Molecular systematics of the neotropical shovelnose catfish genus *Pseudoplatystoma* Bleeker 1862 based on nuclear and mtDNA markers

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**Abstract**

*Pseudoplatystoma* is a commercially important genus of Neotropical migratory catfishes widely distributed in all major river basins of South America. Historically, only three species were recognized, but a recent revision proposed eight putative morphospecies for the genus. A molecular study based on mitochondria DNA (mtDNA) provided support for recognition of only some of the species and raised questions about species boundaries in this group. We present a more encompassing analysis based on mtDNA (cytochrome b, 818 bp) and nuclear DNA-based phylogenies (Rag1 intron 1, 664 bp and S7 intron 1, 635 bp) for a more extensive sampling (279 individuals from 42 localities) of all putative species in all major river basins. Patterns generated by individual gene genealogies and a multispecies coalescent analysis provided evidence to suggest recognition of only four distinct species in this genus: *Pseudoplatystoma magdaleniatum*, *Pseudoplatystoma corruscans*, *Pseudoplatystoma tigrimum* (*sensu lato*) and *Pseudoplatystoma fasciatus* (*sensu lato*). The species phylogeny places *P. magdaleniatum* as the sister group to all the other species in the genus, but the relationships among *P. fasciatus s.l.*, *P. tigrimum s.l.*, and *P. corruscans* could not be resolved with confidence.

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**1. Introduction**

The Neotropics harbour the most diverse ichthyofauna of the world, representing 46% of all freshwater fish species and 10% of extant vertebrates (Vari and Malabarba, 1998; Lundberg et al., 2000; Reis et al., 2003). Among the freshwater fishes, catfishes are a major synapomorphic group, with 2,400 species, and 1,700 genera recognized (Lundberg and Littmann, 2003). *Pseudoplatystoma* Bleeker 1862 (Bleeker, 1862) is an economically important pimelodid genus from South America, with species reaching large size. Their piscivorous and migratory habits make them key top-down regulators of the trophic structure of all major river drainages (Burgess, 1989; Reid, 1983; Barthem and Goulding, 1997), but current anthropogenic activities in most of South America, such as damming and overfishing, are reducing the effective size of their populations and raising conservationist concerns.

A recent revisionary study of *Pseudoplatystoma* (Buitrago-Suárez and Burr, 2007) proposed that eight species should be recognized in this genus. Before this publication, most taxonomists recognized only three, that could be distinguished mainly by coloration pattern (Lundberg and Littmann, 2003; Burgess, 1989): (i) *Pseudoplatystoma corruscans* (Spix and Agassiz, 1829), the spotted surubim or “pintado”, distributed in the São Francisco and Paraná–Paraguay–Uruguay basins; (ii) *Pseudoplatystoma fasciatus* (Linnaeus, 1766), the striped catfish (“bagre rayado” or “surbim/cachara/pintadillo”), is widely distributed in the Amazonas, Magdalena, Orinoco, Paraná–Paraguay, and drainages from Guyana and Suriname and Northeastern Brazil; and (iii) *Pseudoplatystoma tigrimum* (Valenciennes, 1840), the tiger surubim or “caparari”, distributed in both Amazonas and Orinoco basins. External morphological differences among these species involve minor variation in body shape so the species are usually recognized by coloration (dark vertical bars, loops, or spots), as described. In their recent study, Buitrago-Suárez and Burr (2007), recognize eight species based on these characters plus evidence from skeletal anatomy, vertebral numbers, and geographic distribution (namely, river basin). On this basis, the widely distributed striped surubim...
previously assigned to *P. fasciatum* has been split into five species: *P. fasciatum* (*sensus stricto*); restricted to Guyana and Suriname river basins; *Pseudoplatystoma punctifer* (Casteuau, 1855): present in the Amazonas basin and, presumably, in Northeastern Brazilian drainages; *Pseudoplatystoma reticulatum* (Eigemann and Eigemann, 1889): distributed widely in the Paraná–Paraguay system and presumably also restricted to an area of the central Amazonas river (near Manaus); *Pseudoplatystoma orinocoense*: restricted to the Orinoco basin; and *Pseudoplatystoma magdaleniatum*: distributed only in the Magdalena basin. The tiger catfish (*P. tigrinum*) populations from the Orinoco drainage were assigned to a new species (*Pseudoplatystoma metaeanae*), restricting the name *P. tigrinum* to the tiger catfish of the Amazonas basin. The species status of *P. corruscans* and its geographic distribution remained unchanged.

Two years later, *Torrero et al.* (2009) assessed the taxonomy and phylogeny of *Pseudoplatystoma* based on mitochondrial DNA (mtDNA) markers (cytochrome *b* and control region sequences). Their study supported four clades of mitochondrial haplotypes, corresponding to: (i) *P. tigrinum*, (ii) *P. corruscans*, (iii) *P. reticulatum* + *P. punctifer* + *P. fasciatum*, and (iv) *P. magdaleniatum* (following the taxonomy proposed by Buitrago-Suárez and Burr). In addition, for some of the included species the mtDNA haplotypes did not form monophyletic groups, casting doubt about their taxonomic status; however, many important issues could not be addressed by this study due to incomplete taxonomic sampling and evidence limited to a single molecular locus (mtDNA).

In the present study, we present new evidence to assess the taxonomy and systematics of this group by using two nuclear genes in addition to mtDNA markers. We include specimens obtained from an extensive sampling of all major river basins in South America where *Pseudoplatystoma* is distributed, covering some critical drainages that were not sampled in the previous studies. In addition to analyzing single gene genealogies, we use a recently developed coalescent approach to estimate a species trees from multilocus data (*Heled and Drummond*, 2010).

2. Materials and methods

*Pseudoplatystoma* specimens were sampled from all major river basins where the genus occurs, except the Gurupi and Munin rivers (Northeastern Brazil) and some drainages from Guyana and Suriname (*Table 1, Fig. 1*). Samples were identified based on the old taxonomy, the only one available at the time of sampling. Considering that the new taxonomy is generally concordant with species distribution (river basin), we reassigned species names based on their geographic distribution (*Buitrago-Suárez and Burr*, 2007). This allowed comparison of the old and new taxonomies in the light of the molecular phylogenies unraveled in our study. Voucher information is provided in *Appendix D*. DNA was extracted from fin clips or muscle tissues following a rapid salt-extraction protocol (*Aljanabi and Martinez*, 1997) or using the DNaseasy Blood and Tissue Kit (*QIAGEN* Inc.).

The complete mitochondrial Cytochrome *b* gene (*Cytb, 1140 bp*) and two nuclear gene fragments containing intron sequences were analyzed in this study. The nuclear genes targeted were Rag1 (*recombination activating gene intron one; Rag1int1, 800 bp*) and S7 ribosomal gene (*first intron, S7int1, 1000 bp*). All gene fragments were amplified via PCR (*polymerase chain reaction*), in a final reaction volume of 30 µl containing 10–50 ng of DNA, 200 µM of dNTPs (*dATP, dGTP, dCTP* and *dTTP*), 1 × PCR buffer, 0.2 µM of each primer, 1.5–2.0 mM of MgCl2 and 1 U of *Taq* polymerase (*Invitrogen Life Technologies*). All reactions were conducted in either PTC100 (*MJ Research*) or Mastercycler (*Eppendorf*) thermocyclers, following the amplification program: 94 °C for 5 min, 35 cycles of 94 °C for 30 s, annealing temperature (*Table 2*) for 35 s, 72 °C for 40 s and a final extension step (72 °C for 5 min). PCR primers for Cytb and S7int1 were available from the literature (*Table 2*), while those for Rag1int1 were designed using exons 1 and 2 sequences available on GenBank for other fishes. PCR products were purified (*Illustra GFX PCR DNA and Gel band purification, GE HealthCare*) and sequenced on a MegaBACE 1000 (*GE HealthCare*) using EtDye kit (*GE HealthCare*). All fragments were directly sequenced using forward and reverse primers. Sequences were checked on CodonCode 3.0 (*CodonCode Corp.*) and aligned using Clustalw (*Thompson et al.*, 1994) with Bioedit (*Hall*, 1999). Heterozygous individuals for a single nucleotide site at nuclear loci were resolved manually. Otherwise, haplotype phases were determined using Phase 2.1 (*Stephens et al.*, 2001; *Stephens and Donnelly*, 2003) that implements a Bayesian method for haplotype reconstruction. Posterior probabilities higher than 0.9 were accepted if repeated throughout five runs of 500 iterations each. Possible instances of recombination events on nuclear alleles were assessed with Rdp3 3.34 (*Martin et al.*, 2005) using the RDP and Bootscan/RECSCAN methods (*Salminen et al.*, 1995; *Padidam et al.*, 1999), the method applied in the program GENECOVN (*Padidam et al.*, 1999; *Sawyer*, 1989), the MaxChi method (*Maynard-Smith*, 1992; *Posada and Crandall*, 2001), and the 3SEQ approach (*Posada and Crandall*, 2001).

Overall variation among DNA sequences was characterized using Mega 4.0 (*Tamura et al.*, 2007) and DnaSP 4.10 (*Rozas et al.*, 2003). Uncorrected *p*-distances were calculated with Mega and neutrality tests (*Tajima’s D, F*, and *D’*) (*Tajima*, 1989; *Fu and Li*, 1993) were conducted using DnaSP 4.10. Maximum likelihood (ML) gene genealogies were estimated for each gene separately using Treefinder (*Jobb*, 2008). Each data set was reduced to distinct haplotypes or alleles for each gene before phylogenetic analysis (the full list of “collapsed” alleles/haplotypes is shown in *Appendices A–C*). The evolutionary model for each gene also was estimated using Treefinder, based on the Akaike Information Criterion (AIC). Cytochrome *b* sequences were partitioned by grouping 1st and 2nd codon positions into one partition and 3rd codon positions into another, each fitted with an independent model. Sequences from *Brachyplatystoma* and *Zungaro* were used as outgroup. Statistical support for nodes was estimated by bootstrap analysis with 1000 pseudoreplicates (*Felsenstein*, 1985). Topological tests were conducted for each gene genealogy *a posteriori* to compare the best tree to alternative hypotheses using the Shimodaira and Hasegawa (SH) and the Approximately Unbiased tests (AU) *Shimodaira and Hasegawa*, 1999; *Shimodaira*, 2002; both testing procedures are available in Treefinder and use the RELL technique (*Kishino et al.*, 1990).

The species tree was estimated under a Bayesian Markov chain Monte Carlo method for the multispecies coalescent with the `Beast protocol (*Heled and Drummond*, 2010) implemented in the program BEAST v1.5.3 (*Drummond and Rambaut*, 2007a). All sequences obtained in the study for all genes and individuals were used as input for this analysis. This includes redundant haplotypes and alleles. For the nuclear genes, both alleles for each individual were included in the input file, even for homozygous individuals. The species from which each allele/haplotype was obtained was used as the trait value for the species tree and specified using the program BEAUTI, a simple user interface for creating input files to run BEAST. Other parameters for this analysis included specifying a relaxed clock and coding for ploidy types (haploid for mtDNA and diploid autosomal for the nuclear genes). Population sizes were assumed to be constant and all other priors used default conditions. The xml file used as input is available upon request from the corresponding author. Two runs, each of 10 million generations, were conducted and stationarity was checked using the program TRACER (*Drummond and Rambaut*, 2007b), a graphical tool for visualization and diagnostics of MCMC output.
3. Results

A total of 279 individuals were obtained from 42 localities throughout South America from all the major river basins where the genus is distributed (Fig. 1 and Table 1). Most individuals were screened for mtDNA variation first and subsequently nuclear gene sequences also were obtained. A Cytochrome b gene fragment of 818 bp was sequenced for 243 individuals. Variation among sequences was restricted to 121 variable sites that collectively defined 59 distinct haplotypes (H1-H59, Table A1, Appendix A, GenBank: GU593097–GU593157). The average number of nucleotide differences among sequences (k) was to 25.3. Fu and Li’s D*
(1.29432, P > 0.10), Fu and Li’s $F$’ (1.10681, P > 0.10) and Tajima’s $D$ (0.53560, P > 0.10) tests did not reject the null hypothesis of neutrality. Most haplotypes were exclusive to each species, but in several cases haplotypes were shared among species (Appendix A). For example, haplotype 4 [H4_pun(1)fass(1)] was shared between one specimen each from $P$. punctifer and $P$. fasciatum. Similarly, haplotype 10 [H10_ori(4)pun(3)] was shared among three $P$. punctifer and four $P$. orinocoense specimens. Shared haplotypes among these three putative species suggests either a recent divergence with retention of ancestral haplotypes among species, or that the species boundaries are fuzzy and there is significant gene flow (see below the alleles shared among species for the nuclear genes and Fig. 2a for discussion on the “$P$. fasciatum sensu lato” clade).

A total of 227 individuals were sequenced for the nuclear locus Rag1int1 (664 bp). Among the sequences we detected 50 polymorphic sites that defined 45 distinct alleles (R1–R45, Table B1, Appendix B, GenBank: GU593198–GU593242). Only 72 individuals were heterozygous for this locus and in 24 cases the allelic phases were resolved using the program Phase, the rest were trivial to solve because they implied a single polymorphism. Average number of nucleotide differences was $\bar{k}$ = 7.2. All neutrality tests (Fu and Li’s $F$’ and $P$. fasciatum. Similarly, haplotype 10 [H10_ori(4)pun(3)] was shared among three $P$. punctifer and four $P$. orinocoense specimens. Shared haplotypes among these three putative species suggests either a recent divergence with retention of ancestral haplotypes among species, or that the species boundaries are fuzzy and there is significant gene flow (see below the alleles shared among species for the nuclear genes and Fig. 2a for discussion on the “$P$. fasciatum sensu lato” clade).

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and between \( P. \) \textit{tigrinum} and \( P. \) \textit{metaense} \cite{e.g., R36_met(9)tig(1) and R37_tig(16)met(18)}. A total of 121 samples were sequenced for S7int1 (635 bp, 49 variable sites, 41 distinct alleles, S1–S41, Table C1, Appendix C, GenBank: GU593158–GU593197), where 68 were heterozygous.
(25 were resolved by Phase, the rest were trivial to solve because they implied a single polymorphism). Average number of nucleotide differences was $k = 6.7$, and no significant departure from neutrality was observed (Fu and Li’s $F = -0.04091, P > 0.10$; Fu and Li’s $D^* = 0.39149, P > 0.10$; Tajima’s $D = -0.58284, P > 0.10$). Two separate indels were observed: a two bp deletion present in *P. corruscans*, *P. magdaleniatum* and *P. metaense*; and a four bp deletion (the first two bp seemed to be homologous with the two bp found in *P. metaense*) only found in *P. tigrinum*. Shared haplotypes between different species also were observed (Fig. 2c, Appendix C), again especially among specimens in the “*P. fasciatum s.l.*” clade [e.g., S5_pun(7)ret(5)ori(4) and S8_ret(10)pun(4)ori(2)].

No signal of recombination was detected in both intron fragments for any of the tests performed (data not shown). Within and between species distances (uncorrected “p-distances”) are shown in Table 3, where Rag1int1 presents the smallest values (most conserved marker). Comparisons of genetic divergence between species did not take into account those haplotypes shared between different species. *P. magdaleniatum* and *P. corruscans* have the greatest distances to the other species (1–6%). *P. tigrinum* differs less than 0.3% from *P. metaense*, and *P. reticulatum* weakly diverged from *P. punctifer* (0.6–0.8%) and *P. fasciatum* (0.5–0.7%). *P. fasciatum* p-distances ranged from 0.4–0.8% in relation to *P. punctifer*. *P. orinocoense* showed large values in Cytb (2–2.3%) from *P. punctifer*, *P. fasciatum* and *P. reticulatum*, while it presented 2.1–3.3% in sequence divergence from its co-occurring species in the Orinoco basin (*P. metaense*).

**Fig. 2** displays the inferred evolutionary relationships among haplotypes/alleles from *Pseudoplatystoma* based on each of three markers. The “*P. fasciatum clade*” (*P. fasciatum*, *P. punctifer*, *P. reticulatum*, *P. orinocoense*, *P. magdaleniatum* and *P. corruscans*) suggested by morphological characters in Buitrago-Suárez (2006) was not recovered. However, a *P. tigrinum* clade was observed. The mtDNA haplotype phylogeny (Fig. 2a) is resolved into five different clades: (i) *P. magdaleniatum*, (ii) *P. corruscans*, (iii) *P. tigrinum* + *P. metaense* (herein defined as *P. tigrinum s.l.*), (iv) *P. orinocoense*, and (v) *P. reticulatum* + *P. fasciatum* + *P. punctifer* (named *P. fasciatum s.l.*). The latter included 4 individuals from the Orinoco (putatively *P. orinocoense*) that carried haplotype H10. Also based on the Cytb analysis, we found support for clades composed of samples of *P. punctifer* from the Maranhão basins, excepting Turiaçu, and Xingú. In addition, *P. corruscans* populations from São Francisco and Paraná–Paraguay–Uruguay basins also were well differentiated from each other for this marker (p-distance = 1.5%).

Nuclear gene markers were able to distinguish only monophyletic groups comprising alleles obtained from *P. magdaleniatum* and *P. corruscans* (Fig. 2b and c). *P. tigrinum s.l.* was a distinct clade on the intron phylogenies, but for Rag1 this group was subdivided into two highly supported clades (2.9% in sequence divergence):

**Table 3**

Uncorrected average p-distances for Cytb (first value), Rag1int1 (second value) and S7int1 (third value). Short names follow Table 1.

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<th>fas (0/0.008/0.005)</th>
<th>cor (0.009/0.003/0.003)</th>
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one containing all \( P. \) tigrinum samples and most \( P. \) metaenae and the other one composed of few \( P. \) metaenae sequences (R33, R34, and R3, with a 12 bp deletion and many fixed substitutions, but two of them inferred by PHASE) (Fig. 2b). \( P. \) orinocoense alleles mixed extensively with those from \( P. \) fasciatum sensu lato (including a diagnostic 15 bp deletion). \( P. \) fasciatum s.l. was not well delimited in Rag1 and S7, since many alleles from \( P. \) orinocoense were included or had close affinities with this clade, suggesting that this species also should be included in this species complex (Fig. 2b and c).

The mtDNA and nuclear gene trees disagree about the position of \( P. \) corrucans and \( P. \) tigrinum sensu lato. For the intron trees, \( P. \) corrucans alleles have closer affinities to the \( P. \) fasciatum sensu lato + \( P. \) orinocoense clade, whereas in the mtDNA tree \( P. \) tigrinum s.l. holds this position to the exclusion of \( P. \) tigrinum. The topology tests shown no significant differences (P values between 0.96 and 1.0) when the \( P. \) corrucans clade was constrained to be sister to the \( P. \) fasciatum s.l. + \( P. \) orinocoense clade for Cytb or when it was placed in a clade with \( P. \) tigrinum s.i. for the nuclear genealogies.

\( P. \) reticulatum haplotypes H30–H34 formed a moderately supported clade (bootstrap value = 70%) within the “\( P. \) fasciatum s.l.” clade on the Cytb genealogy (Fig. 2a). For Rag1int1, \( P. \) reticulatum shared haplotypes with \( P. \) punctifer (Amazonas), although a highly supported clade (R1 and R2) also was observed (Fig. 2b). The same reticulated pattern holds for \( P. \) fasciatum (Guyana and Suriname), whose samples shared haplotypes with \( P. \) punctifer for Cytb (Fig. 2a) and with \( P. \) punctifer and \( P. \) orinocoense in Rag1int1 (Fig. 2b). Nevertheless, \( P. \) fasciatum (Guyana and Suriname) also presented exclusive haplotypes in all markers (Fig. 2).

Due to the complex pattern of haplotype and allele sharing among putative species, a concatenated analysis of DNA sequences from each individual is not simple or desirable. Instead, a multispecies coalescent approach was taken to infer the most likely species tree on the basis of gene tree topologies estimated for each molecular marker. The species tree obtained with ”BEAST is shown in Fig. 3. The “\( P. \) fasciatum s.l.” clade is well supported in this tree, with very shallow divergences among the putative species included (\( P. \) fasciatum, \( P. \) punctifer, \( P. \) reticulatum and \( P. \) orinocoense). Based on the posterior probabilities obtained for each of the putative species in this clade (0.58–0.69), this approach fails to provide support for the recognition of barriers to gene flow or lack of interbreeding among populations of these fishes. The same lack of evident species boundary is observed for the two taxa in the clade that includes \( P. \) tigrinum and \( P. \) metaenae (\( P. \) tigrinum s.l.). Therefore, this analysis supports the distinction of four well-supported groups in the genus (that may correspond to four species), given the high posterior probabilities (\( P = 1 \)) supporting \( P. \) magdaleniatum and \( P. \) corrucans. The relationship among \( P. \) corrucans, \( P. \) tigrinum s.l., and \( P. \) fasciatum s.l. is not well resolved, as implied by the overlapping confidence intervals for speciation times separating these three clades (Fig. 3).

4. Discussion

Complex gene genealogies have emerged for the three markers used in this study, which sampled more than 2000 bp of both nuclear and mitochondrial genomes of \( P. \) pseudoplatystoma. As expected, the cytochrome b genealogy shows more resolution in terms of well-supported clades, while the S7-based evolutionary history was more resolved than Rag1, which seemed to have a slower rate of molecular evolution. Only five clades were recovered with the molecular markers used: \( P. \) magdaleniatum, \( P. \) corrucans, \( P. \) tigrinum s.l., \( P. \) fasciatum s.l., and \( P. \) orinocoense. The latter however, is seem to be part of the \( P. \) fasciatum sensu lato group, especially in light of results of the species tree analysis.

Although some issues from previous studies were confirmed, others remain to be discussed. First of all, we have detected topological incongruence concerning the \( P. \) corrucans/\( P. \) tigrinum s.l. branch placement among mitochondrial and nuclear DNA genealogies. For mtDNA, Torrico et al. (2009) also reported the same evolutionary relationship that we obtained for the cytb gene. On the other hand, a morphology-based phylogeny (Buitrago-Suárez, 2006) agrees with the nuclear trees. Nonetheless, topology tests performed here show no significant differences when alternative topologies for those taxa were constrained on each marker. The different mutation rates between nuclear and mitochondrial genomes might produce such discrepancy between the gene trees used to infer species trees (Zhang and Hewitt, 2003). However, as nuclear loci tend to be less affected by the effect of homoplasy (Avise, 2004) the well resolved relationships of \( P. \) corrucans and \( P. \) tigrinum in the nuclear markers could be a good hint of the reality of the deep relationships in \( P. \) pseudoplatystoma. However, lineage sorting at this level also may explain the discrepancy, as suggested by the species tree result (Fig 3). Therefore, the issue remains poorly resolved with the evidence at hand and more markers might be necessary to solve this question.

The results of our study show geographically distinct clades defined by the mtDNA analysis, Cytb for \( P. \) corrucans, clearly separating fish from the São Francisco and Paraná–Paraguay–Uruguay drainages. Buitrago-Suárez (2006) found no differences between those populations, but the genetic differences suggest a substantial time of divergence. Cytogenetic differences between these populations have also been reported (Swarça et al., 2005). Such distinctness, however, was not observed in the nuclear DNA markers, perhaps due to the longer time required for lineages to be completely sorted for autosomal loci (Avise, 2000). Torrico et al. (2009) did not address this issue since no samples from the São Francisco basin were included in their phylogeny. Whether or not this evolutionary divergence is related to isolating
reproductive barriers is yet to be determined in future studies, since the geographical separation of these populations for extended periods of time could be a sufficient explanation.

Our results are congruent with those from Buitrago-Suárez and Burr (2007) and Torrico et al. (2009) regarding the evolutionary uniqueness of *P. magdaleniatum*, which used to be considered a geographically isolated population of *P. fasciatum* inhabiting the Magdalena basin (Colombia). This is not surprising since this clade has been probably isolated since the uplift of eastern Andean Cordillera about 13–11.5 million years ago, which explains the higher sequence divergence observed for this species. Furthermore, the morphological study by Buitrago-Suárez and Burr (2007) report strong and reliable anatomical characters supporting it.

Our study also conveyed information about the lack of distinction of *P. metaense* and *P. tigrinum* samples, which clustered together in all DNA genealogies. We refer to this clade as *P. tigrinum* s.l., which seems to represent what Buitrago-Suárez and Burr (2007) called the “*P. tigrinum* clade”. The genetic cohesiveness between these putatively different species might invalidate the status of *P. metaense* as a separate species from *P. tigrinum* populations in the Orinoco basin. One single species of *Pseudoplatystoma* (*P. tigrinum*) seems to be widely distributed in the Orinoco and Amazonas basins, given that inter-basin dispersal is feasible via the physical connection through the Casiquiare river (Armbruster and Provenzano, 2000). Nonetheless, a 2-bp deletion in S7int1 found only in *P. metaense* and exclusive haplotypes in each river reveal some level of population differentiation at this macro-geographical level. It is worth noticing that the diagnosis of *P. metaense* given by Buitrago-Suárez and Burr (2007) is mostly based on body shape and color pattern, which, according to the authors, might be variable and therefore does not provide unambiguous support for the differentiation of these species. The highly supported clade in Rag1int1 for few *P. metaense* haplotypes might be due to an idiosyncratic evolutionary history for the intron lineages during their lineage sorting process, or due to artifactual divergent alleles reconstructed by the program PHASE.

The phylogenies show a discrete clade of *P. orinocoense* samples (formerly known as a *P. fasciatum* population from the Orinoco) only on Cytb and Rag1int1, but some samples shared haplotypes found within the *P. fasciatum* s.l. clade. That is the case of four samples (three from the region next to the Casiquiare) that presented the same haplotype (H10) found in *P. fasciatum* s.l. in cytb (Fig. 2a). These same individuals also carried shared haplotypes with *P. fasciatum* s.l. on Rag1 intron, including a 15 bp deletion and many substitutions (Fig. 2b). Misidentification of samples cannot explain this observation because *P. orinocoense* is endemic to Orinoco. Ruling out ancestral polymorphism in cytb for *P. orinocoense*, given well-delimited genetic populations, these fish might have migrated from Amazonas to Orinoco, which means that the *P. fasciatum* s.l. clade might have representatives in Orinoco. Past dispersal between Amazonas and Orinoco basins already have been reported for other fishes (Lovejoy and Araújo, 2000; Hubert et al., 2007; Willis et al., 2010). Our results provide evidence for introgression of both mitochondrial and nuclear DNA genes from the Amazonas to the Orinoco. However, theoretical expectations and empirical evidence suggest that mitochondrially inherited genes are more likely to undergo introgression than their counterparts in nuclear autosomal DNA (Matos and Schaal, 2000). Genes from nuclear genome are usually responsible for interspecific incompatibility, unless cytonuclear incompatibilities exist or if incompatibility is linked to females (Abe et al., 2005). Although sequences from some of these samples are available for S7, the boundary between *P. orinocoense* and *P. fasciatum* s.l. is not clear with this marker. Ancestral polymorphism might explain the existence of a Rag1 haplotype from the Meta River (tributary of Orinoco) that is identical to the one found in fish from Maranhão and Amazonas (Fig. 2b). Different effective population sizes of some loci (particularly those from mtDNA) or different patterns of selection might lead some loci to reach reciprocal monophyly sooner than others (Di Candia and Routman, 2007), probably explaining why Cytb delimited species better than the autosomal loci, even differentiating conspecific populations of *Pseudoplatystoma*. The species tree analysis, however, provides no support for the recognition of *P. orinocoense* as a divergent set of populations in the *P. fasciatum* s.l. clade (Fig. 3).

*P. reticulatum* was not supported as a monophyletic group, except with moderate support in the mtDNA genealogy, but showing low genetic distance from *P. fasciatum* s.l. A recent speciation event among these putative species could lead to insufficient time for the polymorphism to be completely sorted, albeit reproductive barriers might be already present. Nevertheless, Torrico et al. (2009) argue that this species represents a highly supported clade, but support from nuclear genes is lacking. Among our samples from Maranhão, we observed 1.1% sequence divergence in cytb from the remaining haplotypes in the *P. fasciatum* s.l. clade, and *P. corruscans* haplotypes from the São Francisco are on average 1.5% divergent from the Paraná–Paraguay–Uruguay populations. Therefore, unless the status of these other conspecific populations is reviewed, the species status of *P. reticulatum* seems doubtful. Buitrago-Suárez and Burr (2007) describe *P. reticulatum* as inhabiting the Central Amazonas and the Paraná–Paraguay basin, even though no sample from Amazonas was examined other than the holotype. This diagnosis is mainly on the basis of color pattern, which seems to be very polymorphic in *Pseudoplatystoma*. Thus, it may be more appropriate to regard this species as a natural variation of *P. fasciatum* s.l.

Likewise, no differences were found supporting the distinct status of *P. fasciatum* (to the exclusion of all other taxa in the *fasciatum* s.l. group). Although we studied few samples from only two localities in Guyana and Suriname, these results would, at minimum, indicate incomplete lineage sorting. Samples presented unique haplotypes but also shared haplotypes with *P. fasciatum* s.l. (Fig. 2). If *P. fasciatum* is not different from the species occurring in the Amazonas, then ancestral polymorphism or current gene flow can explain the shared haplotypes.

Unless one shows that the non-monophyletic *Pseudoplatystoma* species are recently split taxa and are effectively isolated meta-populations, our study suggests that the group of nominal species that includes *P. punctifer* (Amazonas, Maranhão basins, Tocantins–Araguaia), *P. reticulatum* (Paraná–Paraguay), *P. fasciatum* (Guyana and Suriname), and *P. orinocoense* may in fact constitute a single widespread taxon as was considered in the older taxonomy (*P. fasciatum*). Only *P. magdaleniatum* is supported as a completely distinct species from the former *P. fasciatum* terminology as was proposed by Buitrago-Suárez and Burr (2007). The same rationale holds for *P. tigrinum* and *P. metaense*, where *P. tigrinum* may have to be revalidated for the Orinoco basin.

5. Final considerations

In conclusion, we were able to confirm some results presented by a previous revisionary study of this group by Buitrago-Suárez and Burr (2007) and a partial analysis of mtDNA by Torrico et al. (2009), such as the phylogenetic distinctness of *P. magdaleniatum*, and *P. corruscans*, but also instances of non-monophyletic species (*P. punctifer*, *P. metaense*, *P. tigrinum*, *P. fasciatum*, *P. orinocoense*, and *P. reticulatum*). Given the relevant implications of this information for conservation and fishery purposes, since *Pseudoplatystoma* is one of the most important resources in inland fishery of South America, we strongly suggest that a critical reevaluation of the morphological characters used for separating these species – mostly supported by color pattern – be reconsidered. Morpholog-
clical characters and additional genetic information will help efforts to delineate units for the sustainable management of this resource.

Acknowledgments

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Appendix A

Table A1. Cytochrome b haplotypes (H1–H59) are listed next to the individual samples from which they were isolated. These labels are at the tips of the tree in Fig 2a. Species names are abbreviated as in Table 1 and the locality codes follow the specimen number. The haplotype label contains information of the species of origin (in parenthesis) of the number of individuals from that species where the haplotype was found. A complete list of specimens with their cytochrome b haplotype and their linked nuclear genotypes is presented in Appendix D.

<table>
<thead>
<tr>
<th>H1_pun(3)</th>
<th>[pun10AMTa, pun7122AMTe, pun02To]</th>
</tr>
</thead>
<tbody>
<tr>
<td>H2_pun(12)</td>
<td>[pun31AMTa, pun2AMTa, pun04AMTa, pun30AMTa, punAM07Ta, pun08AMTa, pun09AMTa, pun751AMik, tig633AMik, pun2548AMMa, pun927AMMa, pun979AMMan]</td>
</tr>
<tr>
<td>H3_pun(2)</td>
<td>[pun28AMTa, pun994AMMa]</td>
</tr>
<tr>
<td>H4_pun(1)fas(1)</td>
<td>[pun750AMik, fas1312RU]</td>
</tr>
<tr>
<td>H5_pun(1)</td>
<td>[pun3AMTa]</td>
</tr>
<tr>
<td>H6_pun(2)</td>
<td>[pun05AMTa, pun29AMTa]</td>
</tr>
<tr>
<td>H7_pun(1)</td>
<td>[pun06AMTa]</td>
</tr>
<tr>
<td>H8_pun(1)</td>
<td>[pun753AMik]</td>
</tr>
<tr>
<td>H9_pun(1)</td>
<td>[pun980AMMa]</td>
</tr>
<tr>
<td>H10_ori(4)pun(3)</td>
<td>[ori110RCu, ori120RCu, ori130RCu, ori8650Rat, pun5156AMRB, pun1258AMRB, pun1313AMRB]</td>
</tr>
<tr>
<td>H11_pun(4)</td>
<td>[pun1382AMXi, pun1433AmXi, pun1537AMXi, pun1541AMXi]</td>
</tr>
<tr>
<td>H12_pun(2)</td>
<td>[pun1539AMXi, pun1540AMXi]</td>
</tr>
<tr>
<td>H13_pun(1)</td>
<td>[pun01AR]</td>
</tr>
<tr>
<td>H14_pun(1)</td>
<td>[pun01To]</td>
</tr>
<tr>
<td>H15_fas(1)</td>
<td>[fas60RU]</td>
</tr>
<tr>
<td>H16_fas(1)</td>
<td>[fas61RU]</td>
</tr>
<tr>
<td>H17_pun(4)</td>
<td>[pun38TU, pun65TU, pun41TU, pun36TU]</td>
</tr>
<tr>
<td>H18_pun(6)</td>
<td>[pun01TU, pun33TU, pun40TU, punsp5Tu, pun56TU, pun39TU]</td>
</tr>
<tr>
<td>H19_pun(32)</td>
<td>[punA03ME, punA04ME, pun45ME, pun69ME, pun27ME, pun47ME, pun55ME, punA07ME, pun59ME, punE10ME, punD08ME, punD10ME, pun11ME, pun51ME, punC06ME, punSP8ME, punB09PM, punB11PM, punC02PM, punA06PM, punC09PM, punC10PM, punC12PM, punD01PM, punD02PM, punD05PM, punS7PM, punS9PM, punE11PM, pun58PM, punF04PM, pun268PBS]</td>
</tr>
</tbody>
</table>

H20_pun(2)         | [pun67ME, punAC10ME] |
| H21_pun(5)         | [punC07ME, punC11PM, punD09PM, punF05PM, pun53PM] |
| H22_pun(8)         | [punC08ME, punC03PM, punC04PM, punC05PM, pun59PM, pun57PM, punE12PM, pun12PM] |
| H23_pun(1)         | [punSF4ME] |
| H24_pun(1)         | [punD07ME] |
| H25_pun(1)         | [punD03PM] |
| H26_pun(1)         | [punD04PM] |
| H27_pun(1)         | [punB07ITCo] |
| H28_pun(2)         | [punC01ITCo, pun216ITRo] |
| H29_pun(3)         | [pun2611PBsJ, pun212PBGd, pun218PBsQ] |
| H31_ret(2)         | [ret107PG, ret136PG] |
| H32_ret(1)         | [ret97PG] |
| H33_ret(2)         | [ret132PG, ret123PG] |
| H34_ret(1)         | [ret133PG] |
| H35_ori(1)         | [ori373ORPo] |
| H36_ori(3)         | [ori4460RCi, ori4450RCi, ori4470RCi] |
| H37_ori(4)         | [ori4820RtE, ori3710RPo, ori5470RAP, ori6140RCa] |
| H38_ori(17)        | [ori4780RPP, ori4660RRc, ori1220RMr, ori1200RMr, ori1210RMr, ori1500RtM, ori1140RMr, ori4810RtC, ori3760Rpo, ori4140RPA, ori4380RPA, ori5020RPz, ori6040RCA, ori6120RCA, ori6130RCA, ori6870Rat, ori8690Rat] |
| H39_cor(17)        | [corB04PG, cor145PG, cor147PG, cor158PG, cor160PG, cor156PG, cor169PG, cor144PG, cor01PnRc, cor02PNRc, cor03PNRc, cor1316PnCr, cor212UR, cor213UR, cor214UR, cor215UR, cor216UR] |
| H40_cor(1)         | [corD12PG] |
| H41_cor(1)         | [cor143PG] |
| H42_cor(1)         | [corF06PG] |
| H43_cor(2)         | [cor148PG, cor155PG] |
| H44_cor(1)         | [cor149PG] |
| H45_cor(2)         | [cor150PG, cor146PG] |
| H46_cor(2)         | [cor232PG, cor1315PnCr] |
| H47_cor(1)         | [corB05PG] |
| H48_cor(7)         | [corD11SF, corF05SF, cor191SF, cor199SF, corE01SF, corE04SF, corAC15SF] |
| H49_cor(3)         | [corF11SF, corH02SF, corSP3SF] |
| H50_cor(1)         | [corF12SF] |
| H51_cor(8)         | [cor170SF, cor171SF, cor172SF, cor174SF, cor175SF, cor176SF, cor192SF, corE03SF] |

(continued on next page)
Appendix A (continued)

H52_cor(2) [cor173SF, corAC2SF]
H53_cor(1) [corSP2SF]
H54_met(18)tig(10) [met116ORMt, met117ORMt, met020Ray, met030Ray, met040Ray, met520Ray, met527ORMt, met528ORMt, met886ORMt, met411ORPA, met413ORPA, met433ORMr, met375ORPo, met486ORTc, met488ORTc, met489ORTc, tig22AMTa, tig24AMTa, tig25AMTa, tig27AMTa, tig675AMIk, tig701AMIk, tig755AMIk, tig756AMIk, tig7129AMTe, tig7132AMTe]
H55_tig(1) [tig23AMTa]
H56_tig(1) [tig26AMTa]
H57_tig(1) [tig671AMIk]
H58_tig(2) [tig4501AMSt, tig4502AMSt]
H59_mag(4) [mag168MD, mag167MD, mag150MD, mag158MD]

Appendix B

Table B1. Rag1 intron 1 alleles (R1–R45) are listed next to the individual samples from which they were isolated. These labels are at the tips of the tree in Fig 2b. Species names are abbreviated as in Table 1 and the locality codes follow the specimen number. The haplotype label contains information of the species of origin and (in parenthesis) of the number of individuals from that species where the allele was found. For 24 individuals the allelic phases were resolved using the program Phase. Alleles reconstructed by this approach are marked with an asterisk. A complete list of specimens with their rag1 genotype and their linked nuclear and mitochondrial genotypes is presented in Appendix D.

R1_ret(4) [ret95APG, ret106PG, ret126APG, ret133PG]
R2_ret(2) [ret95BPG, ret126BPG]
R3_ret(6)pun(3) [ret124PG, ret98PG, ret100APG*, ret94APG*, ret123APG*, ret1314PNCr, pun77AAMTa, pun753AAMIk*, pun5155AMRB]
R4_pun(10)ret(6) [ret96PG, ret108PG, ret130PG, ret100BPG*, ret94BPG*, ret123BPG*, pun109BAR, pun05BAMTa, pun750BAMIk*, pun997BAMMa, pun1433BAMXi, pun1534BAMXi, pun1541BAMXi, pun01BTO*, pun02BTO*]
R5_pun(61)fas(2)ori(1) [pun27ME, pun43ME, pun28ME, pun62ME, pun44ME, pun68ME, pun67ME, pun45ME, pun55ME, pun05ME, pun61ME, pun47ME, pun31ME, pun46ME, pun24ME, pun29ME, pun66ME, pun8ME, pun69ME, pun51ME, pun60ME, pun11ME, pun49ME, pun52ME, pun10ME, pun54ME, pun21PM, pun20PM, pun17PM, pun23PM, pun25PM, pun35PM, pun73PM, pun13PM, pun16PM, pun63PM, pun26PM, pun18PM, pun72PM, pun71PM, pun30PM, pun6PM, pun22PM, pun70PM, pun15PM, pun58PM, pun57PM, pun53PM, pun59PM, pun09PM, pun12PM, pun03IT, pun04IT, pun40BU, pun28TU*, pun39BU*, pun06BAMTa, pun31BAMTa, pun75BAMTa*, pun994BAMMa, pun5158BAMRB, ori121ORMt, fas60BRU, fas61ARU]
R6_pun(9) [pun217PBSQ, pun218PBSQ, pun219PBSQ, pun2110PBSQ, pun2111PBSQ, pun212PBSQ, pun2610PBSJ, pun2611PBSJ, pun2612PBSJ]
R7_pun(9) [pun34TU, pun38TU, pun56TU, pun41TU, pun65TU, pun33TU, pun36BU*, pun2ATU*, pun39ATU*]
R8_pun(1) [pun40ATU, pun01ATO*]
R9_pun(2) [pun40ATU, pun01ATO*]
R10_pun(17)fas(1)ori(1) [pun109AAR, pun06AAMTa, pun05AAMTa, pun753AAMIk, pun09AAMTa, pun07AAMTa, pun03AAMTa, pun748AAMIk, pun31AAMTa, pun77BAMTa*, pun7122BAMTe, pun994AAMMa, pun997AAMMa, pun5156AMRB, pun5158AAMRB, pun980BAMMa, pun1433AAMXi, fas61BRU, ori11AORCi]
R11_pun(3) [pun753BAMIk, pun7122AAMTe, pun980AAMMa]
R12_pun(2) [pun75AAMTa*, pun02ATO*]
R13_pun(1) [pun633AAMIk*]
R14_pun(1) [pun633AAMIk*]
R15_pun(2) [pun1534BAMXi, pun1541BAMXi]
R16_pun(1) [pun1313AAMRB*]
R17_pun(1) [pun1313BAMRB*]
R18_fas(2) [fas1312ARU, fas60ARU]
R19_fas(1) [fas1312BRU]
R20_ori(1) [ori11BORCu]
R21_ori(1) [ori12AORCu*]
R22_ori(1) [ori12BORCu*]
R23_ori(1) [ori13AORCu*]
R24_ori(1) [ori13BORCu*]
R25_ori(2) [ori869ORAt, ori478ORPP]
R26_ori(13) [ori4850ORPz, ori1220ORMt, ori6140ORCa, ori140ORMt, ori5020ORFz, ori6120ORCa, ori1220ORMt, ori4830ORCr, ori3710ORPo, ori3722ORPo, ori3730ORPo, ori4120ORPA, ori4660ORCr]
R27_cor(18) [cor148APG, cor150APG, cor169PG, cor157PG, cor231APG, cor227PG, cor160PG, cor221APG*, cor146APG*, cor147APG*, cor153APG*, cor02PNRG]
Appendix B (continued)

Table C1. S7 intron 1 alleles (S1–S41) are listed next to the individual samples from which they were isolated. These labels are at the tips of the tree in Fig 2c. Species names are abbreviated as in Table 1 and the locality codes follow the specimen number. The haplotype label contains information of the species of origin and (in parenthesis) of the number of individuals from that species where the allele was found. For 25 individuals the allelic phases were resolved using the program Phase. Alleles reconstructed by this approach are marked with an asterisk. A complete list of specimens with their S7int1 genotype and their linked nuclear and mitochondrial genotypes is presented in Appendix D.

| S1_pun(30) | [pun5AME, pun8BME, pun44BME, pun27ME, pun29ME, pun31ME, pun32ME, pun42ME, pun45ME, pun54ME, pun55ME, pun66ME, pun06PM, pun07PM, pun13PM, pun16PM, pun17APM, pun18BPM, pun19PM, pun20PM, pun21BPM, pun22PM, pun23PM, pun25PM, pun30APM, pun35APM, pun72PM, pun73PM, pun09PM, pun03IT] |
| S2_pun(6) | [pun5BME, pun8AME, pun18APM, pun21APM, pun30BPM, pun35BPM] |
| S3_pun(1) | [pun44AME] |
| S4_pun(1) | [pun17BPM] |
| S5_pun(7)ret(5)ori(4) | [pun1ATU, pun02AAMTa, pun03AAMTa, pun05AAMTa, pun08BAMTa, pun750AAMIk, pun751AAMIk, ret106APGTq, ret127APGcb, ret135BPGcb, ret133APGMi, ret137APGcb, ori604AORCa, ori612AORCa, ori613AORCa, ori113AORMt] |
| S6_pun(1) | [pun18TU] |
| S7_ori(3)pun(1) | [pun2TU, ori11BORCu, ori13AORCu, ori445AORCu] |
| S8_ret(10)pun(4)ori(2) | [ret95APGMi, ret105PGMi, ret106BPGTq, ret107APGcb, ret108APGcb, ret127APGcb, ret135BPGcb, ret128BPGcb, ret97BPGmi, pun109BAR+, pun28BAMTa, pun05BAMTa, pun750BAMIk, ori445BORCi, ori447AORCi] |
| S9_ret(4) | [ret95BPGmi, ret107BPGcb, ret108BPGcb, ret142BPGTq+] |
| S10_ret(2) | [ret126BPGcb, ret142APGTq+] |
| S11_ret(3) | [ret128APGcb+, ret133BPGmi+, ret137BPGcb+] |
| S12_ret(1)pun(1) | [ret97APGMi, pun109BAR+] |
| S13_pun(1)ori(1) | [pun28AAMTa, ori11AORCu+] |
| S14_pun(2) | [pun02BAMTa, pun08AAMTa] |
| S15_pun(1) | [pun03BAMTa] |
| S16_pun(1) | [pun06AAMTa] |
| S17_pun(1) | [pun751BAMIk] |
| S18_fas(1) | [fas1312AAMRB] |
| S19_fas(1) | [fas1312BAMRB] |
| S20_ori(19) | [ori376BROr, ori120BORMt, ori1306ORCG, ori1373ORPo] |
Appendix C (continued)
ori484ORTc, ori122BORMt, ori485ORPz, ori371AORPo,
ori483BORTc, ori372BORPo, ori466AORCr, ori482BORTc,
iR478ORPP, ori412ORPA,
iR113BORMt, ori547BORAp,
or604BORCa, ori113BORMt, ori547BORAp,
or612BORCa, ori613BORCa,

S21_ori(5)
io120AORMt, ori122AORMt, ori483AORTc, ori13BORCu,
ori547BORAp,
or604BORCa, ori612BORCa

S22_ori(2)
io371BORPo, ori466BORCr,

S23_ori(4)
io372AORPo, ori115ORMt, ori121ORMt, ori447BORCi

S24_ori(1)
io482AORTc

S25_cor(11)
cor149APGSL, cor153PGCb, cor160PGCb, cor232PGSL,
cor169PGGb, cor212JUR, cor213JUR, cor211BURL, cor02PNRG,
cor191BSF, cor206ASF

S26_cor(4)
cor149BPGSL, cor160BPGGb, cor216AUR, cor01APNRG

S27_cor(3)
cor169BPGGb, cor216BURL, cor01BPNRG

S28_cor(2)
cor211AUR, cor191ASF

S29_cor(4)
cor187ASF, cor206BSF, cor208BSF, cor210BSF

S30_cor(3)
cor187BSF, cor199BSF, cor205BSF

S31_cor(4)
cor199BSF, cor205BSF, cor208BSF, cor210BSF

S32_cor(9)
cor413BORPa, cor489BORTc, cor526ORAp, cor375AORPt,
cor488AORTc, cor469AORCr, cor170ORMt, cor118BORMt, cor190ORMt

S33_cor(6)
cor469BORCr, cor413AORPA, cor486BORTc, cor389AORCr,
cor118AORMt, cor527AORAp

S34_cor(2)
cor486AORTc, cor488BORTc

S35_cor(2)
cor375BORPo, cor527BORAp

S36_tig(6)
tig676AAMLk, tig755AAMLk, tig756AAMLk, tig24AMTa,
tig26AMTa, tig27BAMTa

S37_tig(4)
tig676BAMLk, tig755BAMLk, tig756BAMLk, tig26BAMTa

S38_tig(1)
tig27BAMTa

S39_mag(6)
mag164MD, mag08MD, mag09MD, mag12MD, mag13MD, mag14AMD

S40_mag(1)
mag14BMD

S41_Zungaro(1)
Zungaro

Appendix D

Table D1. List of individuals sequenced for this study, with their associated genotypes for the three molecular markers used (CITB, RAG1, and S7), voucher availability, and collector information.

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