Cox-Fernandes et al., 2009; Hilton and Cox-Fernandes, 2006).

Within Apteronotinae, in addition to *Adontosternarchus*, our MBTE analyses obtained three main clades: (i) Apteronotini, (ii) Sternarchorhynchini, and (iii) Navajini (Figs. 3 and 6). The monophyly of Sternarchorhynchini including *Platyurosternarchus* and *Sternarchorhynchus* is not corroborated by the molecular analyses (Fig. 2A), in which *Sternarchorhynchus* is found to be the sister group to Navajini (Fig. 2A). In the molecular (Fig. 2A) and MBTE (Figs. 3 and 6) analyses, Apteronotini includes the genera *Parapteronotus, Megadontognathus*, and *Apteronotus sensu stricto*. The Apteronotini is sister to the clade Sternarchorhynchini + Navajini, and both of these branches have high statistical support (Table 3).

Within Apteronotini, our analyses support a sister group relationship between *Megadontognathus* + *Apteronotus sensu stricto* (Campos-da-Paz, 1999), and the monophyly of the clade *Apteronotus sensu stricto*, with the exclusion of the "A." *bonapartii* clade (Figs. 2 and 6). Our results propose that *Apteronotus sensu stricto* includes three clades: *A. albifrons* clade, *A. leptorhynchus* clade, and *A. magdalenensis* clade (Figs. 2 and 6). The monophyly of *A. sensu stricto* is partially congruent with the results of de Santana (2007) who obtained a clade with similar species composition, although also with the inclusion of *Parapteronotus*. *Apteronotus sensu stricto* is readily recognized by features of pigmentation on the caudal and middorsal regions (see Tagliacollo et al., in press – Data in Brief).

In studies using morphology and parsimony (Albert and Campos-da-Paz, 1998; Albert, 2001; Albert and Crampton, 2005a; de Santana, 2007), the Sternarchorhynchini (Sternarchorhynchus + Platyurosternarchus) is one of the most highly supported clades by numbers of synapomorphies. Yet, our molecular analyses (Fig. 2A) do not support the monophyly of Sternarchorhynchini, indicating instead and with high statistical support (Table 3) the position of Sternarchorhynchus as sister to the Navajini. However, the MBTE analyses (Figs. 3 and 6), obtain Sternarchorhynchus + Platyurosternarchus as sister taxa, corroborating results from previous studies (Albert, 2001; de Santana, 2007). A novel finding of the MBTE analyses is the sister group relationship between Sternarchorhynchini and Navajini, instead of with Sternarchorhamphinae (Albert, 2001), or as the sister group to all apteronotids except Sternarchorhamphinae (de Santana, 2007). This close relationship between Sternarchorhynchini and Navajini is statistically well-supported (Table 3).

The clade Navajini was originally recognized by Albert (2001) to include seven genera, and subsequently expanded to include eight genera with the description *Pariosternarchus* (Albert and Crampton, 2006). Our analyses propose that Navajini is comprised of seven genera, including those recognized by Albert and colleagues but excluding *Adontosternarchus* (Figs. 2, 3 and 6). Members of the Navajini are restricted to deep river channels and many display cranial sexual dimorphism (Hilton and Cox-Fernandes, 2006; Albert and Crampton, 2009; Cox-Fernandes et al., 2009). All our

analyses obtained two subclades within the Navajini: one subclade comprised of the "Apteronotus" bonapartii group, Compsaraia, Porotergus, and Sternarchogiton, and the other subclade called the Sternarchellini (Ivanyisky and Albert, 2014). In this present study, the relationships within Sternarchellini are based mainly on morphological characters alone due to the absence of molecular data for the genera Magosternarchus and Pariosternarchus. Our morphological (Fig. 2B) and MBTE (Figs. 3 and 6) analyses are similar to the parsimony-based cladogram proposed by Ivanyisky and Albert (2014) in suggesting that Pariosternarchus is the sister group to Sternarchella + Magosternarchus, and that Sternarchella is not monophyletic. Synapomorphies supporting these relationships are mostly associated with modifications of mouth and head shape that are known to be highly homoplastic in apteronotids (see in Tagliacollo et al., in press – Data in Brief).

All our analyses supported these two subclades as sister taxa (Ivanyisky and Albert, 2014; Figs. 2 and 6). The subclade comprised of "Apteronotus" bonapartii group, Compsaraia, Porotergus, and Sternarchogiton includes the same genera as that of the Albert's clade AH, with the exclusion of Adontosternarchus (Albert, 2001). Relationships within this subclade differs substantially among the analyses inferred using morphological and molecular datasets (Figs. 2 and 6). MBTE analyses (Figs. 3 and 6) indicate novel evolutionary relationships: Sternarchogiton as the sister group to all other three genera, and Porotergus as closely related to the "A." bonapartii group (Albert, 2001; Albert and Crampton, 2005a, 2005b; de Santana, 2007). Although this relationship has high statistical support values (Table 3), no morphological characters are yet known that unambiguously diagnose this clade (see in Tagliacollo et al., in press – Data in Brief).

4.3.2. Phylogenetic relationships of Sternopygidae

The monophyly of Sternopygidae (*sensu* Mago-Leccia, 1978, 1994) has been discussed by previous molecular and morphological studies (Alves-Gomes et al., 1995; Alves-Gomes, 1998; Albert, 2001). Using mitochondrial markers, Alves-Gomes et al. (1995) concluded that Sternopygidae is not monophyletic, with *Sternopygus* as sister group to all other Gymnotiformes, and the other genera forming a clade more closely related to Apteronotidae. Our results statistically support (Table 3) the monophyly of Sternopygia and Eigenmanninae.

In the Eigenmanninae, relationships within a clade comprised of Archolaemus, Distocyclus, Eigenmannia, Rhabdolichops, and Japigny differ between morphological (Albert, 2001) and molecular (Alves-Gomes et al., 1995; Alves-Gomes, 1998) studies. One important difference is the relationship of Rhabdolichops, as either the sister group to Eigenmannia (Albert, 2001), or to all other Eigenmanninae (Alves-Gomes, 1998). Morphologically, Eigenmannia and Rhabdolichops share several synapomorphies associated with snout, head, and neurocranial morphology (Mago-Leccia, 1978; Albert, 2001). Our molecular (Fig. 2A) and MBTE (Figs. 3 and 6) analyses found similar relationships within Eigenmanninae to those of previous molecular studies (Alves-Gomes et al., 1995; Alves-Gomes, 1998), in which Rhabdolichops is the sister group to all other genera of Eigenmanninae. However, the monophyly of Rhabdolichops is still uncertain; a recent and as of yet unpublished molecular study by Maldonado-Ocampo (2011) found Rhabdolichops lundbergi to be more closely related to Eigenmannia than to other Rhabdolichops species. This species, and the phenotypically similar R. nigrimans, were not included in our analyses, and the consequences of including these two Rhabdolichops species on the phylogeny of Eigenmanninae are uncertain.

Another incongruence in Eigenmanninae refers to the relationships between *Distocyclus* and *Archolaemus*, which have been inferred based on morphology to be either sister groups (Triques, 1993), or *Archolaemus* as the sister group of a clade comprised of *Distocyclus, Eigenmannia*, and *Rhabdolichops* (Lundberg and Mago-Leccia, 1986; Albert, 2001; Correa et al., 2006). Following previous molecular studies (Alves-Gomes et al., 1995; Maldonado-Ocampo, 2011) and Triques (1993), our molecular (Fig. 2A) and MBTE (Figs. 3 and 6) analyses obtained a close relationship between *Distocyclus* and *Archolaemus*. Unlike molecular analyses Fig. 2A, MBTE results do not have high statistical support (Table 3) for the relationship of *Distocyclus* + *Archolaemus* sister to *Eigenmannia* (Eigenmannini), perhaps because of the incongruence between data partitions (molecular vs. morphological), which suggest alternative phylogenetic hypotheses in Eigenmannini (Fig. 2A and B).

This study is the first to include morphological data for *Japigny* into a formal phylogenetic analysis. Our morphological (Fig. 2B) and MBTE (Figs. 3 and 6) analyses found *Japigny* nested within the *Eigenmannia*, based on character states of mouth position. Mouth position is a variable character that has independently evolved in multiple clades of Gymnotiformes (see in Tagliacollo et al., in press – Data in Brief).

Acknowledgments

We are grateful to all the individuals and institutions that assisted us in the collection and identification of the specimens that served as the basis for this study, with special thanks to the Academic of Natural Science of Philadelphia (ANSP) and the Museum of Natural History, Lima - Peru (MUSM). For loan of specimens, hospitality during visits and other assistance we thank Joseph Neigel (ULL), Luiz R. Malabarba (UFRGS), Hernán Ortega (MUSM), Roberto E. Reis (MCP), Osvaldo T. Oyakawa (MZUSP), Mark H. Sabaj (ANSP), and John G. Lundberg (ANSP). We are also thankful to Ricardo Campos-da-Paz, Tiago P. Carvalho, William G. R. Crampton, Stephen J. Ivanyisky, Fábio F. Roxo, Nathan R. Lovejoy, Emmanuel L. Maxime, Gisela Farinelli Tagliacollo, Matt Starr, Kory M. Evans, Brandon T. Waltz, and Damian Green for comments, suggestions and/or technical assistance during the development of this project. VAT was supported by Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP) - Brazil (2012/09990-0). JSA was supported by National Science Foundation - United States (grants 0614334, 0741450 and 1354511). CO is supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) -Brazil (309632/2007-2).

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