MUSEU PARAENSE EMÍLIO GOELDI
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CURSO DE DOUTORADO EM ZOOLOGIA

SISTEMÁTICA, FILOGENIA E BIOGEGRAFIA DO GÊNERO *CAMPYLORHAMPHUS* (AVES: DENDROCOLAPTIDAE)

CARLOS EDUARDO B. PORTES

Tese de doutorado apresentada ao Programa de Pós-graduação em Zoologia, Curso de Doutorado, do Museu Paraense Emílio Goeldi e Universidade Federal do Pará como requisito para obtenção do grau de Doutor em Zoologia.

Orientador: Dr. Alexandre Aleixo

BELÉM – PARÁ
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Sumário

Sumário

Lista de Tabelas e Figuras

Capítulo 1

Capítulo 2

Capítulo 3

combinations by BPP: 1st—large ancestral N_e and deep divergences; 2nd—small ancestral N_e and shallow divergences and 3rd—large ancestral N_e and shallow divergences. PP $\geq$ 0.95 are marked with an asterisk. Taxonomy follows Marantz *et al.* (2003), with updates from Portes and Aleixo (2009), Portes *et al.* (2013), Aleixo *et al.* (2013) 74

Figure 4 - Graphical results of ancestral distributions at each node of the *Campylorhamphus* phylogeny obtained from S-DIVA (left) and BBM (right) as implemented by RASP based on the output (.trees file) produced by *Beast Analysis. Bootstrap support values (50% and higher; S-DIVA) and Bayesian credibility values (PP; BBM) are indicated close to each node. In the lower left corner are the color keys to possible ancestral ranges at different nodes. Biogeographical regions: A: Atlantic Forest (blue); B: Central America and Chocó area of endemism (purple); C: Amazonia (beige); D: Central South America (red); and E: Eastern slope of the Andes (green). The number in each node represents de ID for ancestral relation for each lineages (see supplementary information) 75

Lista de Appendix

Capítulos 2 e 3

Capítulo 3

Appendix

1.0. Introdução Geral

1.1 – Hipóteses de diversificação na Região Neotropical

As regiões tropicais são conhecidas por possuírem uma grande diversidade biológica, entretanto, as razões pelas quais são mais ricas em espécies do que regiões temperadas e árticas ainda permanecem pouco esclarecidas (Stotz et al. 1996; Gaston 2000; Weir e Schluter 2007). Dentre as florestas tropicais, destacam-se a Amazônia por ser a maior em extensão, compreendendo mais de 6,8 milhões de Km², nos quais a maior diversidade de plantas superiores (40.000 espécies) e de vertebrados (2.523 espécies) do mundo está concentrada (Mittermeier et al. 2003, Hubert e Renno, 2006), além da Floresta Atlântica que se estende pela costa Atlântica da América do Sul, desde o Norte do Rio Grande do Sul até norte da região nordestina do Brasil. A origem e manutenção de tamanha biodiversidade vêm intrigando naturalistas por mais de um século (Chapman 1917, 1926, Mayr, 1963, Wallace 1852), trazendo à tona várias hipóteses na tentativa de explicá-las.

Uma das primeiras hipóteses evolutivas para explicar a história de diversificação dos vertebrados amazônicos foi lançada pelo naturalista inglês Alfred Russel Walace (1852) e, desde então, várias hipóteses alternativas, a partir de fatores ecológicos ou históricos, foram propostas (Haffer 1969, 1993, Endler 1977, Colinvaux 1993, Bush 1994, Marroig e Cerqueira 1997). Dentre as abordagens históricas merecem destaque aquelas formuladas a partir de mecanismos vicariantes, tais como o soerguimento dos Andes (Chapman 1917), os refúgios florestais do Pleistoceno (Haffer 1969), os rios como barreiras (Walace 1852, Sick 1967) e as transgressões marinhas (Nores 1999). A hipótese dos Refúgios propõe que uma série de mudanças climáticas alternadas causadas pelos ciclos de Croll-Milankovitch combinada com a elevação dos Andes e outras grandes elevações, permitiu a formação de refúgios de florestas úmidas intercaladas com florestas secas e áreas abertas (Thoysi et al. 2010). Dentro dos refúgios, as espécies permaneciam isoladas, criando oportunidade para especiação alopátrica, evidenciado pelos atuais centros de endemismos (Hafer 1969, 1997). O conceito de interflúvios como áreas de endemismo está corroborado para Aves (Ribas et al. 2012), e também para primatas (Ayres e Clutton-Brock 1992; van Roosmalen et al., 2002) e foi uma das bases conceituais mais importantes na formulação das celebradas “ecorregiões” (Olson et al., 2001) usadas para priorizar áreas para a conservação na Amazônia. Divergências alopátricas dentro da Amazônia também tem sido hipotetizadas como resultado da restrição de fluxo gênico causado pelos grandes rios dentro da bacia Amazônica. Esse modelo de barreiras pelo rio prevê linhagens independentes ocorrendo em lados opostos do rio como resultado a restrição do fluxo gênico (Ayres e Clutton-Brock 1992, Gascon et al. 2000). Além destas, processos ecológicos, tais como os gradientes ambientais, também foram utilizados como modelo de especiação parapátrica (Endler 1982). Estas hipóteses tentam inferir eventos biogeográficos históricos que promoveram especiação a partir das distribuições e relações filogenéticas dos táxons atuais (Haffer 1997, Moritz et al. 2000).

O contexto histórico da Floresta Atlântica é diferente, o que repercute em uma diversificação distinta da Amazônia. Dentre as principais razões podem ser citados as diferenaças latitudinais encontradas neste bioma, os mecanismos geológicos e climáticos envolvidos nesta região. Uma visão realista da diversificação da Floresta Atlântica pode considerar multiplos mecanismos operando em diferentes escalas de tempo e espaço. Ainda, padrões de endemismo de aves, pequenos mamíferos, e outros vertebrados são amplamentes concordantes na distribuição geográfica (Costa and Leite, 2000; Sigrist and Carvalho, 2008), sugerindo que um mecanismo comum pode ter um papel importante na distribuição de multiplos táxons neste megadiverso bioma (Thome et al. 2010). Paleomodelos de distribuição de espécies complementam inferências filogeográficas de refúgios do Pleistoceno com base em dados genéticos (Carnaval and Moritz, 2008, Waltari et al., 2007). Paleomodelos do Bioma Atlântico prevê várias contrações florestais ao sul do Estado de São Paulo e grande estabilidade florestal na região norte durante a Última Máxima Glacial (LGM), seguido pela expansão do Holoceno (Carnaval and Moritz, 2008). Este cenário é compativo com divergência genetic observada de várias linhagens no nordeste da Floresta Atlântica (Cabanne et al., 2008; Carnaval et al., 2009, Pellegrino et al., 2005), mas linhagens divergentes também podem ser observadas no sudeste da Mata Atlântica (Cabanne et al., 2007; Fitzpatrick et al., 2009; Grazziotin et al., 2006), onde refúgios não sao previstos pelos lapeomodelos (Thome et al., 2010).

Dentre os grupos biológicos, as aves vêm se mostrando um ótimo objeto de estudo na compreensão da história evolutiva da região Neotropical (Bates 2001). Devido a sua fisiografia bastante heterogênea, a região Neotropical é responsável em abrigar a mais diversificada avifauna do mundo, também é caracterizada por apresentar comunidades de aves com histórias evolutivas completamente distintas (Mittermeier et al., 2003). Silva et al. (2005) reconhecem pelo menos oito grandes áreas de endemismo para a Amazônia, onde grupos únicos de espécies e subespécies de animais e plantas são encontrados. Apesar de diferentes táxons muitas vezes apresentarem similaridades quanto as suas distribuições e áreas de endemismos, estudos filogenéticos com espécies endêmicas de uma mesma área vêm demonstrando que tais semelhanças compartilhadas nem sempre resultam de iguais processos históricos de diversificação (Cracraft e Prum 1988; Cracraft 1988, Aleixo 2002, 2006, Marks et al., 2002, Cortés-Ortiz et al. 2003).

Sabe-se que ciclos glaciais/interglaciais, soerguimento de montanhas, rios como barreiras, dispersão e diferenciação genética foram fatores importantes na diversificação das aves neotropicais (Wallace 1852, Chapman 1917, 1926), porém o papel relativo de cada um destes processos ainda gera muitas controvérsias (Bates et al. 1998). Isto se deve, em parte, ao potencial limitado das hipóteses biogeográficas existentes quanto ao esclarecimento de estudos evolutivos na região amazônica, já que elas são baseadas quase que inteiramente em dados de distribuição de táxons morfologicamente distintos (Zink 2004). Assim, estas hipóteses tornam-se problemáticas, pois somente dados de distribuição dos táxons não englobam os componentes filogenéticos dos mesmos, os quais são importantes em estudos evolutivos (Moritz et al. 2000). Além disso, estudos genéticos recentes têm mostrado que táxons morfologicamente definidos podem subestimar padrões de diversidade genética em aves Neotropicais (Marks et al. 2002; Irestedt et al. 2004a, 2004b, Aleixo et al. 2013, Whitney et al. 2013a, Whitney et al. 2013b, Whitney et al. 2013c, Portes et al. 2013).

Contudo, a grande dificuldade está na ausência de contextos geográfico-temporais específicos na formulação de muitas das hipóteses biogeográficas propostas, tornando-as difíceis de serem falseadas por métodos filogenéticos (Patton e Silva 1998, Moritz et al. 2000). Mais recentemente, com o intuito de testar estas hipóteses, vários pesquisadores têm adotado uma abordagem filogeográfica para estudar a diversificação das biotas neotropicais (Patton e Silva 1998, Silva e Patton 1998, Lougheed et al. 1999, Moritz et al. 2000, Marks et al. 2002). Entre estas hipóteses suscetíveis a falseação por métodos filogenéticos e de genética populacional, três podem ser destacadas por suas generalidades ao tratar da diversificação de vertebrados, pricipalmente hipóteses Amazonicas: a hipótese dos rios como barreiras, a dos refúgios e a das incursões marinhas do Mioceno (Capparella 1991, Moritz et al. 2000, Bates 2001).

1.2 - Estudos em Filogeografia

Filogeografia é a ciência que funciona como ponte entre os processos da micro e macro-evolução (Berminghan e Moritz 1998), preocupada com os princípios e processos que governam a distribuição geográfica de linhagens genealógicas, especialmente de espécies proximamente relacionadas (Avise 2000). O termo foi utilizado por Avise et al. (1987), incorporando uma perspectiva filogenética e de genética populacional na biogeografia, bem como integrando abordagens de várias disciplinas micro e macroevolutivas (etologia, demografia histórica, genética popuacional, genética molecular, paleontologia, filogenia, entre outras) nas análises e interpretações dos arranjos espaciais dos grupos de haplótipos (Avise 1998, Bermingham e Moritz, 1998).

A origem da filogeografia está intimamente relacionada a estudos de DNA mitocondrial (mtDNA) animal (Avise et al. 1979). Por apresentar herança materna (Hutchinson et al. 1974), o mtDNA permite a interpretação de relações genealógicas que não foram afetadas por recombinação. Além disso, suas sequências não possuem um mecanismo de reparo para mutação, o que possibilita uma taxa de evolução mais rápida quando comparada à dos genes nucleares, tornando-as suficientemente variáveis para fornecer informações sobre as relações evolutivas de indivíduos dentro e entre populações, em uma variedade de escalas temporais (Avise 2000).

A maioria dos estudos filogeográficos em animais têm se focado no mtDNA (Moore 1995, Zink e Barrowclough 2008), nos quais forneceu uma melhor resolução para eventos de especiação recentes. Outros autores têm incorporado genes nucleares em seus trabalhos (Hare 2001, Crawford 2003), mas o mtDNA ainda permanece o marcador dominante em abordagens deste cunho (Antonelli et al. 2010). Entretanto, a eficiência de inferências filogeográficas é diretamente proporcional ao número de linhas independentes de evidência. Assim, a utilização de marcadores nucleares também pode fornecer indícios robustos que corroborem (ou refutem) uma hipótese filogeográfica gerada somente a partir de mtDNA, e então refletir melhor a história do organismo (Templeton 1998). Desde que árvores filogenéticas representam a história evolutiva de um particular gene ou sequ~encia de DNA, elas podem ser chamadas de *árvore de gene.* Se estas árvores de gene representam as relações entre as espécies e podem ser consideradas árvores de espécie. Vai depender se os genes alinhados são ortólogos ou parálogos. Uma nova técinica, ainda em fase de experimentação, chamada de "Nova Geração", envolve um número elevado de genes, o que permitirá responder muitas questões de cunho filogeográfico e evolutivo.

Alguns padrões filogeográficos podem ser categorizados a partir das árvores de genes de mtDNA ou de outros *loci* (Avise 2000). Assim, são reconhecidos quatro tipos de estruturas filogeográficas: I – árvores de haplótipos profundas, geograficamente estruturadas; II - árvores profundas que não são estruturadas; III - árvores de haplótipos não profundas, mostrando estrutura geográfica; e IV - árvores não profundas e não estruturadas (Avise et al. 1987). Os grupos de haplótipos geograficamente estruturados (tipos I e III) são típicos resultados de isolamento por barreiras ambientais ou ecológicas, enquanto que as demais categorias, II e IV, são caracterizadas por expansão populacional recente com ausência de barreiras de isolamento, podendo, portanto, resultar em árvores de haplótipos sem uma boa resolução; contudo, existindo variação suficiente que diagnostique os grupos de haplótipos, tais árvores não estruturadas fornecem um grande indício de história populacional recente (Zink 2002).

Apesar da objetividade das quatro categorias filogeográficas (Kuchta e Meyer 2001), apenas uma única divisão objetiva existe: se as genealogias de haplótipos apresentam-se reciprocamente monofiléticas ou não (Zink 2002). Grupos que exibem um padrão geográfico de monofilia recíproca não compartilham mais nenhum dos haplótipos ancestrais, comportando-se como linhagens evolutivas distintas (Avise et al. 1987).

Nesse aspecto, a filogeografia pode fornecer um contexto evolucionário e geográfico para as espécies, compreendendo melhor as comunidades ecológicas, assim, permitindo determinar as influências históricas e espaciais dos padrões de riqueza das espécies (Berminghan e Moritz 1998, Lemey 2009).

Existem muitos processos geológicos e ecológicos que podem afetar os padrões na radiação de linhagens que abrange continentes inteiros e longos períodos de tempo, incluindo as maiores mudanças climáticas e eventos geológicos Derryberry et al. (2011). A evidência molecular através de vários táxons suporta um cenário onde muitos dos eventos de especiação e divergência observados ocorrem a *priori* no Pleistoceno (Moritz, et al. 2000), e são associados, também, a eventos paleogeográficos do Mioceno tardio (Thoysi et al. 2010). Muitas hipóteses têm sido propostas para explicar a grande diversidade de espécie na Amazônia, mas apenas pequenas generalizações têm surgido (Ribas et al. 2011). Alguns autores (Herbert e Fischer 1986, Olsen 1986, Bartlein e Prentice 1989, Berger et al. 1989, Zachos et al. 1997, 2001, Bennett

1997) aplicam também à diferenciação biótica durante o Cenozóico e, mais cedo (como durante o Quaternário), quando os ciclos de Milankovitch causaram oscilações no nível do mar, alterações rítmicas nas fácies de estratos geológicos e mudanças climático-vegetacionais nos continentes.

Com base nessas teorias, técnicas de análises de inferência de genética populacional usando genealogias (coalescência) vêm sendo aplicadas para corroborar entendimento da origem das linhagens com os eventos vicariantes que podem explicar a atual diversidade da região Neotropical. Genealogias contêm informações sobre história demográfica e os processos que tem atuado para formar a diversidade das populações (Lemey et al. 2009).

Comparações genéticas também permitem uma avaliação independente das divergências populacionais, no qual permite uma forte inferência em relação às bases filogenéticas da variação fenotípica.

Diferenciações genéticas também podem proceder em diferentes velocidades através do genoma (Wu 2001), com algumas regiões divergindo especificamente mais rápido e outras permanecendo mais homogêneas devido tanto pelo fluxo gênico ou por insuficiente tempo para acumulação de diferenças neutras (Via e West 2008, Nosil et al., 2009). Nestes casos, sequenciar mais genoma é importante não apenas para aumentar a probabilidade de decobrir regiões raras, regiões genômicas divergentes, mais também, para uma perspectiva filogeografica e de genética populacional, em ordem para amostrar um suficiente número de genes de envolvimento neutro para detectar sinal de demografica histórcica (McCormack et al., 2012). Por causa deste comportamento genômico e todas suas implicações, filogenias envolvendo um maior número de marcadores tornam-se importantes em estudos desta natureza (Rokas e Abbot 2009, Holsinger 2010, Emerson et al., 2010). Novas tecnologias envolvendo informações genéticas tem surgido recentemente em estudos filogeográficos e de genética populacional, entre elas o uso do método denominado Nova Geração (*Next Gen*). Hoje, a discussão e padronização de protocolos eficientes que priorizam o custo-benefício desta técnica ainda não chegaram a um consenso. Da mesma forma, a literatura ainda é escassa do uso de técnicas de Nova Geração em estudos filogeografico.

1.3 - Taxonomia do gênero *Campylorhamphus*

Embora a dificuldade em diagnosticar as espécies de *Campylorhamphus,* mesmo entre ornitólogos experientes, a história taxonômica do gênero como um todo, sofreu poucas alterações, principalmente nos últimos 70 anos. Zimmer (1934) foi o primeiro autor a propor uma diagose consistente entre as espécies com base no Conceito Biológico de Espécie. Nesta obra, Zimmer também descreve novos táxons para o gênero. Posteriormente, outros autores (Pinto 1933, Todd 1948, Pinto & Camargo, 1955) propuseram novos táxon para o gênero. Revisões não foram propostas até o inicio dos anos 2000, quando Marantz et al. (2003) revisaram toda a Família Dendrocolaptidae, propondo sinonimizações. As inferências filogenéticas começaram a surgir, Aleixo (2002) e Irestedt et al (2004) mostraram coom base em dados moleculares a monofilia do gênero *Campylorhamphus.* Atualmente são reconhecidas quatro espécies bilógicas dentro do g~enero (SACC 2014).

Gênero *Campylorhamphus* (Bertoni 1901).

A espécie-tipo desse gênero é o que hoje se reconhece como *C. falcularius.* Atualmente são reconhecidas quatro espécies para o gênero (SACC 2013). Recentemente duas novas espécies foram descritas (Aleixo et al. 2013, Portes et al. 2013). Nestes trabalhos, os autores também sugerem a elevação ao nível de espécies para todos os táxons reconhecidos no compleco *C. procurvoides.*

Campylorhamphus falcularius (Vieilot 1822).

Esse táxon monotípico foi descrito por Vieilot, 1822 inicialmente dentro do gênero sinonimizado *Dendrocopus*, na localidade-tipo denominada Serra dos Órgãos, no Rio de Janeiro, Brasil. Segundo Marantz et al. (2003), alguns autores no passado sugeriram a formação de uma superespécie com *C. trochilirostris*. Autores recentes (Claramunt et al. 2010, Aleixo et al. 2013, Portes et al. 2013 – Capítulo 2) mostram que *C. falcularius* é um clado que se diversificou primeiro dentro do gênero, formando um grupo monofilético e irmão de todos os demais *Campylorhamphus*. Distribuem-se no Paraguai, norte a Argentina (Missiones) e Brasil meridional, do centro da Bahia (Chapada Diamantina) até o norte do Rio Grande do Sul, se estendendo inclusive a leste de Minas Gerais (rio Doce) (Pinto 1978, Marantz et. al. 2003). São facilmente visualizados em floresta secundaria da Mata Atlântica, assim como em reflorestamento de eucalipto (obs. pess.CEBP).

Campylorhamphus procurvoides (Lafresnaye 1850).

Campylorhamphus procurvoides (Lafresnaye 1850) foi descrito como pertencente ao gênero *Xiphorhynchus* (*Xiphorhynchus procurvoides*).

Esta espécie politípica é endêmica da Amazônia, sendo suas diferentes raças se substituíndo em cada um dos centros de endemismo reconhecidos na Amazônia (sensu Silva, 2005). Este complexo é formado por quatro subespécies (*procurvoides, sanus, probatus* e *multostriatus*).

Campylorhamphus p. procurvoides (Lafresnaye 1850).

A espécie nominal se restringe ao escudo Guianesne, ocorrendo na calha norte do Rio Amazonas, até a margem leste do rio Negro. Portes & Aleixo (2009) mostraram com base em caracateres morfológicos que a população deste complexo distribuídos a nordeste da Venezuela, que tradicionamente era reconhecida como *C. p. sanus,* é na verdade pertencentes a *procurvoides.* Este resultado mostrou que não há mais populações disjuntas em *sanus.*

Campylorhamphus p. sanus (Zimmer 1934).

Esta subespécie é a única deste complexo a ocorrer em mais de um centro de endemismo reconhecidos para a Amazônia (Silva, 2005). Zimmer (1934) quando descreveu a espécie, estendia a distribuição de *sanus* até o noroeste da Guiana. Portes & Aleixo (2009) mostraram que a população do noroeste da antiga área supostamente habitada por *C. sanus* (estado de Bolívar na Venezuela e Guiana) são na verdade pertencentes a espécie nominal *procurvoides.* Com base nesse trabalho, *sanus* restringe-se agora apenas aos Centros de Endemismo (CEs) Napo e Imeri, distribuindo-se no noroeste da Amazônia, do sudeste da Colômbia (oeste de Meta e Caqueta), nordeste do Equador (Sucumbios) e extremo nordeste do Peru e extremo noroeste do Brasil (acima do Rio Negro) e sul da Venezuela.

Campylorhamphus p. multostriatus (Snethlage, 1907)

Esse táxon é conhecido do sudeste da Amazônia brasileira, entre os rios Tapajós e Tocantins (Marantz et al. 2003). Os padrões vocais e morfológicos sugerem que as populações separadas pelo rio Xingu são distintas e que revisões são necessárias (obs. pes).

Campylorhamphus p. probatus (Zimmer 1934)

Distribuem-se no centro sul da Amazônia brasileira, entre os rios Madeira e Tapajós, em Rondônia e no noroeste do Mato Grosso, Brasil. Se assemelha vocalmente e morfologicamente a população de *C. p. multostriatus* que ocorre na margem oeste do rio Xingu.

Campylorhamphus trochilirostris (Lichtenstein 1820).

Essa espécie originalmente descrita dentro do gênero *Dendrocolaptes* tem a localidade-tipo pouco precisa. Durante a descrição, o autor menciona apenas o Estado da Bahia, Brasil (Marantz et. al. 2003). Como atualmente definida, *C. trochilirostris* é uma linhagem considerada irmã de *C. procurvoides* (Claramunt et al. 2010). Inconsistência taxonômicas e evolutivas são presentes na nesta espécie politípica. Como nenhuma análise filogenética estava disponível para a grande maioria dos táxons agrupados em *C. trochilirostris*, análises preliminares de caracteres morfológicos permitem dividir *C. trochilirostris* em três grupos distintos, a saber: o grupo "venezuelensis" (inclui *brevipennis*) no leste do Panamá e norte da América do Sul, o grupo "*thoracicus*" (inclui *zarumillanus*) ao longo da costa do Pacifico na América do Sul e o grupo "*trochilirostris*" (incluindo os demais táxons) da Amazônia, da Floresta Atlântica e interior da América do Sul; o táxon *sucessor* que anteriormente era reconhecido dentro de *C. procurvoides* foi sinonimizado com *C. t. notabilis* Zimmer (1934) (Portes e Aleixo 2009) e pertence a esse último grupo. Nesse último grupo, as raças de distribuição amazônica são problemáticas: *napensis* é morfologicamente próximo ao grupo "*thoracicus*" da costa do Pacifico, onde *notabilis* e *devius* são aparentemente próximos, e *snethlageae* tem um posicionamento filogenético incerto. As raças descritas *omissus* (leste do Brasil) e *guttistriatus* (sul de Goiás, Brasil) ambas foram sinonimizadas com *major*. São reconhecidas atualmente doze subespécies (Marantz et al. 2003).

Subespécies e Distribuições (segundo Marantz et al. 2003).

C. t. brevipennis Griscon, 1932 – centro e leste do Panamá (norte de Coclé e leste do Panamá até Darién) e noroeste da Colômbia (costa do Pacifico Sul até norte de Chocó).

C. t. venezuelensis (Chapman 1889) – no norte da Colômbia ao leste de Córdoba até o Vale de Magdalena (sul do norte de Huila), ilhas caribenhas e leste do leste dos Andes (norte de Santander sul até oeste de Meta), e norte e centro da Venezuela (leste até Sucre, do sul ao Rio Orinoco, precisamente noroeste e sul de Bolívar), registros da Guiana Francesa aparentemente referem-se a *C. procurvoides*.

C. t. thoracicus (Sclater 1860) – costa do sudoeste da Colômbia (sudoeste de Narino) e oeste do Equador.

C. t. zarumillanus Stolzman 1926 – costa do extremo noroeste do Peru (Tumbes, Piura).

C. t. napensis Chapman 1925 – oeste da Amazônia, no leste do Equador e leste do Peru.

C. t. notabilis Zimmer 1934 – oeste da Amazônia brasileira, sul da Amazônia, entre o Rio Purús e o baixo Rio Madeira.

C. t. snethlageae Zimmer 1934 – Distribuem-se em florestas de várzea no Centro da Amazônia brasileira, em ambas as margens do Rio Amazonas do leste do Rio Madeira ao Rio Tapajós, incluindo as ilhas do Rio Amazonas. Ainda se faz necessárias análises mais complexas envolvendo um número maior de amostras de *snethlageae* (Marantz et al. 2003).

C. t. devius Zimmer 1934 – sudoeste da Amazônia no norte da Bolívia; populações adjacentes no sudeste do Peru e oeste do Brasil (Acre e Sudoeste da Amazônia) podem representar essa raça.

C. t. lafresnayanus (d'Orbigny 1847) – Centro da América do Sul e leste da Bolívia (Santa Cruz), sudoeste do Brasil (oeste do Mato Grosso, oeste do Mato Grosso do Sul) e oeste do Paraguai (sul do Rio Pilcomayo).

C. t. hellmayri Laubmann 1930 – Sudoeste do Paraguai (Nheembucú) e norte da Argentina (Salta, Formosa e oeste de Corrientes, sul até La Rioja, Santiago del Estero, norte de Santa Fe e Entre Rios).

C. t. major Ridgway 1911 – interior leste e sul do Brasil, do Piauí e sul do Ceará até Minas Gerais e extremo oeste do Paraná.

C. t. trochilirostris (Lichtenstein, 1820) – costa leste do Brasil, do sul de Pernambuco a sudeste da Bahia (Ilhéus).

Campylorhamphus pusillus (Sclater 1869).

Essa espécie foi descrita originalmente dentro do gênero *Xiphorhynchus*, cuja localidade-tipo é Nova Grenada. As raças da América Central são consideradas por alguns autores como uma espécie separada (*C. p. borealis*; Marantz et al. (2003). Da mesma forma que em *C. trochilirostris*, atribuir padrões de variação geográfica com base em caracteres de plumagem é complicado devido a variação individual na coloração geral e extensão das estrias. As raças *borealis* e *olivaceus* são pouco diferenciadas uma da outra. As variações em *tachirensis* e *guapiensis* baseiam-se provavelmente em uma variação individual do que geográfica. São reconhecidas atualmente cinco subespécies (Marantz et al. 2003).

Subespécies e Distribuições (segundo Marantz et. al. 2003).

C. p. borealis Carriker 1910 – Costa Rica (Caribe, sudoeste do Pacifico e ilhas adjacentes) e oeste do Panamá (oeste de Chiriquí, oeste de Boca del Toro).

C. p. olivaceus Griscon 1927 – centro e leste do Panamá (leste de Veraguas e Darién).

C. p. tachirensis Phelps e Phelps 1956 – Perijá e extremo leste dos Andes no nordeste da Colômbia e Noroeste da Venezuela (oeste de Zulia, sudoeste de Táchira).

C. p. pusillus (Sclater 1860) – norte e centro dos Andes em ambos os lados na Colômbia (exceto extremo nordeste) e Equador, e no lado leste do norte do Peru (do sul até Cajamarca e San Martn).

C. p. guapiensis Romero-Zambrano 1980 – ilhas da costa do sudoeste da Colômbia (Cauca).

1.4 – Objetivos

1.4.1 – Objetivo Geral

- Reconstruir a história evolutiva do gênero *Campylorhamphus* através de análises morfológicas, moleculares e vocais.

1.4.2 – Objetivos Específicos

- Revisar a taxonomia e limites inter-específicos dentro do gênero *Campylorhamphus*, propondo revalidações e/ou sinonímias, e descrições de novas espécies;
- Realizar análise filogenética incluindo maior número possível táxons reconhecidos atualmente no gênero, de forma a obter hipóteses sobre as relações de parentesco;
- Propor uma diagnose para cada táxon considerado válido no gênero *Campylorhamphus*, com base em análises multicaráter.

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Capítulo 1

Molecular systematics and taxonomic revision of the Curve-billed Scythebill complex (*Campylorhamphus procurvoides*: Dendrocolaptidae), with description of a new species from western Amazonian Brazil

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The difficulty in separating the Amazonian endemic Curve-billed Scythebill *Campylorhamphus procurvoides* from the sympatric taxa grouped under the more widespread Red-billed Scythebill (*C. trochilirostris*), both in the hand and in the field, is notorious among ornithologists working in the Neotropics. J. T. Zimmer (1934) listed several morphological characters separating these two polytypic species, and he was the first to classify the different *Campylorhamphus* taxa occurring in lowland Amazonia as either *C. procurvoides* or *C. trochilirostris*, according to the theoretical background of the Biological Species Concept (BSC). Over the next 76 years, Zimmer's taxonomic treatment of *C. procurvoides* and *C. trochilirostris* has been followed without change (e.g, Todd 1948, Peters 1951, Ridgely and Tudor 1994, Marantz et al. 2003), despite some qualitative evidence indicating that some taxa grouped under *C. procurvoides* (the so called *multostriatus* group) are in fact vocally and morphologically more similar to *C. trochilirostris* (Marantz et al. 2003).

The morphological attributes distinguishing populations of *Campylorhamphus procurvoides* distributed west of the Madeira and south of the Solimões rivers in the Inambari area of endemism (sensu Silva et al. 2005), were first pointed out by Zimmer (1934) when discussing a female (AMNH 309432) from Tefé, in the Brazilian state of Amazonas. Zimmer (1934) could not classify this specimen as *C. procurvoides* or *C. trochilirostris* with certainty, although the shape of its pectoral spots was similar to those of birds grouped under *C.*

procurvoides. The next time the Tefé *Campylorhamphus* was mentioned was by N. Gyldenstolpe (1945a), who studied a female *Campylorhamphus* (NR 569483) obtained by the Olalla family at Igarapé Grande, upper Juruá River, near Eirunepé, Amazonas, Brazil. Gyldenstolpe concluded that this particular specimen and two males also housed at the NR and collected by the Olallas along the Purus River valley at Lábrea and Jaburú, Amazonas, Brazil (respectively NR 569481 and 569482), closely matched the characters shown by the Tefé specimen discussed by Zimmer (1934), and that as a whole, these specimens probably represented an undescribed taxon allied to *C. procurvoides*. Three years later, Todd (1948) studied the Tefé specimen and a series of 19 *Campylorhamphus* obtained by the collector Samuel M. Klages at six different localities along the Purus, Solimões, and lower Amazon rivers, and concluded that they all belonged, along with the male from the upper Juruá housed at the NR, to the new taxon recognized but not named by Gyldenstolpe (1945a); he then provided a brief description of the new taxon, named *Campylorhamphus procurvoides successor* Todd 1948 (type locality Nova Olinda, on the left bank of the middle Purus River, Amazonas, Brazil). Subsequently, in his detailed study on the ornithology of the Purus River region in Brazil, Gyldenstolpe (1951) also assigned his Lábrea and Jaburú specimens mentioned above to *C. p. successor*, without having examined the type series at the CM.

Recently, Portes and Aleixo (2009) showed that the type series of *successor* consists of a mix of individuals belonging to *C. trochilirostris* (including the holotype for *C. p. successor*) and specimens whose plumage characters closely match those of the Tefé, upper Juruá, and Purus specimens discussed, respectively, by Zimmer (1934) and Gyldenstolpe (1945a, 1951). Between 2002 and 2009, five additional specimens with those same characteristics were collected by us and colleagues at four new localities in the Brazilian states of Rondônia and Amazonas and later sequenced for two mtDNA genes. Together, these birds form a statistically well-supported and reciprocally monophyletic group with respect to all other lineages grouped under *C. procurvoides*. Because the name *successor* can no longer be applied to birds grouped in this clade, we propose to name them as:

Campylorhamphus gyldenstolpei **sp. nov.**

Tupana Scythebill

arapaçu-do-tupana (Portuguese)

Illustrated: Hilary Burn

Holotype.— Museu Paraense Emílio Goeldi (MPEG) 62267, skin, adult male, skull 100% ossified, no bursa of fabricius; left testis 5 x 3 mm; brood patch present; 38 g with little fat and no molt. Collected (shot) in the understory of creek-side upland (*terra-firme*) forest by AA and tape-recorded by AW on 4 July 2007 at Tupana Lodge, located at km 158 of the BR 319 road in the municipality of Careiro, Amazonas, Brazil (04º 05' 00.2''S; 60º 39' 37.8''W); prepared by AA under field number TUP 001. Pectoral muscle tissue preserved in approximately 96% alcohol; field number TUP 001. Hologenetype (Chakrabarty 2010) sequences of the mitochondrial genes cytochrome *b* (1,076 pb) and NADH subunit 2 (1,041bp) deposited in GenBank (accession numbers KC237252 and KC242874, respectively). Tape-recordings of vocalizations archived at the British Library of Natural Sounds under accession number (183248; available at http://www.bl.uk/listentonature/main.html). Digital pictures of the recently collected individual, before preparation, deposited at MPEG.

Diagnosis: Morphology — Alphanumeric color designations determined through direct comparison with Smithe (1975). Phenotypically, the new species can be unambiguously assigned to the genus *Campylorhamphus* (Dendrocolaptidae) based on its narrow, long, and curved bill, which distinguishes the genus; within *Campylorhamphus* it can be placed in the *C. procurvoides* complex on the basis of its small and narrowly tipped pectoral stripes, which possess a characteristic sagittal format (Zimmer 1934), being nearest to those of specimens assigned to *C. p. sanus* and *C. p. procurvoides*, but distinct from all other members of the complex by a unique combination of size, color, and shape. In comparison with taxa currently grouped under *C. procurvoides* (*sensu* Zimmer 1934), the new species can be phenotypically diagnosed as follows: 1) from *multostriatus* by significantly smaller and sagittate (acutely shaped) whitish pectoral stripes, less pronounced or even absent streaking on the back, narrower head and neck stripes, and belly and back Cinnamon-Brown (33) or Russet (34) (vs. Cinnamon 39); 2) from *probatus* by narrower and whitish (vs. Pale Horn 92) pectoral stripes, and belly and back Cinnamon-Brown (33) or Russet (34) (vs. Cinnamon 39); 3) from closely related *sanus* by distinctly larger culmen, wing, and tail measurements (Table 1 in supplementary Information – SI), wider and whitish (vs. Pale Horn 92) pectoral stripes, with a more contrasting black edge (vs. black edge absent), and belly Cinnamon-Brown (33) or Russet (34) (vs. bright Antique Brown 37); and 4) from closely related *procurvoides* by distinctly broader head, throat, and pectoral stripes, the latter with a more contrasting black edge (vs. black edge absent), and belly Cinnamon-Brown (33) or Russet (34) (vs. Brownish Olive 29). ***Voice.***— The loudsong is immediately distinguished in the field from those of all other members of the complex and, in spectrographic analysis, by the shape and syntax of the notes (described below; see Figs. 1 and 2). Within the *C. procurvoides* complex, *C. gyldenstolpei* is the only taxon possessing D note types (characterized by an abrupt frequency peak before its end; Fig. 1d) in its loudsong (Fig. 2c). ***Genetic divergence*** — Separated from its closely related taxa *sanus* and *procurvoides* by approximately 0.8 and 1.2 % sequence divergence, respectively, in the mitochondrial genes cytochrome *b* and NADH subunit 2 (Fig. 3).

***Distribution* —** *Campylorhamphus gyldenstolpei* has been documented from several localities west of the Madeira and south of the Solimões rivers in the Inambari area of endemism (*sensu* Silva et al. 2005) in Brazil (Fig. 4). The species is likely to be found in the neighboring departments of Loreto (south of the Amazon / Marañón rivers) and Ucayali in Peru near the Brazilian border but so far no records exist (under the name *C. procurvoides*; Schulenberg et al. 2007).

Description of holotype **-** Alphanumeric color designations determined through direct comparison with Smithe (1975). Plumage fresh and unworn, tail and wing not in molt; skull 100% ossified. Head uniformly Sepia (119) with short, light-brownish stripes, including the forehead, lores, and cheeks. Mantle Sepia (219) with thin and rather long light brown streaks restricted to the upper parts, with unmarked lower parts. Primaries, secondaries, and wing coverts Warm Sepia (221A). Tips and inner webs of primaries with a contrasting Fuscous (21) tinge. Lower mantle and upper parts of rump Sepia (219), gradually changing into Warm Sepia (221A) in the lower rump. Rectrices essentially concolor with lower rump. Tail graduated, each rectrix with a stiff shaft, softer at the tips. Throat Sepia (119) heavily streaked with whitish-creamy feathers with a scaly shape. Lower throat and breast Sepia (219) covered with arrow-shaped (i.e., sagitatte) whitish-creamy streaks with thin but contrasting black edges. Upper belly Cinnamon-Brown (33) with some obsolete thin and rather long whitish streaks. Lower belly concolor with upper belly, but unstreaked. Undertail coverts Cinnamon-Brown (33) with feathers with somewhat contrasting whitish shafts. **Soft parts in life**: Iris dark brown with a contrasting yellow-mustard eyering. Maxilla Burnt Orange (116) with a dark brownish wash around the nostrils; mandible light Burnt Orange (116); tarsi and feet bluish-green. **Measurements of holotype:** wing (100.7 mm), tail (96.4 mm), tarsus-metatarsus (20.8 mm), bill length from the anterior edge of nares (53.3 mm), bill height at nares (6.2 mm), bill width at nares (5.4 mm); average length of pectoral spots (6.8 mm), average width of pectoral spots (1.5 mm), average length of back spots (8.0 mm), average width of back spots (0.8 mm), average length of head spots (3.4 mm), and average width of head spots (0.9 mm).

Etymology.— We are pleased to name the new species after the Swedish ornithologist Count Nils Gyldenstolpe, who was the first to characterize the distinctiveness and distribution of the new *Campylorhamphus* described herein, separating it from all other taxa known at the time grouped under both *C. procurvoides* and *C. trochilirostris* (Gyldenstolpe 1945a, 1951). Furthermore, the name of the new species represents a tribute to Gyldenstolpe’s great contribution to Neotropical, and particularly, Amazonian ornithology, as shown by his unique and thorough monographs on the birds of northern Bolivia and the upper Juruá and Purus rivers in Brazil (Gyldenstolpe 1945a,b, 1951).

REMARKS

Type series.— The allotype of *C. gyldenstolpei* is MPEG 68870, skin, adult female, ovary 7 x 3 mm with ova minute, convoluted oviduct, no molt; collected (shot) and tape-recorded in the understory of *terra-firme* forest by AA on 29 September 2009 at Tupana Lodge (same locality as the holotype); prepared by M. Santa-Brígida under field number TUP 059. Tissue samples deposited at MPEG and mitochondrial cytochrome *b* and NADH subunit 2 sequences deposited in GenBank (KC237250 and KC242872, respectively). Tape-recordings of vocalizations archived at Xeno-canto under accession numbers (XC107627; available http://www.xeno-canto.org/107627). Paratypes of *C. gyldenstolpei* are the following fourteen specimens: MPEG 60081: skin, adult male, left testes 7 x 5 mm, molt; carcass preserved in 70% ethyl alcohol under field number CUJ 25; collected (shot) on 10 March 2006 by AA in the understory of *terra-firme* forest at Reserva de Desenvolvimento Sustentável do Cujubim, ca. 390 km SW of Jutai (05^{o} 13' 11.5''S; 69^{o} 19' 00.0''W), Amazonas, Brazil, and prepared by Fabíola Poletto; tissue sample deposited at MPEG and mitochondrial cytochrome *b* and NADH subunit 2 sequences deposited in GenBank (KC237251 and KC242873, respectively). MZUSP 76641: skin, adult male with well developed gonads; collected by Luís Fábio Silveira and Fábio Olmos at Estação Ecológica Antônio Mujica Nava (09^{o} 24' S; 64^{o} 56' W), Rondônia, Brazil, on 12 February 2002; tissue sample deposited at Instituto de Biologia da Universidade de São Paulo (IB-USP). INPA 1630: skin, male, Campos do Tupana (ca. 120 km south of Manaus: 4^{o}09´S; 60^{o}08´W), Amazonas, on 6 July 2007, collected by M. Cohn-Haft; tissue sample deposited at INPA. NR 569483: skin, female, Igarapé Grande (ca. 15 km north of Eirunepé: 6^{o}38´S; 69^{o}50´W; coordinates from Gyldenstolpe 1945a), Amazonas, Brazil, 30 August 1936, collected by A. M. Olalla and crew. NR 569481: skin male, Lábrea (ca. 7^{o}18´S; 64^{o}35´W; coordinates from Gyldenstolpe 1951), right bank of the Purus River, Amazonas, Brazil, 7 January 1936, collected by A. M. Olalla and crew. NR 569482: male, Jaburú (ca. 5^{o}36´S; 64^{o}12´W; coordinates from Gyldenstolpe 1951), left bank of the Purus River, Amazonas, Brazil, 10 December 1935, collected by A. M. Olalla and crew. AMNH 309432: female, Santo Isidoro, Tefé (ca. 3º22´S; 64º42´W; coordinates from Paynter and Traylor 1991), Amazonas, Brazil, 31 July 1928, collected by A. M. Olalla and crew. CM 96192: male, São Paulo de Olivença (ca. 3º27´S; 68º48´W; coordinates from Paynter and Traylor 1991), Amazonas, Brazil, 2 April 1923, collected by Samuel M. Klages. CM 91898: male, Nova Olinda (ca. 5º40´S; 64º18´W; coordinates from Gyldenstolpe 1951), left bank of the Purus River, Amazonas, Brazil, 14 July 1922, collected by Samuel M. Klages. CM 86702, 87386, and 87857: males, Hyutanaãn (ca. 7º40´S; 68º45´W; coordinates from Gyldenstolpe 1951), right bank of the Purus River, Amazonas, Brazil, collected, respectively, on 26 December 1921, 19 January 1922, and 9 February 1922 by Samuel M. Klages. CM 99363: male, Caviana (coordinates not located), south bank of the Solimões River, Amazonas, Brazil, 30 May 1924, collected by Samuel M. Klages. UMMZ 150237 (ex-CM 93949): male, Arimã (ca. 5º47´S; 63º38´W; coordinates from Gyldenstolpe 1951), right bank of the Purus River, Amazonas, Brazil, 9 November 1922, collected by Samuel M. Klages. **Variation in the type series**: The most noticeable variation in the type series pertains to the chest and belly color of the different specimens, which ranges from Cinnamon-Brown (33) to Russet (34), with a nearly Amber (36) tinge in some specimens (AMNH 309342, CM 91898, NR 569481, NR 569482, MZUSP 76641, MPEG 60081). Apparently, this variation has no geographical, seasonal, ontogenetic, or sexual basis, since series of adult male and female specimens collected between July and September at the same or nearby localities (such as Tupana) varied noticeably in chest and belly color (MPEG 62267, MPEG 68870, and INPA 1630). The same applies to the color of the throat and pectoral spots, which range from pure white (CM 86702, CM 87857, MPEG 60081) to whitish with a Buff (24) hue (NR 569481, NR 569482, NR 569483, CM 87386), with the tendency of the contrasting black edge to be more conspicuous in the birds with whiter pectoral spots; three male specimens collected at the same locality (Hyutanaãn) between late December and early February exhibited both white (CM 86702 and CM 87857) and more buffy (CM 87386) spots, therefore suggesting that the variation in this character is of an individual nature. Head color varied less, with most specimens being Fuscous (21), although UMMZ 150237 (ex-CM 93949) and NR 569482 had conspicuously faded head coloration, with an overall Raw Umber (23) color. Therefore, it is more likely that all aforementioned variation in plumage color has an individual basis that could possibly be explained by differences in the amount of wear due to differences in foraging and roosting, for example. No specimens in the type series exhibit signs of immaturity, with all those for which age-related data are available being full adults based on skull ossification and gonad development data (MZUSP 76641, MPEG 60081, MPEG 62267, MPEG 68870, and INPA 1630).

Ecology and behavior.— *Campylorhamphus gyldenstolpei*, like other members of the *C. procurvoides* complex, forages alone or in pairs in the understory and sometimes midstory of *terra firme* forest, usually found along forest creeks, and will occasionally join mixed-species flocks that pass through its territory. The species seems particularly tied to *terra-firme* forest growing on sandy soils such as at Tupana Lodge and Reserva de Desenvolvimento Sustentável do Cujubim, where the local forest possesses a dense understory dominated by short *Lepdocaryum sp.* palm trees. Its nest and eggs remain unknown.

Vocalizations.— When compared to loudsongs of other taxa in the *C. procurvoides* complex, the loudsong of *gyldenstolpei* is unique, mainly in the shape and syntax of the notes. Within the complex, this vocalization typically consists of three notes types (B, C, and D; Fig. 1), with D note types being found only in *C. gyldenstolpei*. Note syntax for a typical loudsong of *C. gyldenstolpei* is as follows: an introductory sequence of 2-4 D notes, followed by 1-4 B notes, and terminating with 6-12 C notes (N = 8, Figs. 1 and 2c). This loudsong type contrasts with that of other members of the *C. procurvoides* complex, whereby the syntax is similar between *procurvoides* and *sanus* (including only note types A, B, and C), varying only in the number of each note type delivered.

Hence, the composition and structure of the notes in *sanus* loudsong normally includes an introductory sequence of 1-2 A notes, followed by 2-3 B notes, and concluding with 4-9 C notes (N = 3, Figs. 1 and 2b), whereas that of *procurvoides* consists of 1-4 A notes, 2-9 B notes, and 4-23 C notes (N = 21, Figs. 1 and 2a,b). Furthermore, the dominant frequency values of the notes in *gyldenstolpei* loudsongs vary little, whereas in both *sanus* and *procurvoides*, loudsongs increase significantly in frequency, with C type notes having higher frequencies compared to notes A and B (Figs. 1 and 2a,b).

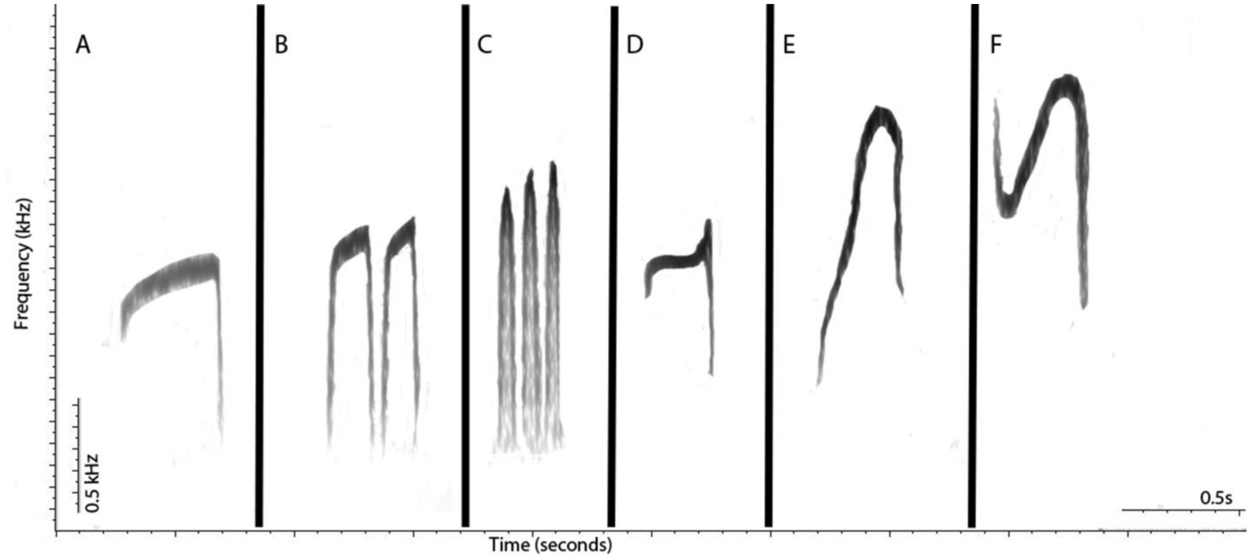

Figure 1 - Representative spectrograms of note-types used to diagnose the loudsongs of taxa currently grouped under the polytypic *Campylorhamphus procurvoides.* Letters refer to the note-type nomenclature used in this study. Notes A, B, and D are restrictedto the so-called "procurvoides" group (*sensu* Marantz et al. 2003; which includes the new taxon *gyldenstolpei*, described herein), whereas notes E and F are found only in the "*multostriatus* group" (sensu Marantz et al. 2003).

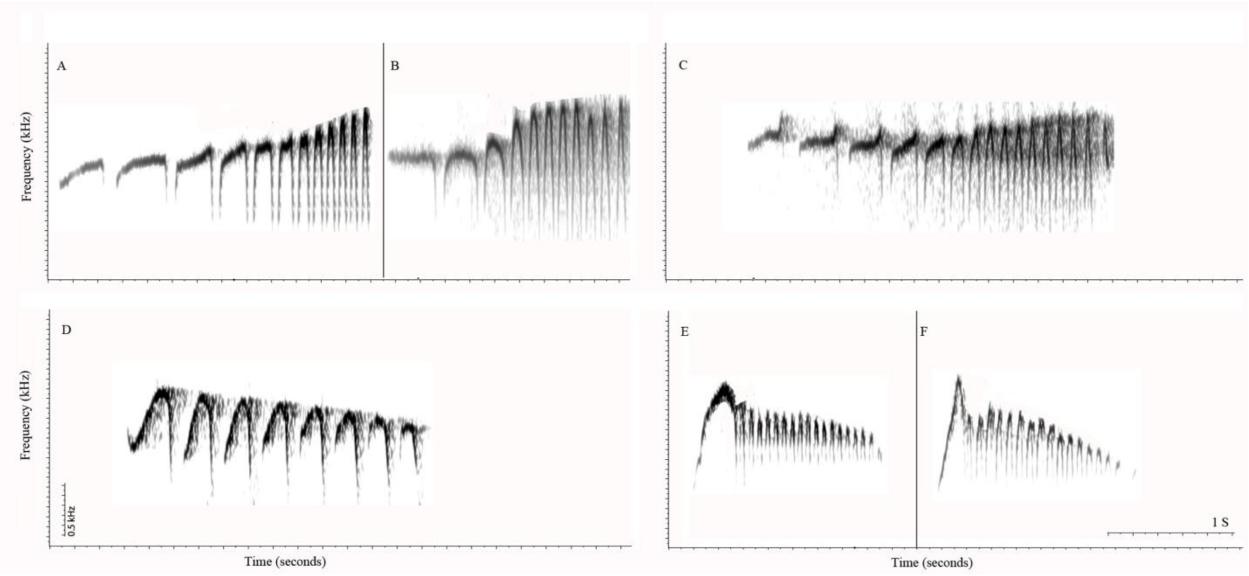

Figure 2 - Representative spectrograms of loudsongs of taxa currently grouped under the polytypic *Campylorhamphus procurvoide* and the new taxa described in this volume: A) *procurvoides*: Venezuela, Rio Grande, El Palmar (LNS-65702_2c); B) *sanus*: Venezuela, Amazonas, San Carlos (LNS-65706_6); C) *gyldenstolpei*: Brazil, Amazona, Tupana Lodge (AW3B3_2b); D) *multostriatus*: Brazil, Pará, Salobo Road, Carajas (AW5A2_1 0); E) unnamed taxon described by Portes et al. (2013): Brazil, Mato Grosso, Alta Floresta, Rio Crista/ina (LNS-1 06114_24b); and F) *probatus*: Brazil, Amazonas, Borba, eastern bank of the Madeira River (LNS-127698_3b).

Phylogenetic relationships — DNA sequence data for the mitochondrial genes cytochrome *b* (cyt *b*, 1,076 bases pairs) and NADH subunit 2 (ND2, 1,041 bases pairs) were obtained for 41 individuals (see Table 4 in the SI file for a list of specimens sequenced) of all species in the genus *Campylorhamphus*, including all taxa currently grouped under the polytypic *C. procurvoides* (sensu Marantz et al. 2003; i.e., *multostriatus*, *probatus*, *procurvoides*, and *sanus*; Fig. 4). Trees were rooted in *Lepidocolaptes fuscicapillus*, which belongs with one of the sister genera to *Campylorhamphus* (Derryberry et al. 2011). The phylogeny estimated by Bayesian inference strongly supports that *C. procurvoides*, as currently defined, represents a polyphyletic species, with taxa currently classified as its subspecies found in three separate clades with disparate phylogenetic affinities (Fig. 3). The three highly supported and reciprocally monophyletic clades group taxa currently classified as subspecies of the polyphyletic *C. procurvoides,* as follows: (1) birds occurring south of the Amazon and east of the Xingu River in the Xingu center of endemism (Silva et al. 2005; corresponding to the taxon *multostriatus,* whose type locality lies in this area of endemism; Fig. 4); (2) birds found south of the Amazon and west of the Madeira River (in the Inambari center of endemism, corresponding to the new taxon described herein, i.e. *gyldenstolpei*) and birds distributed north of the Amazon, which correspond to the taxa *sanus* (found in the Napo and Imeri areas of endemism) and *procurvoides* (corresponding to the Guiana area of endemism; Fig. 4); and (3) birds found south of the Amazon and between the Madeira and Xingu rivers, corresponding to the taxon *probatus* (distributed in the Madeira center of endemism; Fig. 4) and to the taxon formerly known as *multostriatus* but which in fact represent an unnamed taxon described by Portes et al. (2013) in this volume, endemic to the Tapajós area of endemism; Fig. 4). The fact that the Bayesian phylogeny recovered *gyldenstolpei, procurvoides,* and *sanus* as reciprocally monophyletic taxa with strong statistical support (Fig. 3) in conjunction with morphological and vocal diagnoses of these taxa, support their recognition as valid species level taxa (De Queiroz 2007). Thus, we recommend the recognition of three species and vernacular names in the *C. procurvoides* complex, henceforth defined as consisting of only three taxa (*gyldenstolpei*, *procurvoides,* and *sanus*): Tupana Scythebill (*C. gyldenstolpei*; distributed west of the Madeira and south of the Solimões rivers in Amazonian Brazil; Fig. 4); Curve-billed Scythebill (*C. procurvoides*; distributed on the Guianan shield north of the Amazon and east of the Negro - Branco rivers in Venezuela, Brazil, Guyana, Surinam, and French Guiana); and Zimmer's Scythebill (*C. sanus*;

distributed west of the Branco - Negro rivers in Amazonian Brazil and Venezuela westward towards the base of the Andes in Colombia, Ecuador, and Peru north of the Amazon/Solimões rivers).

Conservation — *Campylorhamphus gyldenstolpei* is a low-density species in its preferred habitat. Because it is endemic to one of the least disturbed parts of Amazonia (the Inambari area of endemism), it is not currently threatened by anthropogenic alteration of its habitat or other sources. Of particular concern in the long term is the recent advancement of soybean plantations in parts of the range of *C. gyldenstolpei* such as around Lábrea, in the southern part of Amazonas, Brazil. If the advancement of agro-business at the core of *C. gyldenstolpei*'s range becomes more widespread, it could imperil this and many other endemic *terra-firme* species of the Inambari region in the long run.

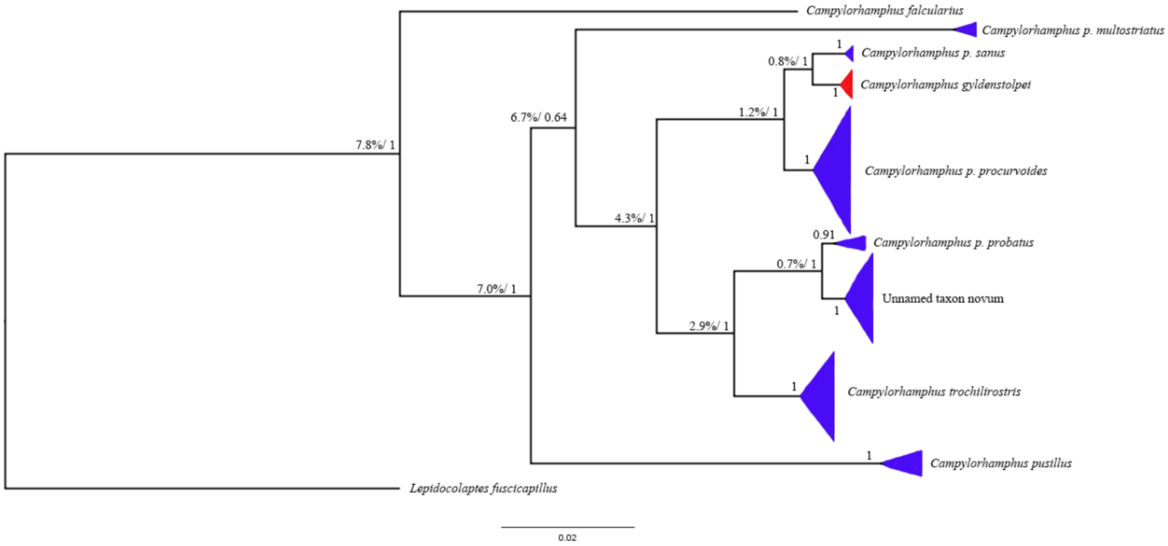

Figure 3 - Bayesian estimate of the phylogeny of the genus *Campylorhamphus* based on two mitochondrial genes (cytb and ND2). Numbers refer to posterior probability values and genetic distances (% of average uncorrected *p* sequence divergence) between sister groups associated with the labeled nodes. Note the polyphyly of taxa currently grouped as subspecies of *C. procurvoides* (*multostriatus*, *probatus*, *procurvoides*, and *sanus*) and the new taxon *gyldenstolpei* and a second unnamed taxon described by Portes et al. (2013). High support values *i.e.*, 1) associated with nodes grouping *procurvoides*, *sanus* and *gyldenstolpei* are consistent with their recognition as species-level tax

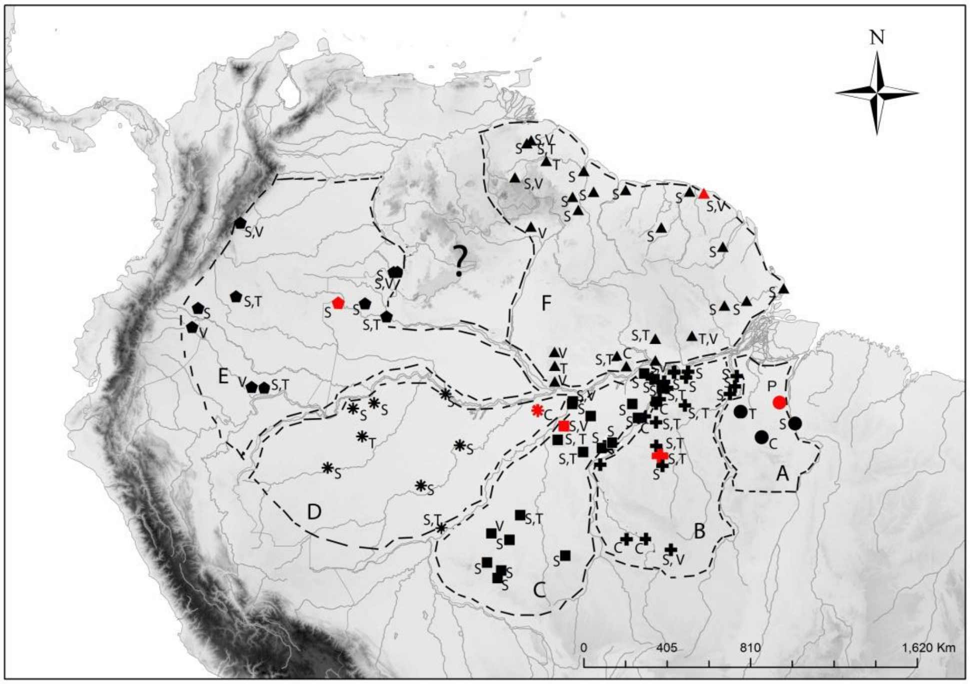

Figure 4 - Geographic distribution of specimens, vocalizations, and tissues of *Campylorhamphus procurvoides* taxa analyzed in this study. Asterisks = *C. gyldenstolpei*; dots = *C. multostriatus*; crosses = unnamed taxon described by Portes et al. (2013) in this volume; triangles = *C. procurvoides*; squares = *C. probatus*; and pentagons = *C. sanus*. Type localities for each taxon are shown as red symbols. Letters next to a symbol represent material available for that given locality: "P" = photographs only; "S" = skins only; "V" = tape-recordings only; "T" tissues only; "S,V" = skins and vocalizations only; "S,T" = skins and tissues only; "C" = tape-recordings, skins, and tissues. Dashed lines delimit main lineages recovered by a molecular phylogeny and interpreted as natural populations as follows: A = *multostriatus*, B = *cardosoi*, C = *probatus*, D = *gyldenstolpei*, E = *sanus*, and F = *procurvoides*. The question mark denotes an area between the Branco and Negro rivers where the taxonomic identity of any taxon of *C. procurvoides* is unknown.

Acknowledgments.— We thank the curators and curatorial assistants of the following collections for allowing us to use skins, tissues, and vocal recordings under their care: AMNH, ANSP, BLNS, CM, COP, FMNH, INPA, LSUMZ, MCZ, MLS, MN, MZUSP, NHMW, NR, UMMZ, USNM, and ZMB. M. A. Raposo (through CNPq grant# 479049/2006-8) kindly sent us high resolution digital pictures of the type specimen of nominate *procurvoides* deposited at the MCZ. S. Dantas and B. M. Whitney generously allowed us to analyze recordings from their personal archives. M. Ferreira and L. J. dos Anjos provided assistance in designing some figures presented in this study. Field and laboratory work related to this study was funded through the following agencies and institutions: CI-Brazil, WWF-Brazil, MMA, CNPq (#476212/2007-3, 490387/2007-1, "INCT em Biodiversidade e Uso da Terra da Amazônia" # 574008/2008-0, "Evolução da Fauna de Vertebrados Terrestres Brasileiros do Cretáceo ao Presente: Paleontologia e Filogenia" # 565046/2010-1, and 471342/2011-4), FMNH Marshall Funds, and NSF (DEB-0515672, DEB-0543562, and DEB-01120054). AA is supported by a productivity fellowship from CNPq. DNA sequencing for this project was carried out in part at the Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution, operated with support of the Pritzker Foundation.

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Capítulo 2

A new species of *Campylorhamphus* (Aves: Dendrocolaptidae) from the Tapajós – Xingu interfluve in Amazonian Brazil

Publicado como: **Carlos Eduardo B. Portes**, Alexandre Aleixo, Kevin J. Zimmer, Andrew Whittaker, Jason D. Weckstein, Luiz Pedreira Gonzaga, Camila C. Ribas, John M. Bates, and Alexander C. Lees. A new species of Campylorhamphus (Aves: Dendrocolaptidae) from the Tapajos- Xingu interftuve in Amazonian Brazil. In: J. del Hoyo, Bret, W. (Eds)., Hand Book of the world, Special Edition. Lynx Edicions, Barcelona, Spain.

The difficulty in visually separating the Amazonian endemic Curve-billed Scythebill *Campylorhamphus procurvoides* from the sympatric taxa grouped under the more widespread Red-billed Scythebill (*C. trochilirostris*), both in the hand and in the field, is notorious among ornithologists working in the Neotropics. J. T. Zimmer (1934) listed several morphological characters separating these two polytypic species, and he was the first to classify the different *Campylorhamphus* taxa occurring in lowland Amazonia as either *C. procurvoides* or *C. trochilirostris*, according to the theoretical background of the Biological Species Concept (BSC). Over the next 76 years, Zimmer's taxonomic treatment of *C. procurvoides* and *C. trochilirostris* has been followed without change (e.g, Todd 1948, Peters 1951, Ridgely and Tudor 1994, Marantz et al. 2003), despite some qualitative evidence indicating that some taxa grouped under *C. procurvoides* (the so called *multostriatus* group) are in fact vocally and morphologically more similar to *C. trochilirostris* (Marantz et al. 2003).

More recently, two of us (AW and KJZ) noticed that even the *multostriatus* group was vocally heterogeneous, with birds from the Carajás region of south-eastern Amazonian Brazil singing very differently from birds found across the Xingu River. Consistent with this finding, a molecular phylogeny, based on mitochondrial DNA data, showed that the two populations separated by the Xingu River and attributed to *multostriatus* are not each other's closest relatives, with birds from the eastern bank (labeled as *C. p. multostriatus*) appearing outside the core Amazonian *Campylorhamphus* clade with unresolved affinities within the genus *Campylorhamphus* (Fig. 1). In contrast, populations from the west bank of the Xingu (labeled in Fig. 1 as the new taxon described herein) grouped with strong support and were vocally close to *probatus* from the neighboring Madeira – Tapajós interfluve, with those two groups clustering together as sisters of *C. trochilirostris* (Fig. 1).

As shown below, birds found between the west bank of the Xingu and the east bank of the Tapajós rivers are morphologically and genetically diagnosed from all remaining *Campylorhamphus* taxa, including those in the closely related *probatus*. However, due to their overall plumage similarity, historically they have all been treated under the name *multostriatus*, which in fact applies only to birds from the Xingu – Tocantins interfluve (Snethlage 1907; Figs. 1 and 2). Therefore, since no valid name is applicable to birds from the fully diagnosable population in the Tapajós – Xingu interfluve, we propose to name these as:

Campylorhamphus cardosoi **sp. nov.**

Tapajós Scythebill

arapaçu-do-tapajós (Portuguese)

Illustrated: Hilary Burn

Holotype.— Museu Paraense Emílio Goeldi (MPEG) 63875, skin, adult female, skull 85% ossified, no bursa of fabricius; 38 g; ovary 7 x 4 mm with ova minute; oviduct convoluted; little fat and tail molt. Collected (shot) in the understory of upland (*terra-firme*) forest by AA on 22 November 2007 at Floresta Nacional de Altamira, municipality of Altamira, Pará, Brazil (06° 04'S; 55° 19'W); prepared by Fabíola Poletto under field number TM 002. Pectoral muscle tissue preserved in approximately 96% alcohol; field number TM 002. Hologenetype (Chakrabarty 2010) sequences of the mitochondrial genes cytochrome *b* (1,048 pb) and NADH subunit 2

(1,041bp) deposited in GenBank (accession numbers KC237254 and KC242876, respectively).

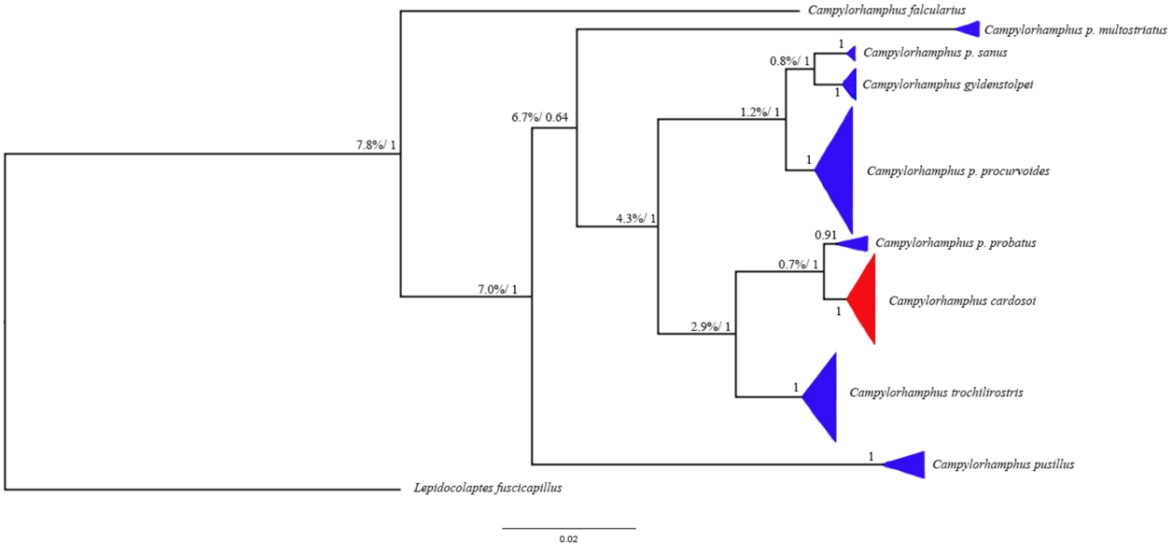

Figure 1 -Bayesian estimate of the phylogeny of the genus *Campylorhamphus* based on two mitochondrial genes (cyt *b* and ND2). Numbers refer to posterior probability values and genetic distances (% of average uncorrected *p* sequence divergence) between sister groups associated with the labeled nodes. Note the polyphyly of taxa currently grouped under *C. procurvoides* (*multostriatus*, *probatus*, *procurvoides*, and *sanus*) and the new taxa *cardosoi* and *gyldenstolpei* described in this volume.

Diagnosis: Morphology.— Alphanumeric color designations determined through direct comparison with Smithe (1975). Phenotypically, the new species can be unambiguously assigned to the genus *Campylorhamphus* (Dendrocolaptidae) based on its narrow, long, and curved bill, which readily characterizes the genus. Within *Campylorhamphus*, it is morphologically similar to the phylogenetically distant taxon *multostriatus* (Fig. 1) but distinguished from it by the following features: 1) reddish-brown maxilla, the latter distinctly blackish in live or recently collected *multostriatus* specimens; 2) much narrower dorsal streaks typically not extending all the way onto the lower back; and 3) whiter rather than buffier pectoral streaks, resulting in the blackish edge of the buffy-yellow pectoral streaks being conspicuously more contrasting than in *multostriatus*. A secondary effect easily observed when the pectoral (and to a lesser extent the dorsal) streaks of *cardosoi* and *multostriatus* are compared, is that in *cardosoi* the contrasting blackish edge is visible along the edges and towards the tip of each individual stripe, whereas in *multostriatus* they are usually barely visible and only along the edges, resulting in *multostriatus* having pectoral streaks not acutely shaped as in *cardosoi*. From the remaining taxa currently grouped in the “*procurvoides*” group (*gyldenstolpei*, *procurvoides*, and *sanus*; see Fig. 1), *cardosoi* is diagnosed by significantly bigger and more cylinder-like buffy pectoral streaks, with more pronounced black edges and a Raw Amber 223 belly (vs. Cinnamon-

Brown-33 or Russet-34). From its sister taxon *probatus*, *cardosoi* can be unambiguously diagnosed by a conspicuously contrasting blackish head, significantly broader head and pectoral spots, mantle covered with longer and broader buffy-whitish streaks (vs unmarked), and significantly shorter tarsi (Fig. 3; Table 3 in SI). ***Voice.***— The loudsong is immediately distinguished in the field and in spectrographic analysis from those of all other members of the polytypic *C. procurvoides*, except *probatus*, by the shape and syntax of the notes (described below; see Figs. 4 and 5). Along with *probatus*, *cardosoi* is the only taxon in the polytypic *C. procurvoides* possessing E note types (characterized by a typical bell shape; Fig. 3e) in its loudsong, followed by a sequence of C note types (Fig. 5e,f). No clear-cut differences could be detected between the loudsongs of *cardosoi* and *probatus*, but there is a tendency for the first note (C type) to be higher in frequency in *probatus* than *cardosoi*. Furthermore, loudsong pace tends to be faster in *cardosoi* than in *probatus*. ***Genetic divergence.***— Separated from its sister taxon *probatus* by approximately 0.7 % sequence divergence in the mitochondrial genes cytochrome *b* and NADH subunit 2 (Fig. 1). Based on these genes, both *cardosoi* and *probatus* diverge from their sister group (*C. trochilirostris*) by 2.9% and from the remaining taxa in the polytypic *C. procurvoides* by ca. 4.3% (Fig. 1).

Distribution — *Campylorhamphus cardosoi* has been documented from several localities in the Tapajós-Xingu interfluve (i.e. Tapajós area of endemism; *sensu* Silva et al. 2005) in the Brazilian states of Pará and northern Mato Grosso. Its distribution is thus bounded to the north by the Amazon River, to the east by the Xingu River and to the west by the Tapajós River. The southern limit of the species range is unclear. The southernmost records come from *terra firme* forest on both banks of the middle Teles Pires River (Zimmer et al. 1997) but the species was unrecorded from transitional white sand forest 90 km south of there (Lees et al. 2008), a vegetative physiognomy that may mark the species' distributional limit.

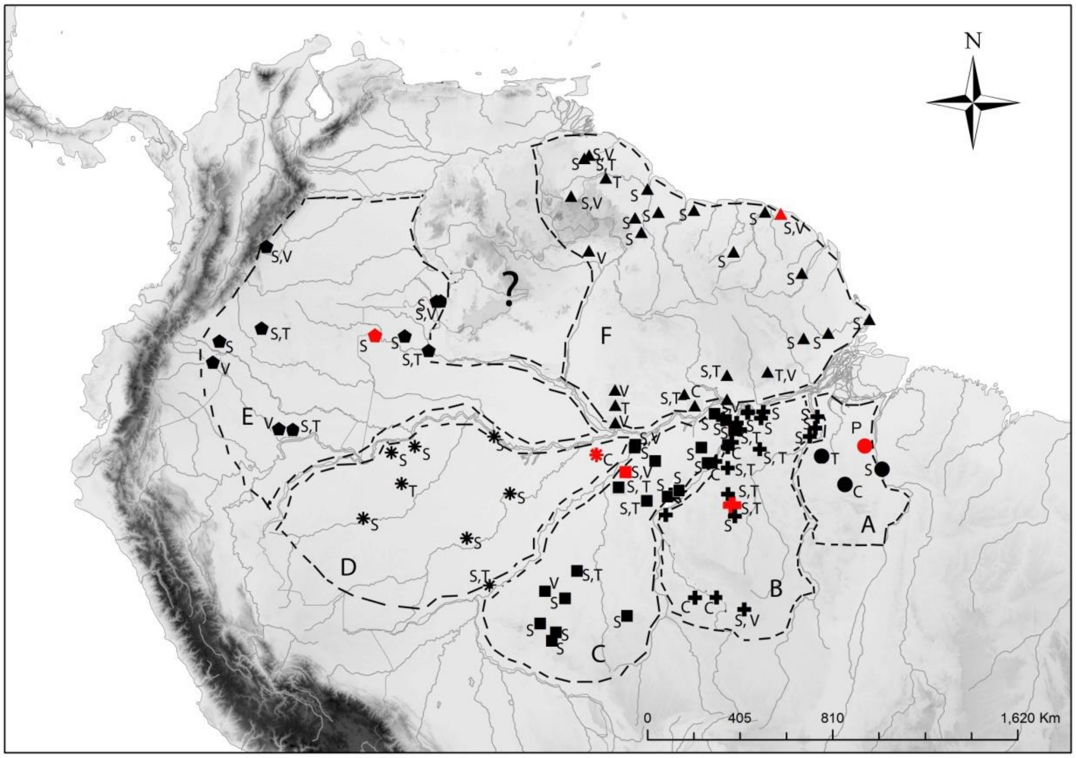

Figure 2 - Geographic distribution of specimens, vocalizations, and tissues of *Campylorhamphus procurvoides* taxa analyzed in this study. Asterisks = *C. gyldenstolpei*; circles = *C. p. multostriatus*; crosses = *C. cardosoi*; triangles = *C. p. procurvoides*; squares = *C. p. probatus*; and pentagons = *C. p. sanus*. Type localities for each individual taxon are shown as red symbols. Letters next to a symbol represent material available for that given locality: "P" = photographs only; "S" = skins only; "V" = tape-recordings only; "T" tissues only; "S,V" = skins and vocalizations only; "S,T" = skins and tissues only; "C" = tape-recordings, skins, and tissues. Dashed lines delimit main lineages recovered by a molecular phylogeny and interpreted as natural populations as follows: A = *multostriatus*, B = *cardosoi*, C = *probatus*, D = *gyldenstolpei*, E = *sanus*, and F = *procurvoides*. The question mark denotes an area between the Branco and Negro rivers where the taxonomic identity of any taxon of *C. procurvoides* is unknown.

Description of holotype — See color illustration. Alphanumeric color designations determined through direct comparison with Smithe (1975). Plumage fresh and unworn, tail in molt; skull 85% ossified. Forehead, lores, crown and upper neck black covered with buff streaks. Cheeks Dark Brownish Olive (129) heavily covered with buff streaks of varying lengths. Mantle Dark Brownish Olive (129), with conspicuous buff streaks possessing a contrasting black edge, gradually turning thinner and obsolete towards the lower back. Primaries, secondaries, and wing coverts unmarked and Warm Sepia (221A) in color. Tips and inner webs of primaries with a contrasting Fuscous (21) tinge. Rump Warm Sepia. Rectrices essentially concolorous with lower rump. Tail graduated each rectrix with a stiff shaft, softer at the tips. Upper throat Dark Brownish Olive (129) heavily covered with broad whitish-creamy scaly-shaped spots, which become gradually smaller towards the lower throat and chest, resulting in a nearly mottled whitish-brownish lower throat and chest. Chest Dark Brownish Olive (129) covered with arrow-shaped Buff (124) streaks with thin but contrasting black edges. Upper belly Cinnamon-Brown (33), with some indistinct thin and rather long buff streaks. Lower belly concolor with upper belly, nearly unstreaked, with only a few indistinct buff streaks. Undertail coverts Cinnamon-Brown (33) with feathers having contrasting whitish shafts. **Soft parts in life**: Iris dark brown with a contrasting yellow-mustard eyering. Maxilla Burnt Orange (116) with a dark brownish wash around the nostrils; mandible Burnt Orange (116) getting blackish at the tip; tarsi and feet greenish-gray. **Measurements of holotype:** wing (86.9 mm), tail (91.9 mm), tarsus-metatarsus (18.5 mm), bill length (46.4 mm), bill height (5.6 mm), bill width (4.9 mm), average length of pectoral spots (10.7 mm), average width of pectoral spots (2.4 mm), average length of back spots (11.2 mm), average width of back spots (1.0 mm), average length of head spots (4.2 mm), and average width of head spots (0.9 mm).

Figure 3 - Ventral views of representative specimens illustrating plumage diagnoses between *Campylorhamphus cardosoi* and its sister species *C. probatus*. (A) Males; from left to right: first three *C. probatus* (MPEG 75591, MPEG 69627, MPEG 39677) and second three paratypes of *C. cardosoi* (MPEG 69378, MPEG 51427, MPEG 65687). (B) Females; from left to right: first three *C. probatus* (MPEG 57584, MPEG 64133, MPEG 37033) and second three holotype (MPEG 63875) and paratypes (MPEG 69002 and MPEG 63454) of *C. cardosoi*. Note the characteristic broader pectoral streaks of *C. cardosoi*, which had until now been regarded as belonging to taxon *multostriatus* based on overall appearance and similarities in streaks widths, while sister *C. probatus* is closest plumage to the distantly related *C. procurvoides*. Photos: Alexander C. Lees.

Etymology.— We are pleased to name the new species after the our colleague José Maria Cardoso da Silva whose biogeographic studies led to the subdivision of the former Pará center of endemism (*sensu* Cracraft 1985) into the Tapajós and Xingu centers of endemism (Silva et al. 1995, 2002, 2005). The new species described herein was formerly lumped with a distantly related taxon, and both were treated under the same subspecies name (*C. p. multostriatus*), and thought to be endemic to the Pará center of endemism. Our studies, on the other hand, showed that they are only distantly related evolutionary units, each endemic to a distinct interfluve within the former Pará center of endemism, thus supporting Silva's treatment of separating this center of endemism into two: the Tapajós and Xingu centers of endemism (Silva et al. 2002, 2005).

REMARKS

Type series.— The allotype of *C. cardosoi* is MPEG 51427, skin, adult male, testes 9 x 5 mm, no molt; netted in the understory of *terra-firme* forest by a MPEG team on 9 December 1993 at Mato Grosso; Alta Floresta, left bank of Teles Pires River, ca. 7 km above the mouth of the Cristalino River; prepared by Dionísio C. Pimentel Neto under field number JH 444. Paratypes of *C. cardosoi* are the following four specimens: MPEG 63454: skin, adult female, ovary 7 x 4 mm; oviduct straight; collected (netted) in *terra-firme* forest on 7 November 2007 by a MPEG tem at Pará; left bank of the Xingu River, Arroz Cru, Igarapé de Maria; prepared by Manoel Santa Brígida under field number BMP 009; tissue sample deposited at MPEG and mitochondrial cytochrome *b* and NADH subunit 2 sequences deposited in GenBank (KC237257 and KC242879, respectively). MPEG 65687: skin, male, apparently immature; testes 2 x 1 mm; netted by Marcos Pérsio D. Santos and M. Villegas at Pará; Jacareacanga, Floresta Nacional do Crepori, Cocho River, on 1 August 2008; tissue sample deposited at MPEG under field number MPDS 1315; mitochondrial cytochrome *b* and NADH subunit 2 sequences deposited in GenBank (KC237258 and KC242880, respectively). MPEG 69378: skin, adult male, gonads not measured; collected by Marcos Pérsio D. Santos and team at Mato Grosso; Paranaíta, left bank of Paranaíta River, Fazenda Aliança (09º34'S; 56º42'W) on 29 September 2009; tissue sample deposited at MPEG under field number TLP(A) 314; mitochondrial cytochrome *b* and NADH subunit 2 sequences deposited in GenBank (KC237260 and KC242882, respectively). **Variation in the type series**: No apparent sexual dimorphism exists in plumage. The most noticeable variation in the type series pertains to the overall plumage brightness, with MPEG 51427 and 69378 from northern Mato Grosso having drabber under and upperparts than the remaining specimens in the type series from further north in Pará. Apparently, this variation has no seasonal or ontogenetic basis, since the type series includes adult and immature specimens collected between August and December, with the drabber adult Mato Grosso specimens collected in September and December. Thus, unless future studies show a significant genetic subdivision between northern and southern populations of *C. cardosoi* (which is not apparent in Fig. 1), it is more likely that plumage brightness has an individual basis that could possibly be explained by individual differences in the amount of wear due to individual differences in foraging and roosting, for example. The only apparent immature specimen of the type series (inferred as such based on gonad size data) has a visibly shorter culmen, wing, and tail than the adult specimens, but plumage is essentially undifferentiated.

Ecology and behavior.— *Campylorhamphus cardosoi*, like other members of the genus, forages alone or in pairs in the understory and midstory of *terra firme* forest, often along creeks (venturing occasionally into adjacent seasonally flooded forests), and virtually always forages in association with mixed-species flocks and, occasionally, army antswarms passing through its territory. It is known to show a strong affinity for *Guadua* sp. bamboo thickets, or vine tangles e.g. around Alta Floresta (Zimmer et al. 1997), and is probably largely dependent on structurally complex forest microhabitats within primary forest. Individuals typically forage by hitching along tree trunks, where they glean for arthropods from the surface or underneath the bark and they may also use their long bills to procure prey items in dead bamboo shoots and tree trunks. Populations may not be temporally stable: periodic disappearances have been reported from well-inventoried sites (e.g. Zimmer et al. 1997), which may be associated with periodic large-scale *Guadua* die-offs. Its nest and eggs remain unknown.

Vocalizations.— When compared to loudsongs of other taxa in the polytypic *C. procurvoides*, the loudsong type shared by *cardosoi* and *probatus* is unique in the shape and syntax of the notes. The syntax of the loudsong in *cardosoi* typically begins with a single introductory E note, followed by a series of 12-33 C notes (N = 24, Figs. 4 and 5e), being very close to that of *probatus* (1 E followed by 12-29C; N = 16, Figs. 4 and 5f). There is a tendency for the first loudsong note (C type) to be higher in frequency in *probatus* than *cardosoi*, and the two taxa also tendency to differ in traits such as pace and change in pace. Among members of the polytypic *C. procurvoides*, both *cardosoi* and *probatus* also uniquely share a distinct vocal type that we name the “long-call”, consisting of a long series of C-type notes gradually rising in frequency towards the middle part of the vocalization, then stabilizing for a variable amount of time, before gradually descending (Fig. 6). The number of “long-call” notes is highly variable, but tends to average higher in *probatus* (40; range 28-63; N = 8) than *cardosoi* (35; range 10-57; N = 12).

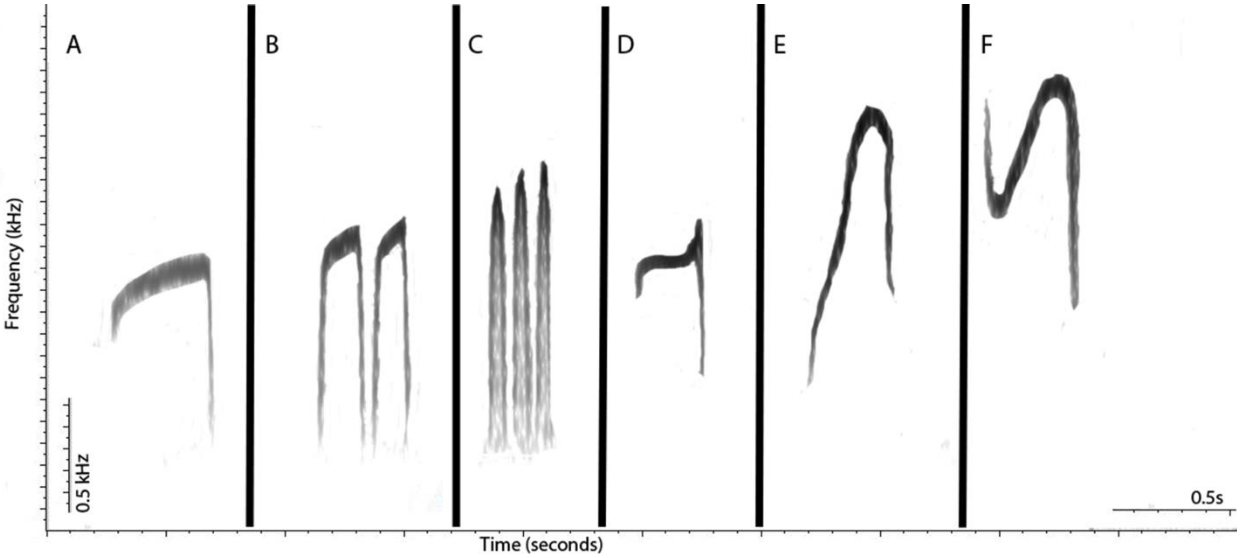

Figure 4 - Representative spectrograms of note-types used to diagnose the loudsongs of taxa currently grouped under the polytypic *Campylorhamphus procurvoides*. Letters refer to the note-type nomenclature used in this study. Notes A, B, and D are restricted to the so called "*procurvoides*" group (sensu Marantz et al. 2003; which includes the new taxon *gyldenstolpei*, described in this same publication). Note E is uniquely shared by *cardosoi* and *probatus*, whereas F notes are unique to *multostriatus* from the Xingu – Tocantins interfluve.

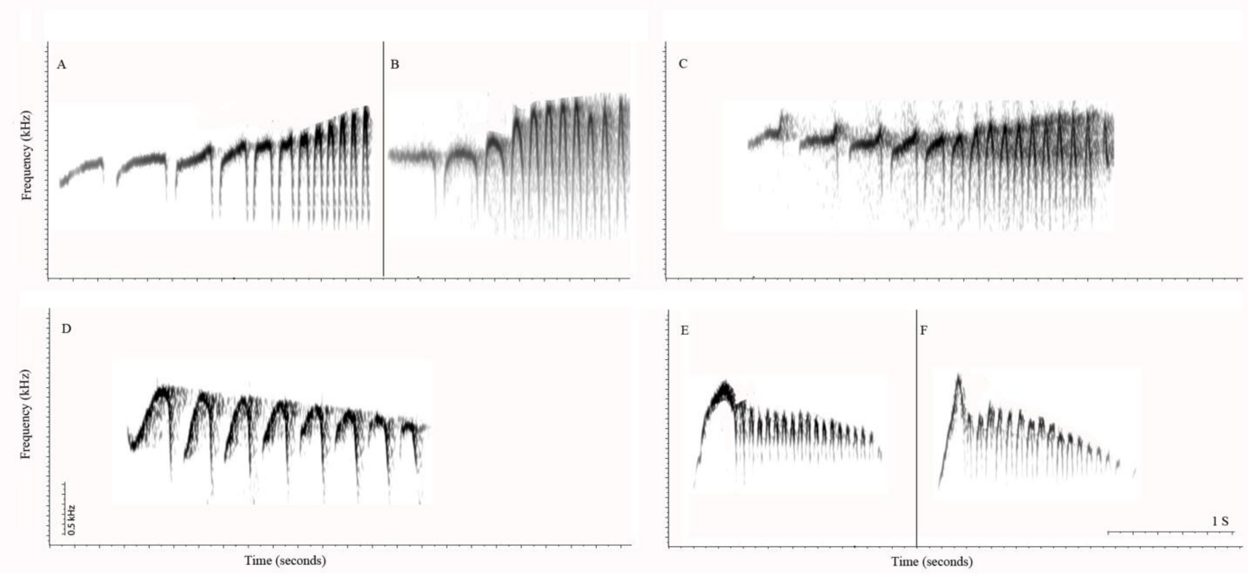

Figure 5 - Representative spectrograms of loudsongs of taxa currently grouped under the polytypic *Campylorhamphus procurvoides* and the new taxa described herein: A) *procurvoides*: Venezuela, Rio Grande, El Palmar (LNS-65702_2c); B) *sanus*: Venezuela, Amazonas, San Carlos (LNS-65706_6); C) *gyldenstolpei*: Brazil, Amazonas, Tupana Lodge (AW3B3_2b); D) *multostriatus*: Brazil, Pará, Salobo Road, Carajás (AW5A2_10); E) *cardosoi*: Brazil, Mato Grosso, Alta Floresta, Rio Cristalino (LNS-106114_24b); and F) *probatus*: Brazil, Amazonas, Borba, eastern bank of the Madeira River (LNS-127698_3b).

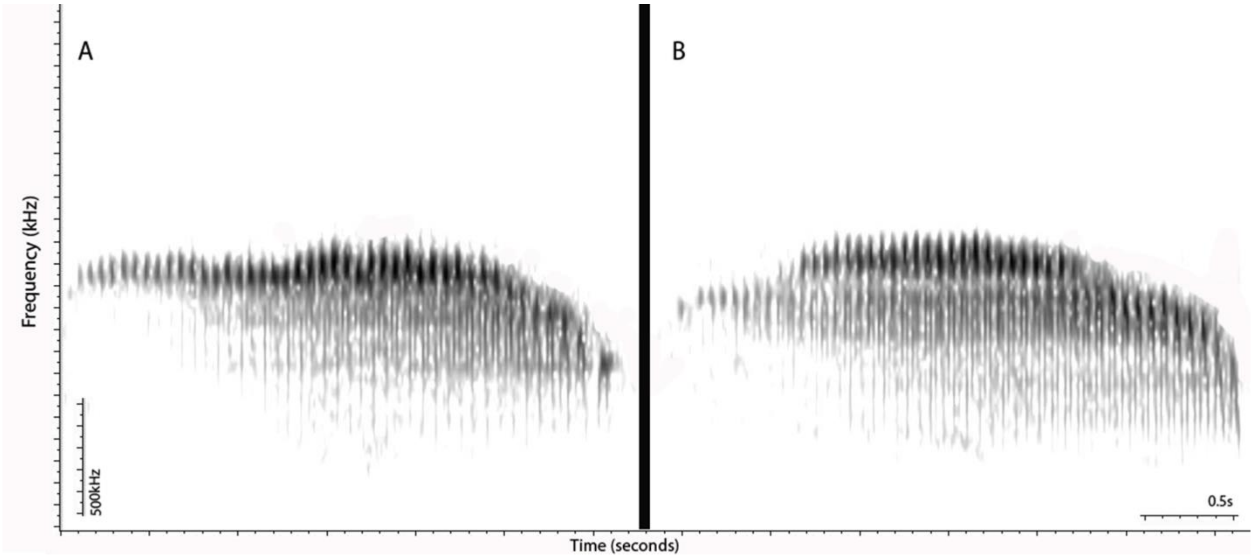

Figure 6 - Representative spectrograms of "longcalls" of *cardosoi* (A; Brazil, Mato Grosso, Cristalino Lodge; KJZ 634B0000_2b) and *probatus* (B; Brazil, Amazonas, Borba, eastern bank of the Madeira River; LNS-127699_3e).

Phylogenetic relationships.— DNA sequence data for the mitochondrial genes cytochrome *b* (cyt *b*, 1048 bases pairs) and NADH subunit 2 (ND2, 1041 bases pairs) were obtained for 41 individuals (see Table 4 in the SI file for a list of specimens sequenced) of all species in the genus *Campylorhamphus*, including all taxa currently grouped under the polytypic *C. procurvoides* (sensu Marantz et al. 2003; i.e., *multostriatus*, *probatus*, *procurvoides*, and *sanus*), and *C. gyldenstolpei* (Fig. 1). Trees were rooted on *Lepidocolaptes fuscicapillus*, which is one of the sister genera of *Campylorhamphus* (Derryberry et al. 2011). The phylogeny obtained with Bayesian inference strongly supports that *C. procurvoides*, as currently defined, represents a polyphyletic species, with taxa currently classified as subspecies of *procurvoides* found in three separate clades with disparate phylogenetic affinities (Fig. 1). The three highly supported and reciprocally monophyletic clades that group taxa currently classified as subspecies of the polyphyletic *C. procurvoides* are as follows: (1) birds occurring south of the Amazon and east of the Xingu River in the Xingu center of endemism (Silva et al. 2005; corresponding to the taxon *multostriatus*, whose type locality lies in this area of endemism; Fig. 2); (2) birds found south of the Amazon and west of the Madeira rivers (in the Inambari center of endemism, corresponding to the other new *Campylorhamphus* taxon described in this same publication, i.e. *gyldenstolpei*) and birds distributed north of the Amazon, which correspond to the taxa *sanus* (found in the Napo and Imeri areas of endemism) and *procurvoides* (corresponding to the Guiana area of endemism; Fig. 2); and (3) birds found south of the Amazon and between the Madeira and Xingu rivers, corresponding to the taxa *probatus* (distributed in the Madeira center of endemism; Fig. 2) and *cardosoi*, endemic to the Tapajós area of endemism; Figs. 1 and 2). Since *C. multostriatus* appears to be the sister group to all remaining taxa grouped until now in *C. procurvoides* and *C. trochilirostris*, and the clade C. *probatus* / *cardosoi* was recovered with high statistical support as sister to *C. trochilirostris* (Fig. 1), the *C. procurvoides* complex cannot include *C. multostriatus*, *C. probatus*, and *C. cardosoi* (see also the *C. gyldenstolpei* account above). The fact that the Bayesian phylogeny recovered *multostriatus*, *probatus*, and *cardosoi* as reciprocally monophyletic taxa with strong statistical support (Fig. 1) in conjunction with morphological and (in the case of *multostriatus*) vocal diagnoses of these taxa, support their recognition as valid species level taxa (De Queiroz 2007) as follows: Snethlage's Scythebill (*C. multostriatus*; distributed in the northern portion of the Xingu - Tocantins interfluve (lineage A in Fig. 2); Rondonia Scythebill (*C. probatus*; distributed in the Madeira - Tapajós interfluve (lineage C in Fig. 2); and Tapajós Scythebill (*C. cardosoi*; distributed in the Tapajós - Xingu interfluve (lineage B in Fig. 2).

Conservation — *Campylorhamphus cardosoi* is generally uncommon but it can be locally common in its preferred habitats (e.g., vine tangles near forest creeks). It occurs in several conservation units, e.g. Floresta Nacional dos Tapajós (Henriques et al., 2003); Parque Estadual do Cristalino and RPPN Cristalino (Zimmer et al. 1997); the Reserva Biológica Nascentes da Serra do Cachimbo (Santos et al. 2011); Parque Nacional do Jamanxin and Floresta Nacional de Altamira (AA pers. obs. and specimens deposited at MPEG). Nevertheless, it has one of the most restricted global populations of any species in the genus *Campylorhamphus*, being endemic to one of the most heavily anthropogenically affected parts of Amazonia (the Tapajós area of endemism) which has already lost 25% of its primary forest cover (Vale et al. 2008). This species is restricted to primary forest habitats and although it does appear to tolerate light selective-logging, it was not found in burnt primary forest nor secondary forest during an extensive survey around Santarém (A. C. Lees et al. unpublished data). Much of this species' distribution is threatened by the expanding agricultural frontier (particularly cattle ranching and soybean plantations) and hydroelectric schemes; these and other infrastructure improvements (such as road-paving) may catalyze forest loss and hence imperils this and many other endemic *terra-firme* species within the interfluve unless adequate government controls on deforestation are enforced. Based on past and predicted future forest loss, fragmentation and degradation within this species limited range (cf. Bird et al. 2012) this species is likely to qualify for Vulnerable status on the IUCN Red List and the Brazilian National List of Endangered Species, currently under revision.

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Appendix 1 - **Supporting Information for the description of *Campylorhamphus gyldenstolpei* and *Campylorhamphus cardosoi***

***Morphometric and plumage analyzes* —** We measured morphometric and plumage characters of 176 specimens of known taxa grouped under the polytypic *Campylorhamphus procurvoides* deposited in the following museums: American Museum of Natural History, New York (AMNH), Carnegie Museum of Natural History, Pittsburgh (CM), Colección Ornitológica Phelps, Caracas, Venezuela (COP), Field Museum of Natural History, Chicago (FMNH), Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA), Museum of Natural Science, Louisiana State University, Baton Rouge (LSUMZ), Museu Nacional, Rio de Janeiro, Brazil (MNRJ), Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP), Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG), Naturhistoriska Riksmuseet, Stockholm, Sweden (NR), and University of Michigan Museum of Zoology (UMMZ) (Tables 1 and 2). An additional six *C. procurvoides* specimens were visually inspected and photographed at the Naturhistorisches Museum, Vienna, Austria (NHMW) and Naturhistorisches Forschunginstitut, Museum für Naturkunde, Zentral Institut der Humboldt-Universität zu Berlin, Berlin, Germany (ZMB). We directly examined holotypes of all *C. procurvoides* taxa, except for nominate *procurvoides*, which was studied through high resolution digital pictures generously provided by M. A. Raposo. We tried to exclude from the morphometric analyzes as many immature specimens as possible. To this end, we regarded as immature those specimens whose label explicitly contained some age-related data (percentage of skull ossification or presence of the bursa of Fabricius); whenever age-related data was not available, specimens with unusually short bills and tails were assumed to be immature (Marantz et al. 2003). When not directly taken from original labels, locality coordinates of the specimens examined were determined with the aid of ornithological gazetteers available for South American countries (Paynter and Traylor 1981, 1991, Paynter 1992), and Brazilian Amazonia (Oren 1999). All localities obtained were plotted on a map using the ArcView GIS 3.3 software (ESRI 2002; Figure 4). **Characters analyzed**: Our analyses were based on morphometric as well as continuous and discrete plumage characters. For each specimen examined, we measured with a Mitutoyo© digital caliper to the nearest 0.01 mm or counted the following morphometric and continuous plumage characters: 1) wing length – flattened (hereafter abbreviated W); 2) tail length – from the rectrices' insertion into the pygostyle to their outermost tip (T); 3) tarsometatarsus length – from the tibia – tarsometatarsus articulation to the base of the hallux (TM); 4) culmen – from the anterior edge of nares to the tip of the bill (LB); 5) bill height - taken along the nares (BH); 6) bill width - taken along the nares (BW); 7) number of feather stripes within a 0.7 cm^2 square placed at the center of the breast (PS); 8) number of feather stripes within a 0.7 cm^2 square placed at the top of the head (HS), and 9) number of feather stripes within a 0.7 cm^2 square placed at the center of the back (BS). The following continuous plumage characters were obtained from measurements of five different randomly chosen feathers in the body part of interest: 10) average length of pectoral stripes (LPS); 11) average width of pectoral stripes (WPS); 12) average length of back stripes (LBS); 13) average width of back stripes (WBS); 14) average length of head stripes (LHS), and 15) average width of head stripes (WHS). Only two discrete plumage characters were systematically evaluated for each specimen examined: 16) head color (HC) and 17) black edge of pectoral, head, and dorsal stripes (BES), which was characterized as: a) absent; b) weakly contrasting, and 3) strongly contrasting.

General color designations for describing the plumage of the specimens analyzed followed Smithe (1975). **Statistical analyzes**: Since all continuous characters measured passed the Kolmogorov – Smirnov test of normality, only parametric tests were employed. Therefore, all continuous characters were tested for sexual dimorphism within any given taxon with the two-sample T-test; because a strong sexual dimorphism was detected for most morphometric characters in all taxa studied, when testing for differences among taxa and clades defined by the molecular phylogeny, only male specimens (for which a greater sample size was available) were considered, unless stated otherwise. Two-sample T-tests and One-way ANOVA were used to test for significant differences in all continuous characters measured among closely taxa of *C. procurvoides* as defined by the molecular phylogeny. When significant results were obtained with ANOVA, a Tukey HSD test was employed (Table 3). All tests were performed with the SYSTAT version 10.2 software (SPSS, 1998) at the 95% confidence level.

Vocal analyzes.— We analyzed of 393 bouts of loudsongs of 84 individuals, from 34 localities throughout the Amazon, belonging to all taxa currently grouped under the polytypic *Campylorhamphus procurvoides* (sensu Marantz *et al.* 2003) in addition to the new taxa *cardosoi* and *gyldenstolpei* described herein.

Samples used in vocal analysis: Numbers following the recordists' names identify the number of cuts per recordist per location.

Campylorhamphus cardosoi (24 recordings). **BRAZIL**: Mato Grosso: Reserva do rio Cristalino (A. Whittaker 1, K. Zimmer 10), Alta Floresta (A. Whittaker 1, K. Zimmer 2), rio Teles Pires (LNS - T. A. Parker 6); Pará: Pará (A. Aleixo 2), Parque Nacional do Jamanxim (A. Aleixo 1), Floresta Nacional de Altamira (A. Aleixo 1).

Campylorhamphus gyldenstolpei (8 recordings). **BRAZIL**: Amazonas; Tupana Lodge (A. Aleixo 2, A. Whittaker 5, K. Zimmer 1).

Campylorhamphus multostriatus (11 recordings). **BRAZIL**: Pará; Serra dos Carajás (S. Dantas 3, A. Whittaker 5, K. Zimmer 3).

Campylorhamphus probatus (16 recordings). **BRAZIL**: Pará; Juruti (A. Aleixo 1). Amazonas; Rio Roosevelt (A. Whittaker 9), right bank of Madeirinha river (A. Whittaker 3), Borba, right bank of the Madeira river (LNS – C. A. Marantz 3).

Campylorhamphus procurvoides (21 recordings). **BRAZIL**: Pará (A. Aleixo 1), Almerim, REBIO Maicuru (A. Aleixo 1). Amazonas; Manaus (A. Whittaker 3), Presidente Figueiredo, Cachoeira da Iracema (A. Whittaker 3), Rodovia de Balbina, Fazenda Salto do Ype (A. Whittaker 1). VENEZUELA: Venezuela: Bolivar; Rio Grande, El Palmar (LNS - P. Schwartz 8). **FRENCH GUYANA:** (A. Whittaker 2). **GUYANA**: Essequibo (LNS – D. Finch 2).

Campylorhamphus sanus (4 recordings). **ECUADOR**: Cuyabeno (B. M. Whitney 1). PERU: Sucusari Camp (B. M. Whitney 1). **VENEZUELA**: Amazonas; San Carlos, Rio Negro, Isla Cigarron (LNS – P. Schwartz 2).

Vocalizations were categorized as 'loudsongs' and 'calls' (*sensu* Willis 1967) through auditory and visual comparisons of spectrograms. Loudsong and call frequency measurements were made using audiospectrograms. The syntax and note structure (sensu Isler et al. 1998) were analyzed qualitatively through a blind inspection and grouping of printed sonograms followed by an assessment of whether the groupings matched the populations under study. Audiospectrograms and all song and call measurements were carried out using the Raven Pro 1.3 (Cornell Laboratory of Ornithology, Ithaca, NY) with all vocalizations digitized at a sample rate of 44.1 kHz and 16 bits in the mono pattern.

Molecular analyzes*.— Taxa sequenced:** We sequenced all known taxa grouped under the polytypic *Campylorhamphus procurvoides* in addition to the new taxa *cardosoi* and *gyldenstolpei* described herein (29 specimens; Table 4). We sampled at least one specimen of all remaining *Campylorhamphus* species, including most taxa grouped under *C. trochilirostris* (8 specimens belonging to *devius*, *notabilis*, *lafresnayanus* and *major*; Table 4). Due to the close relationship between the genera *Campylorhamphus* and *Lepidocolaptes* in Dendrocolaptidae (Aleixo 2002, Irestedt *et al*. 2004; Claramunt *et al.* 2010; Derryberry *et al.* 2011), we used *L. albolineatus* sequences available in GenBank as the outgroup in our analyzes (Table 3). **DNA sequencing:* Standard methods were used to extract, isolate, amplify and sequence mitochondrial genes. Total genomic DNA was extracted from frozen or ethanol preserved tissue samples (n = 38) and dry skin patches or feathers extracted from museum specimens (n = 2) using a Qiagen tissue extraction kit or a standard phenol/chloroform method (Hillis *et al.* 1990). We obtained sequences of the mitochondrial genes cytochrome *b* [1076 pb, primers L14841 (Kocher *et al.* 1989) and H16065 (Helm-Bychowski and Cracraft 1993)] and NADH dehydrogenase subunit 2 – ND2 [1041 pb, primers L5215 and H6313 (Johnson and Sorenson 1998, Sorenson et al.1999)]; for the amplification of more degraded DNA from the dry skin patches and feathers, the following internal primers developed by JDW and CEBP were used: Lwood2 (CGTAACCTCCAYGCAAACGGAGCC), Lwood3 (GGRGGATTCTCAGTAGACAACCC), Lwood4 (GGTGTACTAGCTATATTCTCACC), Lwood5 (CCTATTCCTAGTCCCATTCCTCC), Hwood1 (GCCTCGTCCGATGTGGAGG), Hwood2 (GGAAGTGTAGGGCRAAGAATCG), Hwood3 (GGAGGGGTTACTAGTGGGTTTGCAGG), and Hwood4 (GGGGRCGRAARGTTATTGTTCG). All primer numbers refer to the 3' base of the published chicken mtDNA sequence (Desjardins and Morais 1990). Fragments were PCR amplified using standard conditions available upon request. A small aliquot of each amplification was electrophoresed on agarose gel to check for the correct fragment size and to ensure that only a single amplification product was obtained. Amplification products were cleaned with a Qiagen PCR purification kit and cycle-sequenced using a Big Dye Terminator kit (Perkin Elmer, Norwalk, Connecticut), and all amplification primers listed above. Cycle sequencing reactions were NH_4OAC precipitated, dried, resuspended in a formamide EDTA, and run on ABI 3130 and 3730 DNA sequencing machines. We aligned and reconciled sequences from both strands within and between species using Sequencher 3.1.1 (Genecodes, Madison, Wisconsin). The following measures outlined by Sorenson and Quinn (1998) and Bates et al. (1999) were taken to ensure that the DNA fragments amplified were accurate and of mitochondrial origin (not pseudogenes): (1) most sequences were amplified in large fragments (> 1,000 bp); (2) both DNA strands were sequenced; (3) sequences were aligned with the chicken complete mtDNA sequence, and inspected for insertions, deletions, and stop codons that would result in a nonfunctional protein; and (4) sequences were expected to exhibit high transition to transversion substitution ratios characteristic of mitochondrial, not nuclear substitution patterns. **Phylogenetic analyzes:** We performed a Bayesian inference (hereafter BI) of phylogeny using the MrBayes software, version 3.1.2 (Ronquist and Huelsenbeck 2003). Evolutionary models for BI were selected by MrModeltest2.3 (Nylander 2004), under the Bayesian information criterion (BIC). Bayes factors (referred to as BF) were employed to determine the optimal number of partitions to be used in the BI. Convergence for all parameters was assessed by evaluating whether stationarity was reached by the Markov chain using the Tracer v1.4.1 software (Rambaut and Drummond 2007). BI were run with two heated chains for 20 million generations, with resulting trees and parameters being sampled every 1000 generations. We discarded the first 2 thousand generations as “burn-in” after finding that stationarity was reached well before this number in each run. To assess the clades’ nodal support, we used the remaining 4001 sampled trees to calculate posterior probabilities.

Table 1 – Body measurements (in millimeters) of taxa currently grouped under the polytypic *Campylorhamphus procurvoides* (*sensu* Marantz et al. 2003) in addition to the new taxa *cardosoi* and *gyldenstolpei* described herein. Mean values with corresponding standard deviations in parentheses are shown, along with the number of specimens measured for each sex. The only two females of *multostriatus* measured were excluded from this table. See text for character abbreviations. Number in parentheses after the sex refer the total of the specimens measured.

Taxon	*procurvoides*		*sanus*		*gyldenstolpei*		*cardosoi*		*probatus*		*multostriatus*
Character	Male (25)	Female (14)	Male (17)	Female (6)	Male (10)	Female (4)	Male (30)	Female (20)	Male (23)	Female (13)	Male (4)
Wing Length	95.59 (4.17)	92.03 (2.84)	92.35 (3.52)	91.46 (3.30)	96.73 (3.07)	95.84 (3.28)	94.50 (3.75)	90.88 (2.64)	95.14 (2.94)	92.03 (2.80)	95.44 (1.79)
Tail Length	93.65 (6.01)	89.61 (5.47)	87.83 (4.52)	88.30 (4.78)	93.24 (2.81)	90.26 (3.24)	93.34 (5.30)	89.31 (6.52)	91.54 (3.94)	87.40 (5.89)	93.39 (4.66)
Tarsometatarsus	19.15 (0.96)	19.22 (1.36)	18.52 (1.04)	18.54 (1.01)	18.95 (1.430	19.53 (1.16)	19.27 (1.20)	18.57 (1.41)	18.21 (0.91)	18.75 (1.21)	18.38 (0.80)
Length of Beak	52.22 (2.36)	51.32 (4.85)	48.52 (1.78)	49.02 (1.86)	53.22 (2.21)	54.31 (1.62)	50.79 (3.26)	50.94 (3.85)	51.62 (1.88)	53.27 (2.62)	52.48 (1.96)
Bill height	5.70 (0.42)	5.67 (0.29)	5.52 (0.18)	5.44 (0.32)	5.65 (0.22)	5.75 (0.27)	5.81 (0.78)	5.62 (0.28)	5.70 (0.25)	5.88 (0.99)	5.81 (0.41)
Bill Width	4.45 (0.37)	4.54 (0.23)	4.27 (0.30)	4.63 (0.31)	4.47 (0.43)	4.45 (0.20)	4.57 (0.33)	4.33 (0.34)	4.50 (0.33)	4.53 (0.32)	4.54 (0.42)
PS	5.28 (1.27)	4.71 (0.99)	5.58 (1.32)	5.50 (1.05)	5.50 (1.67)	5.40 (0.89)	5.05 (1.04)	5.40 (1.27)	5.00 (1.38)	5.15 (1.72)	5.25 (0.50)
HS	3.16 (0.76)	3.21 (0.89)	3.29 (0.85)	3.50 (0.83)	3.25 (1.42)	3.40 (0.89)	3.44 (0.86)	3.50 (1.10)	3.52 (0.89)	3.30 (1.03)	3.25 (0.50)
BS	0.76 (0.67)	1.14 (0.77)	1.70 (0.68)	1.50 (0.54)	1.00 (0.85)	1.4 (0.54)	1.91 (1.05)	2.00 (0.85)	1.47 (0.84)	1.46 (0.87)	2 (0.816)
LPS	8.21 (1.15)	8.16 (1.01)	7.46 (1.32)	8.18 (0.92)	8.55 (2.54)	9.67 (1.55)	11.35 (2.41)1	10.81 (1.66)	9.74 (1.16)	9.36 (0.93)	10.96 (0.29)
WPS	1.62 (0.32)	1.67 (0.30)	1.59 (0.16)	2.02 (0.21)	1.91 (0.37)	1.57 (0.38)	2.76 (0.60)	2.74 (0.44)	2.10 (0.33)	2.03 (0.29)	3.16 (0.46)
LBS	9.63 (1.82)	8.86 (1.56)	8.79 (0.96)	10.89 (3.47)	10.35 (1.36)	12.31 (1.35)	12.43 (1.66)	11.73 (1.70)	10.08 (1.36)	9.51 (0.88)	12.51 (1.29)
WBS	0.75 (0.15)	0.75 (0.17)	0.97 (o.40)	0.88 (0.20)	1.03 (0.17)	0.75 (0.19)	1.07 (0.36)	1.21 (0.35)	0.89 (1.47)	1.01 (0.26)	1.39 (0.35)
LHS	4.27 (0.96)	4.70 (0.90)	4.02 (0.45)	4.54 (0.78)	4.44 (0.45)	4.41 (0.87)	5.14 (0.98)	5.31 (0.98)	5.08 (1.15)	4.57 (0.75)	4.49 (1.14)
WHS	0.98 (0.24)	1.00 (0.17)	1.08 (0.12)	1.21 (0.24)	1.48 (0.27)	1.29 (0.16)	1.26 (0.24)	1.17 (0.23)	1.14 (0.197)	1.09 (0.16)	1.23 (0.25)

List of specimens examined in this study belonging to all known taxa currently grouped under the polytypic *Campylorhamphus procurvoides* (*sensu* Marantz et al. 2003) in addition to the new taxa *cardosoi* and *gyldenstolpei* described herein. Institution's acronyms are found in the text.

Campylorhamphus procurvoides. 40 specimens. **BRAZIL: Amapá:** Macapá, Amapari River, Igarape Novo, Iratapuru River 00º30'N,52º30'W (MPEG 16510, 17252, 20486, 29507, 29508, 59510); Araguari River 01º15'N,49º55'W (MPEG 21043). **Pará:** Faro, Castanhal 02º07'S,56º43'W (AMNH 284142, 284144, 284145, 284146); FLOTA de Faro 01º42'S,57º12'W (MPEG 64656, 64557); Óbidos (CM 83573); FLOTA de Trombetas 00º57'N,55º31'W (MPEG 65036, 65037). **FRENCH GUYANA:** Germanaco, Mana River (AMNH 233882); Cayenne, Ipousin 04º52'N,52º37'W (AMNH 525230); Saut Tamanoir 05º09'N,53º45'W (CM 61239, 61603, 62347, 62392, 62461). **GUYANA:** Adarro River 5º15'N,60º30'W (CM 4258); Tumatumary, Potaro River 05º15'N,59º08'W (AMNH 125799); Carimang River 05º49'N,60º37'W (AMNH 525231); Mines District (AMNH 525232, 525233); Katarbo 06º24'N,60º12'W (AMNH 805820, 805821, 805822); Bartica District 06º24'N,58º37'W (AMNH 805823). **SURINAME:** Nickerie, Kaiserberg Airstrip, Zuid River 04º44'N,57º07'W (FMNH 260353); Neger kreek 05º35'N,54º12'W (AMNH 461481). **VENEZUELA: Bolivar**: Altiplanice de Miura, Sierra del Imataca 07º32'N,61º04'W (COP 16949, 16950); Camborere, Cano el Buey 06º00'N,61º30'W (COP 46105); El Venamo (COP 67923, 67924).

Campylorhamphus sanus. 24 specimens. **BRAZIL: Amazonas:** Tahuapunto, Uaupés River, Tatu 00º04'N,67º15'W (AMNH 271133, 434734, 434735, 434736); Igarape Turi, Povoação Santa Cruz (MPEG 31684). **COLOMBIA: Cauca:** Caqueta, La Murelias 03º48'N,75º52'W (AMNH 116480), Putumayo, San Antonio Guamez 00º17'N,73º58'W (FMNH 286993, 293224); **Cundinamarca:** Vilavicencio 04º06'N,73º29'W (AMNH 122111). **PERU: Loreto:** Quebrada Oran 03º19'N,72º35'W (LSUMZ 119612, 119613, 119614). **VENEZUELA: Amazonas:** Negro River, Curycuryai (AMNH 310843, 310844). Solano 02º00'N,66º57'W (AMNH 433077); Orinoco River, Oçamã River 04º25'N,67º48'W (AMNH 432076); Cassiquiare River 02º01'N,67º07'W (AMNH 433078); Yavita-Pumichin 02º53'N,67º30'W (COP 34384); Cerro de la Neblina 00º50'N,66º00'W (FMNH 319013); Monte Duida 03º25'N,65º40'W (AMNH 271131, 274268, 274269, 274270, 274272).

Campylorhamphus gyldenstolpei. 13 specimens. **BRAZIL: Amazonas:** Tefé, Santo Isidoro 03º22'S,64º42'W (AMNH 309342); Hyutanaãn 07º40'S,68º45'W (COP 62702, 87386, 87857); Lábrea, Purus River 07º20'S,64º48'W (NR 569481, 569482, 569483); Nova Olinda 05º40'S,64º18'W (COP 91898); São Paulo de Olivença 03º27'S,68º48'W (COP 96192); Reserva de Desenvolvimento Sustentável Cujubim 05º13'S,68º19'W (MPEG 60081); Careiro, Tupana Lodge 04º05'S,60º39'W (MPEG 62267, 68870). **Rondônia:** Estação Ecológica Antônio Mujica Nava 09º24'S,64º56'W (MZUSP 76641).

Campylorhamphus multostriatus. 5 specimens. **Pará:** Floresta Nacional de Carajas 05º22'S,50º12'W (MPEG 35289, 36736, 38290, 68871); Tucuruí, Rio Tocantins (left bank) 03º44'S,49º50'W (MPEG 36086).

Campylorhamphus cardosoi. 58 specimens. **Mato Grosso:** Alta Floresta, Cristalino Lodge 09º42'S,55º55'W (MPEG 51427, 51428); Peixoto de Azevedo River 10º10'S,54º50'W (MPEG 33625); Paranaíta 09º43'S,56º46'W (MPEG 67340, 67341, 67342, 67343, 67344, 67345, 67346, 69377, 69378, 69379); **Pará:** Aveiro 03º15'S,55º35'W (MZUSP 14654, 14655); Rio Xingu (left bank), 02º35'S,51º57'W (MPEG 63454); Altamira 03º02'S,52º02'W (MPEG 30164, 55385); Floresta Nacional de Altamira 06º04'S,55º19'W (MPEG 63875, 63877, 63878); Floresta Nacional do Trairão 04º36'S,55º29'W (MPEG 69002); Placas, Comunidade Fortaleza 03º52'S,54º13'W (MPEG 67667); Itaituba Transgarimpeira, Jardim do Ouro 06º32'S,55º50'W (MPEG 72229); Parque Nacional do Jamanxin 05º38'S,55º28'W (MPEG 63879); Mina do Palito 06º19'S,55º47'W (MPEG 72148, 72149); Jacareacanga, Floresta Nacional do Crepori 06º27'S,57º55'W (MPEG 65687); Piquatuba 03º03'S, 55º07'W (AMNH 286953, 286954); Aranamay, Tapajós River 02º45'S,55º11'W (AMNH 286955, 286956); Caxiricatuba 02º36'S,54º56'W (AMNH 286957, 286958, 286959); Santarém 02º33'S,54º43'W (CM 71504, 73210, 73459, 74484, 74750, 74791, 75067, 78142, FMNH 254755, MPEG 36490, 36491, 40591, 47710, 66980); Miritituba 04º18'S,55º56'W (CM 76698, 77164, 77522, 77622); Novo Progresso 06º30'S,55º12'W (MPEG 69543); Amazonas River 02º39'S,55º10'W (MZUSP 23337, 23338); Urucurituba 02º24'S,55º32'W (MZUSP 40672); Fordlândia 03º40'S,55º30'W (MZUSP 58540).

Campylorhamphus probatus. 36 specimens. **Amazonas:** Aveiro 03º15'S,55º35'W (MPEG 64132, 64133); Vila Bela Imperatirz 03º42'S,55º35'W (AMNH 278074, 278075, 278077, 278078, 278744); Rosarinho 03º42'S,59º06'W (AMNH 282309); Manicoré 08º39'S,61º25'W (MEPG 57584). **Pará:** Boim, Tapajos River 03º07'S,55º14'W (AMNH 128596); Rio Madeira, Igarapé Auará 03º22'S,58º45'W (AMNH 279769, 279770, 279771, 279772, 279773); Tapajós River, Igarapé Bravo 01º57'S,55º11'W (AMNH 286952); Tapajós River, Igarapé Amazonia (AMNH 288694, 288695, 288696); Vila Braga 04º25'S,56º17'W (CM 75291, 75726, 76065, 76145, 76584); Itaituba 04º27'S,55º30'W (CM 77107, MPEG 58469); Juruti 02º28'S,56º00'W (MPEG 60954); Jacareacanga, Sítio Chicão do Abacate 05º36'S,57º35'W (MPEG 69627, 69637). **Rondônia:** Pedra Branca 04º25'S,56º17'W (FMNH 343880); Ouro Preto do Oeste 11º04'S,62º15'W (MPEG 37033, 37034); Alvorada d'Oeste 11º24'S,62º24'W (MPEG 38737); Cachoeira Nazaré 09º44'S,61º53'W (MPEG 39676, 39677); Aripuanã River, Cachoeira Dardanelos 10º25'S,47º27'W (MPEG 31049).

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Capítulo 3

Historical diversification and species limits in the genus *Campylorhamphus* (Aves: Furnariidae)

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Abstract

The genus *Campylorhamphus* is distributed from southern Central American to northern Argentina, encompassing almost the entire Neotropical region. Historically, the number of species and subspecies recognized in this genus has been controversial. To understand the historical diversification and address the main unsettled issues of *Campylorhamphus* systematics and taxonomy, we built several phylogenies, tested inter-specific limits, and reconstructed area relationships with sequences from three mitochondrial (Cyt *b*, ND2, and ND3) and two nuclear genes (β-fibint5 and MUSK). Seventeen well- supported lineages of *Campylorhamphus* were recovered clustering in at least five major clades. Our results showed that *C. trochilirostris* is polyphyletic with at least six species-level taxa clustering in three unrelated clades, and that *C. pusillus* comprises two species-level lineages separated by the Andes. Furthermore, the split of *C. procurvoides* into six species-level taxa proposed recently is corroborated herein by the multilocus data. Ancestral area reconstructions and a multilocus coalescent species tree support that the initial diversification of *Campylorhamphus* took place in the Atlantic Forest and both sides of the Andes during the Pliocene, followed by several splitting events taking place mostly during the Pleistocene in Amazonia, and a relatively more recent presence in Central America west of the Panama isthmus, as well as in the drier habitats of central South America.

Key-words: Historical biogeography; molecular systematics; Neotropics; phylogeography; taxonomy

Resumo

O gênero *Campylorhamphus* é distribuído do sul da América Central ao norte da Argentina, compreendendo toda a região Neotropical. Historicamente, o numero de espécies e subespécies reconhecidas neste gênero tem sido controverso. Para entender a diversificação histórica e abordar questões não resolvidas das relações filogenéticas e taxonômicas, nós produzimos diversas filogenias, testamos limites inter-específicos, e reconstruimos relações de áreas ancestrais através de dados genéticos de três genes mitocondriais (*Cytb, ND2* e *ND3*) e dois genes nucleares (*β-fibint5* e *MUSK*). Dezessete linhagens bem apoiadas de *Campylorhamphus* agrupam-se em pelo menos cinco grandes clados. Nossos resultados também mostraram que *C. trochilirostris* é parafilético com pelo menos seis táxons em nível de espécies, agrupados em três clados não relacionados, e que *C. pusillus* compreende duas linhagens em nível de espécie separadas pelos Andes. Além disso, a separação de *C. procurvoides* em seis espécies em nível de espécie proposto recentemente é corroborado aqui pelos dados multilocus. Reconstrução de área ancestral e árvore de espécies com base em dados multilocus suportou que a diversificação inicial de *Campylorhamphus* iniciou-se na Floresta Atlântica e em ambos os lados dos Andes durante o Plioceno, seguido por vários eventos de separacao durante o Plesitoceno na Amazônia, com relativamente mais recente presença no oeste da América Central do Istmmo do Panamá, bem como nos ambientes seco da América do Sul central.

Palvras-chave: Biogeografia histórica, sistemática molecular, Neotrópico, filogeografia, taxonomia.

1.0. Introduction

The matrix of forest types in the Neotropics represents one of the most heterogeneous on Earth, allowing these areas to maintain extraordinary species diversity (Smith et al., 2012). The high diversity in the Neotropics has been a major focus for studies of endemism and processes of biodiversity formation (Wallace, 1852; Haffer 1969, 1997; Cracraft 1985; Bates et al., 1998). Biologists have formulated a variety of hypotheses about the patterns and processes that may have led to the high levels of Neotropical biotic diversity, and have used a variety of analytical methods to test these hypotheses (Tuomisto, 2007; Antonelli et al., 2010; Leaché and Rannala, 2011). Although allopatric speciation is widely acknowledged as the primary mechanism underlying Amazonian species richness and endemism, debates about the temporal and spatial history of diversification, as well as the drivers and rate controls of these patterns, remain unresolved (Near and Benard, 2004, Hoskin et al., 2005; Ribas et al., 2011). There are several hypotheses that aim to explain processes of diversification within the Neotropics (see Eberhard and Bermingham, 2005; Fuchs et al., 2011). Some studies have analyzed the distributions among subspecies, species, and genera, and have shown phylogenetic divergence within smaller areas such as the highlands and lowlands flanking the Andes ranges (Brumfield and Edwards, 2006, Sedano and Burns, 2010, Patel et al., 2011), across the Amazon River (Sick, 1967; Capparella 1991; Ribas et al., 2011), and even smaller tributaries such as the Aripuanã, and Ji-Paraná (Cohn-Haft et al., 2013; Fernandes et al., 2012; Fernandes et al., 2013). Independently of the proposed mechanism, however, this pattern has been corroborated in relation to birds of lowland forest, including recent studies using vocal analysis (Isler et al., 1999; Carneiro et al., 2012), and genetic markers (Hackett, 1993; Aleixo 2002). Although previously alternative explanations were thought as mutually exclusive, recent studies recognize that several of them may have played a role in creating patterns of species distribution and diversity (Bates et al., 1998; Tuomisto, 2007, Costa 2000), and that multiple factors have, on multiple occasions, impacted the genetic structure within species (Fuchs et al., 2011).

Historical biogeography reconstructions based on molecular phylogenies are now an important way to clarify the evolutionary history of organisms in space and time (Ali et al., 2012). Birds of the genus *Campylorhamphus* (known as scythebills) are ideal targets to address some hypotheses of Neotropical diversification they have a wide distribution ranging from Central America, through the northern and central Andes, the entire Amazonian lowlands, down to the Atlantic Forest in eastern Brazil, northeastern Argentina, and eastern Paraguay (Marantz et al., 2003). This genus includes species occurring in different types of habitats, such as dry, foothill, and lowland humid forests, including both *terra firme* (upland) and seasonally flooded forests (*várzea* and *igapó*). Scythebills are characterized by exceptionally long and decurved bills, which are associated with highly specialized feeding behaviors, making them particularly sensitive to habitat disturbance (Stotz et al., 1996; Portes et al., 2013).

Taxonomically, the number of species and subspecies recognized in the genus *Campylorhamphus* has been controversial due mainly to the great morphological similarity among taxa (Claramunt et al., 2010; Portes and Aleixo 2009). Currently, 22 taxa (Marantz *et al.* 2003; Portes and Aleixo 2009) and four species are recognized (Claramunt et al., 2010; Remsen et al., 2010), with two additional species recently described (Aleixo et al., 2013; Portes et al., 2013). The Black-billed Scythebill (*Campylorhmaphus falcularius*) is monotypic and endemic to lowland and montane Atlantic Forest in eastern Brazil, northeastern Argentina, and eastern Paraguay. The Brown-billed Scythebill *Campylorhamphus pusillus* has five subspecies distributed in both lowland and montane humid forests from northwestern South America on both sides of the Andes to Central America in Panama and Costa Rica. The Curve-billed Scythebill (*Campyloramphus procurvoides*) comprised originally of four subspecies endemic to the Amazonian upland (*terra-firme*) lowland forests (Marantz et al., 2003); however, Aleixo et al., (2013) and Portes et al., (2013) suggested the split of this complex into six valid species (*C. procurvoides, C. sanus, C. probatus* and *C. multostriatus*), including two new taxa they described therein (*C. cardosoi* and *C. gyldenstolpei*). Finally, the Red-billed Scythebill *Campylorhamphus trochilirostris* includes 12 subspecies and it is the most widespread species of the genus, ranging from Panama south to northern Argentina, including most of central-northern South America, where it is found in dry as well as humid lowland and montane forest types, including Amazonian seasonally-flooded forests (*várzea*; Marantz et al., 1997).

Herein we estimated the evolutionary history, divergence time and biogeographic diversification patterns of the scythebills across the Neotropical region. We provide a comprehensive temporal and spatial analysis of the diversification history of this group based on a dense taxonomic sampling of multilocus DNA sequence data from three mitochondrial and two nuclear genes.

2.0. Methods

2.1. Genetic Sampling

Through loans from several institutions and sequences available on GenBank, we were able to include samples throughout from the distribution of *Campylorhamphus*

(Table 1S in supplementary information). Sampling localities encompassed Central America, both sides of the Andes (cis – trans), all major Amazonian river basins, central and southwestern of South American (savanna and Chaco), and the Atlantic Forest on the Brazilian coast. The ingroup included 138 samples from 20 of 24 recognized taxa of *Campylorhamphus* (Marantz et al., 2003; Portes and Aleixo, 2009; Aleixo et al., 2013; Portes et al., 2013), distributed among 94 localities (Fig. 1S; Table 1S). We were unable to find available samples from two subspecies of *C. trochilirostris* (*brevipennis* and *venezuelensis*) and two subspecies of *C. pusillus* (*tachirensis* and *guapiensis*). To incorporate some of the variation suggested in current subspecific designations in our sampling, as well as to investigate possible unknown intraspecific variation, every taxon was represented by 2-20 individuals, except for *C. t. hellmayri*, from which only one sample was available (Table 1S). Sequences of *Lepidocolaptes angustirostris, L. falcinellus, L. albolineatus* and *Dendroplex picus* were used as outgroups based on the close relationship recovered by previous studies between *Campylorhamphus* and the genera *Lepidocolaptes* and *Dendroplex* (Aleixo, 2002; Irested et al., 2004; Derryberry et al., 2011) (Table 1S).

We extracted total DNA from fresh tissue samples with a DNEasy Tissue Kit (Quiagen, Valencia, CA), following the manufacture's protocols and with standard Phenol-chloroform methods (Sambrook *et al.* 1989). For the dry skin (toe-pad) samples, we added 30µl 100mg/ml DTT (dithiothreitol) on the proteinase K digestion step. DNA concentration was quantified with a NanoDrop spectophotometer. For the majority of samples we obtained DNA sequence for three mitochondrial DNA genes [Cytochrome b (Cytb); NADH dehydrigenase subunit 2 (ND2); NADH dehydrigenase subunit 3], one non-coding nuclear intron [beta-fibrinogen intron 5 (BF5)], and one sex-linked nuclear intron locus [muscle, skeletal, receptor tyrosine kinase (Musk)]. The mitochondrial and nuclear markers were amplified via polymerase chain reaction (PCR) in 12.5 µL reactions using the following protocols: initial denaturation at 94^{o}C for 10 min, followed by 35 cycles at 94^{o}C for 30 s, 48^{o}C, 54^{o}C, 51^{o}C, 54^{o}C and 55^{o}C (for Cytb, ND2, ND3, Musk and BF5, respectively), and the cycle was finished at 72^{o}C for 1 min, and completed by a final extension at 72^{o}C for 10 min and then 4^{o}C soak. Information on the primers used are included in Table 2Sa. PCR amplicons were sequenced in both directions. We used an additional set of primers to sequence the mitochondrial fragments (Table 2Sb). PCR products were sent to the Beckman Coulter Genomics for all subsequent steps. All sequences were deposited in GeneBank (accession numbers listed in Table 1S). Given the condition of some ancient samples, in which the extraction produces an extract with low concentration and DNA fragmented, we were not able to amplify all genes for some individuals (Table 3S). For the DNA sequencing protocols (see supplementary information).

2.1.1. Phylogenetic analyses

Precautions against nuclear copies included sequencing both heavy and light strands checked using Bioedit v.7.0.5 (Hall, 1999), and using overlapping fragments and confirming that amino acid translation was possible without stop codons or gaps as verified with Dambe5 (Xia, 2013). Heterozygous sites in the nuclear loci (double peaks) were coded using the appropriate IUPAC code. We phased nuDNA haplotypes with PHASE 2.1.1 (Stephens et al., 2001; Stephens and Scheet, 2005) after preparing the dataset with Bioedit v.7.0.5 (Hall, 1999). Sites that had posterior probabilities <0.90 were labeled as ambiguous (Smith et al., 2012; Maley and Brumfield, 2013). For each clade/lineage recognized by mtDNA and species trees, pairwise genetic distances between lineages were averaged to provide a single lineage-level estimate of genetic distance. The mtDNA *p* uncorrected mean genetic distance based on Cytb and Nd2 genes was calculated using MEGA 5 (Tamura et al., 2011).

The phylogeny was reconstructed using two approaches: Maximum likelihood (ML) and Bayesian inference (BI), implemented in RAxML version 7.0.4 (Stamatakis, 2006) and MrBayes version 3.1.2 (Ronquist and Huelsenbeck, 2005), respectively. First, we identified the best-fit finites-sites models of sequence evolution for each locus using jModelTest 2 (Darriba et al., 2012) under the Akaike information criterion (AIC) for ML and Bayesian Information Criterion (BIC) for Bayesian analysis. We estimated a gene tree for two different dataset, one nuDNA dataset, and other mtDNA dataset. In all Bayesian analysis, four Metropolis-coupled Markov Chains Monte Carlo, one cold and three heated were run for 20 million interactions with trees sampled every 1000 interactions. Nodal support was assessed by bootstrap replicates of 1000 for each dataset with the program RAxML version 7.0.4 (Stamatakis, 2006). Those nodes with PP ≥ 0.95 and bootstrap ≥70% were considered strongly supported. We assessed MCMC convergence (p >200) and determined burn-ins by examining ESS values (> 200), and likelihood plots in the program Tracer version 1.5 (Rambaut and Drummond, 2010). Analyses were done twice to confirm that different starting trees could recover equivalent optimal posterior probabilities (PP) (Sedano and Burns, 2010).

2.1.2. Species tree and Divergence time estimates

We also estimated species trees as implemented by *Beast (Heled and Drummond, 2010). We used a Relaxed Clock: uncorrelated Lognormal and a randomly generated topology as a starting tree. Defaults prior were generally used unless they involved a uniform prior distribution, in which case we used a lognormal prior distribution (McKay et al., 2013). Following optimization we ran the analysis for 200^6 generations (sampling every 20000 generations and discarding the first 10% as burn-in). We checked for convergence of parameters in Tracer version 1.5 ($p > 200$) (Rambaut and Drummond, 2010) and found the Maximum Clade Credibility tree with TreeAnnotater version 1.6.1 (Drummond and Rambaut, 2007). To designate species in *Beast, we used described taxa (Marantz et al., 2003) and lineages that were recovered as reciprocally monophyletic according to the mtDNA concatenated dataset.

The mtDNA sequence divergence is currently the most reliable marker for inferring a temporal framework of avian diversification and provides a rough age estimate of lineages (Garcia-Moreno, 2004). The most widely used calibration is 2% sequence divergence per million years for birds (Sedano and Burns, 2010). We adopted two different calibration methods: (1) we used only the cytochrome *b* calibration (Cyt *b*: mean = 0.0105, SD = 0.1; Weir and Schluter, 2008) and estimated the divergence times for others loci; and (2) we used independent calibrations available for the mitochondrial genes (Cyt *b*: mean = 0.0105; SD = 0.1; Weir and Schluter, 2008, and ND2: mean = 0.0125, SD = 0.1; Smith and Klicka, 2010), the autosomal marker (BF5: mean = 0.00135, SD = 0.45; Ellegren, 2007), and the sex-linked marker (Musk: mean = 0.00145; SD = 0.45; Ellegren, 2007). We used lognormal distributions for the relaxed uncorrelated rates for all genes, except for ND3, in which divergence was estimated in both approaches due to the lack of a specific calibration for this gene. All analyses implemented a Yule process as the species tree prior. Default priors were generally used unless they involved a uniform prior distribution, in which case we used a lognormal prior distribution (McKay et al., 2013).

2.1.3. Coalescent-based species delimitation

Nuclear and mitochondrial sequence data were used in the coalescent-based species delimitation method implemented by Bayesian Phylogenetics and Phylogeography - BPP v. 2.0 (Rannala and Yang, 2003; Yang and Rannala, 2010), which incorporates a Bayesian modeling approach to generate speciation probabilities of closely related taxa from multilocus sequence data (Rannala and Yang, 2003; Yang and Rannala, 2010). Camargo et al. (2012) showed that the BPP package is the most accurate coalescent-based species delimitation method. BPP uses Bayesian MCMC algorithms that accommodate the species phylogeny as well as coalescent processes in extant and extinct ancestral species (McKay et al., 2013). BPP also tests whether resolving the node into multiple species results in a statistically better fit to the data than collapsing the node into a single species. If resolving the node results in a better statistical fit, BPP recommends splitting that node into multiple species (McKay et al., 2013). A user-specified guide tree is used to reduce the number of possible species delimitations the program must integrate over. At each node on the tree, the program assesses whether the sequence data are compatible with a one-species model or whether a two-species model has to be invoked to explain the data (Mckay et al., 2013). BPP incorporates a model that includes the species divergence times (τ), and the population size parameters θ (see McKay et. al., 2013; Camargo et al., 2012; Leaché and Fujita, 2010 for summary of how BPP works this parameters). We ran the analyses for 200 000 generations, sampling every five and specified a burn-in of the first 50 000 generations. We performed preliminary analyses using algorithms 0 and 1 with different fine-tune. BPP rely on a user-specified guide tree with individuals assigned to a priori defined putative species (McKay et al., 2013). On the guide tree, we used as our a priori species definition the 18 lineages recovered by the species tree estimated by *BEAST (Fig. 2). We implemented the approach of Leaché and Fujita, (2010) and Smith et al., (2012), where performed analyses used three combinations of priors that represented different population sizes and different ages for the root in the species tree: 1) large N_e and deep divergence: θ [theta] and τ [tau] gamma priors G (1, 10) and G (1, 10); 2) small N_e and shallow divergence: θ and τ gamma priors G (2, 2000) and G (2, 2000); and 3) large N_e and shallow divergence: θ and τ gamma priors G (1, 10) and G (2, 2000). BPP generates a posterior distribution of speciation models containing differing numbers of species. Speciation probabilities are estimated from the sum of probabilities of all models for speciation events at each node in the guide tree. Daughter lineages from nodes that had speciation probabilities of >0.95 under all three prior scenarios were classified as species (Leaché and Fujita, 2010; Smith and Klicka, 2013).

2.1.4. *Zoogeographical area reconstruction*

Several methods for geographical range evolution analysis were recently applied to biogeographic studies such as the dispersal-extinction cladogenesis model (Ree et al., 2005; Ree and Smith 2008) and Bayesian island biogeography method (Sanmartín et al., 2008). On the other hand, the dispersal vicariance analysis method (DIVA; Ronquist and Huelsenbeck 2001) has remained the most popular and widely used method for reasons of simplicity (Ali et al., 2012). DIVA reconstructs the ancestral distribution in a phylogeny by optimizing a three-dimensional cost matrix, in which extinctions and dispersals "cost" more than vicariance (Ronquist, 1997; Lamm and Redelings, 2009). These analyzes are important to answer how the ancestral origin of an organism affect its current distribution.

We used a recently developed approach, Bayesian Binary MCMC analysis (BBM) as implemented in RASP to reconstruct the possible ancestral ranges of lineages and species in the genus *Campylorhamphus* based on the obtained phylogenetic trees (Ali et al., 2012). In this method, the frequencies of an ancestral range at a node in ancestral reconstructions are averaged over all trees (Yu et al., 2010). BBM offers a statistical procedure for inferring states, including geographic distributions at ancestral nodes using a full hierarchical Bayesian approach (Ronquist, 2004). In Bayesian inference, relative rates of change among character states under models of range evolution are not fixed. We also estimated ancestral areas with S-DIVA, in which the frequencies of an ancestral range at a node in ancestral reconstructions are averaged over all trees and each alternative ancestral range at a node is weighted by the frequency of the node occurring or by some other measure of support for the node (Yu et al., 2010).

The distribution range of *Campylorhamphus* was divided into five areas, based on the presence of one or more endemic lineages, as follows: A - Atlantic Forest in eastern South America; B - Trans-Andean South America (Chocó) and Central America; C - Amazonian lowlands; D - Central South America (*Cerrado*, *Caatinga*, and *Chaco* biomes); and E – Eastern Slopes of Andes . Each lineage was assigned to one or two zoogeographical regions according to Marantz et al. (2003), complemented by Aleixo et al. (2013) and Portes et al. (2013). Each node was constrained to contain a maximum of two areas in both analysis (BBM and S-DIVA). Although we acknowledge the possibility of more complex scenarios (Sedano and Burns, 2010), this is a simple cladistic procedure for approximating the historical connectivity of areas, which is usually an unknown parameter (Bates et al., 1998; Tuomisto, 2007).

To account for uncertainties in phylogeny, we used 200.004 trees from the MCMC output generated by Beast and ran S-DIVA on all of them, allowing reconstruction. BBM analysis was also conducted in a similar way. The MCMC chains were run simultaneously for four chains for 10,000,000 generations. The state was sampled every 1000 generations. Fixed JC+G (Jukes-Cantor+Gamma) were used for the BBM analysis with a null root distribution (Ali et al., 2012).

3. Results

The final ingroup DNA alignment includes 138 samples of Cytochrome *b* (range 1017 - 1029 bp), 126 samples of ND2 (range 775 - 1041 pb), 120 samples of ND3 (351 pb), 94 samples of BF5 (range 517 - 553 pb), and 99 samples of Musk (range 592 - 656 pb) (Table 1S). We included only partial Cytochrome *b* sequences for ancient samples as we were unable to sequence all genes for these particular samples.

No indels were present in the mitochondrial alignment, but some were identified in the Musk and BF5 datasets. The multilocus dataset ingroup consisted of 107, 132 and 95 individuals for full DNA, mtDNA and nuDNA dataset, respectively (Table 3S). For the species tree, we included all sequences available in our dataset, plus those for the same genes obtained in Genebank adding up to a total ingroup of 138 *Campylorhamphus* specimens (Table 1S and 3S). Transition versus transversion plots did not indicate saturation among ingroup taxa. All substitution models selected for phylogenetic analysis under the AIC and BIC criterion are listed in Table 1. Each Bayesian search were found to have reached stationary in log likelihoods prior to the burn-in, indicating that run length was adequate for sufficient sampling from the posterior probability distribution of trees (Ronquist and Huelsenbeck, 2005). There was no strongly supported conflict between ML and BI analyses of the same dataset for all gene trees and concatenated topologies.

The mean pairwise uncorrected genetic *p*-distances of mtDNA (Cyt *b* and ND2 genes) between the lineages recovered by phylogenies in this study ranged from 0.7% (between nominate *C. trochilirostris* and *C. procurvoides*) and 8.0% (between *C. falcularius* and *C. multostriatus*) (Table 4S in supporting information), while the mean genetic p-distance within lineages varied between 0.0% (in all lineages) to 0.7% (*C. falcularius*) (data not shown). The mean pairwise uncorrected genetic *p*-distances between the major clades are available in Figure 1. The mean divergence between *Campylorhamphus* and outgroup samples is ca. 10.0%.

Table 1 - List of substitutions models selected using jModel Test under the AIC and BIC for each gene, and number of variable and informative sites for each gene.

Loci	Aligment range	Variable/ Informative	Substitution model	Sample size
BF5	517-553 bp	58/45	GTR +I +G	94
Musk	592-656 bp	55/38	GTR+G	99
Cytb	1017-1029 bp	276/221	GTR +G	138
ND2	775-1041 bp	324/256	HKY +Y +G	126
ND3	351 bp	90/72	HKY +G	120

3.1 Phylogenetic analyzes

The Bayesian phylogenetic based in the mtDNA dataset strongly supported the monophyly of the genus *Campylorhamphus*, with the Maximum-likelihood analysis yielding a similar topology (Fig. 1). Both BI and ML analyses recovered seventeen reciprocally monophyletic lineages in *Campylorhamphus* with, 26 of the 29 nodes within the genus estimated phylogeny receiving maximum posterior probabilities (Fig. 1). In contrast, the nuDNA gene tree was much less resolved (Fig. 2S). The monophyly of only three reciprocally monophyletic lineages recovered with both mitochondrial and multilocus analyzes were also strongly supported by the nuclear gene tree: *C. falcularius* (lineage 1), *C. t. snethlageae* (lineage 3B), and *C. multostriatus* (lineage 9; Fig. 1; Fig. 2S).

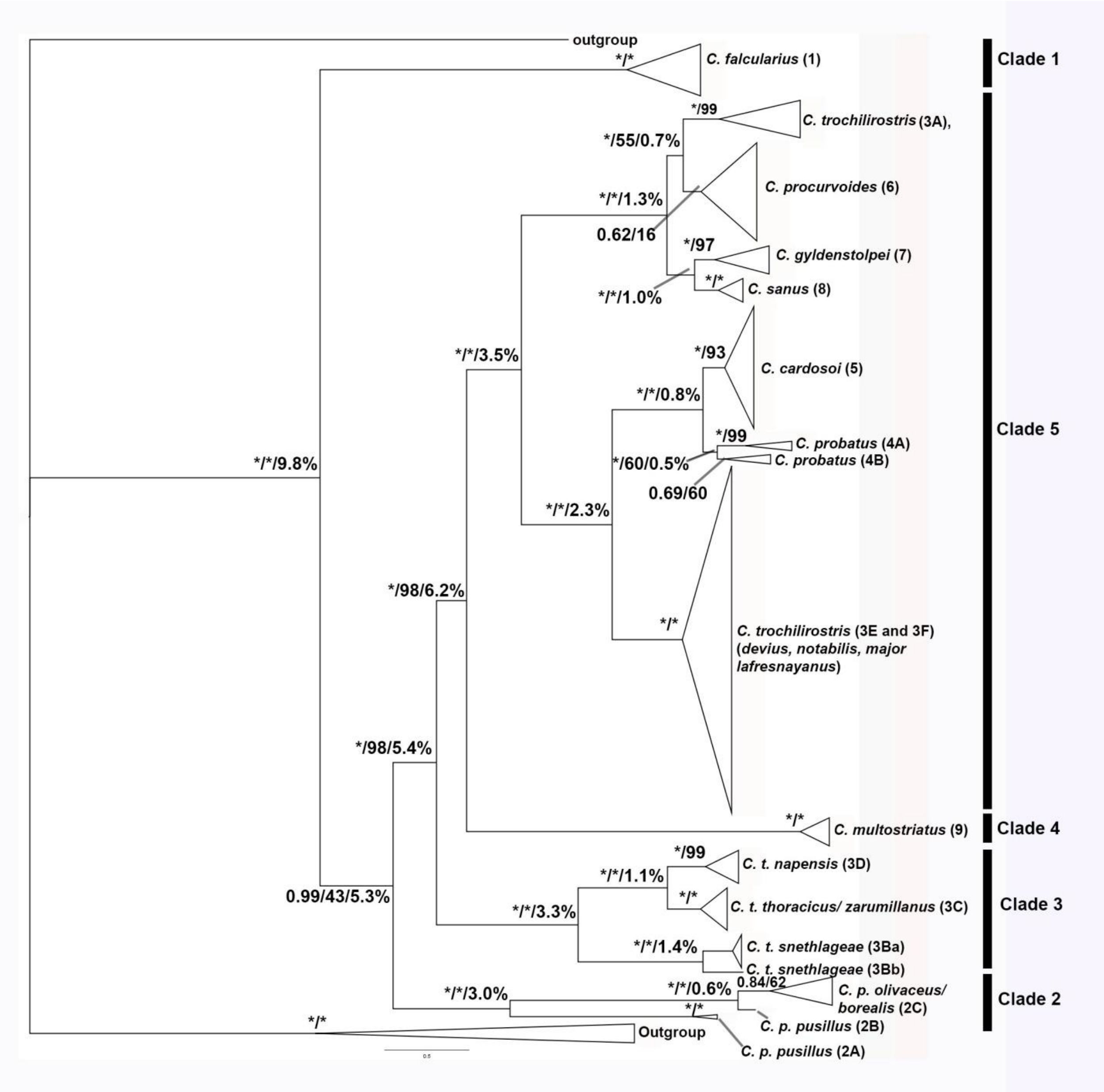

Figure 1 - BI and ML phylogenies estimates based on the mitochondrial dataset (Cyt b, ND2, and ND3). Symbols and numbers close to the nodes are Bayesian posterior probability/ML bootstrap/mean uncorreted *p* mtDNA (Cyt *b* and ND2) distance values, respectively, between sister taxa and between each major clades. Asterisks indicate maximum support according to both BI and ML analyzes. The numbers in parentheses at the tips of terminal branches are associated with the populations sampled (Table 1S). Taxonomy follows Marantz *et al.* (2003), with updates from Portes and Aleixo (2009), Portes *et al.* (2013), Aleixo *et al.* (2013).

The seventeen statistically well-supported reciprocally monophyletic lineages recovered in *Campylorhamphus* by the multi-locus trees are distributed in five main clades as described below. The basal most clade in *Campylorhamphus* (Clade 1) includes only *C. falcularius* (lineage 1), endemic to the Atlantic Forest biome in eastern South America; interestingly, one of the *C. falcularius* specimens sequenced (MPEG

71839/SB008) grouped with samples of another co-distributed lineage in part of the Atlantic Forest (nominate *C. trochilirostris* - lineage 3A) according to the mitochondrial trees (Fig. 1), but not the exclusively nuclear tree (where it groups with other *C. falcularius* samples; Fig. 2S), indicating hybridization between these otherwise phylogenetically distant lineages. The second clade grouped three recovered lineages representing each allopatric populations of *C. pusillus* inhabiting respectively: 1) the eastern slope of the Andes in Colombia, Ecuador, and Peru (lineage 2A); 2) the western slope of the Andes in Ecuador and Colombia (lineage 2B); and 3) Central America in Panama and Costa Rica (lineage 3C; Fig. 1, Fig. 1S). The third clade includes three lineages corresponding to some subspecies of the polyphyletic *C. trochilirostris* inhabiting both side of Andes (*thoracicus*/*zarumillianus*, and *napensis*; lineages 3C and 3D) and the only flooded *várzea* forest specialist *Campylorhamphus* taxon (lineage 3B; *C. t. snethlageae* (Fig. 1, Fig. 1S, Table 1S). The fourth clade consists of a single taxon endemic to eastern Amazonia (*multostriatus*; Fig. 1, Fig. 1S, Table 1S), formerly regarded as a subspecies of *C. procurvoides* (Marantz et al. 2003), but now considered a distinct species (Aleixo et al. 2013; Portes et al. 2013). The fifth and largest *Campylorhamphus* clade group multiple Cis-Andean lineages and taxa traditionally associated with *C. trochilirostris* and *C. procurvoides* (Fig. 1, Fig. 1S, Table 1S): lineages 3E and 3F (*C. trochilirostris devius/notabilis,* and *hellmayri/lafresnayanus/major* from western Amazonia and Central South America in the *Cerrado*, *Chaco*, and *Caatinga* biomes); lineages 5 and 4 (*C. cardosoi* and *C. probatus* from lowland Amazonia between the Madeira and Xingu rivers, and formerly associated with *C. procurvoides*); lineages 7 and 8 (*C. gyldenstolpei* and *C. sanus* from western Amazonia and also formerly associated with *C. procurvoides*); and the sister lineages 6 (*C. procurvoides* from the Guianan shield in Amazonia) and 3A (nominate *C. trochilirostris,* endemic to the coastal Atlantic Forest).

3.2 Species Tree and divergence times

Alternative calibration methods based on the Cyb *b* rate only or those based on specific rates obtained for each marker individually, except ND3, did not result in noticeable changes of estimated divergence times among *Campylorhamphus* lineages (data not shown).

The topology resulting from the *Beast coalescent-based analysis of all loci was well resolved and very similar to the mtDNA Bayesian tree, with 11 of 16 nodes within the genus *Campylorhamphus* having posterior probabilities ≥0.95 (Fig. 2). Two of those five less supported nodes were moderately supported (PP ≥ 0.90, Fig. 2). Among the least supported nodes (PP=0.40) was the sister relationship between *C. multostriatus* and clade 5 (lineages 3A, 3E, 3F, 4, 5, 6, 7, 8, and 9); the sister relationship between clade 3 (lineages 3B, 3C, 3D) and clades 4 (lineage 9) and 5 (lineages 3A, 3E, 3F, 4, 5, 6, 7, 8, and 9; PP = 0.83); the reciprocal monophyly between the two lineages of *C. probatus* (lineages 4A and 4B; PP = 0.89); and the reciprocal monophyly between nominate *C. trochilirostris* (lineage 3A) and those in the *C. procurvoides* complex (lineages 6, 7, and 8). All nodes in the species tree with posterior probabilities of less than 0.95 were also present in the concatenated multi-locus Bayesian tree with high statistical support, except that joining *C. trochilirostris* and the *C. procurvoides* complex reported above, which were recovered by the latter tree with a different relationship, whereby *C. t. trochilirostris* (lineage 3A) and *C. procurvoides* (lineage 6 only) grouped as sister taxa (Fig. 2 and Fig. 3).

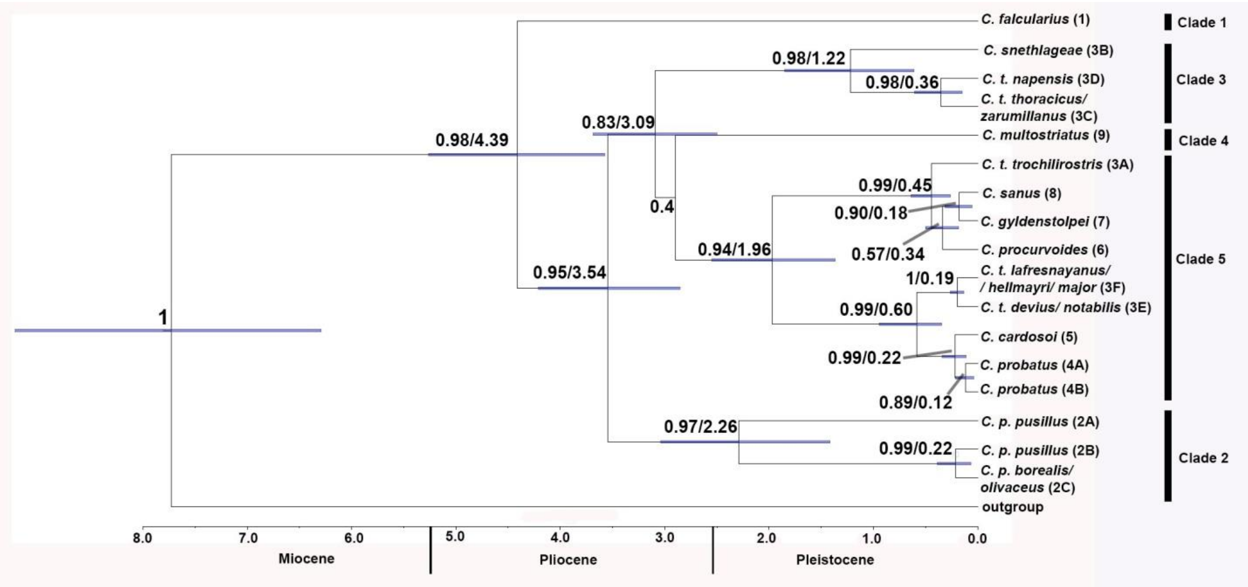

Figure 2 - Species tree obtained using the coalescent approach implemented in *Beast, based on the multilocus DNA (nuDNA and mtDNA) dataset. Values on nodes represent posterior probability and mean divergence times in millions of years ago (mya), respectively. The letters in parentheses at the tips of terminal branches are associated with the populations sampled (Table 1S). Taxonomy follows Marantz *et al.* (2003), with updates from Portes and Aleixo (2009), Portes *et al.* (2013), Aleixo *et al.* (2013).

According to the estimated species tree, all cladogenetic events within the genus *Campylorhamphus* occurred during the Plio-Pleistocene, with the oldest split involving the Atlantic Forest endemic *C. falcularius* and all remaining lineages, with a lower confidence interval almost reaching the Lower Miocene 4.39 mya (95% HPD: 5.26-3.57 mya; Fig. 2). Subsequently, the second oldest split involved the Andean and Trans-Andean clade 2 (*C. pusillus*) and the remaining lineages about 3.54 mya (95% HPD: 4.21-2.85 mya; Fig. 2). Next, clade 3 from the western and central Amazonian and Trans-Andean lowlands split from the remaining Cis-Andean *Campylorhamphus* lineages about 3.09 mya (95% HPD: 3.68-2.50 mya) (Fig. 2). The eastern Amazonian endemic *C. multostriatus* (clade 4) split from the remaining Cis-Andean lineages at an unknown time interval, with the support for this split being too low (PP = 0.4) to allow for a reliable divergence estimate (Fig. 2). Within clade 5, the oldest split separated Central South American and Central Amazonian lineages (3E, 3F, 4, and 5) from those in northern and western Amazonia and the central part of the Atlantic Forest (3A, 6, 7, and 8) between 1.96 mya (95% HPD: 2.54-1.36 mya) (Fig. 2); within each of these subclades, the separation between Central South American (3E and 3F) and Central Amazonian lineages (4 and 5) took place between 0.60 mya (95% HPD: 0.94-0.34 mya), whereas that between northern and western Amazonian (6, 7 and 8) and central Atlantic Forest (3A) lineages occurred between 0.45 (95% HPD: 0.63-0.26 mya) (Fig. 2). Finally, a burst of cladogenetic events took place between 0.22 mya (95%HPD: 0.50-0.10 mya) involving Amazonian lineages isolated in different interfluvia (4, 5 and 6, 7, 8) as well as Amazonian and Central South American lineages (3E and 3F). Therefore, most cladogenetic events associated with the extant lineages recovered in *Camplylorhamphus* are concentrated in the Amazonian lowlands during the Lower Pleistocene (Fig. 2).

3.3 BPP species delimitation

We obtained qualitatively similar results using the different algorithms and starting trees. Using all three prior distributions, 15 of 17 terminal lineages had high speciation probabilities (PP $\geq$ 0.95, Fig. 3). *Campylorhamphus p. pusillus* (lineage 2B, Table 1S) from the west side of the Andes and *C. p. borealis/ olivaceus* (lineage 2C, Table 1C) from Central America did not show significant speciation probabilities for any different priors, thus failing to meet the species criterion of Leaché and Fujita

(2010). Similarly, the split between *C. probatus* lineages separated by the Aripuanã River in southern Amazonia (populations 4A and 4B, Table 1S), did not receive a significant speciation probability either under a model of large N_e and deep divergence (PP=0.79) or a model of large ancestral N_e and shallow divergence (PP=92; Fig. 3), but only when a model of small ancestral N_e and shallow divergence was considered (PP=99; Fig. 3).

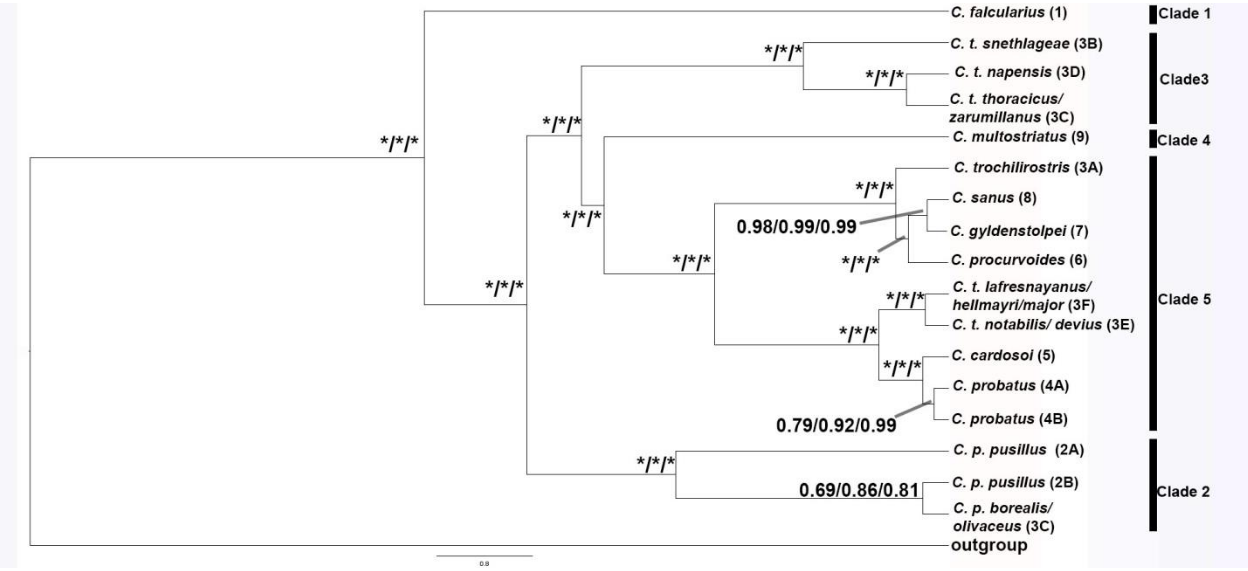

Figure 3 – Bayesian Phylogenetics and Phylogeography analysis (BPP) for the genus *Campylorhamphus* estimated from multilocus (mtDNA and nuDNA) datasets. Nodes represented posterior probabilities using three different prior combinations by BPP: 1st—large ancestral N_e and deep divergences; 2nd—small ancestral N_e and shallow divergences and 3rd—large ancestral N_e and shallow divergences. PP $\geq$ 0.95 are marked with an asterisk. Taxonomy follows Marantz *et al.* (2003), with updates from Portes and Aleixo (2009), Portes *et al.* (2013), Aleixo *et al.* (2013).

3.4 *Ancestral area reconstruction*

Both S-DIVA and BBM postulate that the most favored ancestor of *Campylorhamphus* originated in Atlantic Forest (optimal area reconstruction at basal node 34), although the probabilities have been divided with cis-Andean areas (42.6% A+C, 28.0% A+E, 28.0% A+B and 1.6%* for S-DIVA, and 73.8% A, 13% A+C, 10,4% C, 2.8% * for BBM). The S-DIVA analysis pointed to 8 events of dispersal and 6 events of vicariance, which at least two occurring in the Andes and three occurred in cis-Andean region; the node 35 assigned three dispersal events, but it is impossible to predict where they were because the outgroup includes more than two areas. The BBM analysis pointed to 4 and 6 dispersal and vicariance events, respectively.

Both analysis suggest that node 30 emphasizes the cis-Andean area as the ancestral range of all cis-Andean lineages, not showing any process of re-colonization, except to the node 25 (Fig. 4), which indicate a possible ancestral Atlantic Forest range, but with a very small probability according to BBM. Both analyses showed partial ambiguous results for some nodes. For instance, the ancestral range for lineages 3D and 3E (node 28) had a 100% of marginal probability for B+C according to S-DIVA, while according to BBM its was 93.4% for C and 5,4% for B+C. The analysis of S-DIVA suggests with 100% of marginal probability AC (cis-Andean + Atlantic Forest) as the ancestral areas for the node 25, while BBM analysis suggest C (cis-Andean) as the most likely ancestral range (95.1% C, 4.0% A+C, and 0.5 A). Another instance of ambiguity was recovered for node 32. S-DIVA suggests as the possible ancestral range with 100% of marginal probability B+C (trans-Andean + cis-Andean) for this clade, while the BBM showed splitted probabilities ranging from 40,2% for E as the ancestral range to 38.1% for B, and only 8.1% for C (Fig. 4).

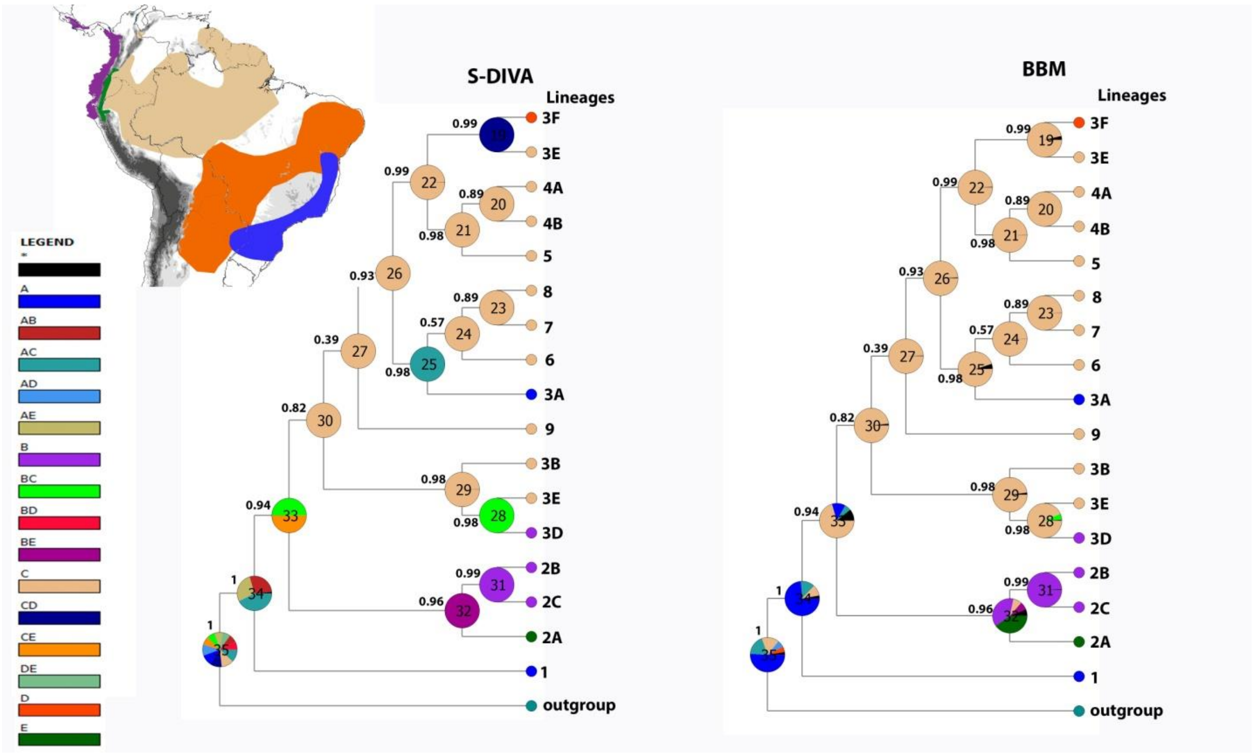

Figure 4 - Graphical results of ancestral distributions at each node of the *Campylorhamphus* phylogeny obtained from S-DIVA (left) and BBM (right) as implemented by RASP based on the output (.trees file) produced by *Beast Analysis. Bootstrap support values (50% and higher; S-DIVA) and Bayesian credibility values (PP; BBM) are indicated close to each node. In the lower left corner are the color keys to possible ancestral ranges at different nodes. Biogeographical regions: A: Atlantic Forest (blue); B: Central America and Chocó area of endemism (purple); C: Amazonia (beige); D: Central South America (red); and E: Eastern slope of the Andes (green). The number in each node represents de ID for ancestral relation for each lineages (see supplementary information).

4.0 Discussion

We obtained the most densely sampled phylogenies for the genus *Campylorhamphus* available to date, which provided a well-resolved estimate of the temporal and spatial contexts of the genus' diversification in the Neotropics. In addition, these phylogenies showed that many recognized polytypic species in *Campylorhamphus* are not monophyletic, and that taxonomic reclassifications are needed. We discuss all these issues in detail below.

4.1 Molecular systematics and species limits in the genus Campylorhamphus

Maximum-likelihood and Bayesian phylogenetic trees as well as the coalescent species tree produced very similar topologies recovering in all instances seventeen statistically well-supported lineages distributed in five major clades (Figs. 1 and 2). In these phylogenies, the following species-level taxa according to some taxonomic treatments (e.g., Remsen et al. 2014) were recovered as polyphyletic: *C. trochilirostris* and *C. procurvoides* (Figs. 1 and 2). Our coalescent-based species delimitation method implemented in BPP showed that at least 15 of these 17 terminal lineages had high speciation probabilities (PP $\geq$ 0.95, Fig. 3) and are best treated as independent species as discussed below.

4.1.1 Campylorhamphus falcularius

The first species to diverge within *Campylorhamphus* was the Atlantic Forest endemic *C. falcularius,* with all but one sample grouping together in one clade with high statistical support according to all phylogeny estimates (Figs. 1 and 2), supporting its long standing treatment as an independent species (Marantz et al. 2003, Derryberry et al. 2011), which is also consistent with the BPP analysis. As reported above, one *C. falcularius* sample (MPEG 71839 / SB008) grouped with the Atlantic Forest *C. t. trochilirostris* clade (lineage 3A) according to the mtDNA tree (Fig. 1), but with other *C. falcularius* samples in the exclusively nuclear tree (Fig. 2Sb), providing evidence of hybridization between these lineages. Given the large phylogenetic distance separating these lineages and their disparate phylogenetic affinities, it is likely that hybridization between them does not happen very frequently or to the extent of causing extensive paraphyly in both nuclear and mtDNA gene trees, as suggested herein with the obtained sampling of 6 *C. falcularius* and 3 *C. t. trochilirostris*. Phenotypically, the hybrid has the typical black bill that readily distinguishes *C. falcularius* from any other taxa grouped under *C. trochilirostris*, mirroring both the nuclear genes sequenced and known high vocal differentiation, and hence not supporting a scenario of extensive gene introgression between these Atlantic Forest lineages, which replace each other altitudinally in coastal Bahia, where they ranges (CEP, pers. obs.). Within *C. falcularius*, no phylogeographic structure could be detected from across its range (Fig. 1), but this pattern should be interpreted with caution given the relatively small sampling obtained for this species according to population genetics standards.

4.1.2 Campylorhamphus pusillus

The second most divergent species in *Campylorhamphus* is *C. pusillus* from both slopes of the Andes and across it into northwestern South America and Central America, and whose 10 samples grouped all together with high statistical support in a single clade (clade 2; Figs. 1 and 2). This supports the current treatment of *C. pusillus* as an independent species (Marantz et al. 2003, Derryberry et al. 2011), but the BPP analysis indicated high speciation probabilities between lineages 2A and 2B+2C, which are found, respectively on the eastern slope of the Andes (*C. p. pusillus*) and northwestern South America and Central America (*C. p. pusillus*, *C. p. borealis*, and *C. p. olivaceus*), hence demonstrating the paraphyly of *C. p. pusillus* under current taxonomy (Marantz et al. 2003). On the other hand, speciation probabilities between lineages 2B (northwestern South America) and 2C (Central America) were not statistically significant, supporting their treatment as single, yet geographically structured species (Fig. 3). Since the type locality of *C. p. pusillus* is Bogotá, Colombia, on the eastern slope of the Andes, this name is applied only to lineage 2A, whereas the oldest name available for the trans-Andean lineages is *C. p. borealis*. Therefore, there is strong evidence for two evolutionary species under the polytypic *C. pusillus*, which are separated by the Andes and a corresponding comparatively high-uncorrected average genetic distance (3%; Fig. 1). However, given the lack of any tissues from farther north in Colombia and Venezuela in our sampling, where two unsampled taxa are found (*C. p. guapiensis* and *C. p. tachirensis*), it seems premature at this point to draw new species limits among all taxa and populations grouped under *C. pusillus*.

4.1.3 Campylorhamphus trochilirostris

The third most divergent clade groups with high support some taxa of *C. trochilirostris* (Figs. 1 and 2). All phylogenies indicated that the polytypic *C. trochilirostris*, as currently delimited (12 subspecies distributed throughout the Neotropics; Marantz et al. 2003), is polyphyletic, comprising taxa distributed in three main clades with disparate phylogenetic affinities. The first of these clades is clade 3, which groups central (*C. t. snethlageae*) and western Amazonian (*C. t. napensis*) populations and those found across the Andes (*C. t. thoracicus* and *C. t. zarumillanus*; which consisted on a single lineage - 3c; Fig. 1). BPP recovered high speciation probabilities between the Amazonian flooded forest *várzea* specialist *C. t. snethlageae* and the remaining taxa in this clade, as well as between the western Amazonian *C. t. napensis* and the trans-Andean *C. t. thoracicus* / *zarumillanus*, supporting their treatment as independent species. This is consistent with significant vocal and ecological differentiation documented among these lineages (Marantz et al. 2003, Derryberry et al. 2011). Again, our sampling of these lineages is small for assessing phylogeographic structure within them, but our samples of *C. t. snethlageae* from the Japurá River basin (where its presence had not been documented previously; Marantz et al. 2003) grouped in a distinct clade separated by an average uncorrected genetic distance of ca. 1.4% from the remaining samples obtained along the mid-lower Amazon river (Fig. 1). Although it is expected that species adapted to flooded environments are good dispersers, able to get out of local and recolonize them, depending on the phase of flood or the successional stage of (Cohn-Haft et al. 2007), this is surprising given the fact that this is a typical *várzea* specialist, for which low levels of phylogeographic structure have been reported (Aleixo 2006, Cadena et al. 2011).

The second set of taxa of *C. trochilirostris* is in the large clade 5 (lineages 3E and 3F; Fig. 1). These lineages were not reciprocally monophyletic according to the mtDNA gene tree, but they group two distinct geographic populations: one, found in southwestern Amazonia (*C. t. devius* and *notabilis*; 3E) and another occurring in central and northwestern South America in the *Chaco, Pantanal, Cerrado,* and the *Caatinga* biomes (*C. t. lafresnayanus*, *hellmayri*, and *major*; 3F; Fig. 1). These two groupings were recovered with high support as sister clades in the multi-locus species tree (Fig. 2) and as separate species according to the BPP analysis (Fig. 3).

Finally, the coastal Atlantic Forest endemic *C. t. trochilirostris* (lineage 3A) is also in clade 5, grouping as the sister taxon of either *C. procurvoides* (lineage 6) from the Guianan shield according to the concatenated analyses (Fig. 1) or the Amazonian *C. procurvoides / sanus / gyldenstolpei* (lineages 6, 7, and 8) according to the multilocus coalescent species tree (Fig. 2). The BPP analysis indicated that *C. t. trochilirostris* has coalesced significantly for the molecular markers sequenced with respect to the other Amazonian lineages in the same clade (Fig. 3), regardless of the uncertainty concerning its sister group (Figs. 1 and 2), and hence that it should also be considered an independent species.

Our combined analyses provide evidence for the splitting of the polyphyletic *C. trochilirostris* into at least six species level taxa as follows: *C. snethlageae* (endemic to the Amazonian flooded forests along the Japurá and the mid-lower Amazon rivers), *C. napensis* (found in western Amazonia along the foothills of the Andes from eastern Ecuador south to the upper Ucayali in eastern Peru), *C. thoracicus* (including *zarumillanus*; occurring in northwestern Peru, western Ecuador, and southwestern Colombia), *C. devius* (including *notabilis*; found in lowland Amazonia in southeastern Peru, northern Bolivia, and western Brazil in the states of Acre and Amazonas), *C. lafresnayanus* (including *hellmayri* and *major*; found in open vegetation biomes of Argentina, Bolivia, Brazil, and Paraguay), and *C. trochilirostris*, endemic to a narrow coastal range in the central part of the Brazilian Atlantic forest. Unfortunately, no tissue samples of the disjunct northern South / Central American taxa *C. t. venezuelensis* and *C. t. brevipennis* were available, preventing the assessment of their phylogenetic position and degree of differentiation. Therefore, given the current degree of uncertainty regarding the evolutionary independence of these taxa, and to avoid any taxonomic changes for which any evidence is lacking, we subscribe to the conservative approach of keeping both *venezuelensis* and *brevipennis* in *C. trochilirostris* until data on their phylogenetic position becomes available.

4.1.4 Campylorhamphus procurvoides

As verified with *C. trochillirostris*, the polytypic *C. procurvoides*, as defined by traditional taxonomy (Marantz et al. 2003), also consists on a polyphyletic assemblage, as already shown by Aleixo et al. (2013) and Portes et al. (2013) based on a smaller and exclusively mitochondrial dataset. Here, both the concatenated and coalescent multilocus trees are in full agreement with those in Aleixo et al. (2013) and Portes et al. (2013) in supporting the splitting of *C. procurvoides* (*sensu* Marantz et al. 2003) into six species (Figs. 1 and 2). In all instances, BPP values supported a species status for these lineages distributed in three highly supported yet unrelated clades, as follows (Fig. 3): (1) *C. multostriatus* (lineage 9 in clade 4), occurring south of the Amazon between the Xingu and Tocantins rivers in a comparatively small portion of the Xingu center of endemism (Fig. 1S; Portes et al. 2013); (2) birds found south of the Amazon and west of the Madeira River (in the Inambari center of endemism), corresponding to C. *gyldenstolpei* (lineage 7 in clade 5) and birds distributed north of the Amazon, which correspond to *C. sanus* (lineage 8 in clade 5; found in the Napo and Imeri areas of endemism) and *C. procurvoides* (lineage 6 in clade 5; from the Guiana area of endemism; Fig. 3); and (3) birds found south of the Amazon and between the Madeira and Xingu rivers, corresponding to *C. probatus* (lineages 4a and 4b in clade 5; distributed in the Madeira center of endemism; Fig. 3) and to *C. cardosoi* (lineage 5 in clade 5), endemic to the Tapajós area of endemism; Fig. 3).

Even though two strongly supported reciprocally monophyletic clades were found in *C. probatus* across the Aripuanã River (Fig. 2Sa), speciation probabilities for this node were not significant according to two of the three modeled demographic scenarios by BPP (Fig. 3), hence not supporting a species level status for these populations.

4.2 The spatio-temporal context of diversification in the genus Campylorhamphus

The combined species tree and ancestral area reconstruction analyses point towards an overall scenario of initial diversification of the genus *Campylorhamphus* in the southern (subtropical) part of the Atlantic Forest and both sides of the Andes throughout the Pliocene (3-5 mya), followed by several splitting events taking place mainly during the Pleistocene in Amazonia (0.10 - 3 mya), and a relatively more recent presence in the drier and more open habitats of central South America (*Caatinga*, *Chaco*, *Cerrado*, and *Pantanal*), starting at ca. 0.6 mya (Figs. 2 and 4).

Both BBM and S-Diva support an Atlantic Forest distribution for the ancestor of all extant *Campylorhamphus* species, with the first split dated to about 4 mya separating the Atlantic Forest endemic (*C. falcularius*) from all remaining lineages, which shared a mainly lowland Amazonian ancestor (Figs. 3 and 4). Studies on other avian groups have also recovered splits dated to the Middle Pliocene in which the Atlantic Forest endemic was basal to all remaining Neotropical lineages (Bates et al., 1998; Eberhard and Bermingham, 2005; Ribas and Miyaki, 2007; Cabanne et al., 2008; Miller et al., 2008; Patel et al., 2011), demonstrating some commonality to this pattern among widespread lineages of Neotropical birds. This period roughly coincides with an early break up of the connection between the Amazon and the Atlantic Forest dated to the Middle / Late Miocene, related, among other things, to geological events such as the Andes uplift (Hoorn et al., 2010) and associated changes in the axial grove to the east—the establishment of broad foreland basins and marine incursions (Wesselingh et al., 2006; Wesselingh and Salo, 2006), which isolated southeastern South America from the rest of the continent (Batalha-Filho et al., 2012).

The second split in *Campylorhamphus*, also dated to the Middle Miocene (ca. 3.5 mya), related to an Amazonian ancestor that reached the Andes (most likely) or the Trans-Andean lowlands in northwestern South America, originating the ancestor of *C. pusillus* (Fig. 4). Later on, but probably still in the Miocene (ca. 2 mya), populations of the Andean / Trans-Andean *C. pusillus* ancestor found across the Andes split, indicating a possible early response to the uplift of this mountain range, whole latest pulse of intense uplift took place from 5 to 2 mya (Gregory-Wodzicki, 2000; Ehlers and Poulsen, 2009). A second split across the Andes took place conspicuously later (Lower Pleistocene, at ca. 0.36 mya), involving an Amazonian ancestor that gave origin to the lowland Amazonian / Andean foothill *C. napensis* and the endemic lowland trans-Andean C. *thoracicus* (Figs 2 and 4). Since the confidence intervals of these two estimates do not overlap, they most likely represent two independent responses to the same vicariant barrier (Fig. 2).

The final closure of the Isthmus of Panama (ca 3.5 ± 0.5 mya; Coates, 1992, Weir et al. 2009) was a crucial event for the exchanges between South and Central American avifaunas (Weir et al. 2009). However, the Central American lineage of *C. pusillus* split off the South American populations during the Pleistocene (ca. 0.22 mya), thus well after the isthmus' closure, indicating a relatively recent presence in Central America. The only Central American taxon of *Campylorhamphus* not sampled in this study (*C. trochilirostris brevipennis*), barely makes it across the isthmus (Marantz et al. 2003), hence also suggesting a recent history in Central America despite the existence of a land bridge since the Pliocene.

Several other studies have shown the pervasive influence of the Andean uplift and the closure of the Panama isthmus on the diversification of Neotropical avian lineages (Miller et al. 2008; Weir et al. 2009; Fernandes et al. 2014), with *Campylorhamphus* fitting a pattern of rather limited diversification across the Andes, derived from at least two independent and relatively recent events of dispersal followed by vicariance (Figs. 2 and 4).

In contrast, starting at ca. 3 mya, most splits in *Campylorhamphus* involved Amazonian ancestors and are best explained by vicariance within this region, with two important exceptions. The first involves the Atlantic Forest endemic *C. t. trochilirostris*, which split off an Amazonian ancestor at ca. 0.45 mya (Figs. 2 and 4). Hence, the two *Campylorhamphus* lineages endemic to the Atlantic Forest, and which were shown to hybridize in this study, have completely different origins, with one (*C. falcularius*) having a much longer history in the area and phylogenetic affinities than the other (*C. t. trochilirostris*). This represents a clear example that hybridization and at least some degree of reproductive compatibility are ancestral characters that can be retained well after lineages split. Quaternary climatic changes are thought to have promoted significant biotic exchanges between Atlantic Forest and Amazonia, thus potentially causing the colonization of an Amazonian ancestor that diversified more recently in the region, as discussed for birds (Batalha-Filho et al., 2012), as well as mammals (Costa, 2003; Percequillo et al., 2011). The second recent episode of diversification in *Campylorhamphus* outside Amazonia involved the splitting of *C. lafresnayanus* (endemic to the *Caatinga*, *Chaco*, *Cerrado*, and *Pantanal* biomes in Central South America), also from a most likely Amazonian ancestor, at ca. 0.6 mya (Figs. 2 and 4). The historical biogeography of lineages endemic to the dry habitats of Central South America is rather complex, with the dominant pattern being a sister relationship between Amazonia and all arid areas, which tend to form a clade (Porzecanski and Cracraft 2005). Therefore, the history of *Campylorhamphus* in these habitats differs from this main pattern by having Amazonian rather than Atlantic Forest lineages as the nearest common ancestors (Fig. 4).

As pointed out earlier, most cladogenetic events in *Camplylorhamphus* are concentrated in the Amazonian lowlands during the Lower Pleistocene (Fig. 2). Some of these splits coincide with the location of major modern Amazonian rivers such as the Negro / Branco (separating *C. procurvoides* from *C. sanus* about 0.3 mya ago), the

Tapajós (between *C. cardosoi* and *C. probatus* at ca. 0.22 mya), the Solimões (upper Amazon, separating *C. sanus* from *C. gyldenstolpei* at ca. 0.18 mya), and the Juruena (between both reciprocally monophyletic lineages of *C. probatus* at ca. 0.12 mya). Rivers have been demonstrated to coincide with multiple splits among lineages of Amazonian upland *terra-firme* birds such as those in clade 5 of *Campylorhamphus* (Ribas et al. 2011). However, the timing of these splits reported herein for *Campylorhamphus* across the same rivers as those reported for other lineages are among the youngest ones, and reveal a very complex scenario whereby rivers can act multiple times as barriers for one or several unrelated lineages (Ribas et al. 2011, Horta et al. 2013, Fernandes et al. 2012, 2014). Supporting this notion is the fact that the Xingu River, which separates the non-sister *C. multostriatus* and *C. cardosoi*, is usually associated with later and younger splits in other Amazonian terra-firme avian lineages (Ribas et al. 2011, Horta et al. 2013, Fernandes et al. 2014); in *Campylorhamphus* however, the Xingu separates clades 4 and 5, whose splitting age could not be estimated with confidence, but which most likely predates that for the origin of the entire clade 5 (i.e., 2 mya), thus consisting in the oldest split recorded among extant Amazonian lineages. Therefore, the diversification of *Campylorhamphus* in Amazonia reinforces a growing body of evidence corroborating the role of rivers are likely important barriers promoting cladogensis in terra-firme lineages, at the same time as it highlights the commonality of idiosyncratic, lineage specific responses to these barriers (Fernandes et al. 2012, 2014).

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Appendix

Table 1S – List of *Campylorhamphus* samples sequenced in this study, with tissue and voucher information. Taxonomy follows Marantz *et al.* 2003, with updates from Portes and Aleixo 2009, Portes *et al.* 2013, Aleixo *et al.* 2013. Lineages refer to evolutionary groupings based on the obtained phylogenies (Figs. 2-4). Abbreviations of institutions housing the tissues / vouchers sequenced: FMNH, Field Museum of Natural History, Chicago, USA; KUNHM, University of Kansas, Natural History Museum, Lawrence, USA; LSUMNS, Louisiana State University, Baton-Rouge, USA; ZMUC, Zoological Museum of University of Copenhagen, Denmark; NRM, Swedish *Museum of Natural History, Swesidh;* ANSP, Academy of Natural Science of Philadelphia, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington; MPEG, Museu Paraense Emilio Goeldi, Belem, Brazil; Camp, ANP and INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; BLM, MZUSP and LFS, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; LGEMA, Laboratorio de Genética e Evolução Molecular de Aves, São Paulo, Brazil; MHNCI Museu de Historia Natural Capão do Imbuia, Curitiba, Brazil; MUSM Museo de Historia Natural de la Universidad Nacional Mayor, Lima, Peru.

				Genes (GenBank Accession numbers)				
Taxon	**Voucher / Code number***	**Lineage**	**Locality**	**BF5**	**Cyt B**	**ND2**	**ND3**	**MUSK**
Campylorhamphus falcularius	LFS 99-378/falcu1	1	Brazil: Bahia, Boa Nova	Pending	AY089810	AY089837	AY089905	Pending
Campylorhamphus falcularius	MHNCI 6083/ML4140	1	Brazil: Paraná, Tijuca do Sul	Pending	Pending	Pending	Pending	Pending
Campylorhamphus falcularius	LGEMA1529/falc1529	1	Brazil: São Paulo, E. Ec. Itabirá	Pending	Pending	GQ906723	GQ922592	Pending
Campylorhamphus falcularius	LGEMA2992/falc2992	1	Brazil: São Paulo, Buri	Pending	Pending	Pending	Pending	Pending
Campylorhamphus falcularius	LGEMA 94908/falc94908	1	Brazil: Rio de Janeiro, Cantagalo	-	Pending	Pending	Pending	Pending
Campylorhamphus falcularius	MPEG 71839/SB008	1	Brazil: Bahia, Camacã, RPPN Serra Bonita	Pending	Pending	Pending	Pending	Pending
Campylorhamphus pusillus pusillus	ANSP 4838/pus4838	2A	Ecuador: Napo, 12 Km NE El Chaco, Mirador	-	Pending	Pending	-	-
Campylorhamphus pusillus pusillus	LSUNMS B33216/pus33216	2A	Peru: Dept. Cajamarca, ca 3 Km NE São José dos Loundes	Pending	Pending	GQ906725	GQ922594	Pending
Campylorhamphus pusillus pusillus	LSUNMS B33822/pus33822	2A	Peru: Dept. Cajamarca, Cordillera del Condor, Picorama	-	FJ222626	-	-	-
Campylorhamphus pusillus pusillus	LSUNMS B11875/pus11875	2B	Ecuador: Esmeraldas, El Placer	-	KC237274	KC242895	-	-
Campylorhamphus pusillus pusillus	LSUNMS B11879/pus11879	2B	Ecuador: Esmeraldas, El Placer	-	FJ222627	-	-	-
Campylorhamphus pusillus olivaceus	LSUNMS 1411/oliv1411	2C	Panama: Darién Province, 9 Km NW Cana, Cerro Pirre	Pending	FJ222628	KC242894	Pending	Pending
Campylorhamphus pusillus olivaceus	LSUNMS B28404/oliv28404	2C	Panama: Panama Province, District Panama, NW Cero Jefe	Pending	Pending	Pending	Pending	Pending
Campylorhamphus pusillus borealis	LSUNMS B52893/bor52893	2C	Panama: Bocas del Toro Province	Pending	Pending	Pending	Pending	Pending

Campylorhamphus pusillus borealis	JTW049	2C	Panama: Bocas del Toro Province, Chiquiri Grande	-	FJ222629	-	-	-
Campylorhamphus pusillus borealis	LSUNMS B16061/bor16061	2C	Costa Rica: Heredia, Finca La Fortuna	Pending	KC237275	KC242896	Pending	Pending
Campylorhamphus trochilirostris trochilirostris	MZUSP 91431/troc91431	3A	Brazil: Bahia, Igrapiúna, Mata do Pacangê	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris trochilirostris	MZUSP 91432/troc91432	3A	Brazil: Bahia, Igrapiúna, Mata do Pacangê	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris trochilirostris	MPEG 70754/Una003	3A	Brazil: Bahia, Ilhéus, Ecoparque de UNA	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris snethlageae	INPA1474/snt1474	3B	Brazil: Amazonas, Itacoatiara	-	Pending	-	Pending	-
Campylorhamphus trochilirostris snethlageae	INPA1475/snt1475	3B	Brazil: Amazonas, Itacoatiara	-	Pending	-	Pending	-
Campylorhamphus trochilirostris snethlageae	INPA1476/snt1476	3B	Brazil: Amazonas, Itacoatiara	-	Pending	-	Pending	-
Campylorhamphus trochilirostris snethlageae	INPA 20646/snt20646	3B	Brazil: Amazonas, Itacoatiara	-	Pending	-	-	-
Campylorhamphus trochilirostris snethlageae	MPEG 43152/snt43152	3B	Brazil: Amazonia, Maraã, Rio Japurá (left bank)	-	Pending	-	Pending	-
Campylorhamphus trochilirostris snethlageae	MPEG 43154/snt43154	3B	Brazil: Amazonia, Maraã, Rio Japurá (right bank)	-	Pending	-	-	-
Campylorhamphus trochilirostris snethlageae	MPEG 56638/snt56638	3B	Brazil: Pará, Juruti, Fazenda São Joaquim	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris snethlageae	MPEG 65250/snt65250	3B	Brazil: Pará, Juruti, Lago Santarém	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris snethlageae	MPEG 65251/snt65251	3B	Brazil: Pará, Juruti, Lago Santarém	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris zarumillanus	LSUNMS183062/zar66415	3C	Peru: Tumbes, El Caucho Biological Station	Pending	Pending	Pending	Pending	-
Campylorhamphus trochilirostris zarumillanus	LSUNMS183061/zar66499	3C	Peru: Tumbes, Campo Verde	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris zarumillanus	LSUNMS183064/zar67005	3C	Peru: Tumbes, Parque Nacional Cerro de Arrotape	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris zarumillanus	LSUNMS183066/zar67112	3C	Peru: Tumbes, Parque Nacional Cerro de Arrotape	Pending	Pending	Pending	Pending	Pending

Campylorhamphus trochilirostris thoracicus	ANSP 2914/tho2914	3C	Ecuador: Manabi, Machalilla, Cerro San Sebastian	-	Pending	Pending	Pending	-
Campylorhamphus trochilirostris thoracicus	ANSP 3120/tho3120	3C	Ecuador: Manabi Machalilla, Cerro San Sebastian	-	Pending	Pending	Pending	-
Campylorhamphus trochilirostris thoracicus	ANSP 3406/tho3406	3C	Ecuador: Manabi Machalilla, Cerro San Sebastian	-	Pending	Pending	Pending	-
Campylorhamphus trochilirostris thoracicus	ANSP 4631/tho4631	3C	Ecuador: Esmeraldas, Muisne, Cabeceras de Bilsa	-	Pending	-	Pending	-
Campylorhamphus trochilirostris napensis	LSUNMS B5507/nap5507	3D	Peru: San Martin, NE Jirillo, Balsapuerto	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris napensis	LSUNMS B5544/nap5544	3D	Peru: San Martin, NE Jirillo, Balsapuerto	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris napensis	LSUNMS B40198/nap40198	3D	Peru: Loreto, ca 86 Km SE Juanjui	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris napensis	MUSM 22898/nap40445	3D	Peru: Loreto , SE Juanju, Rio Pauya	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris napensis	MUSM 23145/nap42960	3D	Peru: Loreto, SE Juanju, Rio Pauya	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	FMNH 433298/dev433298	3E	Peru: Cuzco, Paucartambo, Consuelo	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	FMNH 429954/dev429954	3E	Peru: Cuzco, Paucartambo, San Pedro	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	FMNH 429955/dev429955	3E	Peru: Cuzco, Paucartambo, San Pedro	Pending	KC237265	KC242887	Pending	Pending
Campylorhamphus trochilirostris devius	FMNH 429956/dev429956	3E	Peru: Cuzco, Paucartambo, San Pedro	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	FMNH 429957/dev429957	3E	Peru: Cuzco, Paucartambo, San Pedro	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	FMNH 433295/dev433295	3E	Peru: Madre de Dios, Moskitania	Pending	KC237269	KC242891	Pending	Pending
Campylorhamphus trochilirostris devius	FMNH 433296/dev433296	3E	Peru: Madre de Dios, Moskitania	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	FMNH 433297/dev433297	3E	Peru: Madre de Dios, Moskitania	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	FMNH 397941/dev397941	3E	Peru: Madre de Dios, Quebrada Aguas Calientes	-	Pending	Pending	Pending	-

Campylorhamphus trochilirostris devius	FMNH 433299/dev433299	3E	Peru: Madre de Dios, Moskitania	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	FMNH 433300/dev433300	3E	Peru: Madre de Dios, Moskitania	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	LSUNMS 101916/	3E	Bolivia: La Paz, Rio Beni, N Puerto Linares	-	KC237264	KC242886	Pending	-
Campylorhamphus trochilirostris devius	LSUNMS B1075/dev1075	3E	Bolivia: La Paz, N Puerto Linares	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	LSUNMS B9030/dev9030	3E	Bolivia: Pando, Nicolás Suarez	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	LSUNMS B9278/dev9278	3E	Bolivia: Pando, Nicolás Suarez	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris devius	LSUNMS105879/dev1975	3E	Peru: Pasco, Puerto Bermudez	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris notabilis	LSUNMS B11132/nap11132	3E	Peru: Ucayali, SE Cerro Tahuayo, NE Pucallpa	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris notabilis	MPEG 48154/not48154	3E	Brazil: Acre, Cruzeiro do Sul, Rio Juruá (left bank)	-	Pending	Pending	-	-
Campylorhamphus trochilirostris notabilis	MPEG 52090/not52090	3E	Brazil: Acre, Cruzeiro do Sul, Rio Juruá (left bank)	-	Pending	-	Pending	-
Campylorhamphus trochilirostris notabilis	MPEG 52091/not52091	3E	Brazil: Acre, Cruzeiro do Sul, Rio Juruá (left bank)	-	Pending	Pending	Pending	-
Campylorhamphus trochilirostris notabilis	MPEG 59811/not59811	3E	Brazil: Acre, 78 Km W Assis Brazil, Esec Rio Acre	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris notabilis	MPEG 59949/not59949	3E	Brazil: Acre, Porto Acre, Reserva Humaitá	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris notabilis	MPEG 60597/not60597	3E	Brazil: Acre, Tarauacá, Floresta Estadual do Mogno	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris notabilis	MPEG 52132/not395558	3E	Brazil: Acre, Reserva extrativista Alto Juruá, Tejo River	Pending	KC237270	KC242892	Pending	Pending
Campylorhamphus trochilirostris lafresnayanus	NRM 947183	3F	Brazil: Paraguai	EF212045	AY442987	-	-	-
Campylorhamphus trochilirostris lafresnayanus	LSUNMS B38023/laf38023	3F	Bolivia: Santa Cruz, Estancia Carilouras	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris lafresnayanus	LSUNMS B38893/laf38893	3F	Bolivia: Santa Cruz	Pending	Pending	Pending	Pending	Pending

Campylorhamphus trochilirostris lafresnayanus	LSUNMS B18663/laf18663	3F	Bolivia: Santa Cruz, Cordellera, Estancia Perforacion	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris lafresnayanus	LSUNMS B18673/laf18673	3F	Bolivia: Santa Crus, Prov. Cordillera, 130 Km E Charagua	Pending	KC237266	KC242888	AY089906	Pending
Campylorhamphus trochilirostris lafresnayanus	LSUNMS B18862/laf18862	3F	Bolivia: Santa Cruz, Prov. Cordillera, Estancia Perforacion	Pending	KC237267	KC242889	Pending	Pending
Campylorhamphus trochilirostris lafresnayanus	AMNH 833271	3F	Bolivia: Santa Cruz, Prov. Cordillera, Estancia Perforacion	-	-	GQ906722.1	GQ922591	-
Campylorhamphus trochilirostris lafresnayanus	LSUNMS B37987/laf37987	3F	Bolivia: Santa Cruz, Santa Fe, 138 Km SW San Martin	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris lafresnayanus	LSUNMS B26011/laf26011	3F	Paraguay: Presidente Hayes	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris lafresnayanus	KUNHM 91809/laf3167	3F	Paraguay: 14 km W Baía Negra, Estancia Triunfo	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris hellmayri	KUNHM 90235/hell3302	3F	Paraguay: Missiones, Estancia Santa Ana	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris major	LGEMA 2358/maj126	3F	Brazil: Piauí, Parque Nacional Serra das Confusões	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris major	LGEMA 2359/maj127	3F	Brazil: Piauí, Parque Nacional Serra das Confusões	Pending	KC237268	KC242890	Pending	Pending
Campylorhamphus trochilirostris major	MPEG 47056/maj47056	3F	Brazil: Bahia, Palmas de Monte Alto, Faz. Boa Vista	-	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris major	MPEG 50760/maj50760	3F	Brazil: Maranhão, Caxias, Rio Parnaíba (left bank)	-	Pending	-	Pending	Pending
Campylorhamphus trochilirostris major	MPEG 68201/maj68201	3F	Brazil: Piauí, José de Freitas, Eco Resort Nazareth	Pending	Pending	Pending	Pending	Pending
Campylorhamphus trochilirostris major	FMNH 392474/maj392474	3F	Brazil: Pernambuco	Pending	KC237271	KC242893	Pending	Pending
Campylorhamphus trochilirostris major	MHNCI 5614/Bal3093	3F	Brazil: Paraná, Porto São José, São Pedro do Paraná	Pending	Pending	Pending	Pending	Pending
Campylorhamphus probatus	MPEG 37033/prob37033	4A	Brazil: Rondônia , Jiparaná, Ouro Preto do Oeste	-	Pending	-	-	-
Campylorhamphus probatus	FMNH 390077/prb390077	4A	Brazil: Rondônia, Cachoeira Nazaré, Jiparaná River (rig. bank)	-	KC237262	KC242884	Pending	-
Campylorhamphus probatus	MPEG 57584/prb57584	4A	Brazil: Amazonas, Manicoré, Rod. do Estanho	Pending	KC237261	KC242883	Pending	Pending

Campylorhamphus probatus	MPEG 60954/prb60954	4B	Brazil: Pará, Juruti, Acampamento Barroso	Pending	Pending	Pending	Pending	Pending
Campylorhamphus probatus	MPEG 69627/prb69627	4B	Brazil: Pará, Jacareacanga, Sítio Chicão do Abacate	Pending	KC237263	KC242885	Pending	Pending
Campylorhamphus probatus	MPEG 69637/prb69637	4B	Brazil: Pará, Jacareacanga, Sítio Chicão do Abacate	Pending	Pending	Pending	Pending	Pending
Campylorhamphus cardosoi	MZUSP BLM547/card547	5	Brazil: Pará, Belo Monte, Rio Xingu (left bank)	Pending	Pending	Pending	Pending	Pending
Campylorhamphus cardosoi	MPEG 36490/card36490	5	Brazil: Pará, Estrada de Santarém Cuiabá (84 Km)	-	Pending	-	-	-
Campylorhamphus cardosoi	MPEG 63454/card63454	5	Brazil: Pará, Rio Xingu (left bank), Arroz Cru	-	KC237257	KC242879	-	-
Campylorhamphus cardosoi	MPEG 63875/card63875	5	Brazil: Pará, Altamira, Flona de Altamira	Pending	KC237254	KC242876	Pending	Pending
Campylorhamphus cardosoi	MPEG 63876/card63876	5	Brazil: Pará, Altamira, Flona de Altamira	-	KC237255	KC242877	-	-
Campylorhamphus cardosoi	MPEG 63877/card63877	5	Brazil: Pará, Altamira, Flona de Altamira	-	KC237256	KC242878	-	-
Campylorhamphus cardosoi	MPEG 63878/card63878	5	Brazil: Pará, Altamira, Flona de Altamira	-	Pending	Pending	-	-
Campylorhamphus cardosoi	MPEG 63879/card63879	5	Brazil: Pará, Itaituba, PARNA Jamanxim	Pending	KC237253	KC242875	Pending	Pending
Campylorhamphus cardosoi	MPEG 65687/card65687	5	Brazil, Pará, Jacareacanga, FLONA Crepori	Pending	KC237258	KC242880	Pending	Pending
Campylorhamphus cardosoi	MPEG 67667/card67667	5	Brazil: Pará, Placas	Pending	KC237259	KC242881	Pending	Pending
Campylorhamphus cardosoi	MPEG 69378/card69378	5	Brazil: Pará, Paranaíta, Rio Paranaíta (left bank)	Pending	KC237260	KC242882	Pending	Pending
Campylorhamphus cardosoi	MPEG 75655/card75655	5	Brazil: Pará, Jacareacanga, São Maritm, Rio Tapajós (right bank)	-	Pending	Pending	Pending	Pending
Campylorhamphus cardosoi	MPEG 75800/card75800	5	Brazil: Pará, Jacareacanga, Vila Mamãe Anã	-	Pending	Pending	Pending	Pending
Campylorhamphus cardosoi	MPEG 75969/card75969	5	Brazil: Para, Itaituba, Rio Tapajos (right bank), Terra Preta	-	Pending	Pending	Pending	Pending
Campylorhamphus cardosoi	MPEG 51427/card51427	5	Brazil: Mato Grosso, Alta Floresta, Teles Pires River	-	Pending	Pending	Pending	-
Campylorhamphus cardosoi	MPEG 51428/card51428	5	Brazil: Mato Grosso, Alta Floresta, Reserva Florestal Cristalino	-	Pending	Pending	Pending	-
Campylorhamphus cardosoi	MPEG 67344/card67344	5	Brazil: Mato Grosso, Paranaíta, Rio Teles Pires	Pending	Pending	Pending	Pending	Pending
Campylorhamphus cardosoi	MPEG 67346/card67346	5	Brazil: Mato Grosso, Paranaíta, Rio Teles Pires	Pending	Pending	Pending	Pending	Pending

Campylorhamphus cardosoi	MPEG 74586/card74586	5	Brazil: Mato Grosso, Peixoto de Azevedo	Pending	Pending	Pending	Pending	Pending
Campylorhamphus cardosoi	MPEG 74779/card74779	5	Brazil: Mato Grosso, Marcelândia, Santa Rita	Pending	Pending	Pending	Pending	Pending
Campylorhamphus procurvoides	ASNP 8418/proc8418	6	Guyana: Potaro-Siparuni, Reserva Iwokrama	Pending	KC237237	KC242860	Pending	Pending
Campylorhamphus procurvoides	ANSP 8435/proc8435	6	Guyana: Potaro-Siparuni, Reserva Iwokrama	Pending	KC237241	KC242864	Pending	Pending
Campylorhamphus procurvoides	USNM B9338/proc9338	6	Guyana: Northwest District, Baramita	Pending	KC237238	KC242861	Pending	Pending
Campylorhamphus procurvoides	USNM B9589/proc9589	6	Guyana: Northwest District, Baramita	-	KC237239	KC242862	Pending	Pending
Campylorhamphus procurvoides	USNM B9741/proc9741	6	Guyana: Northwest District, Baramita	-	KC237240	KC242863	Pending	Pending
Campylorhamphus procurvoides	LSUNMS B25514/proc25514	6	Brazil: Amazonas, Estação Ecológica Anavilhanas	Pending	KC237242	KC242865	Pending	Pending
Campylorhamphus procurvoides	INPA 7855/proc7855	6	Barsil: Amazonas, Manaus, Reserva Ducke	Pending	Pending	Pending	Pending	Pending
Campylorhamphus procurvoides	MPEG 64656/proc64656	6	Brazil: Pará, Flota de Faro, c.a. 70Km NW Faro	Pending	KC237243	KC242866	Pending	Pending
Campylorhamphus procurvoides	MPEG 64657/proc64657	6	Brazil: Pará, Flota de Faro, c.a. 70Km NW Faro	-	KC237245	KC242868	-	-
Campylorhamphus procurvoides	MPEG 65036/proc65036	6	Brazil: Pará, Óbidos, Flota Trombetas	Pending	KC237247	KC242870	Pending	Pending
Campylorhamphus procurvoides	MPEG 65037/proc65037	6	Brazil: Pará, Óbidos, Flota Trombetas	Pending	KC237246	KC242869	Pending	Pending
Campylorhamphus procurvoides	MPEG 66219/proc66219	6	Brazil: Pará, Almerim, REBIO Maicurú	Pending	KC237244	KC242867	Pending	Pending
Campylorhamphus gyldenstolpei	MZUSP 76641/gyld111	7	Brazil: Rondônia, Estacao Ecologica Mujica Nava	Pending	Pending	Pending	Pending	Pending
Campylorhamphus gyldenstolpei	INPA 1630/gyld1378	7	Brazil: Amazonas, Campo Tupana, ca 120 Km S de Manaus	-	Pending	Pending	-	-
Campylorhamphus gyldenstolpei	MPEG 60081/gyld025	7	Brazil: Amazonas: RDS Cujubim	Pending	KC237251	KC242873	Pending	Pending
Campylorhamphus gyldenstolpei	MPEG 62267/gyld62267	7	Brazil: Amazonas, Careiro, BR 319 km 158, Tupana Lodge	Pending	KC237252	KC242874	Pending	Pending
Campylorhamphus gyldenstolpei	MPEG 68870/gyld68870	7	Brazil: Amazonas, Careiro, BR 319 km 158, Tupana Lodge	Pending	KC237250	KC242872	Pending	Pending
Campylorhamphus sanus	LSUNMS B7159/sanus7159	8	Peru: Loreto, 5 Km N Amazonia and 85 Km NE Iquitos	Pending	Pending	Pending	Pending	Pending
Campylorhamphus sanus	LSUNMS B7231/sanus7231	8	Peru: Loreto, 5 Km N Amazonia and 85 Km NE Iquitos	Pending	KC237248	KC242871	Pending	Pending
Campylorhamphus sanus	LSUNMS B7501/sanus7501	8	Venezuela: Amazonas, Cerro de la Neblina	Pending	KC237249	GQ906724	GQ922593	Pending

Campylorhamphus sanus	MPEG 77416/sanus77416	8	Brazil: Amazonas, São Gabriel da Cachoeira	-	Pending	Pending	-	Pending
Campylorhamphus multostriatus	ANP083/mult083	9	Brazil: Pará, Belo Monte , Rio Xingu (right bank)	Pending	Pending	Pending	Pending	Pending
Campylorhamphus multostriatus	MZUSP BLM395/mult395	9	Brazil: Pará, Belo Monte , Rio Xingu (right bank)	Pending	Pending	Pending	Pending	Pending
Campylorhamphus multostriatus	USNM B6910/mult6910	9	Brazil: Pará, Altamira, Rio Xingu (right bank)	Pending	KC237273	Pending	Pending	Pending
Campylorhamphus multostriatus	MPEG 36086/mult36086	9	Brazil: Pará, Tucurui, Igarapé Saude	-	Pending	Pending	-	-
Campylorhamphus multostriatus	MPEG 38290/mult38290	9	Brazil: Pará, Serra Carajás, Serra Norte - Fofoca	-	KC237272	Pending	Pending	-
Campylorhamphus multostriatus	MPEG 68871/mult68871	9	Brazil: Pará, Floresta Nacional de Carajás	Pending	Pending	Pending	Pending	Pending
Lepidocolaptes angustirostris	UFPI 7013/angu7013	outgroup	Brazil: Piauí, Castelo do Piauí	Pending	Pending	Pending	Pending	Pending
Lepidocolaptes falcinellus	MPEG 64820/cine64820	outgroup	Brazil: Rio Grande do Sul, Caramba do Sul	Pending	Pending	Pending	Pending	Pending
Lepidocolapes albolineatus	MPEG 59471/albo59471	outgroup	Brazil: Amazonas, Novo Airão	Pending	Pending	Pending	Pending	Pending
Dendroplex picus	MPEG 62684/picu62684	outgroup	Brazil: Amazonas, Japurá	Pending	Pending	Pending	Pending	Pending

***** Code numbers are used to denote samples in phylogenies depicted in figures 1Sa and 1Sb.

Table 2Sa – List of primers used to amplify the three mitochondrial and two nuclear genes; the sequences are in position 5’ to 3’ of the Chicken (Desjardins and Morais 1990).

Primer	5' to 3'	Gene	Reference
L5215	TATCGGGCCCATACCCCGAAAAT	ND2	Hackett 1996
H6313	CTCTTATTTAAGGCTTTGAAGGC		Sorenson et al. 1999
L10755	GACTTCCAATCTTTAAAATCTGG	ND3	Chesser, 1999
H11151	GATTTGTTGAGCCGAAATCAA		
L14841	GCTTCCATCCAACATCTCAGCATGATGAAA	Cytb	Kocher et al. 1989
H16064	CTTCANTYTTTGGYTTACAAGRCC		
Musk 3F	CTTCCATGCACTACAATGGGAAA	MUSK	Kimball *et al.* 2009
Musk 3R	CTCTGAACATTGTGGATCCTCAA		
S713	CGCCATACAGAGTATACTGTGACAT	BF5	Brumfield *et al.,* 2007
AS767	GCCATCCTGGCGATCTGAA		

Table 2Sb – List of primers used to amplify cytochrome *b* of toe pad samples; the sequences are in position 5’ to 3’ of the Chicken (Desjardins and Morais 1990).

Primer	Sequence 5' to 3'
Lwood2	5'-CGT AAC CTC CAY GCA AAC GGA GCC-3'
Lwood3	5'-GGR GGA TTC TCA GTA GAC AAC CC-3'
Lwood4	5'-GGT GTA CTA GCT ATA TTC TCA CC-3'
Lwood5	5'-CCT ATT CCT AGT CCC ATT CCT CC-3'
Hwood1	5'-GCC TCG TCC GAT GTG GAG G-3'
Hwood2	5'-GGA AGT GTA GGG CRA AGA ATC G-3'
Hwood3	5'-GGA GGG GTT ACT AGT GGG TTT GCA GG-3'
Hwood4	5'-GGG GRC GRA ARG TTA TTG TTC G-3'

Table 3S – List of *Campylorhamphus* samples included in different data partitions and analyses. Taxonomy follows Marantz *et al.* 2003, with updates from Portes and Aleixo 2009, Portes *et al.* 2013, Aleixo *et al.* 2013. Lineages refer to evolutionary groupings based on the obtained phylogenies (Figs. 2-4). Abbreviations of institutions housing the tissues / vouchers sequenced: FMNH, Field Museum of Natural History, Chicago, USA; KUNHM, University of Kansas, Natural History Museum, Lawrence, USA; LSUMNS, Louisiana State University, Baton-Rouge, USA; ZMUC, Zoological Museum of University of Copenhagen, Denmark; NRM, Swedish *Museum of Natural History, Swesidh;* ANSP, Academy of Natural Science of Philadelphia, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington; MPEG, Museu Paraense Emilio Goeldi, Belem, Brazil; Camp, ANP and INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; BLM, MZUSP and LFS, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; LGEMA, Laboratorio de Genética e Evolução Molecular de Aves, São Paulo, Brazil; MHNCI Museu de Historia Natural Capão do Imbuia, Curitiba, Brazil, MUSM Museo de Historia Natural de la Universidad Nacional Mayor, Lima, Peru.

Taxon	Voucher	Lineages	Locality	Voucher Code				
					mtDNA	nuDNA	BPP	Specietree
Campylorhamphus falcularius	LFS 99-378	1	Brazil: Bahia, Boa Nova	falcu1	X	X	X	X
Campylorhamphus falcularius	MHNCI 6083	1	Brazil: Paraná, Tijuca do Sul	ML4140	X	X	X	X
Campylorhamphus falcularius	LGEMA1529	1	Brazil: São Paulo, E. Ec. Itabirá	falc1529	X	X	X	X
Campylorhamphus falcularius	LGEMA2992	1	Brazil: São Paulo, Buri	falc2992	X	X	X	X
Campylorhamphus falcularius	MZUSP 94908	1	Brazil: Rio de Janeiro, Cantagalo	falc94908	X		X	X
Campylorhamphus falcularius	MPEG 71839	1	Brazil: Bahia, Serra Bonita	SB008	X	X		
Campylorhamphus pusillus pusillus	LSU B33822	2A	Peru: Cajamarca, Cordillera del Condor, Picorama	pus33822			X	X
Campylorhamphus pusillus pusillus	LSU B33216	2A	Peru: Cajamarca, ca 3 Km NE São José dos Loundes	pus33216	X	X	X	X
Campylorhamphus pusillus pusillus	ANSP 4838	2A	Ecuador: Napo, 12 Km NE El Chaco, Mirador	pus4838	X		X	X
Campylorhamphus pusillus pusillus	ZMUC S1451	2A	Ecuador: Zomara-Chichipe	pus1451				X
Campylorhamphus pusillus pusillus	LSU B11875	2B	Ecuador: Esmeraldas	pus11875	X	X	X	X
Campylorhamphus pusillus pusillus	LSU B11879	2B	Ecuador: Esmeraldas, El Placer	pus11879			X	X
Campylorhamphus pusillus olivaceus	LSU B1411	2C	Panama: Darién Province, 9 Km NW Cana, Cerro Pirre	oliv1411	X	X	X	X
Campylorhamphus pusillus olivaceus	LSU B28404	2C	Panamá: Panama Province, District Panama, NW Cero Jefe	oliv28404	X	X	X	X
Campulorhamphus pusillus borealis	LSU B52893	2C	Panama: Bocas del Toro Province, Gulalace-Chiriqui Grande	bor52893	X	X	X	X
Campulorhamphus pusillus borealis	JTW094	2C	Panama: Bocas del Toro Province, Chiriqui Grande	bor094				X
Campulorhamphus pusillus borealis	LSU B16061	2C	Costa Rica: Heredia, Finca La Fortuna	bor16061	X	X	X	X
Campylorhamphus trochilirostris trochilirostris	MZUSP 91431	3A	Brazil: Bahia, Igrapiúna, Mata do Pacangê	troc91431	X	X	X	X
Campylorhamphus trochilirostris trochilirostris	MZUSP 91432	3A	Brazil: Bahia, Igrapiúna, Mata do Pacangê	troc91432	X	X	X	X

Campylorhamphus trochilirostris trochilirostris	MPEG 70754	3A	Brazil: Bahia, Ilhéus, Ecoparque de UNA	troc70754	X	X	X	X
Campylorhamphus trochilirostris snethlageae	INPA1474	3B	Brazil: Amazonas, Itacoatiara	snt1474	X		X	X
Campylorhamphus trochilirostris snethlageae	INPA1475	3B	Brazil: Amazonas, Itacoatiara	snt1475	X		X	X
Campylorhamphus trochilirostris snethlageae	INPA1476	3B	Brazil: Amazonas, Itacoatiara	snt1476	X		X	X
Campylorhamphus trochilirostris snethlageae	INPA 20646	3B	Brazil: Amazonas, Itacoatiara	snt20646	X		X	X
Campylorhamphus trochilirostris snethlageae	MPEG 43152	3B	Brazil: Amazonia, Maraã, Rio Japurá (left bank)	snt43152	X		X	X
Campylorhamphus trochilirostris snethlageae	MPEG 43154	3B	Brazil: Amazonia, Maraã, Rio Japurá (right bank)	snt43154	X		X	X
Campylorhamphus trochilirostris snethlageae	MPEG 56638	3B	Brazil: Pará, Juruti, Fazenda São Joaquim	snt56638	X	X	X	X
Campylorhamphus trochilirostris snethlageae	MPEG 65250	3B	Brazil: Pará, Juruti, Lago Santarém	snt65250	X	X	X	X
Campylorhamphus trochilirostris snethlageae	MPEG 65251	3B	Brazil: Pará, Juruti, Lago Santarém	snt65251	X	X	X	X
Campylorhamphus trochilirostris zarumillanus	LSU 183062	3C	Peru: Tumbes, El Caucho Biological Station	zar66415	X	X	X	X
Campylorhamphus trochilirostris zarumillanus	LSU 183061	3C	Peru: Tumbes, Campo Verde	zar66499	X	X	X	X
Campylorhamphus trochilirostris zarumillanus	LSU 183064	3C	Peru: Tumbes, Parque Nacional Cerro de Arrotape	zar67005	X	X	X	X
Campylorhamphus trochilirostris zarumillanus	LSU 183066	3C	Peru: Tumbes, Parque Nacional Cerro de Arrotape	zar67112	X	X	X	X
Campylorhamphus trochilirostris thoracicus	ANSP 2914	3C	Ecuador: Manabi, Machalilla, Cerro San Sebastian	tho2914	X		X	X
Campylorhamphus trochilirostris thoracicus	ANSP 3120	3C	Ecuador: Manabi Machalilla, Cerro San Sebastian	tho3120	X		X	X
Campylorhamphus trochilirostris thoracicus	ANSP 3406	3C	Ecuador: Manabi Machalilla, Cerro San Sebastian	tho3406	X		X	X
Campylorhamphus trochilirostris thoracicus	ANSP 4631	3C	Ecuador: Esmeraldas, Muisne, Cabeceras de Bilsa	tho4631	X		X	X
Campylorhamphus trochilirostris napensis	LSU B5507	3D	Peru: San Martin, NE Jirillo, Balsapuerto	nap5507	X	X	X	X
Campylorhamphus trochilirostris napensis	LSU B5544	3D	Peru: San Martin, NE Jirillo, Balsapuerto	nap5544	X	X	X	X
Campylorhamphus trochilirostris napensis	LSU B40198	3D	Peru: Loreto, ca 86 Km SE Juanjui	nap40198	X	X	X	X
Campylorhamphus trochilirostris napensis	MUSM 22898	3D	Peru: Loreto , SE Juanju, Rio Pauya	nap40445	X	X	X	X
Campylorhamphus trochilirostris napensis	MUSM B42960	3D	Peru: Loreto, SE Juanju, Rio Pauya	nap42960	X	X	X	X
Campylorhamphus trochilirostris devius	FMNH 429954	3E	Peru: Cuzco, Paucartambo, San Pedro	dev429954	X	X	X	X
Campylorhamphus trochilirostris devius	FMNH 429955	3E	Peru: Cuzco, Paucartambo, San Pedro	dev429955	X	X	X	X
Campylorhamphus trochilirostris devius	FMNH 429956	3E	Peru: Cuzco, Paucartambo, San Pedro	dev429956	X	X	X	X
Campylorhamphus trochilirostris devius	FMNH 429957	3E	Peru: Cuzco, Paucartambo, San Pedro	dev429957	X	X	X	X
Campylorhamphus trochilirostris devius	FMNH 433298	3E	Peru: Cuzco, Paucartambo, Consuelo	dev433298	X	X	X	X
Campylorhamphus trochilirostris devius	FMNH 397941	3E	Peru: Madre de Dios, Quebrada Aguas	dev397941	X		X	X

			Calientes					
Campylorhamphus trochilirostris devius	FMNH 433295	3E	Peru: Madre de Dios, Moskitania, 14 Km NW Atalaya	dev433295	X	X	X	X
Campylorhamphus trochilirostris devius	FMNH 433296	3E	Peru: Madre de Dios, Moskitania, 14 Km NW Atalaya	dev433296	X	X	X	X
Campylorhamphus trochilirostris devius	FMNH 433297	3E	Peru: Madre de Dios, Moskitania, 14 Km NW Atalaya	dev433297	X	X	X	X
Campylorhamphus trochilirostris devius	FMNH 433299	3E	Peru: Madre de Dios, Moskitania, 14 Km NW Atalaya	dev433299	X	X	X	X
Campylorhamphus trochilirostris devius	FMNH 433300	3E	Peru: Madre de Dios, Moskitania, 14 Km NW Atalaya	dev433300	X	X	X	X
Campylorhamphus trochilirostris devius	LSU B1075	3E	Bolivia: La Paz, Beni river, N Puerto Linares	dev1075	X	X	X	X
Campylorhamphus trochilirostris devius	LSU B978	3E	Bolivia: La Paz, Rio Beni, N Puerto Linares	dev978	X		X	X
Campylorhamphus trochilirostris devius	LSU B9030	3E	Bolivia: Pando, Nicolás Suarez	dev9030	X	X	X	X
Campylorhamphus trochilirostris devius	LSU B9278	3E	Bolivia: Pando, Nicolás Suarez	dev9278	X	X	X	X
Campylorhamphus trochilirostris notabilis	LSU105879	3D	Peru: Pasco, Km 41 de Vila Rica, Puerto Bermudez	dev1975	X	X	X	X
Campylorhamphus trochilirostris notabilis	LSU B11132	3D	Peru: Ucayali, SE Cerro Tahuayo, NE Pucallpa	not11132	X	X	X	X
Campylorhamphus trochilirostris notabilis	MPEG 48154	3E	Brazil: Acre, Cruzeiro do Sul, Sobral, Rio Juruá (left bank)	not48154	X		X	X
Campylorhamphus trochilirostris notabilis	MPEG 52090	3E	Brazil: Acre, Cruzeiro do Sul, Sobral, Rio Juruá (left bank)	not52090	X		X	X
Campylorhamphus trochilirostris notabilis	MPEG 52091	3E	Brazil: Acre, Cruzeiro do Sul, Sobral, Rio Juruá (left bank)	not52091	X		X	X
Campylorhamphus trochilirostris notabilis	MPEG 59811	3E	Brazil: Acre, 78 Km W Assis Brazil, Esec Rio Acre	not59811	X	X	X	X
Campylorhamphus trochilirostris notabilis	MPEG 59949	3E	Brazil: Acre, Porto Acre, Reserva Humaitá	not59949	X	X	X	X
Campylorhamphus trochilirostris notabilis	MPEG 60597	3E	Brazil: Acre, Tarauacá, Floresta Estadual do Mogno	not60597	X	X	X	X
Campylorhamphus trochilirostris notabilis	FMNH395558	3E	Brazil: Acre, Reserva extrativista Alto Juruá, Tejo River	not395558	X	X	X	X
Campylorhamphus trochilirostris lafresnayanus	NRM 947183	3F	Brazil: Paraguai	laf947183				X
Campylorhamphus trochilirostris lafresnayanus	LSU B37987	3F	Bolivia: Santa Cruz, Santa Fe, 138 Km SW San Martin	laf37987	X	X	X	X
Campylorhamphus trochilirostris lafresnayanus	LSU B38023	3F	Bolivia: Santa Cruz, Estancia Carilouras	laf38023	X	X	X	X
Campylorhamphus trochilirostris lafresnayanus	LSU B38893	3F	Bolivia: Santa Cruz	laf38893	X	X	X	X
Campylorhamphus trochilirostris lafresnayanus	LSU B18663	3F	Bolivia: Santa Cruz, Cordellera, Estancia Perforacion	laf18663	X	X	X	X

Campylorhamphus trochilirostris lafresnayanus	LSU B18673	3F	Bolivia: Santa Crus, prov. Cordillera, 130 Km E Charagua	laf18673	X	X	X	X
Campylorhamphus trochilirostris lafresnayanus	LSU B18862	3F	Bolivia: Santa Cruz, prov. Cordillera, Estancia Perforacion	laf18862	X	X	X	X
Campylorhamphus trochilirostris lafresnayanus	AMNH 833271	3F	Bolivia: Santa Cruz, prov. Cordillera, Estancia San Julian	laf2234	X			X
Campylorhamphus trochilirostris lafresnayanus	LSU B26011	3F	Paraguay: Presidente Hayes	laf26011	X	X	X	X
Campylorhamphus trochilirostris lafresnayanus	KU 91809	3F	Paraguay: 14 km W Bahia Negra, Estancia Triunfo	laf3167	X	X	X	X
Campylorhamphus trochilirostris hellmayri	KU 90235	3F	Paraguay: Missiones, Estancia Santa Ana	hell3302	X	X	X	X
Campylorhamphus trochilirostris major	LGEMA 2358	3F	Brazil: Piauí, Parque Nacional Serra das Confusões	maj126	X	X	X	X
Campylorhamphus trochilirostris major	LGEMA 2359	3F	Brazil: Piauí, Parque Nacional Serra das Confusões	maj127	X	X	X	X
Campylorhamphus trochilirostris major	MPEG 47056	3F	Brazil: Bahia, Palmas de Monte Alto, Faz. Boa Vista	maj47056	X		X	X
Campylorhamphus trochilirostris major	MPEG 50760	3F	Brazil: Maranhão, Caxias, Rio Parnaíba (left bank)	maj50760	X		X	X
Campylorhamphus trochilirostris major	MPEG 68201	3F	Brazil: Piauí, José de Freitas, Eco Resort Nazareth	maj68201	X	X	X	X
Campylorhamphus trochilirostris major	FMNH 392474	3F	Brazil: Pernambuco	maj392474	X	X	X	X
Campylorhamphus trochilirostris major	MHNCI 5614	3F	Brazil: Paraná, Porto São José, São Pedro do Paraná	Bal3093	X	X	X	X
Campylorhamphus probatus	MPEG 57584	4A	Brazil: Amazonas, Manicore, Rod. do Estanho	prb57584	X	X	X	X
Campylorhamphus probatus	FMNH 390077	4A	Brazil: Rondônia, Cachoeira Nazaré, Jipaná river	prb390077	X		X	X
Campylorhamphus probatus	MPEG 37033	4A	Brazil: Rondônia , Jiparaná, Ouro Preto do Oeste	prob37033			X	X
Campylorhamphus probatus	INPA 1477	4A	Brazil: Amazônas, Itacoatiara	prob1477	X			X
Campylorhamphus probatus	MPEG 60954	4B	Brazil: Pará, Juruti, Acampamento Barroso	prb60954	X	X	X	X
Campylorhamphus probatus	MPEG 69627	4B	Brazil: Pará, Jacareacanga, Sítio Chicão do Abacate	prb69627	X	X	X	X
Campylorhamphus probatus	MPEG 69637	4B	Brazil: Pará, Jacareacanga, Sítio Chicão do Abacate	prb69637	X	X	X	X
Campylorhamphus cardosoi	MZUSP BLM547	5	Brazil: Pará, Belo Monte, Rio Xingu (right bank)	card547	X	X	X	X
Campylorhamphus cardosoi	MPEG 36490	5	Brazil: Pará, Estrada de Santarém Cuibá (84 Km)	card36490	X		X	X
Campylorhamphus cardosoi	MPEG 63454	5	Brazil: Pará, Rio Xingu (left bank), Arroz	card63454	X		X	X

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Campylorhamphus cardosoi	MPEG 63875	5	Brazil: Pará, Altamira, Flona de Altamira	card63875	X	X	X	X
Campylorhamphus cardosoi	MPEG 63876	5	Brazil: Pará, Altamira, Flona de Altamira	card63876	X		X	X
Campylorhamphus cardosoi	MPEG 63877	5	Brazil: Pará, Altamira, Flona de Altamira	card63877	X		X	X
Campylorhamphus cardosoi	MPEG 63878	5	Brazil: Pará, Altamira, Flona de Altamira	card63878	X		X	X
Campylorhamphus cardosoi	MPEG 63879	5	Brazil: Pará, Itaituba, PABNA Jamanxim	card63879	X	X	X	X
Campylorhamphus cardosoi	MPEG 75969	5	Brazil: Pará, Itaituba, Rio Tapajos (right bank), Terra Preta	card75969	X		X	X
Campylorhamphus cardosoi	MPEG 67667	5	Brazil: Pará, Placas, Assentamento Comunidade Fortaleza	card67667	X	X	X	X
Campylorhamphus cardosoi	MPEG 69378	5	Brazil: Prá, Paranaíta, Rio Paranaíta (left bank)	card69378	X	X	X	X
Campylorhamphus cardosoi	MPEG 75655	5	Brazil: Pará, Jacareacanga, San Marins, Rio Tapajos (right bank)	card75655	X		X	X
Campylorhamphus cardosoi	MPEG 75800	5	Brazil: Pará, Jacareacanga, Vila Mamae Ana, Rio Tapajos	card75800	X		X	X
Campylorhamphus cardosoi	MPEG 65687	5	Brazil, Pará, Jacareacanga, FLONA Crepori	card65687	X	X	X	X
Campylorhamphus cardosoi	MPEG 51427	5	Brazil: Mato Grosso, Alta Floresta, Teles Pires River	card51427	X		X	X
Campylorhamphus cardosoi	MPEG 51428	5	Brazil: Mato Grosso, Reserva Florestal Cristalino	card51428	X		X	X
Campylorhamphus cardosoi	MPEG 67344	5	Brazil: Mato Grosso, Paranaíta, Rio Teles Pires	card67344	X	X	X	X
Campylorhamphus cardosoi	MPEG 67346	5	Brazil: Mato Grosso, Paranaíta,Rio Teles Pires	card67346	X	X	X	X
Campylorhamphus cardosoi	MPEG 74586	5	Brazil: Mato Grosso, Peixoto de Azevedo	card74586	X	X	X	X
Campylorhamphus cardosoi	MPEG 74779	5	Brazil: Mato Grosso, Santa Rita	card74779	X	X	X	X
Campylorhamphus procurvoides	ASNP 8418	6	Guyana: Potaro-Siparuni, Reserva Iwokrama	proc8418	X	X	X	X
Campylorhamphus procurvoides	ANSP 8435	6	Guyana: Potaro-Siparuni, Reserva Iwokrama	proc8435	X	X	X	X
Campylorhamphus procurvoides	USNM B9338	6	Guyana: Northwest District, Baramita	proc9338	X	X	X	X
Campylorhamphus procurvoides	USNM B9589	6	Guyana: Northwest District, Baramita	proc9589	X		X	X
Campylorhamphus procurvoides	USNM B9741	6	Guyana: Northwest District, Baramita	proc9741	X		X	X
Campylorhamphus procurvoides	INPA A7855	6	Barsil: Amazonas, Manaus, Reserva Ducke	proc7855	X	X	X	X
Campylorhamphus procurvoides	LSU B25514	6	Brazil: Amazonas, Estacao Ecologica Anavilhanas	proc25514	X	X	X	X
Campylorhamphus procurvoides	MPEG 64656	6	Brazil: Pará, Flota de Faro, c.a. 70Km NW Faro	proc64656	X	X	X	X
Campylorhamphus procurvoides	MPEG 64657	6	Brazil: Pará, Flota de Faro, c.a. 70Km NW	proc64657	X	X	X	X

			Faro					
Campylorhamphus procurvoides	MPEG 65036	6	Brazil: Pará, Óbidus, Flota Trombetas	proc65036	X	X	X	X
Campylorhamphus procurvoides	MPEG 65037	6	Brazil: Pará, Óbidus, Flota Trombetas	proc65037	X	X	X	X
Campylorhamphus procurvoides	MPEG 66219	6	Brazil: Pará, Almerim, Rebio Maicore	proc66219	X	X	X	X
Campylorhamphus gyldenstolpei	MZUSP 76641	7	Brazil: Rondônia, Estacao Ecologica Mujica Nava	gyld111	X	X	X	X
Campylorhamphus gyldenstolpei	INPA 1378	7	Brazil: Amazonas, Campo Tupana, ca 120 Km S de Manaus	gyld1378	X		X	X
Campylorhamphus gyldenstolpei	MPEG 60081	7	Brazil: Amazonas: RDS Cojubim	gyld025	X	X	X	X
Campylorhamphus gyldenstolpei	MPEG 62267	7	Brazil: Amazonas, Careiro, BR 319 km 158, Tupana Lodge	gyld62267	X	X	X	X
Campylorhamphus gyldenstolpei	MPEG 68870	7	Brazil: Amazonas, Careiro, BR 319 km 158, Tupana Lodge	gyld68870	X	X	X	X
Campylorhamphus sanus	LSU B7159	8	Peru: Loreto, 5 Km N Amazonia and 85 Km NE Iquitos	sanus7159	X	X	X	X
Campylorhamphus sanus	LSU B7231	8	Peru: Loreto, 5 Km N Amazonia and 85 Km NE Iquitos	sanus7231	X	X	X	X
Campylorhamphus sanus	LSU B7501	8	Venezuela: Dept. Amazonas, Cerro de la Neblina	sanus7501	X	X	X	X
Campylorhamphus sanus	MPEG 77416	8	Brazil: Amazonas, Sao Gabriel da Cachoeira, PPBIO	sanus77416	X	X	X	X
Campylorhamphus multostriatus	ANP083	9	Brazil: Pará, Belo Monte , Rio Xingu (right bank)	mult083	X	X	X	X
Campylorhamphus multostriatus	MZUSP BLM395	9	Brazil: Pará, Belo Monte , Rio Xingu (right bank)	mult395	X	X	X	X
Campylorhamphus multostriatus	USNM B6910	9	Brazil: Pará, Altamira, Rio Xingu (right bank)	mult6910	X	X	X	X
Campylorhamphus multostriatus	MPEG 36086	9	Brazil: Pará, Tucurui, Igarapé Saude	mult36086	X		X	X
Campylorhamphus multostriatus	MPEG 38290	9	Brazil: Pará, Serra Carajás, Serra Norte - Fofoca	mult38290	X		X	X
Campylorhamphus multostriatus	MPEG 68871	9	Brazil: Pará, Floresta Nacional de Carajás	mult68871	X	X	X	X
Lepidocolaptes angustirostris	UFPI 7013	outgroup	Brazil: Piauí, Castelo do Piauí	angu7013	X	X	X	X
Lepidocolaptes falcinellus	MPEG 64820	outgroup	Brazil: Rio Grande do Sul, Caramba do Sul	cine64820	X	X	X	X
Lepidocolapes albolineatus	MPEG 59471	outgroup	Brazil: Amazonas, Novo Airão	albo59471	X	X	X	X
Dendroplex picus	MPEG 62684	outgroup	Brazil: Amazonas, Japurá	picu62684	X	X	X	X

***** Code numbers are used to denote samples in phylogenies depicted in figures 1Sa and 1Sb.

Table 4S – Average uncorreted (*p*) distances based on the Cyt *b* and ND2 genes. Numbers refer to the specie tree terminal branches (Fig. 3). Numbers on top and right: 1=*C. falcularius,* 2A= *C. pusillus* nominate form east side of Andes, 2B= *C. pusillus* nominate form west side of Andes, 2C= : *C. pusillus olivaceus/borealis,* 3A= *C. trochlirostris* nominate, 3B= *C. t. snethlageae*, 3C= *C. t. thoracicus/zarumillanus,* 3D= *C. t. napensis,* 3E= *C. t. devius/notabilis,* 3F= *C. t. major/lafresnayanus/hellmayri,* 4A= *C. probatus* from west side of Aripuanã River, 4B= *C. probatus* from east side of Aripuanã River, 5= *C. cardosoi*, 6= *C. procurvoides,* 7= *C. gyldenstolpei*, 8= *C. sanus*, 9= *C. multostriatus.*

	4A	4B	5	3E	3F	8	7	6	3A	9	3B	3C	3D	2C	2B	2A
4A																
4B	0.50%															
5	0.80%	0.70%														
3E	2.50%	2.10%	2.40%													
3F	2.40%	2.40%	2.60%	0.50%												
8	4.10%	4.00%	4.40%	3.80%	4.00%											
7	3.90%	3.90%	4.30%	3.60%	3.80%	0.60%										
6	3.80%	3.80%	4.10%	3.60%	3.70%	1.10%	1.00%									
3A	3.80%	3.90%	4.20%	3.60%	3.80%	1.40%	1.30%	0.70%								
9	5.70%	5.80%	6.00%	5.90%	6.10%	5.70%	5.70%	5.50%	5.50%							
3B	5.90%	5.90%	6.10%	5.80%	5.90%	5.60%	5.40%	5.40%	5.30%	6.60%						
3C	5.10%	5.80%	5.10%	5.40%	5.50%	5.30%	5.10%	4.70%	4.90%	6.10%	3.60%					
3D	5.40%	5.00%	5.30%	5.60%	5.70%	5.40%	5.10%	4.90%	5.10%	6.00%	3.60%	1.10%				
2C	6.80%	6.70%	6.70%	6.80%	6.80%	7.10%	6.70%	6.60%	6.50%	7.60%	6.80%	6.60%	6.30%			
2B	6.10%	6.20%	6.50%	6.60%	6.60%	6.80%	6.50%	6.40%	6.40%	7.40%	6.90%	6.60%	6.30%	0.60%		
2A	5.90%	5.90%	6.00%	6.30%	6.40%	6.40%	6.20%	6.10%	6.20%	6.80%	6.30%	5.80%	5.90%	5.10%	5.20%	
1	7.20%	7.30%	7.40%	7.30%	7.40%	7.40%	7.10%	7.10%	6.90%	8.00%	7.30%	7.30%	7.30%	7.70%	7.70%	7.60%

Figure 1S - Localities where samples used in this study were collected (see also Table 1S). Legend: (A) *Campylorhamphus falcularius;* (B) *Campylorhamphus trochilirostris* complex; (C) *Campylorhamphus procurvoides* complex (; update, Portes et al. 2013); (D) *Campylorhamphus pusillus* complex. Green crosshatched represent the range distribution by Infonatura (www.infonatura.natureserve.otg), in which following Marantz et al (2003); red crosshatched represente the extension range of *C. t. snethlageae;* blue crosshatched represente the extension range of *C. t. notabilis.* The taxonomy follows (Marantz et al. 2003; Portes et al., 2013; Portes and Aleixo, 2009; Aleixo et al., 2013; Remsen et al., 2014; CBRO, 2014).

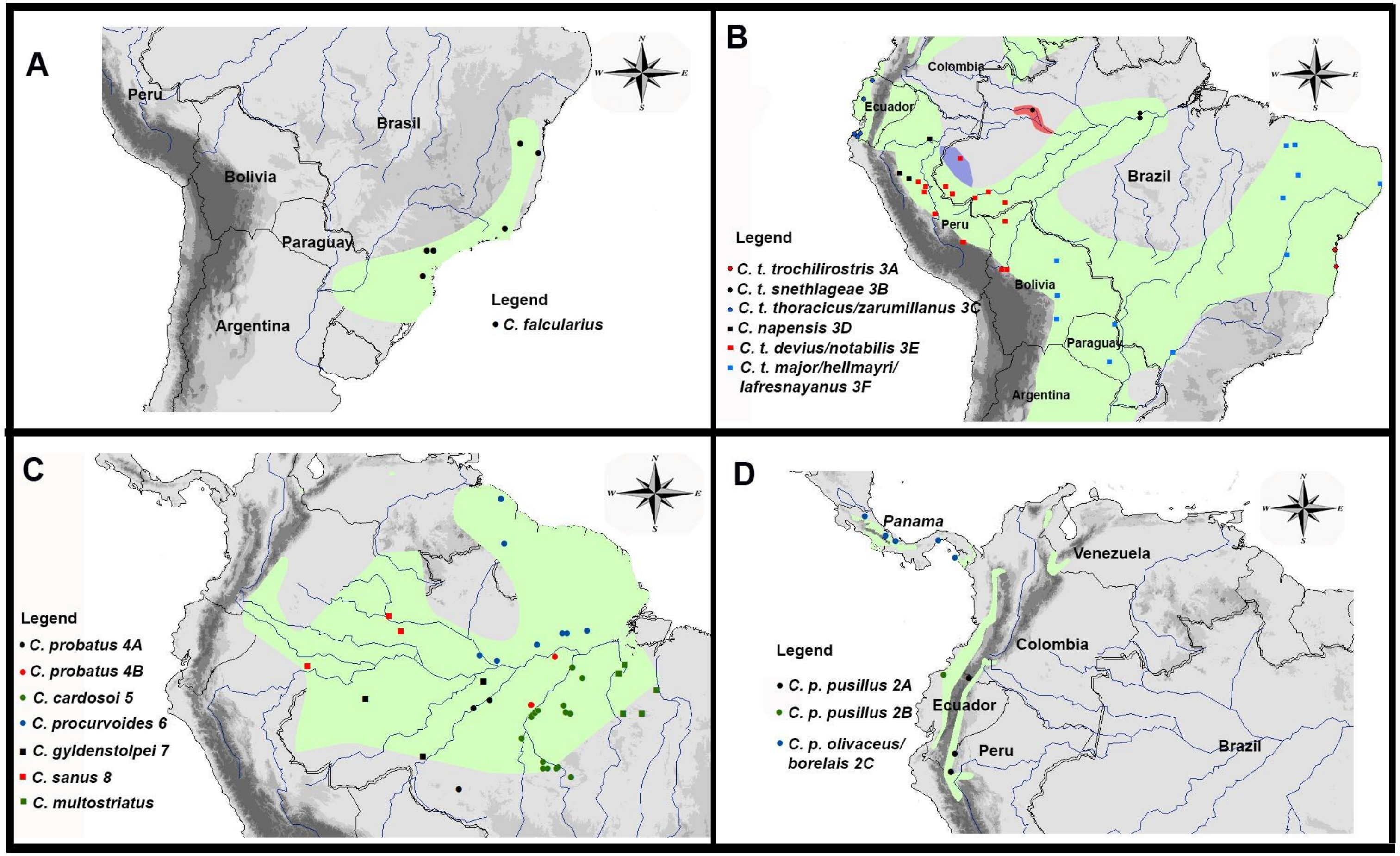
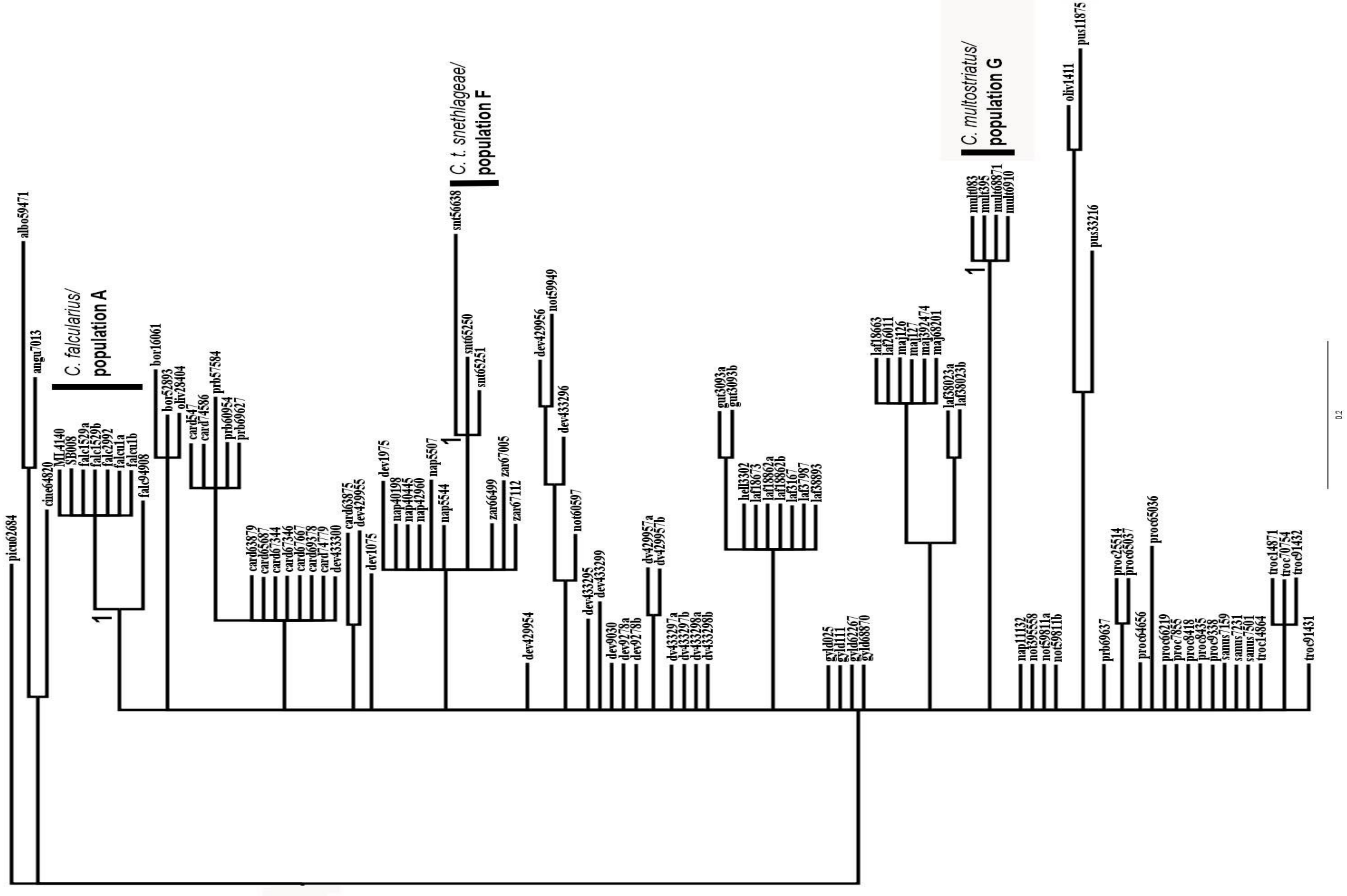


Figure 2S – Bayesian tree based on the concatenated nuDNA dataset (BF5 and Musk genes). Numbers on nodes represent posterior probabilities. Sample and lineage codes are the same as in Table 1S.



Ancestral relation of the lineages

The node number classification in Figure 4 following as:

Taxon id: 1: *C. cardosoi* (lineage 5); 2: *C. devius/notabilis* (3E); 3: *C. falcularius* (1); 4: *C. gyldenstolepei* (7); 5: *C. lafresnayanus/hellmayri/major* (3F); 6: *C. multostriatus* (9); 7: *C. napensis* (3B); 8: outgroup; 9: *C. probatus* (4A); 10: *C. probatus* (4B); 11: *C. procurvoides* (6); 12: *C p. olivaceus/borealis* (2C); 13: *C. p. pusillus* (2A); 14: *C. p. pusillus* (2B); 15: *C. sanus* (8); 16: *C. t. snethlageae* (3B); 17: *C. t. thoracicus/zarumillanus* (3C); 18: *C. t. trochilirostris* (3A).

The distribution at each node: node 19 (anc. of terminals 5-2); node 20 (anc. of terminals 10-9); node 21 (anc. of terminals 10-1); node 22 (anc. of terminals 5-1); node 23 (anc. of terminals 15-4); node 24 (anc. of terminals 15-11); node 25 (anc. of terminals 15-18); node 26 (anc. of terminals 5-18); node 27 (anc. of terminals 5-6); node 28 (anc. of terminals 7-17); node 29 (anc. of terminals 16-17); node 30 (anc. of terminals 5-17); node 31 (anc. of terminals 14-12); node 32 (anc. of terminals 14-13); node 33 (anc. of terminals 5-13); node 34 (anc. of terminals 5-3); node 35 (anc. of terminals 5-8).

Laboratorial Protocols

Fenol-Chloroform Protocol Extraction

1. Weigh out about 50mg of the tissue and transferred to 1.5 mL eppendorf tubes. Add 300 µL of homogenization buffer (STE) and 300 µLof lysis buffer (10% SDS pH 7.2), 30µL RNAse (10mg/mL) to digest RNA.
2. Allow the sample to incubation at 37 °C under continuous stirring for one hour. Then add 30 µl of proteinase K (10mg/mL) and leave over night at 56 °C under continuous agitation. Take the tube at room temperature.
3. Add 500 ul of phenol chloroform isoamyl alcohol (25:24:1 respectively in the following proportion). Stir gently for 5 minutes until homogeneous. Then centrifuge for 10 minutes at 13,000 rpm.
4. Then, transfer the supernatant to a clean tube carefully so as not to move along the protein layer. Add equal volume of chloroform-isoamyl alcohol (500 ul) and stir gently for 5 minutes until complete homogenization.
5. Subsequently, undergo centrifugation at 13,000 rpm for 10 minutes, promoting a separation of the material in 3 phases. Transferring again carefully the supernatant to a clean tube, so that the intermediate layer was not removed
6. Add 100 µL of 3M sodium acetate pH 4.8 and 500 µL of isopropyl alcohol. Shake gently for about 2 minutes until the cloud visualization of DNA.
7. Centrifuge for 2 minutes at 13,000 RPM for the DNA to arrest the bottom of the tube, forming the "pellet".
8. Subsequently, discard the supernatant completely and then add 500 µL of 70% ethanol, centrifuging for 2 minutes under the same conditions above. Then discard the alcohol and then submit to a temperature 37 °C in an oven for about 15 minutes.
9. Add 100 µL of TE. Take the tube at room temperature.

PCR purification protocols with PEG 8000

1. Check the quality of the PCR product on agarose gel.
2. Transfer, where appropriate, the PCR product into a microcentrifuge tube 0.5 ml.
3. Add 1 volume of PEG solution (20% PEG 8000 2.5 M NaCl) into PCR.
4. Incubate at 37 °C for 30 minutes.
5. Centrifuge at 13,000 RPM for 20 minutes. Place the tubes closed with the cover handle toward the outside of the rotor.
6. Remove the supernatant with the aid of a micropipettor P20-200 smoothly.
7. Add 125µl of cold 80% ethanol. Wait 1 minute and centrifuge for 2 minutes at 13,000 rpm.
8. Remove the supernatant with the aid of a micropipettor P20-200 smoothly.
9. Repeat steps 7 and 8.

10. Let evaporate residual ethanol using the dry bath, stove, or leave on the bench. Cover
11. with toilet paper so that no dirt in the tube.
12. Resuspend the pellet with 5 or15 µL of water (Milli-Q water) at least 2 hours.
13. Quantify the purified product on an agarose gel. (1-2µl).

Sequence Reaction

1. The Sequence reaction involved a total of 20µl total as following: 1µl Big Dye Terminator (v3.1), 1.5 µl buffer, 16 µl of water, 0.5µl of each primer, and 1-3 µl of PCR product;

2. The PCR/ reaction condition following: initial denaturation at 96°C for one min, followed by 96°C for 13 seconds, specific annealing temperatures for 15 seconds, and the cycle was finished at 60°C for 4 min;

Precipitation with Isopropanal (final volume = 10 µl)

1. add 30 µl of Milli-Q water;

2. add 80 µl of Isopropanol 100%;

3. leave at room temperature for 20 minutes;

4. Centrifuge for 45 minutes at 4.000 rpm;

5. Invert the tube to discard the Isopropanol;

6. Add 100 µl of ethanol 70%;

7. Centrifuge for 5 minutes and invert the tube to discard the ethanol;

8. dry the tube in hothouse or leave at the branch into complete drying;

9. Resuspend the pellet to the required concentration in 0.01M Tris, 0.001M EDTA, pH 7.5.

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Conclusões Finais

As filogenias recuperadas confirmaram a monofilia de *Campylorhamphus,* reconhecendo dezessete linhagens fortemente apoiadas em sua maioria, por outro lado, em nível sub-específico mostrou parafilia, indicando a necessidade de reclassifições. Tais linhagens estão distribuídas em cinco grandes clados. Com base nas análise dos dados concaternados (mtDNA e nuDNA), a análise da árvore de especie apoiou 11 linhagens com probabilidade posterior máxima, além de ter apoiado de forma moderada outras duas linhagens.

As análises da BBP suportaram com probabilidade de especiação >0.95 15 das 17 linhagens. Estas probabilidades de especiação permitem, segundo os critérios de delimitação de espécie de Leaché e Fujita (2010), reconhece-las como espécies distintas. *Campylorhamphus probatus* que mostrou pertencer a duas linhagens monofiléticas, separadas pelo rio Aripuanã não alcançou a probabilidadede especiação sugerida (P>0.95) para dois dos tres cenarios testados, porem, apoiou a separação quando analisado tamanho populacional efetivo pequeno e baixa divergência. Estes resultados não permitem reconhecer estas linhagens como espécies distintas. Embora haja ausência de amostras para a espécie politipica *C. pusillus* (*tachirensis* e *guapiensis*), os táxons aqui analisados motraram ao menos pertecerem a duas espécies distintas, segundo os critérios de delimitação de espécies de Leaché e Fujita (2010), a nominal *C. pusillus* e uma segunda espécie formada pelos táxons de *C. pusillus* distribuidos a oeste dos Andes e América Central (*borealis*, *olivaceus* e uma táxon não descrito). Os táxons desta ultima linhagem não alcançaram a probabilidade de especiação em nenum dos cenários testados.

Os eventos de cladogeneses tiveram início durante o Plio-Pleistoceno, com a separação mais antiga ocorrendo por volta de 4.3 milhões de anos, seguida pela separação dos táxons cis-trans Andinos, cerca de 3.5 milhões de anos. A clausura do Istomo do Panamá (c.a. 3.5 m.a.) foi um evento crucial para o intercâmbio entre a Américas do Sul e Central para a avifauna, principalmente para o grupo "*pusillus*". Outros eventos de cladogenesis foram concentrados nas planícies Amazonicas durante o Pleistoceno. Algumas desta separações coincidem com o surgimento da drenagem moderna dos rios Amazônicos, tais como o Negro/Branco (separando *C. procurvoides* de *C. sanus* por volta de 0.3 m.a.), o Tapajós (entre *C. cardosoi* e *C. probatus*, por volta de 0.22 m.a.), o Solimões (separando *C. sanus* de *C. gyldenstolpei*, por volta de 0.18

m.a.) e o Juruena (entre ambas as linhagens reciprocamente monofiléticas de *C. probatus*, por volta de 0.12 m.a.).

As análises combinadas da arvore de espécie e distribuição ancestral (S-DIVA e BBM) sugerem uma provável origem de *Campylorhamphus* na Mata Atlântica e uma probabilidade menor proporção, para a região Andina (3-5 m.a.). Esta análises mostraram também que processos de recolonização foram improváveis de ocorrer em *Campylorhamphus,* embora a análise tenha sugerido uma pequena probabilidade de recolonização da Amazonia através *C. trochilirostris* nominal. Vale ressaltar que S-DIVA e BBM mostram ambiguidades em relação a algumas áreas ancetrais.

A filogenia recuperada mostrou que *C. trochilirostris* como tradiciaonalmente reconhecido, é parafilético e distríbuido em três diferentes grandes clados. Um clado formado pelas populações de *snethlageae, napensis, thoracicus* e *zarumillanus,* sendo estes dois ultimos geneticamente iguais e considerados uma única população. A análise da BBP apoia com probabilidade de especiação >0.95 estas três linhagens nos três diferentes cenários testados. Isto permite considerá-las, segundo os critérios de Leaché e Fujita (2012), três espécies disitintas. Um outro clado formado pelos taxosn do oeste da Amazonia (*deviius* e *notabilis*) e os táxons dos biomas seco (Caatinga e Cerrado) e alagados dos Chacos Paraguaios e Argentinos (*lafresnayanus, major* e *hellmayr*). Um último clado formado pelo taxon nominal de *C. trochilirostris* que tem afinidades filogeneticas com os táxons do Escudo Guianense e oeste da Amazônia (*procurvoides, sanus* e *gyldenstolpei*). As relações entre *C. t. trochilirostris* e o grupo "*procurvoides*" precisa ser melhor investigado. Devido a falta de informação de duas subespécies do complexo *trochilirostris* (*venezuelensis* e *brevipennis*), estes dois táxons devem permanecer associados a *trochilirostris* nominal.

Os resultados aqui mostrados são concordantes com a separação da espécie politípica *C. procurvoides*, assim como o reconhecimento das duas espécies recém descritas (Aleixo et al. 2013, Portes et al. 2013), todas suportadas pelas análises da BPP com probabilidade posterior >0.95.

Nossos resultados corroboram a ideia de um complexo padrão nos processos de diversificação da região Neotropical. Estes resultados são inéditos em fornecer um abordagem biogeográfica ampla do gênero *Campylorhamphus.* Os próximos passos são reconhecer as linhagens distintas mostradas aqui, apoiar quando poissível, diagnoses morfológicas e vocais desta linhagens, propondo revisões taxônomicas.

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