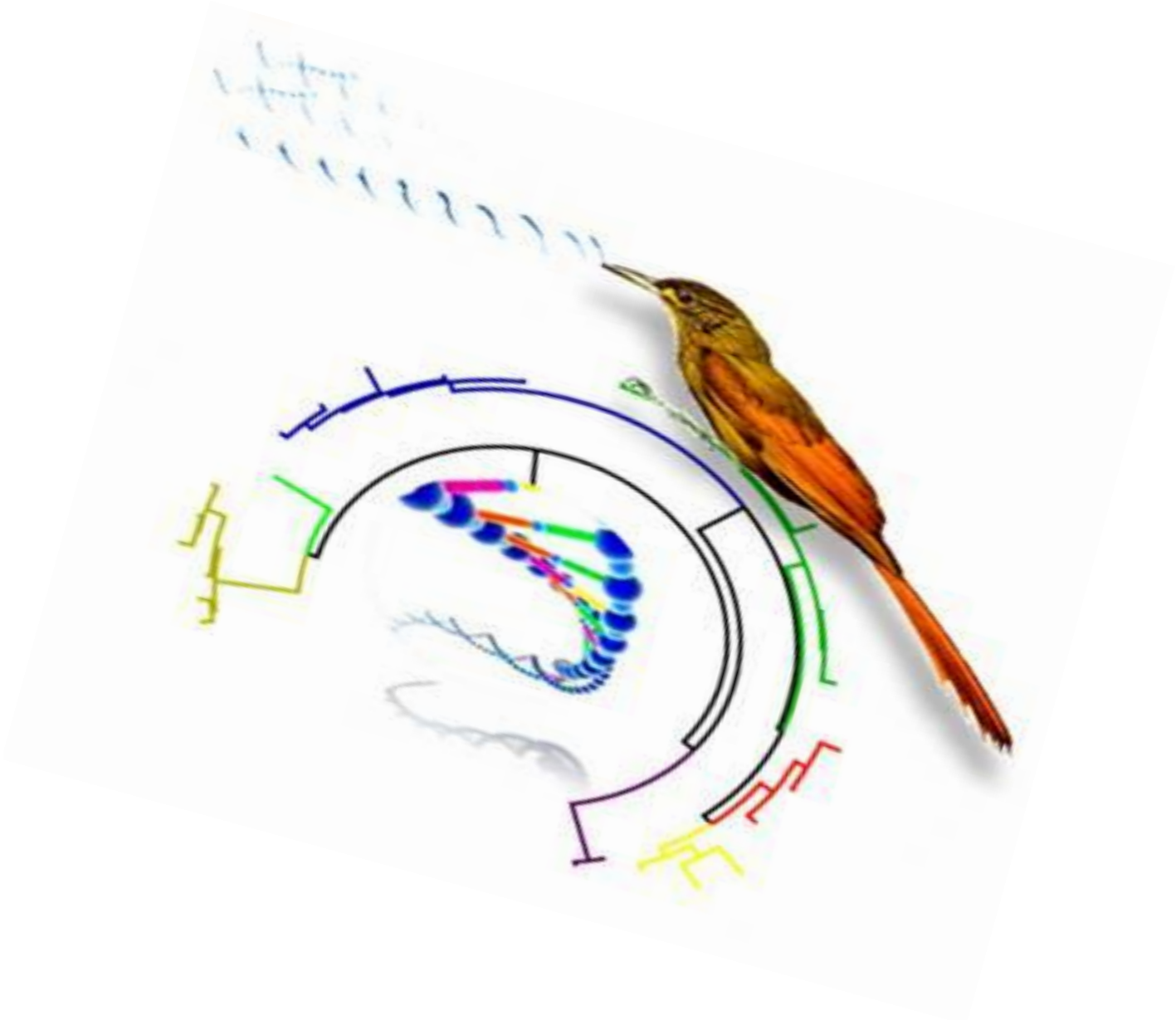
REVISÃO SISTEMÁTICA E FILOGEOGRAFIA DE *DECONYCHURA LONGICAUDA* (AVES – DENDROCOLAPTIDAE)



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CURSO MESTRADO EM ZOOLOGIA

REVISÃO SISTEMÁTICA E FILOGEOGRAFIA DE *DECONYCHURA LONGICAUDA* (AVES – DENDROCOLAPTIDAE)

IVÃ BARBOSA

BELÉM - PARÁ

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Revisão Sistemática e Filogeografia de *Deconychura longicauda* (Aves – Dendrocolaptidae)

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“Era uma vez na Amazônia a mais bonita floresta, mata verde, céu azul, a mais imensa floresta. No fundo d'água as Iaras, caboclos, lendas e mágoas e, os rios puxando as águas. Papagaios, periquitos, cuidavam de suas cores...

Sorria o jurupari, uirapuru, seu porvir era: fauna, flora, frutos e flores. Toda mata tem caipora para a mata vigiar, veio caipora de fora para a mata definhar e, trouxe dragão-de-ferro, prá comer muita madeira e trouxe em estilo gigante, prá acabar com a capoeira. Fizeram logo o projeto sem ninguém testemunhar. Prá o dragão cortar madeira e toda mata derrubar. Se a floresta, meu amigo, tivesse pé prá andar, eu garanto meu amigo, com o perigo não tinha ficado lá...

Depois tem o passarinho, tem o ninho, tem o ar, igarapé, rio abaixo, tem riacho e esse rio que é um mar.

Mas o dragão continua a floresta devorar, e quem habita essa mata, prá onde vai se mudar?

Corre índio, seringueiro, preguiça, tamanduá, tartaruga pé ligeiro, corre-corre tribo dos Kamayurá.

No lugar que havia mata, hoje há perseguição, grileiro mata posseiro só prá lhe roubar seu chão.

Castanheiro, seringueiro já viraram até peão, afora os que já morreram como ave-de-arribação.

Zé de Nata tá de prova, naquele lugar tem cova, gente enterrada no chão. Pois mataram índio, que matou grileiro, que matou posseiro, disse um castanheiro para um seringueiro que um estrangeiro roubou seu lugar...

Era uma vez uma floresta na Linha do Equador”.

Vital Farias – Saga da Amâzonia.

“As águas sendo clara e brilhante refletem aquilo que existe no mais profundo ser.

Ó espelho.

Água fria pelo tédio em teu quadro gelada.

Quantas vezes e durante horas, desolado dos sonhos e buscando minhas lembranças [que são como folhas sob teu vidro de poço profundo].

Apareci-me em ti como uma sombra longínqua. Mas, horror! Certas noites, em tua serena fonte conheci a mudez do meu sonhar disperso e distante...”

(Herodíade)

Revisão Sistemática e Filogeografia de *Deconychura longicauda* (Aves – Dendrocolaptidae)

Resumo.– Os limites interespecíficos da espécie politípica *Deconychura longicauda* (Dendrocolaptidae) foram investigados por uma análise conjunta, incluindo caracteres moleculares, morfológicos e vocais. Um total de 1.108 pares de bases de genes mitocondriais Cit b e ND2 foram usados para construir hipóteses filogenéticas, ao passo que os caracteres morfológicos e vocais foram analisados com métodos estatísticos univariado e multivariado. Todas as árvores filogenéticas recuperadas indicam altos níveis de diferenciação genética e estrutura filogeográfica em *Deconychura longicauda*, com o reconhecimento de quatro grupos principais bem apoiados, geograficamente constituídos por aves (1) do centro de endemismo Guiana no nordeste da América do Sul (2), da bacia amazônica excluindo o escudo das Guianas (3), do sopé oriental dos Andes, e (4), trans-Andinas da América do Sul e América Central. O nível de divergência genética entre estes clados varia de 6-8% (entre as aves Guianenses, não-Guianenses, do sopé dos Andes e trans-Andinas). Embora os caracteres morfológicos contribuam pouco para a diagnose em *Deconychura*, o canto, por outro lado, consistetemente os distinguem. Nós recomendamos com base, principalmente, em sua diagnose molecular e vocal o desdobramento de *D. longicauda* nas seguintes espécies filogenéticas e biológicas: *Deconychura longicauda*, *D. pallida*, *D. zimmeri*, *D. connectens, D. typica* e um táxon ainda não nomeado, endêmico do sopé oriental dos Andes.

Palavras-chave: Amazônia, Dendrocolaptidae, Sistemática Molecular, Neotrópicos, Limites de Espécies, Variação Vocal.

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INTRODUÇÃO

Estudos relativamente recentes têm sido desenvolvidos a fim de elucidar os limites interespecíficos de táxons crípticos na região Neotropical. O incremento recente no número de revisões taxonômicas, subsequentemente o reconhecimento de novas espécies advém, principalmente, da constatação que o uso exclusivo de caracteres morfológicos externos (veja Hillis 1987, Irestedt et al. 2004a, Lôbo-Hajdu 2006) frequentemente é insuficiente para elucidar a história evolutiva de diferentes grupos taxonômicos (Bortolus 2008). Apesar disto, muitos autores têm levantado críticas a esse processo de "inflação taxonômica (elevação dos já conhecidos táxons subespecíficos para a categoria de espécies)" (veja Isaac et al. 2004, Knapp et al. 2005) cujo cerne reside nos diferentes conceitos de espécies adotados na biologia.

Para Mallet e Willmont (2003), o novo entusiasmo sobre a taxonomia é impulsionado em parte pelos avanços na tecnologia, bioinformática e, principalmente, pela insistente crise que ameaça a diversidade biológica. Taxonomias inconsistentes com as histórias evolutivas dos diferentes grupos biológicos afetam a eficiência de manejos ambientais e a conservação das espécies (Agapow et al. 2004, Knapp et al. 2005, Bortolus 2008), consequentemente implicam em uma subestimativa da biodiversidade, principalmente nos Neotrópicos.

Embora o Conceito Filogenético de Espécie (CFE) tenha proporcionado uma redefinição dos limites interespecíficos de muitos táxons (veja Aleixo 2007) com base em um conceito de espécie eminentemente evolutivo (e. g. Assis et al. 2007, Jønsson et al. 2008, Dávalos and Porzecanski 2009, Mauck III and Burns 2009), em

Aves a maior parte das relações filogenéticas dentro dos grupos mais ricos em espécies de linhagens Neotropicais (e. g. famílias Thamnophilidae, Formicariidae, Furnariidae e Dendrocolaptidae) são ainda pobremente entendidas no que se refere aos limites interespecíficos de suas espécies biológicas (e. g. Garcia-Moreno and Fjeldså 1999; Isler et al. 1998, 2002, 2005, 2007; Aleixo 2002; Zimmer 2002; Isler and Isler 2003; Chesser 2004; Irestedt et al. 2004a, b; Chesser and Brumfield 2007; Assis et al. 2007; Rêgo et al. 2007; Krabbe 2008; Portes and Aleixo 2009). Isto se deve principalmente à delimitação de espécies com base no Conceito Biológico de Espécie (CBE) por vários autores durante a primeira metade do século XX, que basearam suas análises apenas em caracteres morfológicos qualitativos e inferiram isolamento reprodutivo ou sua ausência, muitas vezes, a partir de séries incompletas de espécimes ou tratamentos pouco consistentes (e. g. Cherrie 1891; Chapman 1921; Griscom 1929; Zimmer 1929, 1934).

Posteriormente, com o uso de conjuntos de caracteres, novos métodos analíticos (e. g. moleculares com técnicas emergentes de sequenciamento de DNA cada vez mais acessíveis) e avanços tecnológicos e conceituais (e. g. Templeton 2001, Zimmer et al. 2001, Queiroz 2005, Aleixo 2007, Marantz and Patten 2010, Remsen 2010), que permitem uma resolução um tanto mais acurada das relações filogenéticas entre populações e espécies proximamente relacionadas, mostrou-se repetidamente a inconsistência evolutiva de várias espécies politípicas de aves (e. g. Zimmer 1997, Isler et al. 1998, Silva et al. 2001, Aleixo 2002, Chesser 2004, Irestedt et al. 2004a, Maurício 2005, Assis et al. 2007, Rêgo et al. 2007, Nyári 2007, Jønsson et al. 2008, Rheindt et al. 2008).

O reconhecimento do status taxonômico e do relacionamento entre espécies são cruciais para avaliar a biodiversidade e para políticas conservacionistas (veja Avise 2004, Fitzpatrick 2010), já que a designação de distintas unidades taxonômicas pode ter influencias significativas em como elas podem ser manejadas (Yeung et al. 2009). Sangster (2009) examinou 747 propostas de alteração da classificação taxonômica de aves no período 1950-2007, a maioria (84,6%) de espécies recentemente reconhecidas foi apoiada por novos dados taxonômicos. Desse modo, é certo que o número de espécies e níveis de divergência dentro das espécies de aves Neotropicais ainda é mal conhecido.

Assim, a revisão de espécies politípicas tem sido sugerida, não só, para resolver as incongruências envolvendo dados morfológicos e moleculares (veja Omland and Lanyon 2000, Avise 2004, Chesser 2004, Irestedt et al. 2004b, Nyári 2007) e os diferentes conceitos de espécies adotados na taxonomia, (veja Agapow et al. 2004, Queiroz 2005, Aleixo 2007) mas também a fim de identificar corretamente a diversidade dentro dos complexos de espécies (e. g. Zimmer et al. 2001; Zimmer 2002, 2008; Isler et al. 2002; Isler and Isler 2003; Cabanne et al. 2007; Chesser and Brumfield 2007; Rheindt et al. 2008) e fornecer condições para uma avaliação mais precisa da real historia evolutiva dos grupos (e. g. Marks et al. 2002) e seus padrões de diversificação, considerando os diversos fatores que contribuem para diversificação e manutenção das espécies, p. e., as variáveis ambientais que incidem sobre as populações determinando as variações geográficas de populações segregadas espacialmente.

Nesse contexto, um dos grupos onde a taxonomia atual parece ser inconsistente com a história evolutiva do grupo é a espécie biológica politípica

Deconychura longicauda (Aves: Dendrocolaptidae), endêmica da região Neotropical (Marantz et al. 2003). A família Dendrocolaptidae constitui uma linhagem monofilética altamente especializada dentro da radiação dos Suboscines, com táxons predominantes do Novo Mundo e de ampla diversidade interclado (Chesser 2004). A taxonomia usual considera os dendrocolaptídeos como grupo irmão dos Furnariidae excluindo-se os gêneros *Geositta* e *Sclerurus*. (Marantz et al. 2003, Chesser 2004, Irestedt et al. 2004a).

Histórico Taxonômico de *Deconychura* e Nomenclatura

Pelzeln (1868 p. 60) descreveu *Dendrocincla longicauda* (hoje *Deconychura longicauda*) com base em material coletado por Natterer, cinco exemplares de Borba, Marabitanas e Barra do Rio Negro, cujo holótipo não foi designado. Posteriormente, esses exemplares foram alocados no gênero *Deconychura*, originalmente descrito por Cherrie (1891 p. 338-339) com base em *D. typica* (uma fêmea adulta da localidade de Pozo Azul de Pirrís, Costa Rica, número 119943 – Smithsonian National Museum of Natural History), que assumiu o número de dez rectrizes como principal diagnose do novo gênero, distinguindo-o de *Sittasomus* e de *Glyphorynchus.* Hellmayr (1907 e 1925 p. 361) foi quem primeiramente modificou *Dendrocincla longicauda* para *Deconychura longicauda*, designando Manaus como localidade tipo e acresentando em suas análises exemplares de Bartica Grove, Mermuré Mts, Guiana e, exemplares tanto da Costa Rica como do oeste do Panamá, mantendo estes últimos em *D. typica* de Cherrie, mas como subespécie *D. typica typica*. Porém, Chubb (1919 p. 61 e 1921 p. 120) sinonimizou *Dendrocincla longicauda* com *Dendrocincla longicauda guianensis* (de Bartica Grove) e, subsequentemente, modificou-a para o gênero *Dendrocinclopa.*

A última revisão taxonômica do gênero *Deconychura* foi feita por Zimmer (1929), que reconheceu duas espécies politípicas: *Deconychura longicauda* e *D. stictolaema,* a primeira com sete subespécies e diferenciada de *D. stictolaema* principalmente pelo dorso superior mais avermelhado, parte ventral mais intensamente estriada e maior em comprimento total. Na ocasião Zimmer (1929) propôs para *Dendrocincla longicauda* de Pelzeln o trinômio *Deconychura l. longicauda*, por considerar os espécimes da Guiana Britânica indistinguíveis daqueles de Manaus e Marabitanas, sinonimizando, portanto, *Dendrocinclopa longicauda guianensis* com *Dendrocincla longicauda* e, alocando-os no gênero *Deconychura* (sinônimo sênior). Nesta revisão, Zimmer (1929) ainda reconheceu as seguintes subespécies em *D. longicauda*: *pallida*, *connectens*, *typica* e *minor.*

Griscom (1929 p.172) descreveu *D. longicauda darienensis* após a revisão de Zimmer (1929) e, Howell (1956) examinou comparativamente os especimes trans-Andinos pertencentes à *darienensis*, *typica* e *minor*, revisando seus limites geográficos e concluiu tratar-se de um único táxon bastante variável. Por sua vez, *D. longicauda zimmeri* Pinto (1974 p. 177), não havia sido revisto, taxonomicamente, até o presente trabalho.

Recentemente, Derryberry et al. (2010) concluíram, através de dados moleculares, que *Deconychura*, como historicamente definido, é um gênero parafilético, sugerindo *Certhiasomus* como um novo gênero para *D. stictolaema*, não proximamente relacionado à *D. longicauda*, a espécie tipo do gênero, que se agrupa como grupo irmão de *Sittasomus* (Raikow 1994, Irestedt et al. 2004a, Derryberry et al. 2010).

Seguindo Marantz et al. (2003), a distribuição dos táxons trans-Andinos é registrada para o centro-norte e sudoeste da Costa Rica e do leste ao centro do Panamá e, em pontos isolados ao sul de Honduras (*D. l. typica*); leste do Panamá e adjacências do noroeste da Colômbia (*D. l. darienensis*) e centro-norte da Colômbia (*D. l. minor*). Enquanto, os táxons cis-Andinos se sobrepõem aos centros de endemsimos amazônicos (seguindo classificação de Silva et al. 2005), sendo registrados para as Guianas ao norte da Amazônia brasileira, do alto Rio Negro a leste do Amapá (*D. l. longicauda*); ao sul da Amazônia de leste a sudeste do Peru, noroeste da Bolívia e para região central da Amazônia brasileira do leste do Tapajós e ao norte do Mato Grosso (*D. l. pallida*); a oeste e noroeste da Amazônia (norte do Rio Amazonas); leste da Colômbia; sul da Venezuela; norte e leste do Peru (oeste do Rio Ucayali) e alto Rio Negro (*D. l. connectens*); sudeste da Amazônia brasileira (sul o Rio Amazonas, do leste do Rio Tocantins a leste do Maranhão (*D. l. zimmeri*).

As sete subespécies de *Deconychura longicauda* foram basicamente diferenciadas pelo padrão de coloração da plumagem e morfometria externa. De acordo com Marantz et al. (2003), pelo menos, três grupos vocalmente distintos parecem existir agrupando, respectivamente, os táxons trans-Andinos, cis-Andinos e do escudo das Guianas.

Neste trabalho, é proposta uma revisão taxonômica desta espécie politípica com o objetivo de fornecer, através de uma análise combinada de caracteres morfológicos, vocais e moleculares, forte apoio para resolver os limites interespecíficos entre os diferentes táxons nela agrupados. Além disso, a resolução da filogenia dos táxons atualmente agrupados em *D. longicauda* fornecerá mais um estudo de caso onde diferentes hipóteses de diversificação propostas para a biota

Amazônica poderão ser comparadas (veja Bates et al. 1998; Aleixo 2002, 2004; Aleixo e Rossetti 2007; Cabanne et al. 2007; Miller et al. 2008).

OBJETIVOS

O objetivo central desta dissertação foi revisar a taxonomia da espécie politípica *Deconychura longicauda*, a fim de avaliar a hipótese de Marantz et al. (2003) de que existem na verdade três espécies válidas dentre os táxons que integram esta espécie.

Para concluir este propósito, a dissertação foi resumida a um capítulo contemplando seus respectivos objetivos específicos.

Capitulo I (Artigo 1). – Systematic review and phylogeography of *Deconychura longicauda* (Aves - Dendrocolaptidae)

- Propor uma filogenia para os táxons e populações da espécie politípica *Deconychura longicauda* com base em caracteres moleculares*;*
- Verificar se há congruência evolutiva entre os caracteres morfológicos, vocais e moleculares que diagnosticam as populações de *Deconychura longicauda*;
- Documentar a natureza da variação geográfica nos caracteres morfológicos externos entre as populações de *Deconychura longicauda*;
- Documentar as variações geográficas nos caracteres vocais entre as populações de *Deconychura longicauda*.

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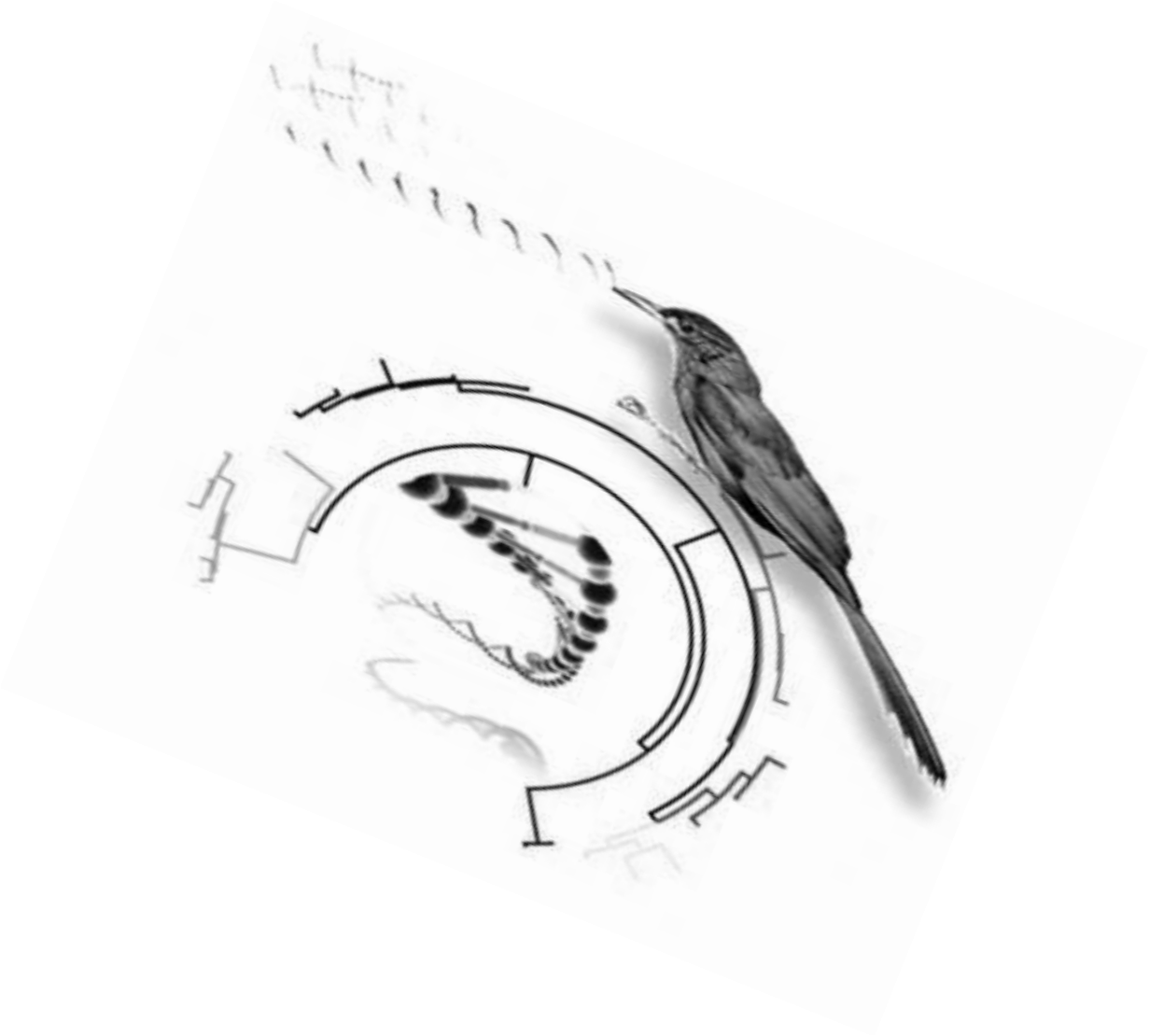
CAPÍTULO I

(Submissão para The Auk)



SYSTEMATIC REVIEW AND PHYLOGEOGRAPHY OF *DECONYCHURA LONGICAUDA* (AVES - DENDROCOLAPTIDAE)

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Abstract. – The interspecific limits of the polytypic specie *Deconychura longicauda* (Dendrocolaptidae) were investigated by a combined analysis including molecular, morphological, and vocal characters. A total of 1,108 base pairs of mitochondrial genes Cyt b and ND2 were used to build phylogenetic hypotheses, whereas the morphological and vocal characters were analyzed with univariate and multivariate statistical methods. All recovered trees indicated high levels of genetic differentiation and phylogeographic structure in *Deconychura longicauda*, with the recognition of four major groups well-supported statistically and geographically consisting of birds from (1) the Guiana area of endemism in northeastern South America, (2) the Amazon basin excluding the Guianan shield, (3) the eastern slope of the Andes and (4) trans-Andean South America and Central America. The levels of genetic divergence between these clades reach 6-8% (among birds from Guianan, non-Guianan, eastern slope of the Andes and, trans-Andean birds). Although morphological characters contribute little to the diagnoses among *Deconychura*, loudsongs, consistently distinguish them. Based on those analyzes, we recommend the splitting of *D. longicauda* into the following phylogenetic and biological species based on their molecular and vocal unequivocal diagnoses: *Deconychura longicauda*, *D. pallida*, *D. zimmeri*, *D. connectens, D. typica* and one yet unnamed taxon endemic to the eastern slope of the Andes.

Key words: Amazonia, Dendrocolaptidae, Molecular systematics, Neotropics, Species limits, Vocal variation.

Revisão Sistemática e Filogeografia de *Deconychura longicauda* (Aves – Dendrocolaptidae)

Resumo.– Os limites interespecíficos da espécie politípica *Deconychura longicauda* (Dendrocolaptidae) foram investigados por uma análise conjunta, incluindo caracteres moleculares, morfológicos e vocais. Um total de 1.108 pares de bases de genes mitocondriais Cit b e ND2 foram usados para construir hipóteses filogenéticas, ao passo que os caracteres morfológicos e vocais foram analisados com métodos estatísticos univariado e multivariado. Todas as árvores filogenéticas recuperadas indicam altos níveis de diferenciação genética e estrutura filogeográfica em *Deconychura longicauda*, com o reconhecimento de quatro grupos principais bem apoiados estatisticamente e, constituídos geograficamente por aves (1) do centro de endemismo Guiana no nordeste da América do Sul (2), da bacia amazônica excluindo o escudo das Guianas (3), do sopé oriental dos Andes, e (4), trans-Andinas da América do Sul e América Central. O nível de divergência genética entre estes clados varia de 6-8% (entre as aves Guianenses, não-Guianenses, do sopé dos Andes e trans-Andinas). Embora os caracteres morfológicos contribuam pouco para a diagnose entre *Deconychura*, o canto, consistetemente os distinguem. Nós recomendamos com base, principalmente, em diagnose molecular e vocal o desdobramento de *D. longicauda* nas seguintes espécies filogenéticas e biológicas: *Deconychura longicauda*, *D. pallida*, *D. zimmeri*, *D. connectens, D. typica* e um táxon ainda não nomeado, endêmico do sopé oriental dos Andes.

Various authors (Haffer 1969, Nores 1999) have suggested that a substantial part of the diversification of Amazonian forest birds occurred during the quaternary and tertiary periods, when active allopatric speciation was supposedly favored. Much of this diversity maintained by areas containing high rates of endemism among Amazonian biota (Bates et al. 1998, Silva et al. 2005). Phylogenetic analyses of a variety of bird lineages provides important evidence to explain the phylogeographic patterns and evolutionary history of the avifauna in general (e.g. Aleixo 2002, 2004; Aleixo and Rossetti 2007; Bates et al. 2008; Burney and Brumfield 2009; Burns and Naoki 2004; Cabanne et al. 2007, 2008; Cracraft 1985; Ribas et al. 2005).

However, phylogenetic relationships within most Neotropical bird lineages are still poorly understood, especially with regard to establishing species limits (e. g. within the families Thamnophilidae, Formicariidae, Furnariidae, and Dendrocolaptidae; see Aleixo 2002, 2004; Assis et al. 2007; Chesser 2004; Chesser and Brumfield 2007; Garcia-Moreno and Fjeldså 1999; Krabbe 2008; Irestedt et al. 2004a, 2004b, 2006; Isler and Isler 2003; Isler et al. 2001a, 2001b, 2009, Rêgo et al 2007; Portes and Aleixo 2009; Zimmer 2002). This is due to several factors, including the delimitation of species based on biological species concept (BSC) by various authors during the first half of the twentieth century (e.g. Chapman 1921; Cherrie 1891; Griscom 1929; Zimmer 1929, 1934). The continuing use of the BSC in the context of a wider diversity of data, including vocal characters, led to the splitting of several formerly recognized single biological Neotropical bird species into between 2 to 6 “novel” biological species (Bierregaard et al. 1997; Isler et al. 1997, 1999, 2007; Zimmer 1997, 2002; Zimmer and Whittaker 2000; Zimmer et al. 2001). A rough estimate, based on the previous studies, indicates that on average three for

every Amazonian biological species studied with a combination of both vocal and morphological characters, two “novel” biological species have been recognized.

The inclusion of molecular data in taxonomic assessments of Amazonian birds has been as widespread as the use of vocal data. A number ever growing studies point towards that “old” polytypic biological species tend to be split in two or more “novel” biological species mainly when there is no evidence of gene flow exist between alleged subspecies or because postulated polytypic species turn out to be paraphyletic and even polyphyletic with respect to other accepted biological species (Aleixo 2002, Marks et al. 2002, Whittaker 2002, Armenta et al. 2005, Nyári 2007, Da Costa and Klicka 2008, but see Brumfield 2005).

Thus, the revision of polytypic species has been suggested as a powerful tool to correctly identify the diversity within complexes of species (e.g. Burney and Brumfield 2009; Rheindt et al. 2008; Stiles 2009; Zimmer 1997, 2002, 2008, Zimmer et al. 2001) and will provide a more accurate assessment of the real evolutionary history of groups (e.g. Marks et al. 2002) and their patterns of diversification.

One group for which the current taxonomy, based on the BSC, appears to be inconsistent with vocal and molecular differentiation is the polytypic Long-tailed Woodcreeper (*Deconychura longicauda*; see Marantz et al. 2003). *D. longicauda* is distributed throughout Central America (southern Honduras, east to Panama) and South America (Guianan Shield, southern Venezuela, northwestern Colombia, eastern slope of the Andes from Ecuador to central Peru, northern Bolivia, and the Brazilian Amazon; Fig. 1).

The genus *Deconychura* (Dendrocolaptidae) was described by Cherrie in 1891, who distinguished it from *Sittasomus* and *Glyphorynchus* by the number of rectrices

(ten). Later, Hellmayr (1907) noticed that some taxa within *Deconychura* had more than ten rectrices, which led Chubb (1920) to synonymize *Deconychura* with *Dendrocinclopa*, adopting *Dendrocinclopa longicauda guianensis* as the holotype. The last revision with morphological inference was made by Zimmer (1929), who included a second species in the genus (*D. stictolaema*) and divided up *D. longicauda* into several subspecies, among them two new taxa described by him in this publication (*Deconychura l*. *pallida* and *D. l. connectens*). Later, subspecies *D. l. darienensis* and *D. l. zimmeri* were described by Griscom (1929) and Pinto (1974), respectively, who followed Zimmer´s (1929) inter-specific species limits in *Deconychura*. However, Derryberry et al. (2010) showed that the genus *Deconychura* is paraphyletic and sister group in fact of *Sittasomus griseicapillus*, proposing the relocation of the polytypic species *Deconychura stictolaema* to the genus *Certhiasomus*, since *D. longicauda* is the type species of the genus.

Thus, prior to this study, seven subspecies have been recognized (e. g. Marantz et al 2003) in the polytypic *D. longicauda*, based on variation in the color pattern of the plumage and external morphology (Zimmer 1929): *D. l. longicauda* (Pelzeln, 1868); *D. l. connectens* Zimmer, 1929; *D. l. pallida* Zimmer, 1929 and *D. l. zimmeri* Pinto, 1974 (all cis-Andean taxa) and *D. l. typica* Cherrie, 1891; *D. l. minor* Todd, 1919 and *D. l. darienensis* Griscom, 1929 (all trans-Andean taxa). Morphological and vocal characters have been suggested to partition this species at least into three main groups, possibly representing separate species. One group, with trans-Andean distribution (including subspecies *typica*, *minor* and *darienensis*), has a comparatively smaller body size than the other subspecies. The second group is cis-Andean in distribution and found across most of Amazonia except for the

Guyana area of endemism (including subspecies *connectens*, *pallida*, and *zimmeri*). Lastly, the third group includes only the subspecies endemic to the Guyana center of endemism (*longicauda*). These three major groups are known to differ from each other conspicuosly by voice (Marantz et al. 2003).

More recently, a molecular phylogeny showed that the trans-Andean taxa *typica* and *darienensis* formed a well supported clade, whereas the monophyly of Cis-Andean taxa was falsified mainly by the position of an unnamed taxon from the Andean foothills; however, no samples of nominate *longicauda* were included in this phylogeny, further complicating the assessment of the evolutionary relationships among the Cis-Andean subspecies (Derryberry et al. 2010).

This prior knowledge and the evidence of conspicuous vocal variation, enough to suspect that several species may be involved in *Deconychura longicauda*, underscore the need for a taxonomic revision of this species complex. Thus, we aim to provide, through a combination of characters (morphological, molecular and vocal), evidence to resolve interspecific limits among the different taxa of *D. longicauda*. Furthermore, the resolution of the phylogeny of the taxa currently grouped in *D. longicauda* provide another case study where different proposals of diversification for the Neotropical biota can be compared (see Bates 1998; Aleixo 2002, 2004, 2006; Aleixo and Rossetti 2007; Borges 2007; Miller et al. 2008).

METHODS

Molecular Analysis.– This study was represented by 25 individuals of *Deconychura longicauda*, corresponding to the taxa currently named *longicauda* (n = 6); *connectens* (n = 5); *pallida* (n = 8); *zimmeri* (n = 3); *darienensis* (n= 1); *typica* (n=

1) and; yet unnamed Andean taxa (n = 1) (Marantz et al. 2003; Derryberry et al. 2010; Appendix 2). In addition, the taxa *Certhiasomus stictolaemus, Dendrocincla merula* and, *Sittasomus griseicapillus* were used as outgroups, following Derryberry et al. (2010). Muscle tissues were provided by the following collections: Museu Paraense Emílio Goeldi in Belém, Brazil (MPEG), Instituto Nacional de Pesquisas da Amazônia in Manaus, Brazil (INPA), Louisiana State University Museum of Natural Science (LSUMNS), Universidade de São Paulo, São Paulo, Brazil (USP). Genomic DNA was extracted from muscle tissue using standard phenol-chloroform extraction protocol (Sambrook et al. 1989). Polymerase chain reaction (PCR; Mullis and Faloona 1987) was used to amplify a fragment of the mitochondrial gene NADH subunit 2 (ND2) using primers L5215 (Hackett 1996) and H6313 (Sorenson et al.1999). Thermocycling in the PCR protocol was as follows: initialization for 5 min at 95°C, followed by 35 cycles including denaturation at 95°C for 1 min, annealing at 58°C for 1 min, and extension at 72°C for 1 min and concluded with final extension at 72°C for 5 min.

Additionally, a fragment of the mitochondrial cytochrome b gene (cyt b) was amplified using primers L15560 and H16064 (Sorenson et al. 1999), with the following protocol: initialization for 3 min at 94°C, followed by 35 cycles including denaturation at 94°C for 0.30 sec, annealing at 55°C for 1 min, and extension at 72°C for 2 min, and concluded with final extension at 72°C for 5 min. Excess reagents in the reaction were eliminated by using EDTA precipitation according to standard protocol for birds. The samples were sequenced directly from PCR in the ABI 3130 Genetic Analyzer (Applied Biosystems) following the manufacturer's instructions. The sequences were aligned with the aid of application CLUSTAL-W

(Thompson et al.1994) and edited manually with the software BioEdit (Hall 1999). A check for possible stop-codons and evidence of saturation was performed in the application Dambe (Xia and Xie 2001) with parameters of penalty suggested by Schneider (2007). Maximum parsimony analysis (MP), maximum likelihood analysis (ML) and Bayesian inference (BI) were used to construct phylogenetic hypotheses using the programs PAUP* 4.0 (Swofford 2002) and MrBayes 3.1 (Ronquist and Huelsenbeck 2003). The appropriate model for ML and BI was chosen using the Akaike Information Criterion in MrModeltest 2.2 (Nylander 2004).

For the BI, we calculated values of the Bayesian Information Criterion (BIC, Posada and Buckley 2004, Sullivan and Joyce 2005) for four different partitioning regimes, ranging from unpartitioned to a maximum of six different partitions (a different model for each codon position of each coding gene, i. e, cyt B and ND2). BIC identified the HKY and HKY+I models as the best models for the first and second codon positions, and the GTR and GTR +Γ models as the best models for the third codon positions. All models had a confidence level estimated to 0.01, as indicated by MrModeltest 2.2 (Nylander 2004). For the four Markov chains that were performed with an initial run of 5×10^6 generations and a random tree, 5,000 trees were obtained, and the first 500 were discarded as burn in the chain.

Morphological Analysis.– In this study, we analyzed the external morphology of 110 specimens (62 males, 48 females), including the cis-Andean taxa *longicauda* (n = 10 males and 7 females), *connectens* (n = 3 males and 10 females), *pallida* (n = 19 males and 7 females), and *zimmeri* (n = 30 males and 24 females). These specimens were sampled from different ornithological collections, including Museu Paraense Emilio Goeldi, Belém, Brazil (MPEG), Museu Nacional do Rio de Janeiro,

Rio de Janeiro, Brazil (MNRJ); Museu de Zoologia da Universidade São Paulo, São Paulo, Brazil (MZUSP) and American Museum National History, New York, United States (AMNH) (see Appendix 1). No specimens of the trans-Andean taxa were measured directly by us for the morphological analysis. So we utilized the characters bill length, wing length and tail length measured by Howell (1956) for *typica* (n = 13 males and 9 females), *darienensis* (n = 2 males and 4 females) and *minor* (n= 6 males and 3 females).

In addition, high resolution photographs of the types were examined. The specimens studied directly by us were measured using a digital caliper (Starrett 799-0.01 mm) for the following external morphological characters and plumage patterns: 1) BL - bill length (the initial point of bill to anterior margin of nostril); 2) BH - bill height (at the anterior edge of the nostrils); 3) BW - bill width (at the anterior edge of the nostrils); 4) WL - total length of the right wing (from the wing bend to the end of the last primary); 5) LT - length tail (from insertion of the tail for the longest of the central rectrizes); 6) TSL - length of right tarsus; 7) PSC - proportion of streaks on the crown; 8) SSL - length of the superciliary spots; 9) SSW - width of the superciliary spots; 10) PPS - proportion of pectoral streaks; 11) PSL - length of the pectoral streak; 12) PSW - width of the pectoral streak and; 13) ESA - extension of the spot in the region of alula. All morphological nomenclature follows Proctor and Lynch (1993).

A 1 cm^2 hollow square made of laminated paper was used to standardize the area for counting the number of streaks on the crown and chest of the each specimen. Plumage characters selected were: 1) throat color; 2) pectoral streak color; 3) color of the edges of pectoral streaks, 4) color of the axillary feathers; 5)

extension of the pectoral streaks; 6) presence of streaks on the abdomen; 7) format of the pectoral streaks (striped, sagital, diamond-like and triangular shape). Names of colors when capitalized indicate direct comparison with color catalog of Smithe (1975), and color codes are given in parentheses hereafter.

Statistical analyzes.– All measured morphological characters were found to be normally distributed and uniform using the Kolmogorov-Smirnov test ($p \leq 0.05$). A logistic regression and a test of Hotelling t^2 were applied to the morphometric dataset to assess the existence of sexual dimorphism. The regression analysis assumes multivariate normality and equal covariance between samples and provides a visual assessment that can be used to reject or confirm the morphological distinction between the two binomial groups (Hair et al. 2005). A Discriminant-Function Analysis (DFA) was applied to the morphological data for each sex separately to evaluate whether the different natural groups of cis-Andean taxa defined by molecular phylogeny were also significantly diagnosable from other taxa based on the continuous morphometric and plumage characters measured. In this analysis, to eliminate the effect of body size, we substracted the raw morphometric data from scores of the first factor of a principal component analysis and these ratios were used in a multiple regression whose residues were employed in classical discriminant analysis independent of size (Reis et al. 1990). Because only three characters were measured by Howell (1956) for trans-Andean taxa, we employed a two-sample T-test and One-way ANOVA to test whether those continuous characters were significantly different among trans and cis-Andean taxa. The groups tested were defined a priori by a molecular phylogeny to evaluate whether clades were also

diagnosable by morphological characters. All statistical analyses were conducted using the software Statistica 7.1 (Statsoft 2005) with a confidence interval of 0.95.

Vocal Analysis.– For each taxon we obtained recordings from geographically distinct regions throughout the Amazon to sample the diversity of patterns of the loudsong of *Deconychura longicauda*. We reviewed 90 vocal recordings of cis-Andean populations, one recording for the trans-Andean population and another single recording for the Andean population, obtained from audio archives and personal files as listed in Appendix 3. Of these, 38 recordings (*longicauda* n = 6, *D. longicauda subsp.*1 of Andean n = 1, *connectens* n = 1, *typica* n = 1, *pallida* n = 16, *zimmeri* n = 12) were used in our analysis. The remaining 54 recordings were eliminated after an initial inspection due to excessive background noise, short recording time, and uncertainty about the type of vocalization (spontaneous or stimulated by play-back) involved. The latter is justified because many woodcreepers often change their songs when subjected to tape playback and string songs together separated by a continuous series of notes, resulting in a “chorus” that may last for minutes at a time. It is often almost impossible to distinguish separate songs in such a series (Marantz 2005).

Occasionaly, two or more recordings of the song belonging to the same individual were present in the vocal records, resulting in a sample size of 187 loudsong recordings (*longicauda* n = 20, *connectens* n = 5, *pallida* n = 64, *zimmeri* n = 92, *typica* n = 2, Andean unnamed taxon n = 4).

We made an individual spectrogram of each recording, using Raven software (version Pro 1.3 for Windows, Krein et al. 2008). All recordings of the song were digitized at 44.1 kHz and 16 bits in the standard mono. For clarity, shape of notes in

all spectrograms was adjusted for a resolution of 116 kHz filter bandwidth, mainly to investigate which could be considered frequency-modulated (FM). We filter some of these songs to remove background noise, observing the lowest minimum frequency and higher maximum frequency of each recording.

We adopt the following terminology: a single note was characterized as a continuous trace in the spectrogram, including associated "overtones" (Isler et al. 1998); long vocalizations were named "loudsong", seen as a series of structurally different notes; short vocalizations were named "call", with a note or pair of identical notes, simply structured (Thorpe 1961, Willis 1967, Warren 2002). Nevertheless, we did not find enough recordings of calls for most of the group considered here, making it impossible to establish call note homologies between the vocal groups analyzed.

Given the complexity of the vocalization present in most recordings, we divided songs in two parts (similar to Marantz 2005), defined by the shape of the notes (from the spectrogram), sound and/or time interval (in seconds) between sequence of notes. The first part called initial element (IE), usually given at the beginning of the song, or isolated in multinotes with note maximum frequencies relatively close in values. The second part called conclusive element (CE), which is always present in the song, distinguishable by the structure of the notes, usually long (relative to IE), and may form sequences with the IE. We divided the CE in three sections (including the beginning of the first note until the end of the last note in the element) with equal intervals of time (similar to Isler et al 1998). Loudsongs with structurally simple notes lacking an IE were classified CE.

To measure and describe variation of vocalizations among the different taxa, we used only the CE to ensure that all vocal characters being compared were

homologous (Remsen 2005). Most of the selected characters were adapted from Isler et al. (1998), except the maximum frequency and interquartile range, which were selected from the Raven Pro 1.3 program (Krein et al. 2008).

The quantitative vocal characters measured were as follows: 1) NN - number of notes (notes were defined as continuous features in the spectrogram) 2) MF - average maximum frequency (provided by the program in Hertz) for all notes of the song, 3) DN - average duration of each note measured in seconds (computed as from the time between the initial and final note) 4) IQR - average interquartile range of frequency of the notes (the difference between the first and third average frequency quartiles; see Charif et al. 2008), 5) TIN - time interval between notes (computed in hundredths of seconds as the first, TIN1, and last, TIN2, section of conclusive element), 6) TS - total duration of the song (computed from the beginning of first note until the end of the last note of the CE, including the time intervals between notes), 7) TP- total pace (computed by dividing the number of notes for the duration of the loudsong until the beginning of the last note, including the respective intervals NN/TS), 8) P - pace for each section of the conclusive element (P1, P2, and P3) defined as the ratio between the number of notes and the total duration in each section including the intervals between them; 9) PD - duration of the pace in each section(PD1, PD2 and PD3) computed from the beginning of the first note to the beginning of the last note in each section, including the respective time intervals between notes. Three measurements were made for each character of each song, to account for individual variation and minimize measurement errors. We found the mean for each individual and later vocal group based on these three measurements

in our analyses to make descriptive comparisons between groups. These measurements were made in the waveform format.

The following vocal qualitative characters were analyzed: 1) composition of song for the presence of the elements defined above, which were classified either as simple (if only CE was present) or compound (if both IE and CE were present); 2) presence or absence of "overtones", defined in the spectrogram as a trace parallel and simultaneous to basal note; 3) presence or absence of harmonics, defined as a series of tones with consecutive integral multiples of the frequency of the basal notes, seen in the spectrogram as notes parallel to fundamental harmonic; 4) changes in the pace observed by the ratio between the total number of notes and duration of loudsong until the beginning of the last note, and so in each section, classified as upward (if the values increase between sections) and downward (if the values decay between sections; 5) changes in the pattern of structure and length of notes/time within sections, seen as acceleration or deceleration; 6) syntax defined as the order in which different notes are arranged.

We used three approaches to describe the variation of loudsong: i) visual classification of elements using the spectrogram; ii) linear correlation to investigate the relationship between variables in song of those vocal groups with more than three recordings and; iii) stepwise Discriminant-Function Analysis (DFA) with Tukey HSD test using vocal groups defined by the molecular phylogeny (Figure 2).

Data were logtransformed, because some variables showed deviations from normality according to the Kolmogorov-Smirnov test ($p \leq 0.05$), and then they were subjected to multivariate analysis, conducted in the Statistica 7 software (StatSoft 2005). After characterizing and identifying each vocal type of *D. longicauda*

populations we mapped them onto the molecular phylogeny to verify the degree of congruence in the phylogenetic signal of these two sets of data.

RESULTS

Molecular Phylogenetics.– We obtained a total of 1108 base pairs (bp), of which 206 bp (ca. 18.59%) were phylogenetically informative, from segments of the mitochondrial Cyt b (494 bp) and ND2 (614 bp) genes. No stop codons, insertions or deletions were observed. The partition homogeneity test showed no significant difference (p = 0. 58) in the phylogenetic signal of the gene partitions and thus we combined in MP and ML phylogenetic analyses. The ML model selected for the combined data set was the HKY85, with frequency of bases (A = 0.30540, C = 0.32490, G = 0.10260, T = 0.26710), substitution model kappa = 8.045145 (Ti/Tv = 3.9342), proportion of invariable sites (I = 0.3899), and rate of variable sites following a Gamma distribution (α = 1.2793).

Phylogeny estimates.– The phylogeny estimated by MP using the heuristic search algorithm with equal weight to all characters (unweighted) resulted in 54 equally most parsimonious trees (length 405, CI = 0805, RI = 0866). A strict bootstrap consensus (based on 1000 pseudo-replications; not shown) of these trees resulted in a tree with identical well supported nodes (> 75%) as those also well supported by ML and BI; both ML and BI trees were identical in topology, with the same well supported nodes (ML bootstrap >75% and BI posterior probability > 0.95; Fig. 2).

All three phylogenetic methods indicated high levels of phylogeographic structure within a well supported monophyletic polytypic *D. longicauda*, with MP, ML

and BI trees converging on the same basic topology. Regardless of the tree-building method chosen, high bootstrap (bt) or posterior probabilities (pp) indicate the existence of eight well-differentiated clades in *D. longicauda* (Figs. 1 and 2). All trees grouped the samples corresponding to the populations of the Guiana center of endemism in a single well-suported clade hereafter named clade 1 (Cl1). This clade together with an Andean unnamed taxon is sister to a second major clade, formed by lowland Amazonian taxa outside of the Guianan shield and trans-Andean taxa. However, this major dichotomy separating Guianan+Andean and lowland Amazonian+trans-Andean populations is not well supported (pp 0.51; Fig. 2). Within this second major clade, trans-Andean birds (*typica* and *darienensis*) form a well supported clade (hereafter named clade 8, i.e. Cl8) sister to another well supported clade grouping all Amazonian populations outside of the Guianan shield (clades 3-7 in Figure 2). However, the statistical support for this trans-Andean / lowland non-Guianan Amazonian sister relationship was low (BI: 0.81, ML: 67.5%, and MP < 50%; Fig. 2).

Within the lowland Amazonian clade excluding Guianan shield populations, three main well supported clades were found: clade 3 (endemic to the Inambari center of endemism), clade 4 (endemic to the Imeri and Napo center of endemism), and clades 5-7, grouping populations found east of the Madeira River (Figure 2). Relationships among those three Amazonian clades are poorly supported and are best interpreted as an unresolved trichotomy (Figure 2). The Madeira, Tapajós, and Xingu areas of endemism harbor respectivelly clades 5, 6, and 7, with good support for a node uniting the populations associated with the Madeira center of endemism with those from the Tapajós and Xingu centers of endemism.

Sequence divergence levels.– The average divergence level ("p" uncorrected) between outgroups and *Deconychura* was 14%, whereas the average divergence level between trans-Andean and Guianan shield populations was 8% (Table 1). Table 1 shows that average pairwise divergence levels among taxa varied from 1% (between clade 6 and clade 7) to 8% (between clade 1 and clade 7).

Morphology.– The logistic regression test and Hotelling's t^2 ($p \leq 0.05$) confirm that the cis-Andean *D. longicauda* are sexually dimorphic. Analyzed together, 98.8% of the polytypic cis-Andean *D. longicauda* specimens are correctly classified as males and females. According to the logistic regression (Chi^2 13 = 79.87, p = 0.00), the characters that best contribute to discriminate males and females in *Deconychura longicauda* are the length and width of the bill, wing length, length of pectoral streaks, and proportion of streaks on the crown (Table 2). To confirm this pattern, we applied the logistic regression to each clade defined by the molecular phylogeny (Figure 2) separately, noting which characters of external morphology were responsible for sexual dimorphism in each clade individually.

In clade 1, characters that best contributed to the sexual dimorphism were length and height of bill, length of wing and tail and number of streaks on the crown and chest (Chi^2_{13} = 19.57 p <0.05). For clade 3, characters that best contributed to the sexual dimorphism (Chi^2_{13} = 23.21 $p \leq 0.00$) were related only to measurements of the bill (BL, BW and BH). Clade 4 is sexually dimorphic (Chi^2_{13} = 16.85 $p \leq 0.00$) by the width of the bill, tarsus length, wing length and tail length. Clade 5 showed sexual dimorphism in measurements of bill and length of the wing, length and width of chest streaks and length of the superciliary spots (Chi^2_{13} = 29.58 $p \leq 0.00$). For clade 6 bill and tail length measurements are sexually dimorphic (Chi^2_{13} = 28.97 $p \leq$

0.00) contribute to the sexual dimorphism in clade 6. Clade 7 is sexually dimorphic (Chi^2_{13} = 28.03 p ≤ 0.00) in bill length, wing length, width of pectoral streaks, length of the superciliary spots and extension of the spot in the region of alula. The logistic regression showed 100% of sexes were correctly classified in all clades.

For trans-Andean taxa measured by Howell (1956) all characters contribute to unambiguously discriminate (Chi^2_3 = 50.58, p ≤ 0.00) males and females, with 100% of specimens correctly classified by sex. The T-test and ANOVA indicate that bill length (t = 7.48, F = 2.62) and wing length (t = 14.47, F = 4.45) are the most important characters contributing to sexual dimorphism in trans-Andean taxa. According to the logistic regression wing length was the character that best contributed to sexual dimorphism in *typica* (Chi^2_3 = 30.78, p = 0.00), *darinensis* (Chi^2_3 = 12.26, p = 0.00) and *minor* (Chi^2_3 = 11.40, p = 0.01) with 100% (in *typica* and *minor*) and 83% (in *darienensis*) of cases correctly classified.

The canonical DFA conducted separately for males (Wilks'Lambda = 0.0349, $F_{15, 145}$ = 4. 75, p = 0.00) and females (Wilks'Lambda = 0.155, $F_{25, 138}$ = 3. 73 p = 0.00) of cis-Andean populations (all clades except clades 2 and 8; Fig. 2) support the hypothesis that the morphometric dataset does not discriminate very well among the clades (Fig. 3; Tables 3, 4, and 5). Among males there is a tendency for clade 1 (endemic to the Guianan shield) and clade 7 (representative from Tapajos-Xingu interfluvium) to distinguish themselves conspicuously from the other clades by the characters wing length, tarsus length, and length of pectoral streaks for males, with respectively ca. 90% and 93% of the specimens classified correctly (Fig. 3A and Table 3). Females, on the other hand, separated more consistently among clades by the characters bill width and height, length of pectoral streaks, proportion of pectoral

streaks, and length of the superciliary spots which together discriminate clades 1, 3, 5 and 7 with 100%, 85%, 100% and 88% of specimens correctly classified (see Figure 3B and Table 4). Therefore, the only instances where morphometric characters contribute to separate clades recognized by the molecular phylogeny involve females of clades 1 and 5.

Characters bill length, wing length and tail length (Fig. 3D, 3C and Table 5) correctly separate males among Guianan (60%), Amazonian non-Guianan (54.7%), and trans-Andean (90.5%) clades, whereas for females, a higher proportion of specimens are classified correctly among Guianan (100%), Amazonian non-Guianan (64.3%), and trans-Andean (100%) clades. Trans-Andean males were discriminated among themselves by morphometric characters such as bill length (*typica* and *minor*, $t_{17} = 3.42$, $p = 0.00$; and *minor* and *darienensis* $t_6 = 3.56$, $p = 0.01$) and tail length (*typica* and *darienensis* $t_{13} = 3.39$, $p = 0.00$), but with a very low variance detected for measurements within each taxon (see data in Howell 1956). Among females, trans-Andean taxa were not discriminated among themselves by any morphometric characters.

Vocalization.– The vocal quantitative and qualitative data, resulting from the visual analyses of the loudsong spectrograms, were adequate to define diagnostic differences among certain clades recovered in the molecular phylogeny (Fig. 4, Table 7).

Clade 1 birds utter an average of nine notes, yielding a longer loudsong (9.17 s) in comparison with the other five clades examined (ca. 3. 36 s longer). The duration of notes (0.4-1.01 s) and time intervals between them (0.2-0.53 s) are longer in clade 1, contributing to the longer total duration of the loudsong. Also, the

average maximum frequency (2897.08 kHz) is higher than in all other clades analyzed. In clade 1 there is a constant change of pace between sections of upward-downward and accelerating-decelerating pace (intermittent pace), which is different than the more constant and accelerated pace of clades 2-8. The song only has the conclusive element with two individual variants in the arrangement of notes (48677 ML and FARO III) and is thus structurally simple (Fig. 4). This is quite different from clades 2, 4, 7, and 8. The syntax shows that the first note is, on average, always of higher frequency (3244 kHz) and longest (0.73 s) on average, whereas the last is always the smallest in frequency (2641 kHz) and shortest kHz (0.54 s; Table 7). All temporal characters are correlated ($p \leq 0.05$), especially those related to the pace. The linear correlations between the character pace (P and P2) and duration of notes ($r = -0.97$) and maximum frequency ($r = -0.91$) were strong. Thus, the correlation between these characters is associated with the change in pace in the loudsong.

We only had access to single recordings of birds from clade 2, representing the unnamed Andean taxon, and clades 4 and 8, which precluded us from including them in discriminant analysis. However, our descriptive analysis show that the loudsong of clade 2 birds is structurally distinct from all other clades according to the following characters: 1) a high number of notes in the conclusive element (12 on average); 2) the duration of notes is shorter than those of the loudsongs of clades 1 and 3, but slightly longer than those of clades 4-8 (Table 7). The maximum frequency is lower and the time intervals between notes is shorter than in all remaining clades; as a consequence clade 2 birds loudsong is longer than those of clades 4 – 8 (due to a higher number of notes) but shorter than in clades 1 and 3 (due to shorter time intervals between notes). The song is structurally composite by

initial and conclusive elements, similar to those of clades 4 and 7-8 (Fig. 4B, table 7). The pace is decelerating, but downward-upward, similar to the loudsong of the clade 1, but in reverse order. The first note is, on average, always of higher frequency (1808 kHz) and longest (0.29 s) on average, while the last is always of smallest frequency (1292 kHz) and shortest (0.23 s), but with variations between the 12 notes of up to 0.37 s (Table 7).

Clade 3 birds utter an average of eight notes in the conclusive element, with an average maximum frequency of 2289 kHz, which is higher than those of clades 2 and 4, but lower than clades 1, and 5-8. The song is structurally composite, due arrangement of notes and includes the initial and conclusive elements (Fig. 4C, table 7). The average total duration of the loudsong (5.81 s) and maximum frequency (2289 kHz) reveals the same pattern as those of clades 2, 4, and 6, but respectively shorter and lower than those of clades 1, 5, 7-8 (Table 7). The notes in clade 3 loudsong last on average 0.49 s, with the shortest interval (0.15 s) at the end of the loudsong. The pace is constantly upward and accelerating-decelerating from the first to the last section (most notably in the latter), except in one individual (XC938 from Loreto, Peru). This is different than the pace in the same section of the loudsongs of clades 2, 4, and 6-8. Spectrograms of the loudsong of clade 3 show pairs of notes with equal frequency in nearly the entire length of the song of the conclusive element (Fig. 4C, table 7). The frequency of the first note (2729 kHz) is greater than the last (1808 kHz), lasting longer (0.57 s) than those that follow, except in one individual (XC 20429 from Acre) which varies with respect to the order of frequency and the duration of notes. For clade 3 the number of notes is positively correlated with pace ($r = 0.79$, $p \leq 0.03$); the duration total of loudsong was positively correlated ($r = 0.99$

$p \leq 0.01$) with the number of notes, and the duration of the pace (DP1, DP2, DP3) was negatively correlated with the pace (P1, P2, P3) in three sections of the loudsong ($r = -0.88, -0.92, -0.80$, $p \leq 0.05$).

Clade 4 sample size was too low for inclusion in thein discriminant analysis due to the low quality of several recordings. Nonetheless, from a qualitative perspective, the single loudsong of clade 4 analyzed is structurally distinct from clades 1 and 4-6 but similar to those in clades 2-3 and 7-8 in that it includes both initial and conclusive elements, categorizing it as structurally composite (Fig. 4D). This bird uttered seven notes in the conclusive element, with the maximum frequency of the notes (1984 kHz) relatively lower when compared to loudsongs of the other clades, except clade 2, which has an even lower frequency (Table 7). The last notes average 0.36 s long with shorter time intervals between them (0.23 s) in the final section of the loudsong. This duration of notes is slightly shorter than in clades 1 and 8 (0.37 s and 0.30 s respectively), but longer than that in loudsong of clades 3, 4, 5 and 7. The pace is constantly upward and decelerating from the first to the last section of loudsongs, which slows down steadily, unlike clades 1-2 and 5-7, but similarly to clades 3 and 8 (Table 7). The initial element is multinoted, followed by seven to eight notes of the conclusive element, varying in frequency and duration. The frequency of the first note (2196 kHz) in the conclusive element is greater than the last (1723 kHz), whereas the duration of the last note is shorter (0.13 s) than the first, which is similar to clades 5-7 (Table 7).

Clade 5 loudsong has the smallest number of notes (four on average) of all clades analyzed, with a maximum frequency (2448 kHz) higher than in the loudsongs of clades 2-4 and 6-8, but lower than loudsong of clade 1. Notes normally

last 0.47 s with the shortest interval between them (of 0.06 s) at the end of the loudsong. The very short time interval between notes of clade 5 loudsong is responsible for the shorter overall time relative to the other sampled clades loudsongs (Table 7). The downward pace also constantly slows down, which is different from all other clades loudsongs. The song is structurally simple in the arrangement sequences of notes, containing only the initial element (Fig. 4E), a characteristic shared only with clade 1 birds. Spectrograms display a downward shift in frequency of the notes across nearly the entire length of the loudsong, with the frequency of first note (2735 kHz) greater than the last (2289 kHz; Table 7).

Clade 6 birds loudsong is similar to those of clade 7 in the number of notes (seven on average) and time interval between them, except for the maximum frequency of the notes (2394 kHz on average), which average higher (by 60 kHz) than those in clades 2-4 and 7-8, but lower than in clades 1 and 5. The pace follows a downward and decelerating-accelerating pattern in the last section, a character also distinguishing clade 6 birds from the other clades. The song is structurally simple (Fig. 4F), with two structural variants (ML88555 and XC39450, both from northern Mato Grosso, where the initial element has eight pairs notes that make harmonic and the conclusive element six pairs of notes, both with modulated frequencies). As observed in the spectrogram (Fig. 4F), pairs of notes have downward frequencies, with the frequency of the first note (2903 kHz) greater than the last (1982 kHz), but both having the same duration of 0.37 s (Table 7). For clade 6 there is a negative correlation between the pace in section three (P3) and the duration of notes in this section ($r = -0.98$, $p \leq 0.01$), as well as a positive correlation between the duration of the pace in the first section (DP1) and duration of notes in

this section (r = 0.95). Also, there is a partial positive correlation between the total duration of the pace and pace (P3) in the final section (r = 0.75) of loudsong. The pace between sections appears controlled by the duration of the notes for this clade.

Clade 7 birds loudsong consists of an average seven to eight notes, with a maximum frequency (2331 kHz) lower than those in clades 1 and 5, but higher than those in clades 2-4 and somewhat similar to clades 6 and 8 (Table 7). The relatively short time (0.17 s) between notes in the first and last sections is kept constant, a distinguishing character of the loudsong of clade 7 (Table 7). The decelerating-accelerating pace is similar to that of clade 6, but differs from it by the upward pace towards the end of the loudsong. The loudsong is structurally composite due to the arrangement sequences of notes (Fig. 4G), with the first note of the conclusive element higher frequency (2773 kHz) than the last (1757 kHz), except for two individual variants (CA2200 and CA3600). As in clade 1 birds, most characters of clade 7 loudsong are auto-correlated ($p \leq 0.01$), except for number of notes, time interval between notes (ITN1 and 2), pace in the second and last section (P2 and P3), and duration of pace of section 2 (DP2). The duration of notes is negatively correlated with the overall loudsong frequency (r = -0.90). However, there is a negative correlation (r = -0.91) between the total duration of pace and duration of the pace in the last section, and a positive correlation (r = 0.85) between the loudsong overall frequency and total duration of pace.

Only a single recording was available for clade 8 birds, thus this clade was not included in the DFA of vocal characters. However, a descriptive analysis indicated that clade 8 has a loudsong that is structurally different from those in the remaining clades. Clade 8 loudsongs have the conclusive element with the smallest number of

notes among all *D. longicauda* clades (Table 7). Furthermore, unlike clades 1-7, clade 8 loudsong is unique in having three elements: initial, intermediate, and conclusive (Fig. 4H). The frequency of the notes in the intermediate element is upward-downward and decelerating-accelerating. The frequency of the notes of the conclusive element is almost constant, going downward towards the end, which is differently from all other clades. The duration of notes in the conclusive element is nearly constant, but the last note is shorter, as in the remaiming clades (Table 7).

The stepwise DFA applied to the five vocal groups with sufficient sample sizes (clades 1, 3, 5-7 as defined in the phylogeny), was statistically significant (Wilks'Lambda = 0021 $F_{30, 50}$ = 4.14 $p < 0.00$) and indicated that clades 1 and 5 are vocally diagnosable, whereas clades 3, 6, and 7 exhibit a lot of variation that does not distinguish these three clades (Fig. 5 and Table 8). According to this analysis, the characters best distinguishing among the different vocal groups are total duration of the song (TS), the time interval between notes in the last section (TIN2), maximum frequency (MF), number of notes (NN), pace in the first and last section (P1e P3), and duration of the pace in the first section (PD1).

A Tukey HSD test which we used to determine the significant differences between vocal group means in an analysis of variance framework, showed no marked differences in character NN among clades ($p > 0.05$). However, marked differences in the character MF were detected between clade 1 and 2 ($p = 0.00$), clade 1 and 3 ($p = 0.00$), clade 1 and 4 ($p = 0.03$), clade 1 and 6 ($p = 0.03$), and clade 1 and clade 7 ($p = 0.01$). Character TIN2 was significantly different between clades 1 and 3, 6 and 7 ($p = 0.00$ for all), whereas character TS was significantly different between clades 1 and 3, and among clades 5-8 ($p = 0.00$ and $p \leq 0.01$

respectivetly). The Tukey HSD test showed significant differences in character R1 between clades 1 and 6 ($p = 0.00$), 5 and 6 ($p = 0.04$), 8 and 1-7 ($p = 0.00$ for all). The character P3 was significantly different between clades 1, 6 and 7 ($p \leq 0.01$), between clades 3 and 5 ($p = 0.00$), between clades 5, 6 and 7 ($p = 0.00$) and, between clades 6, 7 and 8 ($p \leq 0.02$). Finally, the character PD1 was significantly different only between clades 1 and 3 ($p = 0.00$) and, between clades 5-8 ($p \leq 0.01$ for all).

DISCUSSION

The molecular phylogeny based on mtDNA sequences showed that the polytypic *Deconychura longicauda* as currently defined (Marantz et al. 2003, SACC 2010) consists of a strongly supported monophyletic group as demonstrated previously by Derryberry et al. (2010), whose analysis included all main clades of this species, except nominate *longicauda* from the Guiana center of endemism. Within polytypic *D. longicauda*, a total of eight divergent and well supported clades (Fig. 2, Table 1) were recovered: Guianan (including only clade 1 birds distributed in the Guiana center of endemism in northeastern South America), Andean (including only clade 2 birds distributed in the foothills of the eastern slope of the Andes in Peru and Ecuador), Amazonian (including birds in clades 3-7 distributed in lowland Amazonia, except for the Guianan area of endemism), and Trans-Andean (including only clade 8 birds distributed west of the Andes in Colombia and Central America). Genetic distances separating those four main groups of *D. longicauda* are much higher than those separating sister biological species in other woodcreeper genera such as *Xiphorhynchus* (Aleixo 2002) and *Lepidocolaptes* (Garcia-Moreno and Silva

1997) and therefore are indicative of species level status. Although the vocal analyzes included only a single recording for the Andean and Trans-Andean clades, vocal differences among those groups were also great, mirroring genetic differences (Fig. 2 and 4, Table 7). Inter-clade genetic distances were comparatively lower among those five clades (from Napo and Imeri, Inambari, Rondônia and Tapajós-Belém endemism centers, Cl 3-7; Table 1) grouped in the lowland Amazonian group and at least three distinct loudsong types were recognized in this group, indicating that multiple species may be involved in this group (Figure 4, Table 7). While genetic and vocal data support a highly variable polytypic *D. longicauda*, morphological characters were generally ambiguous for distinguishing the different clades recovered by the molecular data (Fig. 3, Tables 3-6). Our morphological analyses did not include specimens from the Andean clade, which appears diagnosably distinct based on the shape and distribution of pectoral streaks (Schulenberg et al. 2007). However, morphological analyses indicated that inter-clade morphological differences are more apparent in females than males, and that Trans-Andean, Guianan, and clade 5 females are consistently diagnosed by a combination of a just few morphological characters (Figure 3, Tables 2-6).

When contrasted with the latest taxonomic assessment of *D. longicauda* (Marantz et al. 2003), our results and those of Derryberry et al. (2010) do not support the speculation that Trans-Andean populations (taxa *darienensis*, *minor*, and *typica*) are more closely related to *C. stictolaemus* but indicate that nominate *longicauda* (Guianan group or clade 1) is genetically and vocally distinct from the remaining clades and that it is better treated as a separate species, particularly because no signs of gene flow were detected between birds in this clade and other nearby *D.*

longicauda taxa. However, our data showed that even though the lowland Amazonian taxa *connectens*, *pallida*, and *zimmeri* are morphologically more uniform as pointed out by Marantz et al. (2003), but are nevertheless distinct vocally in addition to being reciprocally monophyletic in the molecular phylogeny (Figs. 2 and 4; Tables 1 and 7), and thus are better treated as separate species rather than subspecies. Therefore, we propose a *taxon novum*omic treatment, following either the Biological Species Concept (Johnson et al. 1999) or Phylogenetic Species Concept (Queiroz 2005), for the polytypic *D. longicauda*, where six separate species are recognized, including a previously unnamed taxon, described below.

Deconychura longicauda (Pelzeln, 1868)

Taxonomic History.– Pelzeln (1868 p. 60) described *Dendrocincla longicauda*, without designating a holotype, based on five specimens collected by Natterer at Borba, Marabitanas and Barra do Rio Negro (Manaus), all in the Brazilian state of Amazonas. Hellmayr (1907) changed *Dendrocincla longicauda* to *Deconychura longicauda*, designating Manaus as the type locality. Subsequently, Hellmayr (1925 p. 361) followed Chubb (1919, 1921) in synonimizing *Dendrocincla longicauda guianensis* from Bartica Grove, Mermuré Mts, Guianan with *D. longicauda longicauda*. Zimmer (1929) stated the polytypic *D. longicauda*, treating the Guianan clade as *D. l. longicauda*. Here, we found evidence that *longicauda* is genetically and vocally completely diagnosable from all remaining taxa traditionally grouped in the polytypic *D. longicauda*, thus indicating that this taxon is better treated as an independent phylogenetic species. The distinctiviness of *longicauda* loudsong (see below)

Morphological Diagnosis**.–** Throat varying from Canyon-Clay Color (cod. 123 B) to ochraceous in both sexes, but distinctly darker than in any other *Deconychura* clade. Axillaries Cinnamon (cod. 123-A), similar only to those of birds from the eastern slope of the Andes (*D. taxon novum*, clade 2) and *D. zimmeri* (clades 5, 6 and 7). Pectoral streaks Buff (cod. 24) with Olive-Brown (cod. 28) edges (Fig. 6), differing conspicuously from *D. pallida*, *D. zimmeri* and *D. connectens*. Furthermore, unlike all remaining of *Deconychura* species, *D. longicauda* presents the pectoral streaks striped shape less sagital and that extends to the lower region of the abdomen.

Vocal Diagnosis.– The loudsong distinguished from those of birds in all remaining *Deconychura* clades by a significantly longer total duration (around 9s), with longer notes averaging 0.71s separated from each other by longer time intervals (around 0.37s). The Average maximum frequency of notes also is significantly higher than in any other *Deconychura* clade (around 2900 kHz). The loudsong of *D. longicauda* is further distinguished from those of all remaining *Deconychura* clades by the absence of an intial element, i.e. just the conclusive element is present; the loudsong pace is slightly intermittent, but less rapidly than those of birds of *Deconychura connectens* (clade 4) and *D. zimmeri* from the Tapajós center of endemism.

Distribution.– Occurs in the Guiana area of endemism, from the eastern bank of the Guianan Branco River in the State of Roraima to the State of Amapá in Brazil, and the Guianas (Marantz et al. 2003, Naka et al. 2006). Unlike stated by Marantz et al. (2003), Naka et al. (2006) established the Branco rather than the Negro River as the likely geographic barrier between *D. longicauda* and *D. connectens*.

Deconychura pallida (Zimmer, 1929)

Taxonomic History.– Zimmer (1929 pp. 6-7) described *D. l. pallida* based on one adult male from Hyutanahán, on the Purus River, State of Amazonas, Brazil (CM 86902). Zimmer (1929) found significant individual variation in *pallida* and interpreted a series of three specimens from São Paulo de Olivença, on the south bank of the Solimões River, as intermediates between *longicauda* and *pallida*; on the other hand, no intermediates between *pallida* and *D. l. connectens* were found (see below). Zimmer (1929) further discussed that birds he classified as *pallida* east of the Tapajós River might represent a different taxon, which was described only many years later by Pinto (1974). Here, we found evidence that *pallida* is reciprocally monophyletic with high statistical support with respect to all remaining *Deconychura* clades, being also vocally diagnosable by a unique combination of characters; therefore indicating that it is better treated as an independent phylogenetic species. The distinctiveness of *pallida* loudsong added to its reciprocal monophyly, also suggest that it is an independent species. We also found evidence that birds of the Madeira-Tapajós interfluvium (Rondonia center of endemism), which have been historically treated as *pallida*, are in fact sister taxon to those attributed to *zimmeri* (thus mirroring their vocal similarity), and we therefore treat them as such.

Morphological Diagnosis.– Plumage paler overall when compared to *D. longicauda*, with throat and streaks of breast rather than dark Buff (cod. 24), throat feathers with less conspicuous dusky edges, narrower and more indistinct breast streaks and axillaries also less prominent and sometimes lacking (Fig. 7). *Deconychura pallida* is distinguished from *D. longicauda*, *D. zimmeri* and *D. connectens* by the presence of more diamond-like shaped pectoral streaks, absent

in abdomen, thus approaching *D. taxon novum* and *D*. *typica* in this respect, but differing from the latter taxon by larger overall measurements.

Vocal Diagnosis.– The loudsong with both initial and conclusive elements as in *D. zimmeri*, *D. typica*, *D. taxon novum*, and *D. connectens*, but unlike *D. longicauda.* The loudsong average maximum frequency (2290 kHz) lower than those of *longicauda*, *zimmeri* and *typica*, but higher than those of *D. taxon novum*, and *D. connectens*. Average total duration of loudsong (5.81s) is shorter than *longicauda* and *D. taxon novum*, but longer than *D. zimmeri*, *D. connectens*, and *D. typica*. The pace is downward and constant slowing until the second section, unlike the pace in the same section of the remaining *Deconychura* clades.

Distribution.– Amazonia in the Inambari center of endemism, i.e. south of the Amazon / Solimões and east of the Ucayali Rivers in Brazil and Peru, reaching northern Bolivia (Pando) with its eastern limit bounded by the Madeira River.

Deconychura zimmeri (Pinto, 1974)

Taxonomic History.– Pinto (1974 p. 177) described *Deconychura l. zimmeri* based on an adult male from Capim River, in the eastern part of the State of Pará, Brazil (MZUSP 44600). Pinto (1974) showed that Zimmer´s (1929, 1934) original suspicion that birds found south of the Amazon and east of the Tapajós River belonged to a distinct taxon from *pallida* was correct, after analyzing a larger series of specimens from eastern Amazonia. Here, we found evidence that *zimmeri* is indeed a distinct taxon, being reciprocally monophyletic (clades 5, 6, and 7) with high statistical support with respect to all remaining *Deconychura* clades. Furthermore, it is also vocally diagnosable by a unique combination of characters, thus indicating that it is better treated as an independent phylogenetic species. We also found

evidence that birds of the Madeira-Tapajós interfluvium (Rondonia area of endemism), which have been historically treated as *pallida*, are in fact sister to those attributed to *zimmeri* and we therefore treat them as such here, a notion also supported by their loudsong similarity although even tough some important differences exist. Whether or not birds from the Rondonia center of endemism belong to yet another distinct taxon remains to be determined by future analysis (see below).

Morphological Diagnosis.– Morphologically closest to *pallida*, but distinguished mainly by even paler colors, especially the throat which is nearly whitish Smoke-Gray (cod. 44). Pectoral streaks Pale Horn (cod. 92) with Dark Drab (cod. 119B) edges, being longer and possessing a typical sagitate shape, differing from those remaining *Deconychura* clades. The pectoral streaks can extend up to the upper abdomen (Fig. 8).

Vocal diagnosis.– Average total duration of the loudsong´s conclusive element (3.50s) shorter than in all remaining *Deconychura* clades, except *D. typica*, with which there is no overlap. Average loudsong frequency (2393 kHz) is similar to that of *D. pallida* and *D. typica*, but significantly higher than in *D. taxon novum* and *D. connectens*, but lower than in *D. longicauda*. The time interval between notes in first and second sections of the loudsong is held constant, differing from all remaining *Deconychura* clades, but similar to those remaining *D. zimmeri* populations (clades 6 and 7). The clade 5 has a loudsong with fewer notes (four on average) and consequently a shorter total duration (3.11s). The small sample size of vocalizations available for clade 5 (n = 2) precluded any further assessment of the nature of this variation, i.e. whether it is only individual or a fixed apomorphy shared by the whole

clade, which would prompt its diagnosis as an independent species. Similarly, two other *D. zimmeri* populations (clade 6 and 7) loudsongs are very similar, but clade 7 birds utter an initial element in addition to a conclusive element. Again, due to a relatively small sample size and a small geographic coverage of vocal samples, particularly in clade 7, it is impossible to know whether this variation is merely individual or a fixed apomorphy consistently distinguishing those two clades. To further complicate things, no vocal samples east of the Tocantins (i.e. from the Belém center of endemism) were analyzed, thus precluding an accurate assessment of vocal variation of birds in clades 5, 6, and 7, which are kept together in *D. zimmeri* until a more detailed vocal analysis is available.

Distribution.– Distributed south of the Amazon River from the eastern bank of the Madeira westward to the Belém center of endemism in eastern Pará, with a single record for the Marajó Island, also reaching northern Bolivia in Santa Cruz and parts of Beni.

Deconychura connectens (Zimmer, 1929)

Taxonomic History.– Historically, birds west of the Ucayali, north of the Amazon and west of the Negro Rivers (i.e., clade 4 birds occupying the Napo and Imeri center of endemism in Brazil, Peru, eastern Colombia and southern Venezuela) have been treated under the name *connectens*, whose type locality is Puerto Bermudez, on the Río Pichis, Pasco department, Peru. The type of *connectens* is hardly distinguishing from specimens of the highly variable *pallida* from southeastern Peru collected east of the Ucayali, thus possibly indicating that they should be synonymized (D. F. Lane, pers. comm.). To further complicate things, the diagnosis of *connectens* provided by Zimmer (1929) was apparently highly influenced by only

two Ecuadorian specimens from the foothill of the Andes (Sabanilla and Cutucuo / Cutucú), which approach *typica* in their large pectoral spots, whereas the *connectens* holotype from Puerto Bermudez does not, i.e. it has small sagitate pectoral spots much like those of many specimens of *pallida*. As explained above, the Sabanilla and Cutucuo birds belong to an undescribed taxon, which we called *Deconychura taxon novum*. Unfortunately, no genetic or vocal samples are available from nearby the type locality of *connectens*, making it impossible to unambiguosly assign this name to birds of clade 4, which are genetically divergent, reciprocally monophyletic and apparently posess a distinct loudsong (see below). Therefore, for the sake of nomenclatural stability, until tissues and vocal samples are available for populations of the Peruvian lowlands west of the Ucayali and more loudsong samples of clade 4 birds are analyzed, we will keep applying the name *connectens* to birds from west of the Ucayali, north of the Amazon and west of the Negro Rivers.

Morphological Diagnosis.– Very close to *pallida*, but with somewhat darker Cinnamon color (cod. 39), small sagitate pectoral streaks with dark Raw Umber color (cod. 123) edges (Fig. 9), commonly absent in the abdomen, differing from those remaining *Deconychura* clades. Throat is darker than in *pallida* and *zimmeri*, but not so much as on *longicauda*.

Vocal diagnosis.– Loudsong with both initial and conclusive elements as in *D. pallid*a, *D. zimmeri*, *D. typica*, and *D. taxon novum*, but unlike *D. longicauda.* The loudsong average maximum frequency (1984 kHz) significantly lower than those of *longicauda*, *pallida*, *zimmeri*, and *typica*, being slightly higher only than that of *D. taxon novum*, from which it differs by a smaller number of notes (i.e. 7 rather than

12). The pace is constantly upward and decelerating from the first to the last section of the loudsong, unlike *zimmeri* and *D. taxon novum*, but similar to *pallida* and *typica*.

Distribution.– Distributed west of the Ucayali, north of the Amazon and west of the Branco Rivers (Napo center of endemism) in Brazil, Peru, eastern Colombia and southern Venezuela.

Deconychura typica (Cherrie, 1891)

Taxonomic History.– *Deconychura typica* was originally described by Cherrie (1891 p. 338-339) based an adult female from Pozo Azul of Pirro, Costa Rica. Todd (1919 p. 116) described *D. typica minor* based on an adult male from El Tambor in Santander, Colombia, which differed in plumage but mainly body size from nominate *typica* of Cherrie. Zimmer (1929 p. 12) reviewed the systematics of *Deconychura* and proposed treating *typica* and *minor* as a subspecies of *D. longicauda*. Shortly after, Griscom (1929 p.172) described *D. typica darienensis* based an adult female from Cana, eastern Panamá, later also treated as a subspecies of *D. longicauda* (Peters 1951), an arrangement followed until today. Howell (1956) examined all trans-Andean populations of the polytypic *D. longicauda* (*darienensis*, *typica* and *minor*) and concluded that they should all be synonymized into a single highly variable taxon in terms of overall size. Howell (1956) found *darienensis* not separable from *typica* and that *minor* and *typica* (ex- *darienensis*) appear to intergrade in size and color. This notion based solely on morphological characters is also mirrored by the high genetic similarity between *typica* and *darienensis* as shown here and also by Derryberry et al. (2010). No samples of *minor* were sequenced, but given it close morphological similarity to *typica* and *darienensis*, in addition to trans-Andean

distribution, we believe that future genetic evidence will support Howell´s (1956) conclusion to also lump *minor* with *typica* and *darienensis* into a single taxon. Until then, we follow Howell´s (1956) treatment because it is the only one to present actual data involving *minor*. Unlike Zimmer (1929, 1934), we found evidence that clade 8 birds (distributed in trans-Andean South America and Central America) are genetically and vocally completely diagnosable from all remaining taxa traditionally grouped under the polytypic *D. longicauda*, thus indicating that this population is better treated as an independent phylogenetic species. Although only one vocal sample of clade 8 birds was analyzed, the high distinctiveness of their loudsong (see below) indicating that they should be best treated as an independent species.

Morphological Diagnosis.– Diagnosed from all remaining *Deconychura* clades by a combination of conspicuous wide triangular buffy pectoral streaks and dark buffy throat in addition to significantly shorter bills (Fig. 10).

Vocal diagnosis.– Loudsong apparently distinguished from those in all remaining *Deconychura* clades by the presence of an intermediate element in addition to initial and conclusive elements, and also by the shortest notes, lasting on average only 0.05s, which also result in the shortest loudsong of the group.

Distribution.– Distributed in Central America from southern Honduras, Nicaragua, Costa Rica, and Panama to northwestern Colombia.

Deconychura taxon novum

Taxonomic History.– Here, we found evidence that clade 2 birds (distributed in the foothills of the eastern slope of the Andes at ca. 900 – 1750 m in central and northern Peru and eastern Ecuador; Schulenberg et al. 2007) are genetically and

vocally completely diagnosable from all remaining taxa traditionally grouped in the polytypic *D. longicauda*, thus indicating that this taxon is better treated as an independent phylogenetic species. Although only one vocal sample of clade 2 birds was analyzed, the high distinctiviness of its loudsong (see below) added to the high genetic differentiation and apparent lack of introgression with other taxa in the polytypic *D. longicauda*, also indicate that it should be best treated an independent species. A comparison of specimens belonging to clade 2 with the holotype of *D. l. connectens* Zimmer, 1929, the only *Deconychura* taxon approaching the range of clade 2 birds (see also below), revealed that they are not the same taxon (D. F. Lane, pers. comm.) and therefore that no valid name is currently available for this new species, whose morphological and vocal diagnoses are provided below. In fact, two specimens from Sabanilla and Cutucuo in eastern Ecuador discussed by Zimmer (1929, 1934) and reluctantly assigned by him to *connectens* (see below), have the diagnostic morphological features distinguishing this *taxon novum*.

Morphological Diagnosis.– Morphologically distinguished from other *Deconychura* clades mainly by light to whitish large diamond shaped pectoral streaks (Fig. 11), similar in shape but larger than those of *D. pallida* and *D. typica* (Schulenberg et al. 2007, D. F. Lane, pers. comm.). Belly also more distinctly marked than in the remaining *Deconychura* clades (Zimmer 1934).

Vocal diagnosis.– Loudsong with both initial and conclusive elements distinguished from those in all remaining *Deconychura* clades by the lowest average maximum frequency (1650 kHz); the number of notes (12) is higher than in any other *Deconychura* clade, except *D. longicauda*, from which clade 2 birds are also

distinguished by the presence of an initial element, shorter notes, and a downward-upward pace.

Distribution.– Andean foothills of the eastern slope in Peru and Ecuador between 900 and 1750 m (Schulenberg et al. 2007).

Finally our results demonstrate that, although the morphologic diagnosis is minimal, the genus *Deconychura*, comprising at least six phylogenetic and biological species (*Deconychura longicauda*, *D. pallida*, *D. connectens*, *D. zimmeri*, *D*. *typica* and *D*. *taxon novum*), by the high genetic differentiation and apparent lack of introgression with other taxa in the polytypic *D. longicauda*, indicating that they are independent species. All species are genetically and vocally distinct, and geographically being separated by the large Amazonian Rivers. The genetic distance among each clade is enough to consider them distinct taxonomic units and lift them to the species level, as proposed above. We chose to gather the clades 5-7 in *D. zimmeri*, due not only to morphological similarities, but mainly due to small sample vocal. Future work will aim to improve the sampling of taxa, which also inhabit the Amazonian areas under deforestation intense, including the *D. zimmeri* (from endemism center Belém, where begins an area called "arc of deforestation) considered vulnerable.

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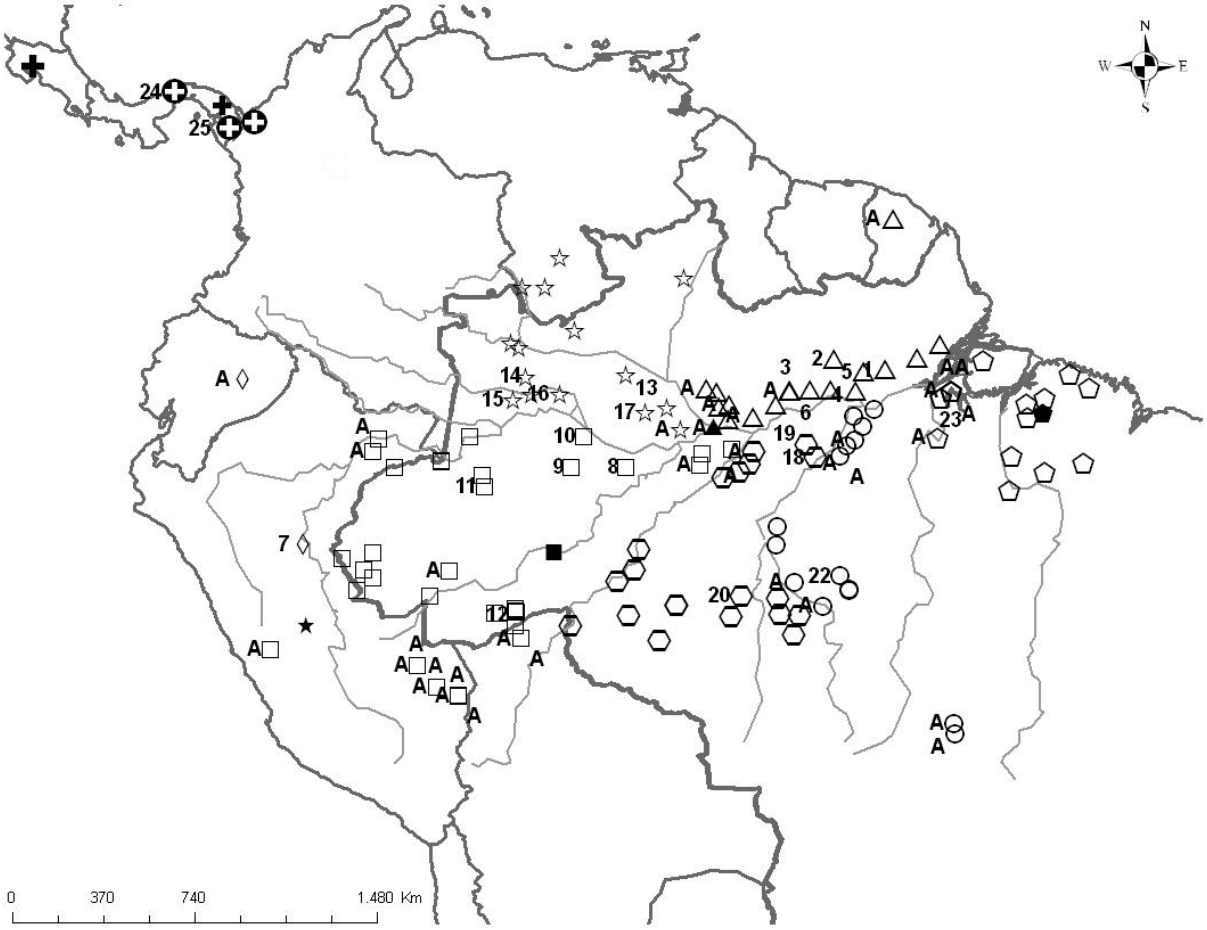

Figure 1. Distribution of sampling points of skins, tissues and vocal recordings of taxa grouped in *D. longicauda* analyzed in this study. The symbols denote locations of samples coded for the different clades they belong as recovered by the molecular phylogenetic data (see Fig. 2 below): Triangles = clade 1 (*Deconychura l. longicauda* of the Guiana center of endemism); diamond = clade 2 (*D. longicauda subsp.* of the eastern fothills of the Andean); squares = clade 3 (*D. l. pallida* of the Inambari center of endemism); stars = clade 4 (*D. l. connectens* of the Imeri and Napo centers of endemism); hexagons = clade 5 (*D. l. zimmeri* of the Rondonia center of endemism); circle = clade 6 (*D. l. zimmeri* of the Tapajós center of endemism); pentagons = clade 7 (*D. l. zimmeri* of the Xingu center of endemism); encircled + = trans- Andean *Deconychura l. darienensis* and *D. l. typica*. Type localities for the *D. longicauda*

taxa associated with the different clades are filled in black. The type localities of *darienensis* and *typica* are shown, respectively as black +. The letter “A” next to a symbol denote localities for which only tape-recordings are available, whereas numbers 1-25 denote localities for the tissues sampled sequenced in Figure 2.

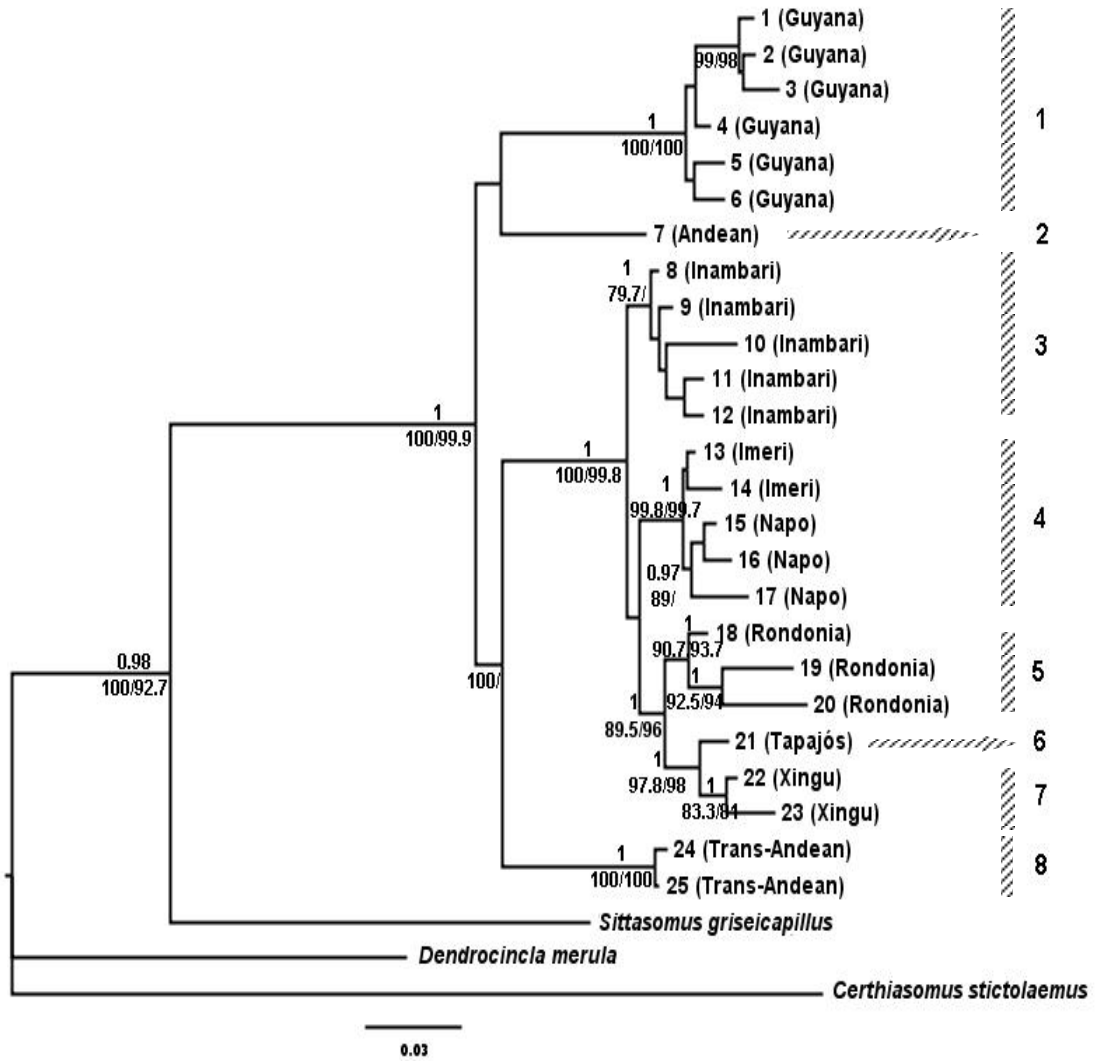

Figure 2. Bayesian phylogenetic tree of *Deconychura* populations based on partial mt DNA sequences (Cyt B and ND2). Numbers above the branches indicate posterior probabilities (BI) and numbers below indicate bootstrap values (MP/ML). Nodes with statistical support below 0.95 (BI) and 75% (MP and ML) are not shown. Numbers at the branch tips refer to tissue collecting localities shown in Figure 1 with names in parenthesis corresponding to Amazonian areas of endemism or major Neotropical regions where those sites are located (see Appendix 2 for detailed locality descriptions). Numbers next to bars represent clades 1-8 (see text).

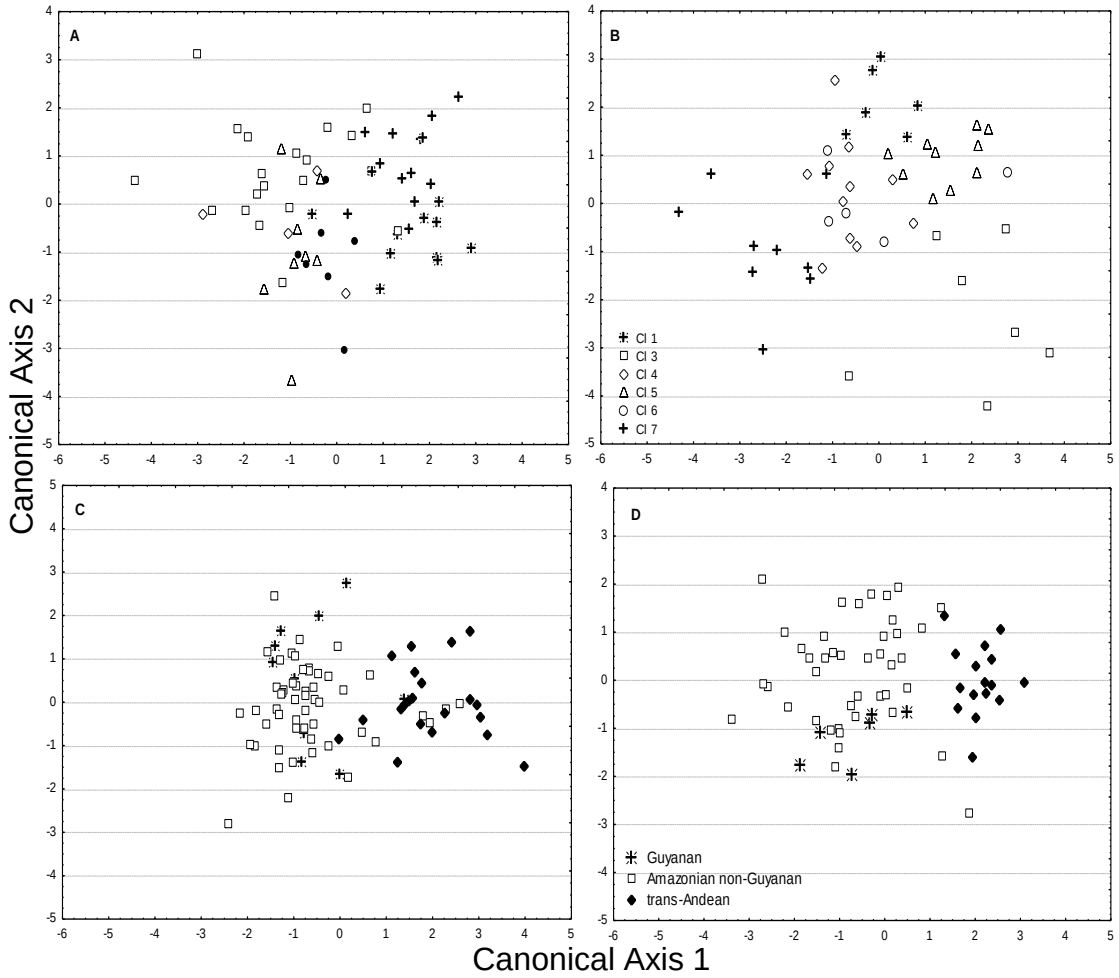

Figure 3. Representation of the stepwise DFA performed with morphometric characters of males (A) and females (B) of the polytypic *D. longicauda*. Those best discriminating between clades 1 and clades 3-7 are pectoral streaks length (both male and female); length of tarsus and of wing (only male), length and height of bill, length of the superciliary spots and, proportion of pectoral streaks (only females). Stepwise DFA performed with morphometric characters of males (C) and females (D) of birds Guianan, Amazonian non-Guyanan and trans-Andean.

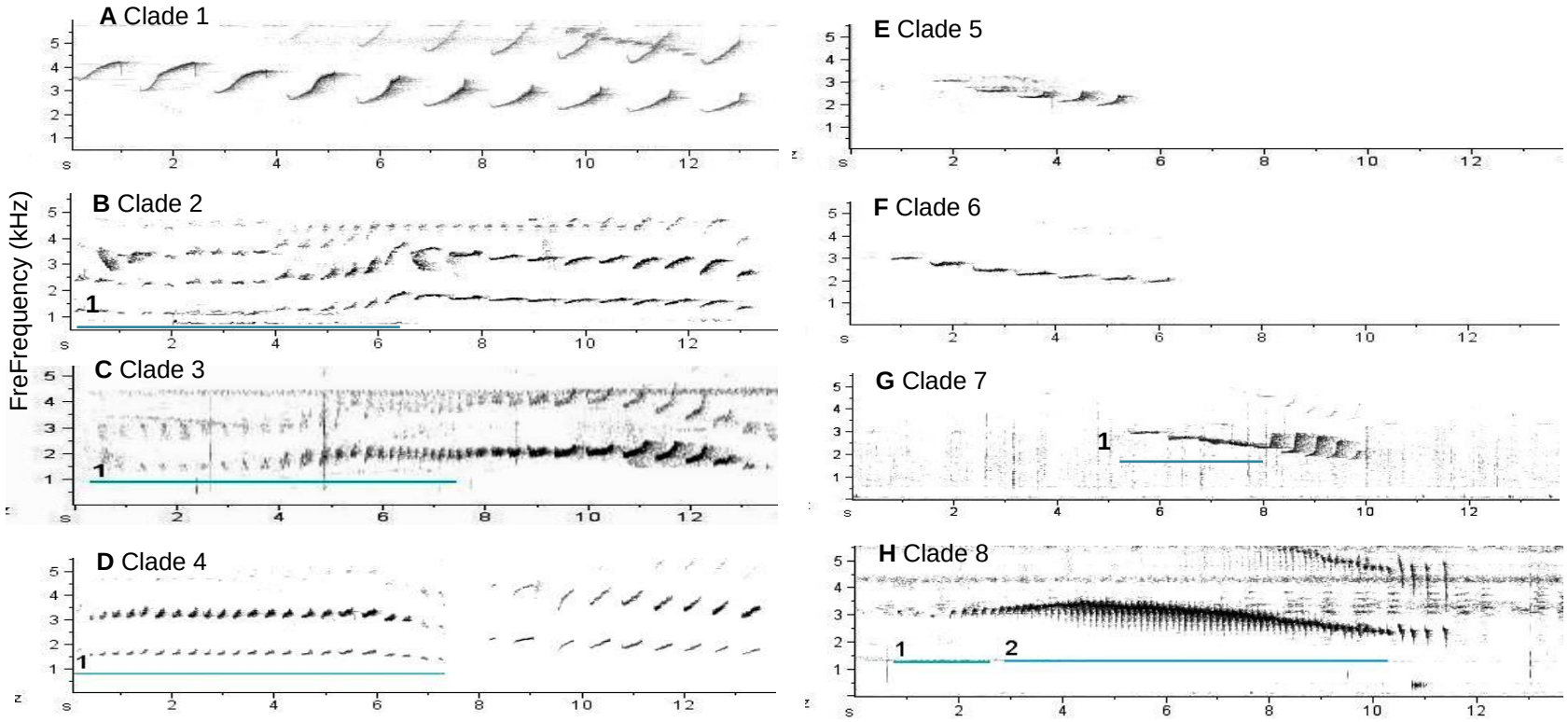

Figure 4. Loudsongs of natural populations of *Deconychura longicauda* (clades 1-8) recovered in a molecular phylogeny (Figure 2). (A) Clade 1: French Guiana, La Trinité (XC 22249); (B) Clade 2: Peru, Loreto: Tierra Blanca (XC20711); (C) Clade 3: Peru, Madre de Dios, Porto Maldonado (ML35539); (D) Clade 4: Brazil, Amazonas, Iranduba, Terra Verde Lodge (ML112796); (E) Clade 5: Brazil, Amazonas, Maués, Pau-Rosa National Forest (AP 1078); (F) Clade 6: Brazil, Pará, Santarém, Tapajós National Forest (BR

163-1); (G) Clade 7: Brazil, Pará, Melgaço Caxiuanã National Forest (CA 4400); (H) Clade 8: Panamá, Darién, Cerro Pirre (ML31184). (1) Marks the initial element and beginning of the conclusive element; (2) Intermediate element present in loudsong of clade 8.

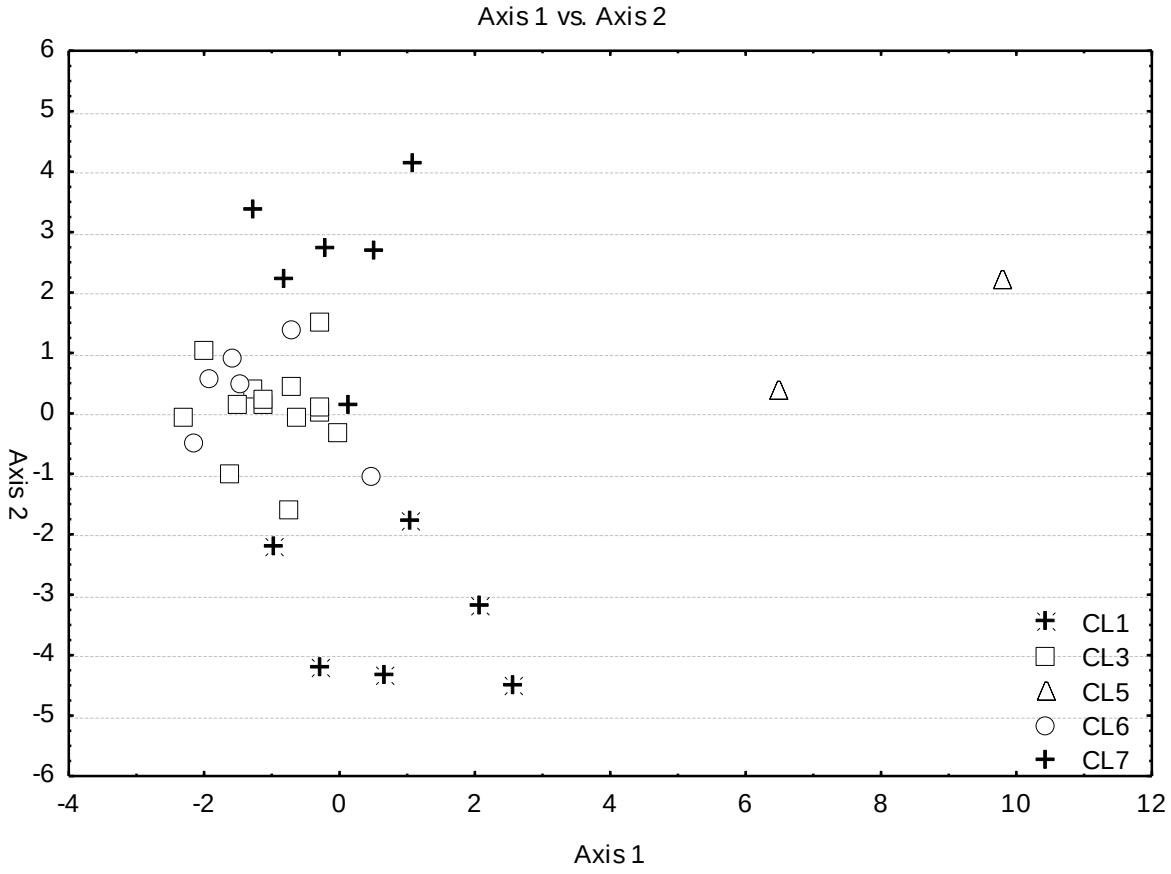

Figure 5. Stepwise DFA with the vocal characters that best discriminate the vocal groups. The clades were those defined by a molecular phylogeny (Figure 2), considering the five vocal groups with more than two recordings.

Figure 6. Serie of *Deconychura longicauda* from Guianan shield (clade 1) showing the conspicuous pectoral streaks that have striped shape less sagital and that extends to the lower region of the abdomen and throat color distinguishing the species. From left to right: MPEG 65986, 65024, 64631, 28627, and 34040. Picture: I. Barbosa.

Figure 7. Serie of *D. pallida* (clade 3) showing the conspicuous presence of more diamond-like shaped pectoral streaks and throat color distinguishing the species. From left to right: MPEG 49918, 48184, 62292, and 55188. Picture: A. Aleixo.

Figure 8. Serie of *D. zimmeri* (clade 5 – 7) showing the pectoral streaks longer and possessing a typical sagitate shape and the throat which is nearly whitish distinguishing the species. From left to right: MPEG: 67312; 53852; 14717; 37353; 38602. Picture: I. Barbosa.

Figure 9. Serie of *D. connectens* (clade 4) showing the conspicuous small sagitate pectoral streaks distinguishing the species. From left to right: AMNH 433089, 274084 and 432963 (Venezuela: Rio Cassiquiare and Esmeralda) and, AMNH 434682, 310809, 434681 (from Brazil: Rio Negro and Uaupés). Picture: A. Aleixo.

Figure 10. Serie of *Deconychura typica* from Costa Rica (clade 8) showing the conspicuous triangular buffy breast streaks and throat distinguishing the species. From left to right: AMNH 525406, 390568, 390570, 390569, 390567, 525407, and 175016. Picture: A. Aleixo.

Figure 11. Serie of *D. taxon novum* (clade 2) showing the conspicuous diamond-shaped whitish breast streaks distinguishing the species. From left to right: AMNH 820999, 821013, and 820931 (Peru: Depto. Huánuco, Cerros del Sira, 1300m and 1550m) and AMNH 820674 (from Peru: Depto. Ayacucho, Huanhuachayo, 1660m). Picture: A. Aleixo.

Table 1. Average pairwise uncorrected genetic P distances between major evolutionary units (clades 1-8 of Figure 2) of *Deconychura longicauda* and outgroups (*Certhiasomus stictolaemus*, *Dendrocincla merula* and *Sittassomus griseicapillus*).

Clades	Outgroups	Clade 1	Clade 2	Clade 3	Clade 4	Clade 5	Clade 6	Clade 7	Clade 8
Outgroups	_								
Clade 1 (Guianan)	0.13	_							
Clade 2 (Andean)	0.14	0.07	_						
Clade 3 (Inambari)	0.14	0.07	0.06	_					
Clade 4 (Imeri, Napo)	0.14	0.07	0.06	0.02	_				
Clade 5 (Rondonia)	0.14	0.08	0.07	0.03	0.04	_			
Clade 6 (Tapajós)	0.13	0.08	0.07	0.02	0.03	0.03	_		
Clade 7 (Xingu)	0.13	0.08	0.07	0.03	0.03	0.03	0.01	_	
Clade 8 (Trans-Andean)	0.14	0.08	0.06	0.06	0.06	0.07	0.07	0.07	_

Table 2. Morphometric measurements of specimens of clades 1, 3-7 of *Deconychura longicauda* (following the molecular phylogeny in Figure 2). Mean ± SD (mm). The characters highlighted are those that best discriminated the different clades separately by sex according to a stepwise DFA independent of size.

	Characters												
Taxa	**BL**	BH	**BW**	**WL**	TL	**TSL**	PSC	**SSL**	**SSW**	PPS	**PSL**	PSW	ESA
D. l. longicauda (clade 1)													
Males (n = 9)	17.83 ± 0.93	5.75 ± 0.36	5.83 ± 0.31	103.87 ± 5.15	111.72 ± 8.24	21.43 ± 0.60	15.64 ± 2.49	11.19 ± 1.76	1.13 ± 0.40	10.97± 1.90	5.78 ± 1.15	1.76 ± 0.24	14.28 ± 3.32
Females (n = 6)	15.34 ± 057	5.30 ± 0.34	5.61 ± 0.36	94.56 ± 3.07	103.60 ± 6.40	19.72 ± 0.88	13.72 ± 1.02	9.52 ± 1.12	1.08 ± 0.26	11.44 ± 1.31	5.95 ± 0.68	1.73 ± 0.32	13.31 ± 1.24
D. l. pallida (clade 3)													
Males (n = 20)	18.42 ± 1.26	5.80 ± 0.39	6.01 ± 0.50	102.30 ± 2.74	104.43 ± 7	18.75 ± 2.12	14.88 ± 2.42	10.56 ± 2.50	1.10 ± 0.35	11.47 ± 1.80	3.96 ± 0.81	1.81 ± 0.30	13.38 ± 1.38
Females (n = 7)	16.71 ± 0.67	5.36 ± 0.31	5.61 ± 0.42	93.01 ± 2.32	94.83 ± 4.91	18.11 ± 1.21	15.05 ± 2.06	11.12 ± 3.29	0.99 ± 0.27	10.95 ± 2.09	3.20 ± 1.36	1.71 ± 0.46	13.12 ± 2.36
D. l. connectens (clade 4)													
Males (n = 4)	18.64 ± 0.42	6.11 ± 0.36	6.33 ± 0.12	104.98 ± 0.39	109.53 ± 4.70	19.59 ± 0.59	15.78 ± 3.98	10.13 ± 0.26	1.30 ± 0.10	13.67 ± 6.89	4.69 ± 0.62	1.58 ± 0.25	11.22 ± 0.29
Females (n = 11)	15.52 ± 1.30	4.86 ± 0.29	5.31 ± 0.68	91.13 ± 5.36	95.89 ± 7.24	18.34 ± 1.26	15.94 ± 4.22	10.61 ± 1.47	0.93 ± 0.17	13.97 ± 3.78	4.33 ± 0.48	1.61 ± 0.52	12.75 ± 2.33
D. l. zimmeri of the Rondonia center of endemism (clade 5)													
Males (n = 8)	17.97 ± 0.40	5.89 ± 0.18	6.11 ± 0.30	104.81 ± 4.07	109.30 ± 3.20	20.51 ± 1.58	15.17 ± 2.04	10.54 ± 1.35	1.03 ± 0.29	11.42 ± 1.77	3.95 ± 0.39	1.46 ± 0.25	14.23 ± 1.78

Females (n = 10)	16.35 ± 1.14	5.57 ± 0.62	5.65 ± 0.45	97.83 ± 6.52	101.15 ± 9.50	18.99 ± 1.38	16.23 ± 2	9.20 ± 1.28	1.25 ± 0.33	13.33 ± 2.71	4.09 ± 0.67	1.46 ± 0.20	13.67 ± 1.85
D. l. zimmeri of the Tapajós center of endemism (clade 6)													
Males (n = 7)	18.05 ± 1.37	5.68 ± 0.27	5.87 ± 0.12	102.49 ± 3.59	107.47 ± 6.07	20.82 ± 2.33	15.86 ± 2.57	11.22 ± 1.45	1.12 ± 0.36	10.62 ± 2.63	4.53 ± 0.60	1.51 ± 0.35	13.43 ± 2.12
Females (n = 3)	16.73 ± 1.49	6.08 ± 0.19	5.83 ± 0.45	99.17 ± 6.23	101.15 ± 9.58	18.99 ± 0.72	13.11 ± 2.83	10.87 ± 1.89	1.11 ± 0.29	10.55 ± 2.04	4.61 ± 0.25	1.66 ± 0.22	12.21 ± 1.62
D. l. zimmeri of the Xingu-Belém center of endemism (clade 7)													
Males (n = 14)	18.21 ± 1.16	5.67 ± 0.52	5.93 ± 0.43	104.50 ± 3.75	112.66 ± 5.62	19.20 ± 1.28	15.07 ± 2.68	11.67 ± 3.15	1.18 ± 0.35	12.24 ± 3.26	5.95 ± 0.77	1.98 ± 0.32	13.81 ± 1.59
Females (n = 11)	16.73 ± 1.24	5.35 ± 0.35	6.09 ± 0.36	95.32 ± 3.89	104.06 ± 3.52	18.55 ± 1.43	16.07 ± 2.70	11.66 ± 1.41	1.19 ± 0.36	12.36 ± 2.36	5.22 ± 0.77	1.90 ± 0.41	12.65 ± 1.40

Table 3. Summary of morphometric classification of males specimens of clades 1, 3, 4, 5, 6, and 7 as defined in the molecular phylogeny in Figure 2 according to a cannonical DFA. *D. l. longicauda* = Cl1, *D. l. pallida* = Cl3, *D. l. connectens* = Cl4 *D. l. zimmeri* of the Rondonia center of endemism = Cl5, *D. l. zimmeri* of the Tapajós center of endemism = Cl6, and *D. l. zimmeri* of the Xingu-Belém center of endemism = Cl7.

Rows: Observed classifications Columns: Predicted classifications							
	Correctness	Cl1	Cl3	Cl4	Cl5	Cl6	Cl7
Cl1(n = 9)	90%	8	1	0	0	0	0
Cl3 (n = 19)	80%	0	16	0	0	0	3
Cl4 (n = 4)	50%	0	2	2	0	0	0
Cl5 (n = 9)	75%	0	0	2	6	1	0
Cl6 (n = 7)	43%	0	2	1	1	3	0
Cl7 (n = 14)	93%	1	0	0	0	0	13
Total (n = 62)	78%	9	21	5	7	4	16

Canonical DFA Males					
Statistic	Value	F-ratio	df		p-value
Wilks's Lambda	0.349	4.748	15	145	0.000
Pillai's Trace	0.796	4.119	15	171	0.000
Lawley-Hotelling Trace	1.466	5.246	15	161	0.000

Table 4. Summary of morphometric classification of female specimens of clades 1, 3, 4, 5, 6, and 7 as defined in the molecular phylogeny in Figure 2 according to a cannonical DFA. *D. l. longicauda* = Cl1, *D. l. pallida* = Cl3, *D. l. connectens* = Cl4, *D. l. zimmeri* of Rondonia center of endemism = Cl5, *D. l. zimmeri* of the Tapajós center of endemism = Cl6, and *D. l. zimmeri* of the Xingu-Belém center of endemism = Cl7.

Rows: Observed classifications Columns: Predicted classifications

	Correctness	Cl1	Cl3	Cl4	Cl5	Cl6	Cl7
Cl1(n= 6)	100%	6	0	0	0	0	0
Cl3 (n= 7)	86%	0	6	0	0	1	0
Cl4 (n= 11)	64%	1	0	8	1	0	1
Cl5 (n= 10)	100%	0	0	0	10	0	0
Cl6 (n= 3)	60%	0	0	1	0	2	0
Cl7 (n= 11)	88%	0	0	1	0	2	8
Total (n= 48)	83%	7	6	10	11	5	9

Canonical DFA Females

Statistic	Value	F-ratio	df		p-value
Wilks's Lambda	0.155	3.734	25	138	0.000
Pillai's Trace	1.310	2.983	25	210	0.000
Lawley-Hotelling Trace	2.923	4.256	25	182	0.000

Table 5. Summary of morphometric classification of male specimens of three major clades in *Deconychura longicauda* as defined in Figure 2 according to a cannonical DFA: Guianan (Cl1G), lowland Amazonian non-Guianan (Cl3-Cl7), and trans-Andean. See text for details.

Rows: Observed classifications Columns: Predicted classifications Males

	Correctness	Cl1G	Cl3-Cl7	t-Andean
Cl1G (n= 9)	60%	6	3	0
Cl3-Cl7 (n= 54)	54.7%	19	30	5
t-Andean (n= 21)	90.5%	0	2	19
Total (n = 84)	64.3%	25	35	24

Canonical DFA Males

Statistic	Value	Approx. F-ratio	df		p-value
Wilks's Lambda	0.417	14.456	6	158	0.000
Pillai's Trace	0.607	11.608	6	160	0.000
Lawley-Hotelling Trace	1.343	17.462	6	156	0.000

Table 6. Summary of morphometric classification of female specimens of three major clades in *Deconychura longicauda* as defined in Figure 2 according to a cannonical DFA: Guianan (Cl1G), lowland Amazonian non-Guianan (Cl3-Cl7), and trans-Andean. See text for details.

Rows: Observed classifications Columns: Predicted classifications Females

	Correctness	Cl1G	Cl3-Cl7	t-Andean
Cl1G (n= 6)	100%	6	0	0
Cl3-Cl7 (n= 42)	64.2%	11	27	4
t-Andean (n= 16)	100%	0	0	16
Total (n = 64)	76.5%	17	27	20

Canonical DFA Females

Statistic	Value	Approx. F-ratio	df		p-value
Wilks's Lambda	0.329	14.634	6	118	0.000
Pillai's Trace	0.760	12.266	6	120	0.000
Lawley-Hotelling Trace	1.771	17.119	6	116	0.000

Table 7. Loudsong measurements (average) of birds in *Deconychura* (clades 1-8) as defined by the molecular phylogeny (Fig. 2). Mean ± SD. SS – sample size analyzed for clade. Characters that best discriminate the different clades according to a stepwise DFA are shown in bold.

Clades	1	2	3	4	5	6	7	8
SS	6	1	14	1	2	6	6	1
NN	**10 ± 4**	12	**8 ± 2**	7	**4 ± 1**	**7 ± 1**	**7 ± 1**	4
MF(kHz)	**2897 ± 87**	1644	**2290 ± 30**	1984	**2448 ± 41**	**2394 ± 08**	**2339 ± 56**	2369
DN (s)	0.71 ± 0.24	0.45	0.49 ± 0.08	0.36	0.47 ± 0.10	0.44± 0.12	0.35 ± 0.13	0.05
IQR (kHz)	237 ± 103	69.38	121 ± 67	111	135 ± 17	103 ± 56	230 ± 175	86.10
TIN1 (s)	0.34 ± 0.11	0.08	0.20 ± 0.08	0.41	0.25 ± 0.09	0.21 ± 0.07	0.18 ± 0.08	0.18
TIN2 (s)	**0.37 ± 0.11**	0.13	**0.15 ± 0.05**	0.23	**0.20 ± 0.06**	**0.18± 0.05**	**0.18 ± 0.09**	0.30
TS (s)	**9.17 ± 2.77**	6.64	**5.81 ± 1.10**	5.28	**3.11 ± 0.71**	**4.05 ± 1.18**	**3.54 ± 1.54**	0.91
TP	1.14 ± 0.35	2.19	2.79 ± 4.25	1.84	1.58 ± 0.28	1.95 ± 0.57	2.36 ± 0.83	4.60
P1	**1.23 ± 0.29**	2.44	**2.21 ± 0.43**	2.25	**1.19 ± 1.68**	**3.38 ± 1.19**	**2.29 ± 1.14**	8.0
P2	1.91 ± 1.48	1.98	2.25 ± 0.53	2.32	2.38	2.33 ± 1.25	2.63 ± 2.49	0.00
P3	**1.71 ± 0.50**	2.74	**2.43 ± 0.36**	2.56	**0.00**	**3.14 ± 0.80**	**3.69 ± 1.15**	0.00
PD1	**2.31 ±**	2.05	**1.25 ± 0.38**	1.33	**0.42 ±**	**0.90 ±**	**0.73 ±**	0.25

	0.78				**0.59**	**0.47**	**0.34**	
PD2	2.39± 1.30	2.02	1.42 ± 0.44	1.29	0.42 ± 0.59	0.73 ± 0.40	0.54 ± 0.59	0.00
PD3	1.03 ± 0.83	1.09	1.32 ± 0. 38	1.17	0.00	0.76 ± 0.35	0.94 ± 0.54	0.00
*MF(FN)	3244	1809	2729	2196	2735	2904	2774	2369
*MF (LN)	2641	1292	1809	1723	2290	1982	1757	2369
*DN (FN)	0.73	0.29	0.57	0.41	0.52	0.37	0.34	0.05
*DN (LN)	0.54	0.23	0.45	0.36	0.43	0.37	0.27	0.05

*Average Maximum frequency (MF) and duration (s) of first note (FN) and last note (LN) for each clades.

Table 8. Summary of the classification obtained by DFA of loudsongs measurements of birds belonging to clades 1, 3-7 in *Deconychura* as defined by the molecular phylogeny (Fig. 2). Clades 2, 4, and 8 were represented by only one recording and therefore were not included in this analysis. *D. l. longicauda* = Cl1, *D. l. pallida* = Cl3, *D. l. pallida* of the Rondônia center of endemism = Cl5, *D. l. zimmeri* of the Tapajós center of endemism = Cl6, *D. l. zimmeri* of the Xingu center of endemism = Cl7.

Classification Matrix Classical DFA of Vocalizatins

Groups	N	Correctness	Cl1	Cl3	Cl5	Cl6	Cl7
Cl1	6	100%	6	0	0	0	0
Cl3	14	93%	0	13	0	1	0
Cl5	2	100%	0	0	2	0	0
Cl6	7	83%	0	1	0	6	0
Cl7	5	83%	0	1	0	0	4
Total	34	92%	6	15	2	7	4

Statistical Test to Classical DFA of Vocalizations

Statistic	Value	F-ratio	df		p-value
Wilks's Lambda	0.012	7.277	28	84	0.000
Pillai's Trace	2.463	5.949	28	104	0.000
Lawley-Hotelling Trace	10.124	7.774	28	86	0.000

Appendix 1. List of specimens of the polytypic *Deconychura longicauda* examined in this study for analyzes of external morphology with reference to the taxon, sex, country, and location (coordinates in decimal degrees). Acronyms: MPEG – Museu Paraense Emílio Goeldi; MNRJ – Museu Nacional do Rio de Janeiro; MZUSP – Museu de Zoologia da Universidade de São Paulo; AMNH – American Museum Natural History; CM – Carnegie Museum; FMNH – Field Museum of Natural History. Subspecies designations follow Marantz et al. (2003).

Deconychura longicauda longicauda: **Males**: **Brazil**: (CM15905, lectotype, examined by digital photography); **Amapá**: (MPEG 28627) Cachoeira Itaboca, R. Macaipe, Mazagão; **Amazonas**: Itacoatiara, (MPEG 66941; MPEG 66942); **Pará**: Flota Faro, Faro, (MPEG 64630; 64631; 64632); Flota of Faro, ca. 70 km NW of Faro, (MPEG 64633); Alenquer, Grão-Pará, (MPEG 65376; 65377). **Females**: **Brazil**: **Amazonas**: Reserve Adolfo Ducke, Manaus, (MPEG 30413); Urucará, Linhão, (MPEG 66911); **Pará**: Porto Trobetas, Oriximiná, (MPEG 34040); Óbidos, Flota do Trombeta, (MPEG 65024); Oriximiná, Port Trobetas, (MPEG 65986); Almerim, Flota do Paru, (MPEG 66442).

Deconychura longicauda pallida: **Males: Brazil: (**CM 86902, holotype, examined by digital photography); **Acre:** Sobral, Cruzeiro do Sul, (MPEG 48183, 48184); Porto Walter, Val Paraíso, (MPEG 52789; 52580); Serra do Divisor, PARNA, (MPEG 58281); Ecological Fundation Antimary, Bujarí, (MPEG 60557, 60558); Plácido de Castro, Novo Horizonte, (MPEG 60559; 60560); Senador Guiomard, Nabor Junior, (MPEG 60561); BR 364, Senador Guiomard, (MPEG 64368); Iquiri, (MZUSP 35655); Station Ecol. Sierra of 3 Brothers, Base São Lorenço, Jaci Paraná, (MPEG 54917); **Amazonas:** River Javari, Estirão do Equador, (MNRJ 17218). River

Javari, (MPEG 18558); River Solimões, São Paulo de Olivença, (MPEG 55188); RDS Cujubim, ca. 390 km SW Jutaí, (MPEG 60141); Coari, River Urucu, Trilha do Papagaio, (MPEG 62291); River Juruá, Igarapé Grande, (MZUSP 23480); River Roosevelt, Esperança, (MZUSP 80631); Paca, RB., River Abacaxis, (MZUSP 76821); **Pará:** Tapajos National Park, Km 120, (MPEG 78046); Rondônia: River Jaci Paraná, Cachoeira Nazaré, (MPEG 39680; 39681; 39682); Ecological Reserve of Samuel, (MPEG 46785); **Mato Grosso:** River Aripuanã, Cachoeira Dar Danelos, (MPEG 31036); Faz. Aliança, left bank, River Paranaíta, Paranaíta (MPEG 7310); Faz. River Paranaíta, right bank, River Paranaíta, Paranaíta, (MPEG 69342); Fazenda João Carvalho, River Teles Pires, Paranaíta, (MPEG 67311); Sete Quedas, right bank, River Teles Pires, Paranaíta, (MPEG 67312). **Females: Brazil: Acre:** River Juruá, South-Sobral, Cruzeiro (MPEG 48182); River Tejo, Taumaturgo, (MPEG 52076); **Amazonas:** Reserve Urucu, River Papagaio-Tefé, (MPEG 57031); Coari, River Urucu, Trilha do Papagaio, (MPEG 62292); River Solimões, right bank, Caitau Uará, (MPEG 49918); Aldeia Traíra, Humaitá, (MPEG 58682); River Abacaxis, left bank, (MZUSP 76822); **Mato Grosso:** Rodovia do Mutum, Apiacás, (MZUSP 83105); Fazenda Aliança, River Paranaíta, left bank, Paranaíta, (MPEG 69343); **Pará:** Igarapé Mutum, Juriti, (MPEG 56610); Igarapé, Mutum, Juriti, (MPEG 56611); Itaituba, AMANA, (MPEG 65616); **Rondônia:** River Ji Paraná, Cachoeira Nazaré, (MPEG 39683; 39684; 39685; 39686); River Jamari, (MPEG 46786); Igarapé, Anibá, (MZUSP 23455).

Deconychura longicauda connectens: **Males**: **Peru**: (FMNH 65866, holotype, examined by digital photography); **Brazil**: **Amazonas:** River Cuiuni, right bank, Barcelos, (MPEG 59453); Japurá, River Acanauí, (MPEG 62631); P. del

Cerro, Mt. Curycuryari, River Negro, (AMNH 310809); **Roraima**: River Mucajaí, Colônia of Apiauí, (MPEG 45788). **Females**: **Brazil**: **Amazonas**: Novo Airão, Igarapé-Açu, (MPEG59454); Japurá, River Mapari, (MPEG 62632); Sitio Bautá, left bank. Alto River Negro, - (MNRJ 37955; 37956); Rodovia S. Gabriel da Cachoeira, Km 15 Cucuí, (MNRJ 38012); Tahuapunto, left bank, River Uaupés, (AMNH 434681); River Negro, Tatui, (AMNH 434682); **Roraima**: River Mucajaí, Colônia do Apiauí, (MPEG 45789); **Venezuela**: River Casiquiare, left bank, Solano, (AMNH 433089); River Huayna, junction with River Casiquiare, (AMNH 432963); Esmeralda, Mt. Duida, (AMNH74084).

Deconychura longicauda zimmeri: **Males**: **Brazil**: (MZUSP 44600, holotype, examined); **Maranhão**: River Itinga, Açailandia, (MPEG 38453); **Mato Grosso**: River Teles Pires, Alta Floresta, (MPEG 51381; 51382); **Pará**: FLONA Caixuanã, (MPEG 61732; 61733); Fazenda Cauaxi, (MPEG 53286); Tomé-Acu, Rodovia Jamic, (MPEG 22934); Flona Tapajós, Purá, Santarém-Cuiabá, Km 117, (MPEG 53852); Rodovia Santarém-Cuiaba, (MPEG 47711); Rodovia Belém-Brasília Km 93, Capim, (MZUSP 44589; 44590; 44591; 44592; 44593; 44594; 44596; 44597; 44599). **Females**: **Brazil**: **Maranhão**: Alto Turiagu, Aldeia Zé Gurupi, (MPEG 38602); Florest CURD, Buruticupú, (MPEG 37353); **Para**: Rodovia Belém-Brasília, Km 93, Capim, (MZUSP 44588; 44595; 44598; 58548); River Alto Cururú, Marajó, (MNRJ A3031); Rodovia Santarém-Cuiabá, (MPEG 36487); Fazenda Jamanxin, Altamira, (MPEG 59220); Rodovia Belém-Brasíliam, Km 75, (MPEG 14714; 14717); River Tocantins, left bank, Marabá, (MPEG 36037); River Tapajós, Vila Braga, (MNRJ 13367).

Deconychura longicauda typica (examined by digital photography)**: Costa Rica**: (AMNH 525406; 390568; 390570; 390569; 390567; 525407; and 175016).

Deconychura taxon novum (examined by digital photography)**:** **Peru:** Depto. Huánuco, Cerros del Sira, 1300m and 1550m (AMNH 820999; 821013; 820931); Depto. Ayacucho, Huanhuachayo, 1660m (AMNH 820674).

Appendix 2. List of tissue samples for taxa included in the phylogenetic analysis of this study.

	Taxa	Clades[a]	Locality	Source[b]	Tissue / voucher numbers
1	*D. l. longicauda*	Cl1	Brazil - PA: FLOTA do Paru, Almeirim	MPEG	CN 1219
2	*D. l. longicauda*	Cl1	Brazil - PA: Óbidos, Flota do Trombeta	MPEG	CN 256/65024*
3	*D. l. longicauda*	Cl1	Brazil - PA: FLOTA de Faro, ca 70 km NW de Faro	MPEG	CN 045/64633*
4	*D. l. longicauda*	Cl1	Brazil - PA: Alenquer, ESEC Grão-Pará	MPEG	CN 382/65376*
5	*D. l. longicauda*	Cl1	Brazil - PA: Alenquer, ESEC Grão-Pará	MPEG	CN 561/65377*
6	*D. l. longicauda*	Cl1	Brazil - PA: FLOTA de Faro, ca 70 km NW de Faro	MPEG	CN 132/64632*
7	*D. l. subsp*	Cl2	Peru - Loreto: Contamana.	LSUMNS	B27966
8	*D. l. pallida*	Cl3	Brazil - AM:Coari, Rio Urucu, Trilha do Papagaio	MPEG	RUR 034/62292*
9	*D. l. pallida*	Cl3	Brazil - AM:Coari, Rio Urucu, Trilha do Papagaio	MPEG	RUR 069/62291*
10	*D. l. pallida*	Cl3	Brazil - AM: Tefé, Base Petrobras/Urucu, Papagaio	MPEG	PUC 025/57031*
11	*D. l. pallida*	Cl3	Brazil - AM: RDS Cujubim, ME Rio Jutaí	MPEG	CUJ 077/60141*
12	*D. l. pallida*	Cl3	Brazil - AC: Plácido de Castro, Novo Horizonte, Km 09	MPEG	UFAC 263/60560*
13	*D. l. connectens*	Cl4	Brazil - AM: Novo Airão, Igarapé-Açu	MPEG	AMZ 160/59454*
14	*D. l. connectens*	Cl4	Brazil - AM: Japurá, Rio Acanauí	MPEG	JAP 594/62631*
15	*D. l. connectens*	Cl4	Brazil - AM: Japurá, Rio Mapari	MPEG	JAP 042/62632*
16	*D. l. connectens*	Cl4	Brazil - AM: ESEC Juami-Japurá, ca 166 km W Japurá	INPA	Dl219
17	*D. l. connectens*	Cl4	Brazil - AM: Parque Nacional do Jaú, MD, "trilha do Nazaré"	INPA	A 2027
18	*D. l. pallida*	Cl5	Brazil - PA: FLONA Amana, MD, Igarapé Montanha, Itaituba	MPEG	AMANA 078/65616*
19	*D. l. pallida*	Cl5	Brazil - PA: Juruti, Igarapé Mutum	MPEG	Dl20336/56610*
20	*D. l. pallida*	Cl5	Brazil - MT: Aripuna	USP	Dl970092
21	*D. l. zimmeri*	Cl6	Brazil - PA: Altamira, Fazenda Jamanxin.	MPEG	BR163-114/59220*
22	*D. l. zimmeri*	Cl7	Brazil - PA: FLONA do Caxiuanã, Plot PPBIO	MPEG	PPBIO 273/61732*
23	*D. l. zimmeri*	Cl7	Brazil - PA: FLONA do Caxiuanã, Plot PPBIO	MPEG	PPBIO 091/61733*
24	*D. l. typica*	Cl8	Panama:prov. Colón, Río Agua Salud	LSUMNS	B26585
25	*D. l. darienensis*	Cl8	Panama:prov. Darién, Cana	LSUMNS	B2084
26	*S. griseicapillus*	Outgroup		Gen Bank	AY089796.1
27	*Dendrocincla merula*	Outgroup	Brazil - AM: Japurá, Rio Acanauí	MPEG	JAP 389
28	*C. sitctolaemus*	Outgroup	Brazil - PA: Alenquer, ESEC Grão-Pará	MPEG	CN432/65378

[a]Natural populations of the polytypic species *Deconychura longicauda* as recognized by the phylogeny (see Fig. 2).

[b]Acronym of the collections are cited in the methods. *Corresponding voucher specimen examined.

Appendix 3. Recordings of vocalizations *Deconychura longicauda* examined in this study. Subspecies designations follow Marantz et al. (2003). Acronym of sound archives: MPEG = Museu Paraense Emilio Goeldi, ML = Macaulay Library, XC = web site Xeno Canto http://www.xeno-canto.org and Pers = personal files kindly provided.

***Deconychura longicauda longicauda*: 6 recordings.** Brazil**: Amazonas**: Manaus (ML127366; ML127468; ML127374, Marantz, Curtis A.); (ML48677, Cohn-Haft, M.); **Pará:** Flota de Faro **(**MPEG Faro III, Aleixo, A.); **French Guiana**: La Trinité (XC22249, Claessens, O.).

Deconychura taxon novum: **1 recording. Peru: Loreto:** Tierra Blanca (XC20711, Athanas, N.).

***Deconychura longicauda pallida* of Inambari center of endemism**: **14 recordings. Bolivia**: **Pando** (ML134997; ML135016, O'Shea, B. J.); **Brazil: Acre:** Manoel Urbano (XC20429, Dantas, S.); Careiro (ML127336 Marantz, Curtis A.); **Peru: Madre de Dios**: Porto Maldonado (ML24328; 29719; 35498; 35539, Parker III, T. A.); (ML55852, Donahue, P. K.); Puerto Tahuantinsuyo: (ML129529 Peter, A.); (ML132302, Michael, A.); (ML136636, Barry, J. H.); **Loreto**: Sta Cecilia (ML37394 Mark, R. B.); (XC938, Vellinga, W-P.).

***Deconychura longicauda connectens* of the Imeri and Napo center of endemism: 1 recording.** Brazil: **Amazonas:** Iranduba (ML112796, Marantz, C. A.).

***Deconychura longicauda pallida* of the Rondônia center of endemism**: **2 recordings. Brazil: Amazonas:** Maués (MPEG AP1078; AP1079, Dantas, S.).

***Deconychura longicauda zimmeri* of the Tapajós center of endemism**: **7 recordings. Brazil: Mato Grosso:** Cristalino, Rio Cristalino (ML88555, Marantz,

Curtis A.); (ML106180 Michael, D.); Paranaíta, Rio Teles Pires (XC36934, Brito, E.); (XC39450, Spencer, A.); **Pará:** Santarém-Cuiabá (ML115073; ML115136, Marantz, Curtis A.); Belterra, Flona do Tapajós (MPEG – BR 163-1, Aleixo, A.).

***Deconychura longicauda zimmeri* of the Xingu center of endemism**: **5 recordings. Brazil: Pará:** Caxiuanã (Pers: CA2 200; CA3 600; CA4 400; CA6 400, Dantas, S.); Belo Monte, Bom Jardim, Anapu (XC18826, Carneiro, L.,).

***Deconychura longicauda darienensis* of Trans-andean South America and Central America. 1 recording. Panama: Darien:** Cerro Pierre (ML31184, Davis, T. H.).