GENETIC DISTANCES AND PHYLOGENETIC ANALYSIS SUGGEST THAT BAILLONIUS CASSIN, 1867 IS A PTEROGLOSSUS ILLIGER, 1811 (PICIFORMES: RAMPHASTIDAE)

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Abstract. – Distances genetic and analyses filogenéticas sugerem que Baillonius Cassin, 1867 faz parte do género Pteroglossus Illiger, 1811 (Piciformes: Ramphastidae). – O género monotípico Baillonius Cassin, 1967 é considerado como próximo dos araçaris Pteroglossus Illiger, 1811, segundo dados morfológicos, comportamentais e moleculares. No presente trabalho, mostramos que análises filogenéticas de um fragmento do citocromo b posiciona Baillonius internamente aos Pteroglossus. Esta associação é fortemente apoiada por bootstrap de máxima verossimilhança e probabilidades posteriores de análise Bayesiana. A árvore filogenética obtida mostra Baillonius bailloni como espécie irmã de Pteroglossus inscriptus, e P. bitorquatus a espécie irmã destas duas. Estas três espécies por sua vez formam um grupo irmão a P. aracari, P. castanotis and P. torquatus. Pteroglossus beauharnaesii é a espécie irmã a todas as demais. Distâncias genéticas entre Baillonius e Pteroglossus estão entre as menores estimadas entre os géneros de Ramphastinae, ou entre qualquer género e Baillonius ou Pteroglossus. Portanto, baseado em nossas análises filogenéticas e distâncias genéticas, e dados não moleculares publicados previamente, sugerimos que Baillonius bailloni deve ser renomeado para Pteroglossus bailloni de acordo com a prioridade cronológica das regras internacionais de nomenclatura.

Key words: Baillonius, Pteroglossus, genetic distances, phylogeny, Ramphastidae.

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INTRODUCTION

Among the Piciformes, toucans, barbets and allies have been subject of many taxonomic studies. One of the main problems within these birds is the assessment of taxa in suprageneric levels (e.g., Peters 1948, Prum 1988, Barker & Lanyon 2000, Short & Horne 2000, Horne & Short 2002). Recently, Moyle (2004) presented the most comprehensive study including several important lineages that provided information on the phylogenetic relationships of these birds. He concluded that New World barbets are more closely related to toucans and aracaris than to Old World barbets. Therefore, the family Ramphastidae should include all six genera of toucans and aracaris in the subfamily Ramphastinae, and the three genera of New World barbets in the subfamily Capitoninae, in exclusion of African and Asian barbets allocated to other families (Sibley & Ahlquist 1986). These results are in agreement with osteological (Prum 1988), DNA hybridization (Sibley & Ahlquist 1990) and allozyme data (Hackett & Lehn 1997), showing a closer approximation of New World barbets and toucans. Although this relationship seems to be generally accepted nowadays, several taxonomic problems still remain to be checked within Ramphastidae, such as the validation of the monotypic *Baillonius* as a separate genus.

Toucans and aracaris are among the most typical endemic birds that inhabit the Neotropical region (Haffer 1974). Haffer (1974) considers that cyclic climatic changes were responsible for the speciation in this group. He believes that their evolution occurred due to fragmentation of the rain forests during dry periods related to glaciations, when forest fragments provided true refuges for most of the surviving fauna. During interglacial periods, by expansion of the forest fragments, the previously isolated fauna came in contact again and, for those taxa that did not achieve reproductive isolation, free mating was possible. In one of these refuges, in southeastern Brazil, diversification of several endemic taxa of the Ramphastinae is assumed to have occurred due to the isolation of the Atlantic and Amazonian forests. Some of these taxa are *Ramphastos dicolorus*, *Selenidera maculirostris* and *Baillonius bailloni* (Haffer 1974). Other piciform taxa as *Melanerpes flavirostris*, *Campophilus robustus* (Winkler & Christie 2002) and *Notharchus swainsoni* (Alvarenga et al. 2002) are also assumed to have diversified for the same reason.

Distinguishing characteristics of toucans and aracaris include a large bill that, in some species, may exceed the size of their body. The bill is, however, light, pneumatic and bright-colored, and in many species may be even more exuberant in its inner side. Another typical feature is the coloration of their plumage: black, green, yellow and brown in various combinations; however, in many species it is less exuberant than the bill. Immature birds have a shorter, less toothed, soft and poorly colored bills (Sick 1997). They are zygodactylous, arboreal, inhabit the canopy of wet and flooded forests, but some species are typical of dry mountain forests, and *R. toco* is the only open country Ramphastid. The presence of a huge toothed bill induced some scientists of the XVIII century to believe that those birds fed on fish. However, they are basically frugivorous and are considered as very important seed dispersers, and occasionally feed on some small animals, invertebrates and eggs (Short & Horne 2001). Toucans and aracaris will nest in preexistent tree or other natural cavities high above the ground. However, nests close to the ground have been also observed. Periodical molts of the tail and wing feathers occur (Sick 1997).

*Pteroglossus* Illiger, 1811 is the largest Ramphastinae genus, comprising 10 species. Their
main features are a clown-like pattern and coloration, brightly marked bill that is long and hooked at the top, and a long tail with graded coloration. *Pteroglossus beauharnaesii* is the most differentiated species with modified feathers on the top of the head that are hard, shiny, black and curly. All species have a very similar constitution and form a rather uniform group of species (Short & Horne 2002). *Pteroglossus viridis*, *P. inscriptus* and *P. bitorquatus* are considered to belong to a group of smaller species while *P. torquatus*, *P. frantzii*, *P. aracari*, *P. castanotis* and *P. pluricinctus* seem to belong to a larger and more colorful group of species (Short & Horne 2002).

The Saffron Toucanet (*Baillonius bailloni*) is the only species in the genus and was initially denominated *Ramphastos bailloni* Vieillot, 1819. It has also been considered as associated to the genus *Andigena* by Gould (in Pinto 1938) and Peters (1948). Unlike all species of *Andigena*, however, *B. bailloni* inhabits the lowlands of the Atlantic forest. Many authors have suggested the association of *B. bailloni* to *Pteroglossus* based on vocalization, plumage coloration, external morphology and allozyme data (Haffer 1974, Hackett & Lehn 1997, Sick 1997, Short & Horne 2002). However, its typical yellow-green plumage is not found in any *Pteroglossus*, and its red and green bill and the red periorbital region, and its longer tail compared to other Ramphastinae, have been used to consider *Baillonius* Cassin, 1867 as a distinct genus.

Further evidence on the close association between *Baillonius* and *Pteroglossus* was provided by intergeneric phylogenetic relationships studied in Ramphastinae (Barker & Lanyon 2000, Nahum et al. 2003, Moyle 2004) using mitochondrial and nuclear DNA sequence data, and Höfling (1995) based on cranial osteological characters. These studies have shown a close association of both genera in exclusion to other Ramphastinae genera.

In order to better investigate the relationship between *B. bailloni* and species belonging to genus *Pteroglossus* we performed mtDNA cytochrome b sequence analysis of *B. bailloni*, six species of *Pteroglossus* and nine species representing the other four genera of Ramphastinae.
MATERIAL AND METHODS

**Taxa.** Table 1 shows all the species of which cytochrome b (cyt b) sequences were used in the present study, including their GenBank accession numbers. For the species with DNA sequences obtained in the present study, approximately 0.1 ml of blood was taken by venipuncture from captive birds. These samples are stored in absolute ethanol at room temperature at the Laboratório de Genética e Evolução Molecular de Aves at the Departamento de Biologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil.

**DNA extraction, amplification and sequencing.** DNA was extracted from the blood samples following standard protocols (Sambrook et al. 1989). Cyt b was isolated by PCR with primers CBL15103 (TGC CGA AAC GTA CAA TAY GG, designed by E. S. Tavares, pers. com.), CBH15331 (Kocher et al. 1989), CBL15298 (Cheng et al. 1994), CBH15764 (Miyaki et al. 1998), CBL15637 (Miyaki et al. 1998), and HThr16092 (Kornegay et al. 1993). DNA amplification and sequencing are described elsewhere (Grau et al. 2003).

**Sequence analysis.** Both strands of the DNA fragments of each bird were visually aligned and corrected for ambiguities in Sequence Navigator (Applied Biosystems). Heterogeneity of base composition was tested using TREEPUZZLE 5.0 (Strimmer & Von Haeseler 1996), excluding constant sites, as the test is sensitive to the proportion of constant sites in the data set (Foster & Hickey 1999). A hierarchical likelihood ratio tests (LRT) and the Akaike Information Criterion (AIC) score as implemented in MODELTEST 3.0 (Posada & Crandall 1998) indicated that the best model for the cyt b sequences used here is the HKY, assuming rate heterogeneity of DNA substitution among sites (HKY + g). Therefore, we estimated uncorrected p-distances and HKY + g in PAUP 4.0b10 (Swofford 2001) and plot them against each other to check for saturation of DNA substitutions. Also, the best-fitting model was used in Bayesian and maximum likelihood analysis. Bayesian analysis (BA) with Markov Chain Monte Carlo sampling was performed in MrBayes 3.0 (Ronquist & Huelsenbeck 2003). The analysis was run for 3,000,000 generations, with one cold and three heated chains. Burnin time was selected at the first 500,000 generations. One tree was sampled in every thousand to assure independency of successive samples. Maximum likelihood (ML) and maximum parsimony (MP) tree searches were carried out in PAUP 4.0 b10.0 (Swofford 2001) using heuristic algorithms and gaps deleted on a pairwise basis. The model parameters estimated from MODELTEST were used as initial estimates to speed up all ML searches. Bootstrap proportions were obtained for ML and MP analysis using 100 replicates, with 10 replicates of random addition of taxa in effect. In all phylogenetic analyses, Ramphastos species were used as outgroups based on previously published phylogenies (Barker & Lanyon 2000, Nahum et al. 2003).

RESULTS

Amplification of each mitochondrial DNA region resulted in single PCR products for all amplifications. The reading frame for cyt b sequences did not show any stop codon or changes in amino acid sequence that could indicate that they represent a nuclear copy of the mitochondrial gene. Final alignment resulted in 1045 bp, which 678 bp overlapped for all species listed in Table 1. Among the sites included in the overlapping region, 434 were invariable and 175 parsimony-informative.

Analysis of variable sites only indicated that these species have homogeneous base
TABLE 2. Uncorrected p-distances and HKY + g distances (below and above the diagonal, respectively) for all species.

<table>
<thead>
<tr>
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<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
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<td>0.208</td>
<td>0.282</td>
<td>0.205</td>
<td>0.178</td>
<td>0.264</td>
<td>0.193</td>
<td>0.187</td>
<td>0.210</td>
<td>0.247</td>
<td>0.167</td>
<td>0.162</td>
<td>0.154</td>
<td>0.364</td>
<td>0.281</td>
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<td>2. <em>A. luminosus</em></td>
<td>0.038</td>
<td>0.212</td>
<td>0.287</td>
<td>0.220</td>
<td>0.172</td>
<td>0.244</td>
<td>0.172</td>
<td>0.191</td>
<td>0.208</td>
<td>0.221</td>
<td>0.180</td>
<td>0.147</td>
<td>0.157</td>
<td>0.408</td>
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<td>3. <em>A. derbianus</em></td>
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<td>0.206</td>
<td>0.248</td>
<td>0.257</td>
<td>0.323</td>
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<td>0.284</td>
<td>0.304</td>
<td>0.253</td>
<td>0.305</td>
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<td>0.310</td>
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<td>0.093</td>
<td>0.091</td>
<td>0.129</td>
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<td>5. <em>B. bailloni</em></td>
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<td>0.123</td>
<td>0.150</td>
<td>0.116</td>
<td>0.050</td>
<td>0.043</td>
<td>0.079</td>
<td>0.099</td>
<td>0.194</td>
<td>0.199</td>
<td>0.197</td>
<td>0.312</td>
<td>0.184</td>
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<td>6. <em>P. aracari</em></td>
<td>0.100</td>
<td>0.099</td>
<td>0.124</td>
<td>0.131</td>
<td>0.059</td>
<td>0.116</td>
<td>0.050</td>
<td>0.043</td>
<td>0.079</td>
<td>0.099</td>
<td>0.194</td>
<td>0.199</td>
<td>0.197</td>
<td>0.312</td>
<td>0.184</td>
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<td>7. <em>P. bitortuatus</em></td>
<td>0.130</td>
<td>0.126</td>
<td>0.142</td>
<td>0.155</td>
<td>0.095</td>
<td>0.077</td>
<td>0.080</td>
<td>0.152</td>
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<td>0.305</td>
<td>0.290</td>
<td>0.488</td>
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<td>8. <em>P. beaumontii</em></td>
<td>0.105</td>
<td>0.099</td>
<td>0.121</td>
<td>0.127</td>
<td>0.065</td>
<td>0.04</td>
<td>0.061</td>
<td>0.073</td>
<td>0.084</td>
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<td>0.213</td>
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<td>9. <em>P. castanotis</em></td>
<td>0.103</td>
<td>0.105</td>
<td>0.130</td>
<td>0.137</td>
<td>0.064</td>
<td>0.035</td>
<td>0.092</td>
<td>0.053</td>
<td>0.109</td>
<td>0.086</td>
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<td>0.299</td>
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<td>10. <em>P. inexpectus</em></td>
<td>0.111</td>
<td>0.111</td>
<td>0.133</td>
<td>0.143</td>
<td>0.062</td>
<td>0.058</td>
<td>0.089</td>
<td>0.060</td>
<td>0.071</td>
<td>0.128</td>
<td>0.258</td>
<td>0.232</td>
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<td>0.284</td>
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<td>0.121</td>
<td>0.115</td>
<td>0.124</td>
<td>0.150</td>
<td>0.079</td>
<td>0.066</td>
<td>0.109</td>
<td>0.072</td>
<td>0.059</td>
<td>0.078</td>
<td>0.261</td>
<td>0.261</td>
<td>0.286</td>
<td>0.403</td>
<td>0.266</td>
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<td>12. <em>S. Gouldii</em></td>
<td>0.090</td>
<td>0.094</td>
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<td>0.137</td>
<td>0.122</td>
<td>0.106</td>
<td>0.139</td>
<td>0.115</td>
<td>0.111</td>
<td>0.124</td>
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<td>0.031</td>
<td>0.165</td>
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<td>13. <em>S. spectabilis</em></td>
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<td>0.086</td>
<td>0.139</td>
<td>0.139</td>
<td>0.171</td>
<td>0.140</td>
<td>0.103</td>
<td>0.115</td>
<td>0.118</td>
<td>0.127</td>
<td>0.096</td>
<td>0.156</td>
<td>0.164</td>
<td>0.143</td>
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<td>14. <em>S. macculatius</em></td>
<td>0.086</td>
<td>0.087</td>
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<td>0.123</td>
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<td>0.135</td>
<td>0.111</td>
<td>0.109</td>
<td>0.129</td>
<td>0.13</td>
<td>0.027</td>
<td>0.090</td>
<td>0.158</td>
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<td>15. <em>T. toco</em></td>
<td>0.149</td>
<td>0.156</td>
<td>0.173</td>
<td>0.173</td>
<td>0.153</td>
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<td>0.174</td>
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<td>0.458</td>
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<td>16. <em>R. vitellinus</em></td>
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<td>0.139</td>
<td>0.148</td>
<td>0.155</td>
<td>0.124</td>
<td>0.105</td>
<td>0.154</td>
<td>0.124</td>
<td>0.117</td>
<td>0.134</td>
<td>0.128</td>
<td>0.296</td>
<td>0.332</td>
<td>0.273</td>
<td>0.100</td>
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</table>
composition for cyt b, except for one of the outgroup species (R. toco, \( P = 0.0309 \)). However, outgroups with deviant base composition do not seem to interfere with ingroup topology in some instances (e.g., Pereira et al. 2002, Pereira & Baker 2004). Indeed, exclusion of R. toco from the analysis resulted in same tree topologies for all methods. Analysis of uncorrected and corrected distances (Table 2) indicated a slight level of saturation of DNA substitution (Fig. 1). The saturation is due to multiple hits at third codon positions. However, exclusion of these positions did not change the results of the phylogenetic analysis. Therefore, we are presenting the results of analysis including all codon positions.

Uncorrected distances between B. bailloni and each Pteroglossus varied from 0.059 to 0.095 with mean of 0.071. This is within the intrageneric range of Pteroglossus (from 0.035 to 0.109 with mean of 0.068) and of Selenidera (from 0.027 to 0.096 with mean of 0.071). Andigena, Aulacorhynchus and Ramphastos had each two species included in our analysis providing only one intrageneric comparison (0.038, 0.104 and 0.1, respectively). HKY + g distances also indicated similar trends. Comparisons of intergeneric genetic distances are shown in Table 3. The mean genetic distances for Baillonius and Pteroglossus are the lowest between any Ramphastinae genera among themselves or between any of them and Baillonius or Pteroglossus.

Trees recovered by BA and ML had the same topology and similar branch lengths. Posterior probabilities from the BA and bootstrap proportions for ML are indicated to the right of the nodes (Fig. 2). Our results showed consistency among the relationships of genera with those published before (Barker & Lanyon 2000, Nahum et al. 2003). Baillonius bailloni was placed within the Pteroglossus clade, being a sister species to P. inscriptus. Posterior probabilities and bootstrap support for this...
association are high. Although *Pteroglossus* and *Baillonius* are well-supported assemblage in exclusion to all other genera, the relationships among the other *Pteroglossus* species are not strongly supported by either BA or ML. Also, our results indicated that *Selenidera spectabilis* is a sister group to *Andigena*, in exclusion of other *Selenidera* species. This relationship is not well supported by either BA or ML.

MP analysis recovered one tree, 545 steps long (Fig. 3). This tree is similar to the BA and ML tree, except that *Selenidera* is a monophyletic group and that of *P. castanotis* and *P. torquatus* is a sister clade to *P. inscriptus* and *B. bailloni*, in exclusion of other *Pteroglossus*. Bootstrap analysis by MP provided high support for the *Pteroglossus-Baillonius* clade in exclusion to other genera, but internal relationships within this group are not well supported.

We performed the Kishino-Hasegawa (KH) test as implemented in PAUP 4.0b10 to check the difference between the BA/ML tree and the MP, and a third tree where *Baillonius* was constrained to be a sister taxon to all *Pteroglossus* species. Our results are summarized in Table 4. The topologies recovered by BA/ML and MP analysis do not differ significantly. The BA/ML tree is eight steps longer than the MP tree. The MP tree is only 0.99 likelihood units worse than the BA/ML tree. These differences are not significant. Constraining *Baillonius* to be a sister species to all *Pteroglossus* resulted in a tree 12 steps longer than the MP tree. This difference is not significant according to the KH test. However, this tree had likelihood significantly worse than the BA/ML tree. Because our data set indicated some level of saturation of DNA substitution at third codon positions and because

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**TABLE 3. Mean uncorrected p-distances and HKY + g distances (below and above the diagonal, respectively) between genera of Ramphastinae.**

<table>
<thead>
<tr>
<th></th>
<th>Andigena</th>
<th>Aulacorhynchus</th>
<th>Baillonius</th>
<th>Pteroglossus</th>
<th>Selenidera</th>
<th>Ramphastos</th>
</tr>
</thead>
<tbody>
<tr>
<td>Andigena</td>
<td>0.247</td>
<td>0.213</td>
<td>0.207</td>
<td>0.161</td>
<td>0.330</td>
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<td>Aulacorhynchus</td>
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<td>0.240</td>
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<tr>
<td>Pteroglossus</td>
<td>0.110</td>
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<td>0.071</td>
<td>0.240</td>
<td>0.310</td>
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<tr>
<td>Selenidera</td>
<td>0.089</td>
<td>0.135</td>
<td>0.121</td>
<td>0.120</td>
<td>0.147</td>
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<tr>
<td>Ramphastos</td>
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<td>0.135</td>
<td>0.138</td>
<td>0.363</td>
<td></td>
</tr>
</tbody>
</table>

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**FIG. 2.** Topology recovered by both BA and ML for the cyt b data set of Ramphastinae, using HKY + g model of DNA substitution. The bar corresponds to the expected number of DNA substitutions per site. Numbers to the right of nodes are BA posterior probabilities/ML bootstrap proportions.
parsimony methods are known to underestimate the number of changes in such cases, we preferred the topology recovered by BA and ML analyses as the best tree representing the relationships among the taxa included in this study.

DISCUSSION

Ramphastid intergeneric relationships have been the topic of several studies using molecular tools (Sibley & Ahlquist 1986, 1990; Lanyon & Hall 1994, Barker & Lanyon 2000, Nahum et al. 2003, Moyle 2004). From these studies it can be concluded that phylogenetic relationships among Ramphastidae genera are very robust. Indeed, addition of nuclear DNA sequences from the seventh intron of the beta fibrinogen to previous mitochondrial cyt b data set resulted in a well-supported tree, the topology of which agrees with previous studies (Moyle 2004).

All the above studies have shown a close association between B. bailloni and Pteroglossus, and Barker & Lanyon (2000) suggested that B. bailloni is more closely related to P. castanotis than this species is to P. inscriptus. Nevertheless, taxonomic sampling of those studies included only one or two representatives of Pteroglossus. Thus, to further investigate the phylogenetic positioning of Baillonius within the group, we analyzed a portion of cyt b from several Ramphastinae, including more Pteroglossus species. Our results are not in agreement with Barker & Lanyon (2000). In fact, B. bailloni was placed as sister to P. inscriptus and these two have P. bitorquatus as a sister species, forming a clade of small-sized aracaris (mean male weight ranges from 121 to 148 grams; mean male wing length ranges from 117 to 128 cm; Short & Horne 2001). In turn, this clade is sister to a clade of large-sized aracaris (mean male weight ranges from 211 to 283 grams; mean male wing length ranges from 135 to 158 cm; Short & Horne 2001). Although posterior probabilities and ML and MP bootstrap proportions are not very high within Pteroglossus, the association of Baillonius to P. inscriptus was well supported in the BA and ML analysis. Lack of support observed in our phylogeny for other associations indicates that more DNA sequence data (Pereira et al. 2002) and/or taxa (Pollock et al. 2002) should be used to improve resolution at that level.

Unfortunately, samples of P. viridis, P. azara, P. frantzii and P. pluricinctus were not available for our study, preventing us to propose a biogeographic hypothesis for their speciation. However, even using a limited taxonomic sampling, our results showed that a similar diversification pattern is reflected in both small-sized and large-sized clades. Both

FIG. 3. MP tree found for the cyt b data set of Ramphastinae. The bar corresponds to the expected number of substitutions. Numbers to the right of nodes are MP bootstrap proportions.
TABLE 4. Results of KH test for comparison among different tree topologies.

<table>
<thead>
<tr>
<th>Tree</th>
<th>BA/ML tree</th>
<th>MP tree</th>
<th>Baillonius as sister to Pteroglossus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (steps)</td>
<td>553</td>
<td>545</td>
<td>557</td>
</tr>
<tr>
<td>Consistency index</td>
<td>0.577</td>
<td>0.585</td>
<td>0.573</td>
</tr>
<tr>
<td>Rescaled consistency index</td>
<td>0.335</td>
<td>0.348</td>
<td>0.328</td>
</tr>
<tr>
<td>Homoplasy Index</td>
<td>0.423</td>
<td>0.415</td>
<td>0.427</td>
</tr>
<tr>
<td>Difference in steps</td>
<td>8</td>
<td>-</td>
<td>12</td>
</tr>
<tr>
<td>t</td>
<td>1.4153</td>
<td>-</td>
<td>1.9507</td>
</tr>
<tr>
<td>$P$</td>
<td>0.1575</td>
<td>-</td>
<td>0.0515</td>
</tr>
<tr>
<td>-lnL</td>
<td>3380.92312</td>
<td>3381.91378</td>
<td>3395.56271</td>
</tr>
<tr>
<td>Difference in -lnL</td>
<td>-</td>
<td>0.99066</td>
<td>14.63959</td>
</tr>
<tr>
<td>$P$</td>
<td>-</td>
<td>0.924</td>
<td>0.040*</td>
</tr>
</tbody>
</table>

* $P < 0.05.$

clades have one representative of the Atlantic forest (B. baillonius and P. aracari) that are more closely related to Amazonian taxa than both Atlantic taxa are to each other. This pattern of phylogenetic relationships has been found in other group of birds (Pereira & Baker 2004) and also in mammals (Cortés-Ortiz et al. 2003).

Despite an incomplete taxonomic sampling for Pteroglossus, our results of genetic distances seem to provide enough evidence to support our conclusions. The proximity of Baillonius and Pteroglossus is more evident by comparisons of intra- and intergeneric distances. This analysis has been applied before to assess species limits of other groups of birds (e.g., Zink & Blackwell-Rago 2000, Grau et al. 2003). Our results showed that comparisons between Baillonius and Pteroglossus species are in the same range as intrageneric comparisons for the other genera, including the Pteroglossus species among themselves.

Furthermore, other non-molecular, independent evidences exist to corroborate our results. Höfling (1995) in her osteological studies of a sample of 100 skulls belonging to 19 species and representing all Ramphastinae genera revealed that there are two osteological characteristics that were exclusively shared by Pteroglossus and Baillonius. In her work, she included four species of Pteroglossus (P. inscriptus, P. bitorquatus, P. aracari and P. torquatus) and found a pointed suprameatic process and a characteristic shape of the lateral apophysis of the lacrimal. Among the vocal repertoires of Baillonius, one was considered to be similar to that of P. azara (Short & Horne 2001, 2002). However, Haffer (1974), analyzing vocalizations recorded by Paul Schwartz, considers that the vocalization of B. bailloni reminds that of P. flavirostris, Selenidera nattereri and Andigena nigroirostris. Morphologically, B. bailloni and all species of Pteroglossus have red upper tails coverts (Sick 1997) and are among the aracaris with gradated and longest tail (Haffer 1974). Haffer (1974) refers to the fact that, in flight, B. bailloni strongly resembles some species of Pteroglossus.

In conclusion, based on our results, we suggest that B. bailloni should be renamed to P. bailloni, following the international rules of zoological nomenclature (International Commission on Zoological Nomenclature 1999), giving chronological priority to the oldest genus described (Pteroglossus Illiger, 1811 instead of Baillonius Cassin, 1867). Our results are corroborated by behavior, cranial morphology, and other external morphology data (Haffer 1974, Höfling 1995, Sick 1997).
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REFERENCES


THE SAFFRON TOUCANET BAILLONIUS IS A PTEROGLOSSUS

(Aves, Cracidae) based on mitochondrial DNA phylogeny. Auk 121: in press.


