Underestimated Neotropical diversity: Integrative taxonomy reveals two unrelated look-alike species in a suboscine bird (*Pachyramphus albogriseus*)

Lukas J. Musher,[1]* Niels K. Krabbe,[2] and Juan I. Areta[3]

[1] Department of Ornithology, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA

[2] Zoological Museum, Natural History Museum, Copenhagen University, Copenhagen, Denmark

[3] Laboratorio de Ecología, Comportamiento y Sonidos Naturales (ECOSON), Instituto de Bio y Geociencias del Noroeste Argentino (IBIGEO-CONICET), Salta, Argentina

* Corresponding author: ljm357@drexel.edu

ABSTRACT

We applied an integrative taxonomic framework to evaluate the systematics of the Neotropical Black-and-white Becard (*Pachyramphus albogriseus* Sclater 1857). Combining phylogenomic (ultraconserved elements), morphological, and vocalization data, we confirmed that this species is polyphyletic; some individuals form a clade sister to *P. polychopterus* and should be afforded species rank as *P. salvini* Richmond 1899 (Slender-billed Becard), whereas the remaining subspecies of *P. albogriseus* (Broad-banded Becard) are sister to *P. major*. We found that *P. salvini* differs from *P. albogriseus* in song, color of the lores, wing-bar width, body size, and bill width. Whereas *P. albogriseus* occurs in montane forest in Costa Rica and Panama (ssp. *ornatus*) and along the eastern slope of the Andes from northern Venezuela to southern Peru (ssp. *albogriseus*), *P. salvini* is found in the lowlands from Pacific Colombia south to northwest Peru and in the Río Marañón drainage. The latter also occurs, possibly only seasonally, along the eastern slope of the Andes, where the two species' ranges approach closely. We treat *P. a. guayaquilensis* Zimmer 1936 as a junior synonym of *P. salvini* Richmond 1899, and *P. a. coronatus* Phelps and Phelps 1953 as a junior synonym of *P. a. albogriseus* Sclater 1857. This study provides a striking example of a major problem for comparative biology: underestimated and mischaracterized diversity. We argue that there are likely many more cases like this awaiting discovery.

Keywords: integrative taxonomy, morphological, Neotropical, phylogenomic, ultraconserved elements, underestimated diversity, vocalization

LAY SUMMARY

- An integrative taxonomic framework reveals that two subspecies in the Black-and-white Becard (*Pachyramphus albogriseus*) are not closely related to that species.
- Two non-sister species differing subtly in plumage but more clearly in morphology and vocalizations are uncovered: Slender-billed Becard (*P. salvini*) and Broad-banded Becard (*P. albogriseus*).
- The two species are largely allopatric but *P. salvini* occurs, possibly only seasonally, on the east slope of the Andes in eastern Ecuador, and north and central Peru, in close proximity to *P. albogriseus*.
- Little data indicate spatial overlap between *P. salvini* (usually to the west, at higher altitude in dry to humid areas) and *P. albogriseus* (usually to the east, at lower altitude often in undisturbed, humid forest).
- Systematic work integrating phenotypic, genomic, and vocalization data, along with dense geographic sampling will increase the probability of detecting unrecognized species in the future.
- We highlight a major problem facing biodiversity science and comparative biology in general; species diversity remains underestimated and mischaracterized, even for well-inventoried groups like birds.

Diversidad neotropical subestimada: taxonomía integradora revela dos especies no emparentadas en un pájaro suboscine (*Pachyramphus albogriseus*)

RESUMEN

Aplicamos un marco de taxonomía integradora para evaluar la sistemática de un ave neotropical, el Cabezón Blanco y Negro, *Pachyramphus albogriseus* Sclater 1857. Combinando datos filogenómicos (elementos ultraconservados), morfológicos y vocales, confirmamos que esta especie es polifilética; algunos individuos formaron un clado hermano a *P. polychopterus* y deben ser elevados al rango de especie como *P. salvini* Richmond 1899 (Cabezón Pico Fino), mientras que las restantes subespecies de *P. albogriseus* (Cabezón Bandas Anchas) son hermanas de *P. major*. Encontramos que *P. salvini* difiere de *P. albogriseus* en canto, color de la región loral, ancho de filetes alares, tamaño corporal y ancho del pico. Mientras que *P. albogriseus* habita bosques montanos en Costa Rica y Panamá (ssp. *ornatus*) y a lo largo de la ladera este de los Andes desde el N de Venezuela al S de Perú (ssp. *albogriseus*), *P. salvini* se encuentra en tierras bajas desde el Pacífico de Colombia hacia el sur hasta el NO de Perú y en el Valle del Río Marañón. Esta última especie también ocurre, quizás sólo estacionalmente, a lo largo de la ladera este de los Andes, donde las distribuciones de ambas especies se aproximan estrechamente. Tratamos a *P. a. guayaquilensis* Zimmer 1936 como un sinónimo junior de *P. salvini* Richmond 1899 y a *P. a. coronatus* Phelps y Phelps 1953 como un sinónimo junior de *P. a. albogriseus* Sclater 1857. Este estudio muestra un impactante caso de un problema mayor para la biología comparada: la subestimación y caracterizatión errónea de la diversidad. Proponemos que existen posiblemente mucho más casos como éste aguardando a ser descubiertos.

Palabras clave: taxonomía integradora; morfología; neotropical; filogenómica; elementos ultraconservados; diversidad subestimada; vocalización

INTRODUCTION

Understanding how avian species arise and diversify is a key goal of ornithology but is hampered because species-level diversity is incompletely documented (Freeman and Pennell 2021). In the Neotropics, phylogenetic and phylogeographic studies have repeatedly shown that many widespread species of birds consist of multiple species-level taxa (Isler et al. 2007, Tavares et al. 2011, Gutiérrez-Pinto et al. 2012, d'Horta et al. 2013, Rheindt et al. 2013, Fernandes et al. 2014, Ferreira et al. 2017, Cadena et al. 2020, Krabbe et al. 2020, Berv et al. 2021). For example, a recent phylogenomic study of the evolutionary history of 1,287 suboscine species discovered 58 cases of non-monophyly in species for which the authors sampled multiple individuals (Harvey et al. 2020). Moreover, the authors found that >11% of intraspecific divergences were deeper than the median sister species divergence across all suboscines. Thus, uncovering previously unrecognized lineages, both in the field and in the laboratory, and clarifying species limits is crucial for unraveling the evolutionary history of modern birds (Freeman and Pennell 2021) as well as for informing conservation action (Zink 2004, Mace 2004, Fernandes 2013, Huntley et al. 2019).

One group of birds that has recently been reviewed is the becards (Tityridae: *Pachyramphus*), which consists of a group of Neotropical suboscines mostly found in forest and edge habitats (Musher and Cracraft 2018). This recent work concluded that most currently-recognized becard species consist of multiple distinct lineages that would be considered species-level taxa according to the evolutionary species concept (De Queiroz 2007, Musher and Cracraft 2018). The Black-and-white Becard (*P. albogriseus* [Sclater 1857]) is a species with historically controversial phylogenetic affinities (Figure 1). Whereas some previous studies found that a sample of *P. albogriseus* from western Peru was sister to *P. polychopterus* based on mitochondrial DNA (Barber and Rice 2007), others have suggested that *P. albogriseus* might be closely-related to *P. marginatus* (Snow 1979) or *P. major* (Sibley and Monroe 1990), the latter of which is phenotypically most-similar (Figure 1). A study using genome-wide molecular markers found that *P. albogriseus* was polyphyletic; some individuals formed a clade sister to *P. polychopterus*, whereas the remaining samples (including the nominate taxon) were recovered to be sister to *P. major* (Musher and Cracraft 2018, Musher et al. 2019), a result replicated in another study (Harvey et al. 2020). Therefore, given the recently discovered polyphyly of this species, both hypotheses of relationships are apparently valid, but apply to different populations historically included within *P. albogriseus*.

Five subspecies have been recognized within *P. albogriseus*, spanning across much of the tropical Andes to southern Central America (Dickinson and Christidis 2014). The nominate taxon *P. a. albogriseus* (type-locality "Bogotá") is thought to inhabit both slopes of the northern Andes in eastern Colombia and the Andes and coastal mountains of Venezuela; *P. a. coronatus* (type-locality Cerro Tamuypejocha, Sierra de Perijá, Zulia, Venezuela) is known only from the Santa Marta and Perijá mountains of northern Colombia and adjacent Venezuela; and *P. a. ornatus* (type-locality Barranca, Alajuela, Costa Rica) is found in the Talamanca-Chiriquí highlands of Costa Rica and western Panama. The distributions of the two remaining subspecies are disputed. Most previous authors describe the range of *P. a. guayaquilensis* (type-locality Chimbo, Bolívar, W Ecuador) as restricted to the tropical lowlands of western Ecuador (Zimmer 1936, Ridgely and Greenfield 2001a, Mobley 2020), whereas it has also been reported to occur on both slopes of the western Andes in northern Peru (Schulenberg et al. 2010). *Pachyramphus a. salvini* (type-locality Chusgón, Huamachuco, La Libertad, Peru) is typically described as inhabiting the eastern Andean slope, apparently crossing to the Pacific slope in northern Ecuador (Zimmer 1936, Ridgely and Greenfield 2001a, Mobley 2020). All *P. albogriseus* subspecies are found in mid- to upper-elevation humid forest (typically 800–2,300 m, occasionally as high as 3,200 m; Ridgely and Greenfield 2001a, Schulenberg et al. 2010), but *P. a. guayaquilensis* has been thought to be most common from sea level to middle elevations in the Tumbesian dry forests and around the Gulf of Guayaquil (Zimmer 1936, Ridgely and Greenfield 2001a, Schulenberg et al. 2010). To complicate matters, *P. a. salvini* is reported in Peru in both humid montane forest from the eastern slope of the central Andes as well as in dry intermontane valleys (Zimmer 1936, Ridgely and Greenfield 2001a, Schulenberg et al. 2010), a distribution that is biogeographically unusual.

In agreement with the conflicting distributional statements, Musher and Cracraft (2018) found that the diagnoses of two taxa (*P. a. salvini* and *P. a. guayaquilensis*) were vague and difficult to assess. For example, they found that specimens ascribed to *P. a. salvini* in multiple collections fell into each of the two clades, one related to nominate *albogriseus*, the other to *guayaquilensis*. Believing to follow Zimmer (1936), but in fact having sequenced a different E Ecuadorian taxon than what Zimmer had examined, they applied the name *salvini* to birds east of the Andes in Ecuador and Peru that were phylogenetically related to nominate *albogriseus* and sister to *P. major*, and applied the name *guayaquilensis* to birds west of the Andes in Ecuador, and Peru and sister to the sympatric *P. polychopterus*. Zimmer (1936) described *guayaquilensis* based on 7 specimens (4 males, 3 females) from western and southwestern Ecuador, diagnosed by having shorter wings and tail than Peruvian birds (*salvini*) and by males having slightly grayer tails. Musher and Cracraft (2018) found that individuals in the nominate group are significantly larger, males usually have entirely black upper rectrices (excepting *P. a. ornatus*), and females have white supraloral and supercilium with a vibrant chestnut crown and a contrasting black border. Thus, more detailed information about the type specimens and diagnoses is needed to assess the correct application of scientific names for the 2 species in this complex.

Given the taxonomic complexity within this group, additional work is needed to (1) test for non-monophyly of *P. albogriseus* using a larger sample of individuals and more genetic markers, (2) verify the geographic distribution of these taxa through careful assessment of specimen material, (3) delineate the diagnosable plumage and song characters differentiating these taxa from one another, and (4) assess the type specimens of each taxon to ensure the correct application of names to the different clades. We sampled thousands of ultraconserved elements across all 5 named taxa within the *P. albogriseus* complex in addition to 8 closely related *Pachyramphus* taxa in order to test monophyly of *P. albogriseus*. Moreover, we examined study skins (including type specimens), georeferenced photographs, and vocalizations of all *P. albogriseus* taxa to achieve the above goals.

As previously stated, Musher and Cracraft (2018) discovered 2 independent clades within *P. albogriseus*. Henceforth, and at the risk of tipping our hand, we refer to these clades as *P. salvini* (western clade referred to as *P. guayaquilensis* by Musher and Cracraft 2018) and *P. albogriseus* (clade of eastern and northern individuals, in part referred to as *P. salvini* by Musher and Cracraft 2018) (see also comments by JIA in Remsen et al. 2021).

METHODS

Sampling, DNA Extraction, and Sequencing

We analyzed ultraconserved elements (UCEs) for 17 samples representing 13 subspecies and 4 species widely recognized by various taxonomic authorities (Dickinson and Christidis 2014, Billerman et al. 2020, Remsen et al. 2021). We first sequenced UCE data for 7 samples, which included 8 vouchered fresh tissue samples and 2 toe-pads cut from museum study skins at the American Museum of Natural History (AMNH) and National Museum of Natural History

Smithsonian Institution (USNM) (*P. a. albogriseus* AMNH 494147 and *P. a. coronatus* USNM 387453, respectively). We also incorporated all UCEs from a previous study by downloading raw Illumina reads for 10 additional samples, including 4 *P. albogriseus* samples across 3 taxa (Musher and Cracraft 2018). We also downloaded raw reads from 1 outgroup taxon, *Tityra cayana*, which were used in previous studies (Musher et al. 2019, Harvey et al. 2020). A list of genetic samples used can be found in Table 1.

For samples of fresh tissue, we extracted genomic DNA using a DNeasy tissue extraction kit (Qiagen, Valencia, California). To extract fragmented historical DNA from museum study skins, we first cut toe pads from the 2 skins. We then cleaned these samples using 2 washes in water and 1 wash in ethanol to remove impurities and superficial contaminant DNA. DNA was then extracted in an ancient DNA lab at AMNH to minimize the risk of contamination from PCR product and other exogenous sources using the same DNeasy tissue extraction kit.

For new samples, we performed target-capture with the Tetrapods-UCE-2.5Kv1 probe set (available at ultraconserved.org), which targets 2,386 UCEs. Specifically, we sent DNA extracts to Rapid Genomics (Gainesville, FL) for sequence capture of UCEs, including DNA shearing, library preparation, and Illumina sequencing. After sequencing we utilized many scripts within the Phyluce pipeline for bioinformatic processing of UCE data (Faircloth et al. 2012, Faircloth 2016). Specifically, we cleaned the raw reads by removing low-quality reads and trimming all barcodes using *illumiprocessor* (Faircloth 2013, Bolger et al. 2014). Newly sequenced and downloaded reads were cleaned separately because they contained overlapping barcodes. We then assembled the cleaned reads for both downloaded and newly sequenced samples together into contiguous sequences using *velvet* (Zerbino and Birney 2008). Because some samples were originally sequenced using the 5-k probeset (which probes for >4,000 loci including all loci in the 2.5-k probeset), we matched assembled contigs to the larger 5-k probeset to maximize the amount of data in our analyses. Finally, we aligned orthologous loci for our final taxon set using MAFFT (Katoh and Standley 2013). We analyzed 2 datasets with various amounts of missing data for our downstream molecular analyses: first, all loci for which at least 50% of the individuals had sequence (50% complete dataset) and all loci for which at least 95% of the individuals had sequence (95% complete dataset).

Phylogenetic Analyses

To test for non-monophyly of samples previously treated as *P. albogriseus* (*sensu lato*) given complete taxonomic sampling of this group, we applied both concatenated and species tree (i.e., multi-species coalescent) methods to both 50% and 95% complete datasets. We first applied a maximum likelihood (ML) approach on the concatenated sequence data using RAxML (Stamatakis 2014). Specifically, we performed 20 ML searches under the GTR + CAT model of sequence evolution. The GTR + CAT model approximates a GTR + Gamma model of sequence evolution, but reduces computational time (Stamatakis 2014). To examine the robustness of the phylogenetic results, we then performed 1,000 bootstrap replicates.

For the species tree approach, we used ASTRAL (Rabiee et al. 2019). ASTRAL estimates the species tree from a set of unrooted gene trees under the multi-species coalescent model. As input for ASTRAL, we automated the estimation of gene-trees for each UCE locus in RAxML, applying 10 ML tree searches for each UCE locus under a GTR+CAT model of substitution. Finally, we assigned individuals to subspecies (except in *P. polychopterus,* in which we lumped all taxa east of the Andes into a single population, and in *P. albogriseus* in which we subsumed the subspecies *coronatus* into the nominate group based on prior work; Musher and Cracraft 2018), and ran ASTRAL using default settings.

Specimen Examination and Morphometrics

We examined and measured 59 specimens at the AMNH and 25 at the Academy of Natural Sciences of Drexel University (ANSDU) to obtain a more precise diagnosis for *P. salvini* and *P. albogriseus* and quantify their morphology. Specifically, we assessed head, tail, and dorsal plumage patterns, and measured the width of the upper and lower wing-bars (length of longest median and greater covert tips, respectively). To supplement these data and better characterize qualitative patterns of plumage variation, we additionally examined photographs of 26 specimens from 5 additional museums (Supplementary Material Table S1).

To evaluate the morphological differences among taxa in *P. albogriseus* and *P. salvini*, LJM took multiple morphological measurements for 84 specimens at AMNH and ANSDU, including the holotype of *guayaquilensis* and 6 of the 10 specimens in the type series of *salvini*. Specifically, we identified these individuals to the appropriate taxon in light of the data presented herein and measured flattened wing and tail length using a wing ruler (measured to 0.5 mm), as well as culmen length (nares to tip), width at nares, and depth at nares using vernier calipers (measured to 0.1 mm). We further obtained body weight data from AMNH, ANSDU, Museo Ecuatoriano de Ciencias Naturales (MECN, now INABIO), Western Foundation of Vertebrate Zoology (WFVZ), the Museum of Comparative Zoology (MCZ), Museo Estación Biológica Rancho Grande (EBRG, Aragua), and the Louisiana State Museum of Natural Science (LSUMNS) databases. Wing and tail length were not taken if feathers were in molt. We then plotted the data as boxplots using *ggplot2* in R (Wickham 2011) and summarized the data with principal components analysis (PCA) using the function *prcomp* in the package *ggbiplot* (Vu 2011). To minimize missing data in the analysis, we included measurements of bill size, tail length, wing length, and wing-bar width in the PCA. To test for statistical differences in morphological measurements among taxa, we first performed a two-tailed *t*-test comparing *P. albogriseus* to *P. salvini*, and then used a Kruskal-Wallis rank sum test to evaluate whether the means of each morphological measurement also differed among subspecies (*P. a. albogriseus*, *P. a. ornatus*, and *P. salvini*). All morphometric statistics were performed in R version 4.0.3 (R Core Team 2019). A list of specimens measured for this study can be found in Supplementary Material Table S2 and obtained weights can be found in Supplementary Material Table S3.

We also obtained photographs of the holotype of *P. albogriseus* Sclater 1857, and of the lectotype and 3 syntypes of *salvini* (Richmond 1899) in the British Museum (Tring), as well as of critical specimens from the Muzeum i Instytut Zoologii Polskiej Akademii Nauk collection (MIZPAN, Warsaw), Field Museum of Natural History (FMNH, Chicago), MCZ (Cambridge), and LSUMNS (Baton Rouge). Dr. Miguel Lentino, scientific director of Fundación W. H. Phelps kindly examined specimens in the Phelps Collection (COP) and in Museo de Historia Natural La Salle (FLS), the latter of which is now housing the Pons collection (CP), all in Caracas. He also sent us comparative photos he had taken of 3 females from the type series of *P. a. coronatus* side-by-side with females of nominate *P. a. albogriseus* from other parts of Venezuela (see Supplementary Material).

Analysis of Vocal Data

We downloaded *P. albogriseus* songs that we deemed as high quality from 2 open-source databases: the Macaulay Library at Cornell University (Ithaca, NY) and Xeno-Canto.org. After filtering out background noise and normalizing the amplitude, we first identified vocalizations qualitatively by listening to recordings from areas where only 1 taxon occurs. This included recordings of 14 individuals from Pacific Ecuador and Peru for *P. salvini*, and 15 from Venezuela and Central America for *P. a. albogriseus* and *P. a. ornatus* (Appendix). Once a qualitative pattern was found, we identified all recordings to taxon, and quantified 6 characteristics of each song using CoolEditPro (Syntrillium Software, Scottsdale, Arizona). Specifically, we measured (1) duration of an entire song phrase, (2) duration of the penultimate note in the phrase, (3) duration of the last note, (4) duration of rising part of the last note, and (5-6) maximum and minimum peak frequency (frequency with highest amplitude) for the falling and for the rising parts of the last song note, respectively (analyzing 0.02 s long sections of the highest and lowest pitched parts of each in separate files, thus avoiding the effect of large FFT sizes overlapping with adjacent sections; see Supplementary Material Table S4). We also measured the pace of the trilled notes that replace song notes in some recordings and attempted to classify the different call types (see Supplementary Material Appendix and Table S4). Sonograms were drawn with CoolEditPro, using a resolution of 512 bands, a Blackmann windowing function, and a window width of 30%.

Estimation of Species Distributions

We took 3 approaches to collect locality data and inform species distribution estimation for taxa within this group. First, we included localities for each clade identified using mitochondrial gene sequences in a previous study (Musher and Cracraft 2018). Second, we identified all specimens available in seven avian collections (Supplementary Material Tables S1 and S2). These first 2 steps resulted in 227 georeferenced data points to inform species distribution estimation. To supplement this dataset, we then identified all records available in an open-source image archive, the Macaulay Library at Cornell University. Specifically, we searched for *P. albogriseus* records and identified all images to subspecies when at least one diagnostic character was visible; heavily post-processed and altered photographs were ignored. This generated an additional 69 records. In addition to recording georeferenced localities, we also recorded elevation rounded to the nearest 10 m to evaluate differences in altitudinal range and habitat preference among the two taxa. Moreover, we added the georeferenced localities for all identified songs (see section on “Analysis of vocal data” above) to complete the list of localities for each species. We then plotted these localities in QGIS (QGIS.org 2021) and drew minimum concave polygons (i.e., minimum concave hull) around all points for each species. Although these polygons cannot precisely define the distributions of each species (i.e., they do not take into account elevation, habitat, etc.), they are useful for visualizing the degree of potential sympatry between the 2 taxa.

RESULTS

Phylogenetic Relationships

We confirmed polyphyly of *P. albogriseus*, indicating that the current treatment of *P. albogriseus* comprises an additional species, *P. salvini* (Figure 2A, B). In total, the 50% complete dataset included 2,060 UCE loci, which resulted in a concatenated dataset totaling 1,185,367 base pairs (bp) in length whereas the 95% compete dataset contained 1,135 loci totaling 671,206 bp in length. Consistent with previous work (Musher and Cracraft 2018), the nominate group of *P. albogriseus* taxa was recovered as sister to *P. major*, forming a clade that was in turn sister to *P. marginatus*, whereas *P. salvini* was sister to *P. polychopterus* (Figure 2A, B). Intraspecific relationships within *P. albogriseus* uncovered *P. a. ornatus* as sister to our *P. a. albogriseus* clade, including a single sample of *P. a. coronatus* embedded within (Figure 2A). These results were robust to levels of missing data and methodology, as concatenated and species tree analyses resulted in identical relationships for both 50% and 95% complete datasets. However, bootstrap values were generally lower for the 95% complete dataset and the relationships among *P. polychopterus* taxa east of the Andes varied among the two datasets (Supplementary Material Figure S1).

Diagnostic Plumage Characters and Morphometrics

We identified multiple subtle plumage and morphological characteristics that distinguish *P. salvini* from *P. albogriseus* (Figures 2 and Supplementary Material Figures S2–S6). In total, we examined 28 specimens of *P. albogriseus* (19 of *P. a. albogriseus* and 9 of *P. a. ornatus*) and 56 of *P. salvini*. All *P. albogriseus* specimens examined of both sexes show a deep black loral spot that contrasts visibly with the pale supraloral and malar plumage patches, and also show a pale nuchal collar that is fairly well-defined and contrasts noticeably with the darker mantle and upper neck (*n* = 26; Supplementary Material Table S2). Females and immature males of *P. albogriseus* (*n* = 12) have a particularly contrasting facial pattern in general, which is apparent due to a thick well-defined black border around a typically bright chestnut crown. This black border extends from the supercilium into the post-ocular eye-line. Moreover, the upper side of the innermost pair of rectrices (r1) in adult males of *P. albogriseus* is typically either entirely black (83.3% of *P. a. albogriseus*; *n* = 6) or partly gray (100% of *P. a. ornatus*; *n* = 3). Two specimens, one of *P. a. albogriseus* (AMNH 820033) and the other of *P. a. coronatus* (COP 2970), however, have some dark gray tones in the anterior half of the innermost pair of rectrices (r1), but the gray in the tail of these two outliers is not as pale or as extensive as in typical *P. salvini* (Supplementary Material Figure S6). Moreover, the alula is uniformly monochromatic in 96% of *P. albogriseus* (*n* = 27), black in adult males and brown in females and immatures, unlike the bicolored alula of *P. salvini* (see below). Only a single specimen from Costa Rica exhibits a barely visible pale margin of the alula (AMNH 182870). Finally, the upper (median covert) wing-bar on all *P. albogriseus* specimens examined is very broad (4.3 ± 0.5 mm, *n* = 27), averaging nearly 60% broader than the lower (greater covert) wing-bar (2.8 ± 0.8 mm, *n* = 27). The ratio of wing-bar breadth was also 36% larger in *P. albogriseus* (1.8 ± 0.6, *n* = 27) than in *P. salvini* (1.3 ± 0.4, *n* = 56, two-sample *t*-test: *t* = 3.7, df = 38.0, *P* = 0.0008). The only character that Phelps and Phelps (1953) used to distinguish *P. a. coronatus* from *P. a. albogriseus*, the darker crown of the female, could not be corroborated: 3 of 7 females of *P. a. albogriseus* had crowns as dark as three females from the type series of *P. a. coronatus* (see Discussion below and Supplementary Material

Figure S8).

We found that the similarly colored alula of *P. salvini* always shows a pale outer margin, typically white in males and buff in females (*n* = 54; 100%) (Zimmer 1936), a feature rarely seen in *P. albogriseus* (*n* = 1; 3.5%). Individuals of *P. salvini* also always have primarily gray to dark gray (*n* = 54; 96%) lores contrasting only slightly with the supraloral and malar plumage patches, and occasionally containing a small number of black feathers near the anterior end of the eyes (*n* = 15; 27%). Males also always show extensive gray on the upper side of the central pair of rectrices (*n* = 24; 100%), and occasionally two central pairs (*n* = 7; 29%). Specimens of both sexes of *P. salvini* lacked the pale collar found in *P. albogriseus* (*n* = 55; 100%). Examination of photographs of additional specimens corroborate these patterns. The upper (median covert) wing-bar on all *P. salvini* specimens examined is narrower than in *P. albogriseus* (2.4 ± 0.4 mm, *n* = 56), averaging only 24% broader than the lower (greater covert) wing-bar (1.9 ± 0.5 mm, *n* = 56).

In addition to diagnosable plumage characters, *P. salvini* differed from *P. albogriseus* in several morphological measurements, averaging smaller and especially more narrow-billed (Figure 4; Table 2). The two-sample *t*-tests revealed that weight ($t = 4.1$, df = 10.6, $P = 0.002$), tail length ($t = 9.5$, df = 42.8, $P < 0.0001$), flattened wing ($t = 5.1$, df = 23.8, $P < 0.0001$), culmen length ($t = 6.2$, df = 27.9, $P < 0.0001$), culmen width ($t = 14.2$, df = 24.4, $P < 0.0001$), and culmen depth ($t = 8.3$, df = 24.0, $P < 0.0001$) were all significantly larger for *P. albogriseus* than for *P. salvini*. The first two PC axes explained a large portion of the variance in morphology (PC1: 59.1% variance explained; PC2 12.2% variance explained) and revealed two non-overlapping clusters in PC space corresponding to the 2 species (*n* = 84; Figure 5). All 6 morphological measurements contributed to variation along PC1 and all but median wing-bar width to variation in PC2 (Supplementary Material Table S5). The Kruskal-Wallis test also showed that these morphological traits differed significantly when separated into subspecies for weight (Kruskal-Wallis $\chi^2 = 16.2$, df = 2, $P = 0.0003$), tail length ($\chi^2 = 33.9$, df = 2, $P < 0.0001$), flattened wing ($\chi^2 = 19.9$, df = 2, $P < 0.0001$), culmen length ($\chi^2 = 39.0$, df = 2, $P < 0.0001$), culmen width ($\chi^2 = 54.1$, df = 2, $P < 0.0001$), and culmen depth ($\chi^2 = 45.4$, df = 2, $P < 0.0001$).

When populations were delimited by recognized subspecies, most subspecies differed only minimally. A PCA separating groups by subspecies showed complete overlap in PC space between *P. s. salvini* and *P. s. guayaquilensis* and some overlap between *P. a. albogriseus*, *P. a. ornatus*, and *P. a. coronatus* (Supplementary Material Figure S7). Individuals assigned to *salvini* were not significantly larger than those assigned to *guayaquilensis* in tail length ($t = –2.0$, df = 20.1, $P = 0.06$), but were roughly 5% larger based on wing length ($t = –3.7$, df = 15.4, $P = 0.002$). Similarly, *P. a. albogriseus* were roughly 5% larger than *P. salvini* (including *guayaquilensis*) based on tail length ($t = 3.0$, df = 12.7, $P = 0.011$) but not based on wing chord ($t = 1.9$, df = 12.5, $P = 0.08$).

Vocalizations

Two different song types were found. A rapid type was given by birds from western Ecuador and north-western Peru, while a slow type was delivered by birds from Central America and Venezuela, regions where only 1 geno- and morphotype is known to occur. Localities for the 2 song types in other areas generally agreed with the geographical distributions of the 2 geno- and morphotypes (see Musher et al. 2022). The 2 song types correspond to those described from both Ecuador and Peru (see Discussion). In both species the song phrase is composed of a 2–3 noted phrase that is usually repeated once or twice in succession, when twice, typically with a short hesitation before the last phrase. The first two notes in each phrase are alike and falling, whereas the third falls and rises. All 3 notes are considerably longer and delivered at a slower pace in *P. albogriseus* (slow type) than in *P. salvini* (rapid type). Another striking difference between songs of the two species is in the structure of the third note, which begins with a slightly falling part and ends with a sharply rising part in *P. albogriseus*, whereas it falls and rises about equally in *P. salvini*. Songs of *P. salvini* are remarkably similar throughout the species' range, whereas those of *P. albogriseus* are more variable. Thus, the duration of the last note in 18 recordings of *P. albogriseus* was 0.29–0.60 s (0.37 ± 0.08 s, $n = 20$), in 10 recordings of *P. salvini* 0.13–0.17 s (0.15 ± 0.01 s; $n = 11$). The last note in song phrases of *P. albogriseus* is similar in all songs, but the preceding notes are subject to some variation. In 5 of the 35 recordings of *P. albogriseus* the preceding notes are replaced by rapid trills (15–19 notes s^{-1}; Figure 7), which are very similar in recordings from both Venezuela, Colombia, eastern Ecuador, and eastern Peru. The PCA of songs recovered two discrete clusters corresponding to the two song-types detected (Figure 5). PC1 explained 64.1% of variation and clearly separated songs of *P. a. albogriseus* and *P. a. ornatus* from those of *P. salvini*, and PC2 explained 13.8% and accounted for variation within these two species (Figure 5). All vocal variables strongly contributed to the separation between species along PC1, whereas the primary contributor to PC2 was maximum frequency of the last note (Supplementary Material Table S6).

Geographic Distributions

After identifying 69 images, 121 museum specimens, and 61 audio recordings, we obtained 90 georeferenced localities for *P. albogriseus* and 127 for *P. salvini* (Figure 2; see kml file in Musher et al. 2022). Localities of *P. a. albogriseus* were entirely restricted to the eastern slope of the Andes (except for one locality in the Río Marañón drainage; see Discussion) ranging from the Cordillera Vilcabamba in southeastern Peru into the northeastern Andes, Santa Marta and Perijá mountains, and coastal mountains of Venezuela, whereas *P. albogriseus ornatus* is isolated in Central America. *Pachyramphus salvini* is primarily found on the western slope from Colombia south to NW Peru and in the Río Marañón drainage. However, *P. salvini* spills over onto the eastern slope, possibly as a partial migrant only, from central Peru north to northeast Ecuador and possibly southeast Colombia (see kml file in Musher et al. 2022). Records of *P. salvini* from western Ecuador and northwest Peru were found to be from all months of the year. The same was the case for records from the Marañón drainage (except November).

Data from a few localities indicate narrow parapatry or possibly sympatry between *P. salvini* (usually to the west and at higher altitude) and *P. albogriseus* (usually to the east and at lower altitude) (see Supplementary Material). Some ecological differences are also apparent between these forms, which might prevent them from establishing a broad area of overlap. *Pachyramphus salvini* is found in dry to humid areas, tolerating considerably more disturbed habitats than *P. albogriseus*, which is often found in undisturbed, humid to wet forest on the east Andean slopes and outlying ridges. A peculiar situation occurs at Loma Santa (=Lomo Santo), where two specimens of *P. albogriseus* (AMNH-185946 and 185947, both on 30 May 1924; ~1,500 meters above sea level [m.a.s.l.]) were collected well inside the range of *P. salvini*, ~5–8 km to the northwest, at a higher altitude, and in a more humid forest than the nearby specimens of *P. salvini* from Jaen (AMNH-185943 and 185945, 7 Jun 1924, collected by H. Watkins; MVZ-161535, 4 Mar 1972, collected by Robert E. Jones; ~730 m.a.s.l.). Note that Harry Watkins collected both species within an 8-day period in the Jaen/Loma Santa area, suggesting spatiotemporal overlap in distribution (see

Supplementary Materials for more detail).

Based on the localities included in this study, *P. a. albogriseus* averaged higher in elevation (1,529 ± 4,081 m, min = 600, max = 2,280, *n* = 75, two-sample *t*-test: $t = 4.3$, df = 221.3, $P < 0.0001$), but *P. salvini* is found in a wider elevational range (1,214 ± 710 m, min = 0, max = 3200, *n* = 155) that overlaps entirely with that of *P. a. albogriseus. Pachyramphus a. ornatus* averaged slightly lower (1,294 ± 339 m, min = 610, max = 1,829, *n* = 11) in elevation than *P. a. albogriseus*.

DISCUSSION

We used genetic, morphological, and vocal data to show that the Black-and-white Becard, *P. albogriseus* (*sensu lato*), consists of 2 distinct and diagnosable species: *P. salvini* and *P. albogriseus* (*sensu stricto*). These 2 species are (1) each recovered as reciprocally monophyletic, (2) non-sister taxa, (3) diagnosable by song and phenotype (plumage and morphology), and (4) parapatric or possibly sympatric in their distributions. Therefore, they unequivocally represent species under a range of commonly applied species concepts (Mayr 1942, Cracraft 1983, De Queiroz 2007). These 2 species differ only subtly with respect to the details of their plumage and morphology, despite being more than 9% divergent across the mitochondrial gene NADH dehydrogenase subunit 2 (Musher and Cracraft 2018) and probably over 5.5 million years diverged based on fossil-calibrated divergence times (Figure 1C, D; Musher et al. 2019).

Taxonomic Confusion and Clarification

The confused use of the name *salvini* stems in part from the rarity of specimens of *P. albogriseus* from eastern Peru and eastern Ecuador. Zimmer (1936) had none at hand; he examined 5 specimens from eastern Ecuador, all *P. salvini*. Having shown that 2 species were involved, one primarily western, the other primarily eastern in distribution, and having sequenced only one specimen from eastern Ecuador, which by chance happened to be *P. albogriseus*, Musher and Cracraft (2018) then assumed that their bird represented the same taxon as the birds from eastern Ecuador that Zimmer had examined (*salvini*). This left only one name available for western birds (*guayaquilensis*), which they then applied to the western species.

Zimmer (1936) noticed that two specimens collected at Lomo Santo in northern Peru (AMNH 185946 and 185947) differed markedly from other Peruvian material and discussed them extensively. However, Lomo Santo is above Jaen (Zimmer 1936), where typical *salvini* had been collected; Zimmer (1936) considered these birds resident and could not believe that 2 species so similar could coexist, so he concluded that the Lomo Santo birds were most likely atypical specimens of *salvini*. We reexamined and rechecked the origin of the 2 specimens, confirming that both agree with *P. a. albogriseus*, and we presume that Lomo Santo is the same as Loma Santa (5.7005°S, 78.8442°W; see also Vaurie and Zimmer 1972, Stephens and Traylor 1983), as we were not able to find any other locality near Jaen with a similar name. Except for the two Lomo Santo specimens, which were collected by Harry Watkins in the Marañón drainage, and a specimen taken at an elevation of 2,000 m near Numbala Bajo at the headwaters of Río Chinchipe in primary forest connected to the forest of the east Andean slope (MECN-7251; tissue Zoological Museum, University of Copenhagen [ZMUC] 146558), all the remaining 15 specimens of *P. albogriseus* from Peru and Ecuador are from the Amazonian slope. None of the over 10,000 bird specimens collected by Watkins in Peru give reason to doubt his localities. As unlikely as it seems, it appears that *P. albogriseus* is not restricted to the Amazonian slope, but also occurs in the Marañón drainage in close proximity to *P. salvini*, possibly above and in more humid habitats. We encourage further fieldwork in the area to address this issue.

Our data support treating *Pachyramphus albogriseus guayaquilensis* Zimmer 1936 as a junior synonym of *Pachyramphus salvini* Richmond 1899. One of the 7 specimens Zimmer used to describe *guayaquilensis* was intermediate with Peruvian birds in tail length. A female-plumaged bird from Mindo, Pichincha, on the Pacific slope of northern Ecuador, however, was no smaller and was left as *salvini* by Zimmer, although this made little biogeographical sense. We consider it highly unlikely that a specimen from San Javier, Esmeraldas, which Zimmer referred to as *guayaquilensis*, should represent a different taxon from birds at Mindo, which Zimmer referred to as *salvini*. Our study of larger series, including all 5 males (with the lectotype) in the type series of *salvini* as well as the holotype of *guayaquilensis*, shows that there is as much variation in the amount of gray in the tail in *salvini* as there is in *guayaquilensis* (Supplementary Material Table S2). Although the shortest tails are found in birds from southwestern Ecuador, the difference in tail length between *salvini* and *guayaquilensis* is not statistically significant (Supplementary Material Figure S7).

We also recommend that *P. a. coronatus* Phelps and Phelps 1953 be considered as a junior synonym of nominate *P. a. albogriseus* Sclater 1857 (Supplementary Material Figure S9). The only diagnostic feature of *coronatus* given in the type description is the darker crown in the female. However, photos comparing three females from the type series of *coronatus* with females from other parts of Venezuela show that this character does not hold. The crowns of 2 females from Lara (COP 72088, COP 18578) and 1 from Táchira (COP 60638) are as dark as in all 3 females of *coronatus* (COP 54975, CP 2974, CP 2976) (Supplementary Material Figure S8). Darker brown-crowned and brighter chestnut-crowned individuals can be found within the same populations, and it is not entirely clear whether this variation is age-related (M. Lentino *in litt.*). Moreover, our genetic analysis could not recover *coronatus* as being distinct from the nominate taxon (Figure 2A).

Two vocal types were recognized in both Ecuador (Ridgely and Greenfield 2001a) and Peru (Schulenberg et al. 2010), and our data support these distinctions. Previous descriptions state that "Western ♂ has pleasant "tu-tu-dwit?" song, repeated three times, then a pause, then the three phrases again. Eastern ♂ gives a more leisurely and longer phrase with the last note strongly inflected, e.g., "twe, tew, tweu, tu wu-wit?" (P. Coopmans)" (Ridgely and Greenfield 2001b, p. 538); (see p. 624 in Ridgely and Greenfield 2001a for match of western to *guayaquilensis* and eastern to *salvini*), and that 'Song (*salvini*) a quiet, musical "*pew-ew-ew-eewee?*"' and 'Song of *guayaquilensis* is an emphatic "*HEW chewy? HEW chewy?*"' (Schulenberg et al. 2007, p. 480). However, as with specimens, the vocalizations have been in part misassigned: vocalizations assigned to *guayaquilensis* pertain to *P. salvini* (including *guayaquilensis*) whereas those assigned to *salvini* pertain to *P. albogriseus*.

Geographic Overlap

Whether *P. salvini* and *P. albogriseus* are narrowly parapatric or sympatric year-round or seasonally remains an open question. In areas in which their distributions approach, *P. salvini* tends to occur in dry to humid areas to the west and at higher altitude than *P. albogriseus*, which seems to prefer undisturbed, humid to wet forest, but further investigation of these presumed ecological differences is necessary. At least some *P. salvini* are resident on the breeding grounds in western Ecuador, northwestern Peru and the Marañón drainage, but seasonal movements on the Pacific slope during the second half of the year have been suggested to occur (Mobley 2020). The species might be partially migratory with some individuals crossing to the eastern slope during the non-breeding season. This would represent an unusual migratory pattern in the region, matched only by *Sporophila luctuosa* and *Conothraupis speculifera* (Schulenberg et al. 2010, Ridgely and Greenfield 2001b), the latter species, however, being wholly migratory, and possibly *Elaenia* (*albiceps*) *modesta*, which is believed to be migratory in Peru (Fjeldså and Krabbe 1990, Schulenberg et al. 2010), but resident in Chile (Jaramillo et al. 2003). There are no fewer than 13 records of *P. salvini* from the east slope of the Andes, from all months of the year except February and March. Those 2 months are the prime breeding season in the west (the peak of the rainy season), but could be missing just by chance, so it remains possible that *P. salvini* is parapatric or even sympatric year-round with *P. a. albogriseus* in portions of their ranges.

Why Are the Plumages of *P. albogriseus* and *P. salvini* So Similar?

Interestingly, *P. salvini* and *P. albogriseus* have quite similar phenotypes, most notably due to the presence of a gray back in males and pale supraloral stripe, which surely contributed to their confused taxonomic history. But the observation that these non-sister species seem to be phenotypically more like each other than like other more closely related taxa begs the question: why are the two species so similar? One potential hypothesis is that evolutionary conservatism limits variation in plumage patch color combinations. For example, the clade that includes *P. albogriseus*, *P. major*, *P. marginatus*, *P. salvini*, and *P. polychopterus* is characterized by striking plumage similarities across the whole group. Males in this clade share steel-blue to blackish crowns, gray to black backs, pale supraloral streaks, relatively broad, white wing-bars, and whitish to grayish underparts, whereas females share brownish/chestnut crowns often with a lower dark border, brownish backs, yellowish underparts, and relatively broad, rusty wing-bars. Exceptions to this pattern are the males of subspecies *nigriventris* and *tenebrosus* (and to some degree, *spixii*) of *P. polychopterus* and the female of the nominate subspecies of *P. major*. It is therefore possible that plumages of *P. albogriseus* and *P. salvini* have converged to some extent, due to the homeoplastic reappearance of features (i.e., homoplasy) produced by a shared plumage plan (Omland and Lanyon 2000) or represent ancestral characters that have been retained over evolutionary time (i.e., symplesiomorphy). Similarly, conspicuous plumage patterns are often shared in other clades of becards, even between non-sister taxa (e.g., pink throats in *P. minor* and *P. aglaiae*; Barber and Rice, 2007; Musher and Cracraft, 2018). Detailed plumage assessments on the lability and genomic architecture of plumage traits in *Pachyramphus* are needed to further test these ideas.

Might *P. salvini* Be a Subspecies of *P. polychopterus*?

In light of the new phylogenetically-informed taxonomy recovering *P. salvini* as sister to *P. polychopterus*, one hypothesis to consider is that these 2 taxa may be conspecific. Despite their phylogenetic affinity, however, there are few phenotypic or behavioral reasons to suggest this is the case. First, although *P. polychopterus* is a widespread polytypic species that varies extensively in phenotype, all its forms share features lacking in *P. salvini*. Males of all have an entirely black mantle, white scapulars, and a dark supraloral region, quite unlike *P. salvini* males, which have gray backs, gray scapulars, and pale supraloral stripe. Moreover, although plumage varies extensively across *P. polychopterus*, typical songs are remarkably similar across all taxa (Boesman 2016), and quite unlike the explosive song of *P. salvini*. For example, Boesman (2016) showed that the song duration for all

P. polychopterus subspecies was always 1–2 s, but the duration of *P. salvini* song is always just under 0.5 s. Similarly, *P. polychpterus* songs typically contain between 5 and 9 notes, compared with the 3-note phrase we identified for *P. salvini*. Finally, the 2 species are sympatric across a large portion of their distribution in W Ecuador and SW Colombia and are not known to hybridize. Importantly, *P. salvini* and *P. polychopterus* are also highly diverged across their genomes, and are likely between 3 and 7.5 my diverged (Figure 1D) (Musher and Cracraft, 2018; Musher et al. 2019). Thus, we can safely reject the hypothesis that they are conspecific.

TAXONOMIC SUMMARY

Pachyramphus salvini Richmond 1899 (Ex. (Salvin 1895) **Slender-billed Becard**

Type locality: Chusgón, Huamachuco, La Libertad, Peru.

Phylogenetic position: Sister to *P. polychopterus*.

Distribution: Pacific Colombia south through western Ecuador to northwest Peru and central Peru in the Río Marañón drainage. Also occurs, possibly only seasonally, on the east slope of the Andes in eastern Ecuador, north and central Peru, and probably also in southeast Colombia, where it can be found in close proximity to *P. albogriseus*.

Diagnosis: Significantly smaller than *P. albogriseus*. Males superficially similar to *P. albogriseus* in plumage, but with multiple diagnostic features. The dorsal side of the tail is gray with the distal end black but tipped white. The alula always shows a narrow pale edge that is white in males and buff or dull cinnamon in females and is not typically present in *P. albogriseus*. *Pachyramphus salvini* also lacks the pale nuchal band and black loral spot of *P. albogriseus*. Females differ significantly in plumage by having a weakly contrasting, narrow or absent black border to the crown, pale gray or smudgy undefined lores, and a light brown or dull chestnut crown (Figure 3). Males differ from sympatric *P. polychopterus dorsalis* by the presence of a gray back and pale supraloral stripe, and females by presence of a dull chestnut crown.

Subspecies: Monotypic. Given the phylogenetic placement and lack of diagnostic features, we consider *Pachyramphus albogriseus guayaquilensis* Zimmer 1936 as a junior synonym of *Pachyramphus salvini* Richmond 1899 (see *Taxonomic confusion and clarification*).

Song description: Quick and explosive *tu-tu-dwit*? typically repeated 2–3 times in close succession (Figure 6).

Pachyramphus albogriseus Sclater 1857 **Broad-banded Becard**

Type locality: New Grenada, Bogotá.

Phylogenetic position: Sister to *P. major*.

Distribution: Montane forests ranging from the eastern slope of the Andes of southern Peru north to southern Colombia, then again from northeastern Colombia east to northern Venezuela. The subspecies, *P. a. ornatus* (Cherrie 1891) occurs in humid montane forests of western Panama and Costa Rica.

Diagnosis: Significantly larger than *P. salvini* with clearly defined black lores, and a broader heavier bill. The upper cheek and nuchal collar are pale and contrasting, the upper wing-bar is considerably broader than the lower, and the alula is typically uniform in color (black in adult males and brown in females and immature males). Males differ minimally from *P. salvini* in other plumage characters, except that rectrices are typically entirely black on the dorsal side in the nominate taxon. Females and immature males differ more obviously in plumage by having a strongly contrasting black border (black post-ocular eye-line and supercilium) to a chestnut crown, and warm cinnamon wing edgings.

Subspecies: Polytypic. We recognize two subspecies: *P. a. albogriseus* Sclater 1857 and *P. a. ornatus* Cherrie, 1891. We consider *P. a. coronatus* Phelps and Phelps 1953 to be a junior synonym of nominate *P. a. albogriseus* Sclater 1857, given its phylogenetic position and lack of diagnostic features (see Taxonomic confusion and clarification).

Song description: Slow, slurred, and with an obviously longer and inflected terminal note *soo soo-EE*, typically given once at long intervals, but sometimes in series of 3 (Figure 6).

Conclusions

We demonstrate that *Pachyramphus albogriseus* (*sensu lato*) does indeed comprise 2 biological species that are not sisters, and that their names should be *P. salvini* and *P. albogriseus*. To eliminate confusion, we propose the vernacular names Slender-billed Becard for *P. salvini* and Broad-banded Becard for *P. albogriseus*, rather than retain “Black-and-white Becard” for either species. We present evidence that the names *P. albogriseus guayaquilensis* Zimmer 1936 and *P. albogriseus coronatus* Phelps and Phelps 1953 are junior synonyms of *P. salvini* Richmond 1899 and *P. a. albogriseus* Sclater 1857, respectively. We retain the taxon *ornatus* of Central America as a valid subspecies of *P. albogriseus* given its disjunct distribution and morphological differences. We call for field work to determine whether the 2 species breed syntopically. Our results suggest that future systematic work should integrate natural history data on vocalizations and dense taxonomic and spatial sampling to the extent possible in order to increase the probability of detecting unrecognized taxa hidden in museum collections (Avendaño et al. 2017, Zuccon et al. 2020). The study highlights a major problem facing biodiversity science in general; biodiversity remains underestimated and the tree of life mischaracterized, even for well-inventoried groups such as birds.

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Data availability: Analyses reported in this article can be reproduced using the data provided by Musher et al. (2022).

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Figure 1. Recent hypotheses for the phylogenetic placement of *P. albogriseus*. (**A**) Sibley and Monroe (1990) hypothesized *P. albogriseus* as sister to *P. major*. (**B**) Barber and Rice (2007) recovered *P. albogriseus* as sister to *P. polychopterus* based on a single mitochondrial gene. Barber and Rice sequenced mtDNA for a *P. albogriseus* specimen from northwestern Peru now known to be *P. salvini*. Bootstrap values <100% are mapped. (**C**) Musher and Cracraft (2018) and (**D**) Musher et al. (2019) found that both hypotheses might be correct and recovered a polyphyletic *P. albogriseus* based on multiple types of genetic markers. Gray bars represent 95% highest posterior densities for node ages based on divergence time analysis on UCEs. Bootstrap values <100% are mapped. *P. albogriseus* 2 is equivalent to the lineage referred to as "*P. guayaquilensis"* in those studies.

Figure 2. Polyphyly and comparison of taxa in *P. albogriseus*. (**A**) Results of the concatenated phylogenetic analysis on the 50% complete dataset. Red stars identify genetic samples new to this study. Bootstrap values are 100% on all nodes except where noted. (**B**) Results of the species tree (coalescent) analysis on the 50% complete dataset. (**C**) Occurrence data and estimated ranges of the 3 taxa recognized in this study. Yellow stars represent type specimens' localities for (from north to south) *P. a. ornatus* (Alajuela, Costa Rica), *P. albogriseus "coronatus"* (Zulia, Colombia), *P. a. albogriseus* (Bogotá, Colombia), *P. salvini "guayaquilensis"* (Chimbo, Ecuador), and *P. s. salvini* (Chusgón, Peru). Specimens shown are (from left to right) AMNH 820700, 820701, 182137, and 182135. Photo by Jon Merwin (AMNH/ANSDU).

Figure 3. Photographs comparing Peruvian specimens of *P. salvini* (blue boxes: AMNH 185945, 182137, 182135, and 182133) and *P. a. albogriseus* (green boxes: AMNH 820701, 821005, 820943, 820700). Photos by Jon Merwin.

Figure 4. Box and whisker plots of morphometric and elevation data for *P. salvini* and *P. albogriseus* taxa, including culmen length, culmen width, culmen depth, relative bill width (culmen width/length), tail length, the length of the widest median covert tip, weight, and elevation. See also Table 2.

Figure 5. The first two axes of the principal components analysis on morphometric (left) and song (right) data.

Figure 6. Songs of birds formerly included within the Black-and-white Becard *Pachyramphus albogriseus*. (**A–D**) Slender-billed Becard *P. salvini* (2 song phrases). (**E–H**) Broad-banded Becard *P. albogriseus* (1 song phrase). (**A**) Pichincha, Ecuador, 25 August 2012 (XC 108575, A. Spencer). (**B**) Piura, Peru, 7 July 2015 (XC 297106, R. Gallardy). (**C**) Cajamarca, Peru, 27 December 2007 (XC 227116, P. Boesman). (**D**) Huánuco, Peru, 22 May 2010 (XC54569, D. Lane). (**E**) Puntarenas, Costa Rica, 7 March 2020 (ML 240493071, J. Alvarado). (**F**) Aragua, Venezuela, 26 May 1969 (ML 62586, P. Schwartz). (**G**) Napo, Ecuador, September 1995 (XC 264752, P. Coopmans). (**H**) San Martín, Peru, 22 September 2013 (XC 150850, H. van Oosten). Note the distinctive termination of each phrase.

Figure 7. Trilled notes of birds formerly included within the Black-and-white Becard *Pachyramphus albogriseus*. (**A**) Slender-billed Becard *P. salvini*. (**B–D**) Broad-banded Becard *P. albogriseus*. (**A**) Guayas, West Ecuador, March 2003 (XC259055, J.V. Moore); (**B**) Aragua, coastal Venezuela, 29 June 1961 (ML62589, P. Schwartz); (**C**) Tungurahua, East Ecuador, 11 September 2011 (XC108656, A. Spencer); (**D**) Huánuco, East Peru, 4 September 1979 (ML17784, V. Emanuel). Note the difference in pace between the two species.

Table 1. List of genetic samples used in this study. Institutions that provided genetic samples included AMNH (American Museum of Natural History), FMNH (Field Museum of Natural History), LSUMNS (Louisiana State University Museum of Natural Sciences), MPEG (Museu Paraense Emilio Goeldi), UAM (University of Alaska Museum), USNM (National Museum of Natural History, Smithsonian Institution), and UWBM (University of Washington Burke Museum).

Material	Institution	Tissue/ Coll. #	Genus	Species	Subspecies	Locality	Latitude	Longitude
Tissue	UWBM	107848	*Pachyramphus*	*major*	*uropygialis*	Mexico: Jalisco; Bolaños	21.8167	–103.8833
Tissue	UWBM	101156	*Pachyramphus*	*major*	*uropygialis*	Mexico: Michoacán; Lázaro Cárdenas	18.1685	–102.3113
Tissue	UAM	KSW 1195	*Pachyramphus*	*major*	*itzensis*	Mexico, Tabasco; Huimanguillo	17.3333	–93.6167
Tissue	LSUMNS	41620	*Pachyramphus*	*albogriseus*	*ornatus*	Panama: Bocas del Toro Province	8.7914	–82.2098
Toe Pad	USNM	387453	*Pachyramphus*	*albogriseus*	*coronatus*	Colombia: Cesar Department	9.3373	–73.3899
Toe Pad	AMNH	494147	*Pachyramphus*	*albogriseus*	*albogriseus*	Venezuela: Kechisera, Merida State	8.6273	–71.1493
Tissue	LSUMNS	6079	*Pachyramphus*	*albogriseus*	*albogriseus*	Ecuador: Morona-Santiago Province	–2.7552	–78.0945
Tissue	LSUMNS	8114	*Pachyramphus*	*albogriseus*	*albogriseus*	Peru: Huánuco Department	–9.9921	–75.8075
Tissue	AMNH	DOT 3866	*Pachyramphus*	*marginatus*	*nanus*	Venezuela: Amazonas	0.8333	–66.1667

Tissue	LSUMNS	33362	*Pachyramphus*	*salvini*	–	Peru: Cajamarca Department	–5.3833	–78.7717
Tissue	LSUMNS	33450	*Pachyramphus*	*salvini*	–	Peru: Cajamarca Department	–5.3833	–78.7717
Toe Pad	FMNH	282130	*Pachyramphus*	*polychopterus*	*dorsalis*	Colombia: Cauca Department	4.2773	–74.7723
Tissue	UWBM	108370	*Pachyramphus*	*polychopterus*	*similis*	Panama: Veraguas Province	7.2417	–80.9057
Tissue	LSUMNS	60813	*Pachyramphus*	*polychopterus*	*similis*	Honduras: Tela	15.7311	–87.4554
Tissue	MPEG	MAD 275	*Pachyramphus*	*polychopterus*	*nigriventris*	Brazil: Amazonas State	–5.8074	–61.4223
Tissue	FMNH	392915	*Pachyramphus*	*polychopterus*	*polychopterus*	Brazil: Sergipe State	–9.6521	–37.9350
Tissue	AMNH	DOT 6149	*Pachyramphus*	*polychopterus*	*spixii*	Bolivia: Santa Cruz Department	–16.5500	–59.6500

Table 2. Results of 5 morphometric measurements for the 3 taxa recognized in this study (*P. salvini*, *P. a. albogriseus*, and *P. a. ornatus*). Shown are the mean ± SD, range, and sample size for each taxon. See also Figure 4.

Taxon	Culmen length (mm)	Culmen width (mm)	Culmen depth (mm)	Tail length (mm)	Wing (mm)	Weight (g)
P. salvini	9.01 ± 0.52	5.54 ± 0.34	4.96 ± 0.32	49.63 ± 2.98	69.66 ± 2.86	16.93 ± 1.95
	(7.81–9.91)	(4.64–6.28)	(3.60–5.75)	(39–55)	(63–75)	(12.5–23)
	n = 56	*n* = 56	*n* = 56	*n* = 48	*n* = 52	*n* = 37
P. a. albogriseus	9.92 ± 0.54	7.10 ± 0.42	5.74 ± 0.33	55.29 ± 1.54	74.35 ± 3.41	22.11 ± 3.05 (17–26)
	(8.82–10.80)	(6.15–7.76)	(5.11–6.31)	(52–57)	(69–81)	*n* = 9
	n = 18	*n* = 18	*n* = 18	*n* = 14	*n* = 17	
P. a. ornatus	10.28 ± 0.48	7.47 ± 0.28	6.07 ± 0.47	52.88 ± 1.96	71.75 ± 3.69	16.2
	(9.76–11.1)	(7.13–7.88)	(5.33–6.67)	(50–56)	(66–76)	NA
	n = 9	*n* = 9	*n* = 9	*n* = 8	*n* = 8	*n* = 1

Figure 1

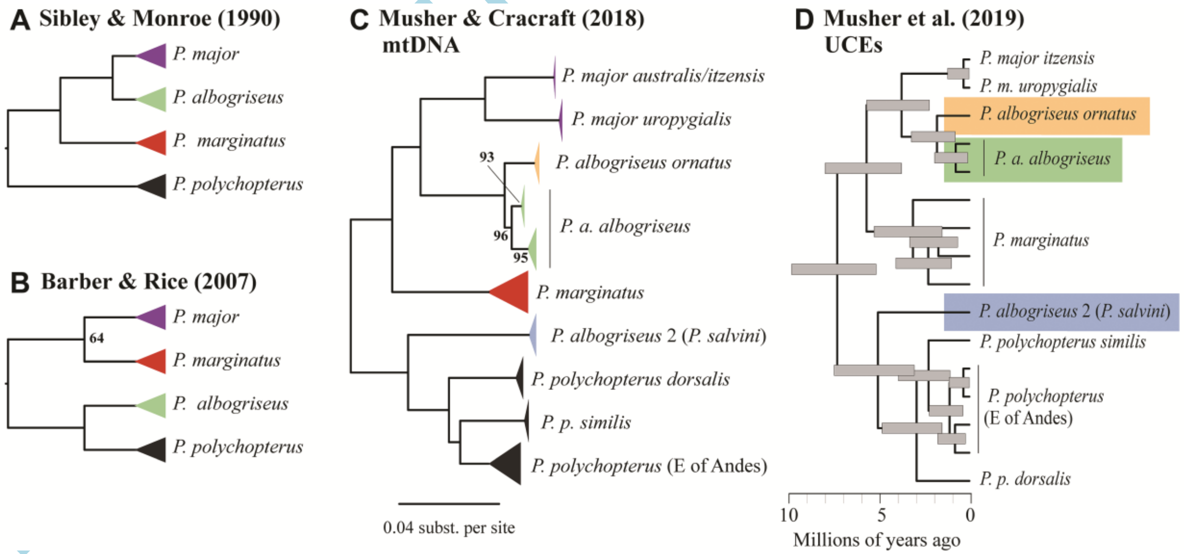

A Sibley & Monroe (1990)
P. major
P. albogriseus
P. marginatus
P. polychopterus
B Barber & Rice (2007)
64
P. major
P. marginatus
P. albogriseus
P. polychopterus
C Musher & Cracraft (2018)
mtDNA
P. major australis/itzensis
P. major uropygialis
93
P. albogriseus ornatus
96
95
P. a. albogriseus
P. marginatus
P. albogriseus 2 (P. salvini)
P. polychopterus dorsalis
P. p. similis
P. polychopterus (E of Andes)
0.04 subst. per site
D Musher et al. (2019)
UCEs
P. major itzensis
P. m. uropygialis
P. albogriseus ornatus
P. a. albogriseus
P. marginatus
P. albogriseus 2 (P. salvini)
P. polychopterus similis
P. polychopterus
(E of Andes)
P. p. dorsalis
10
5
0
Millions of years ago

Figure 2

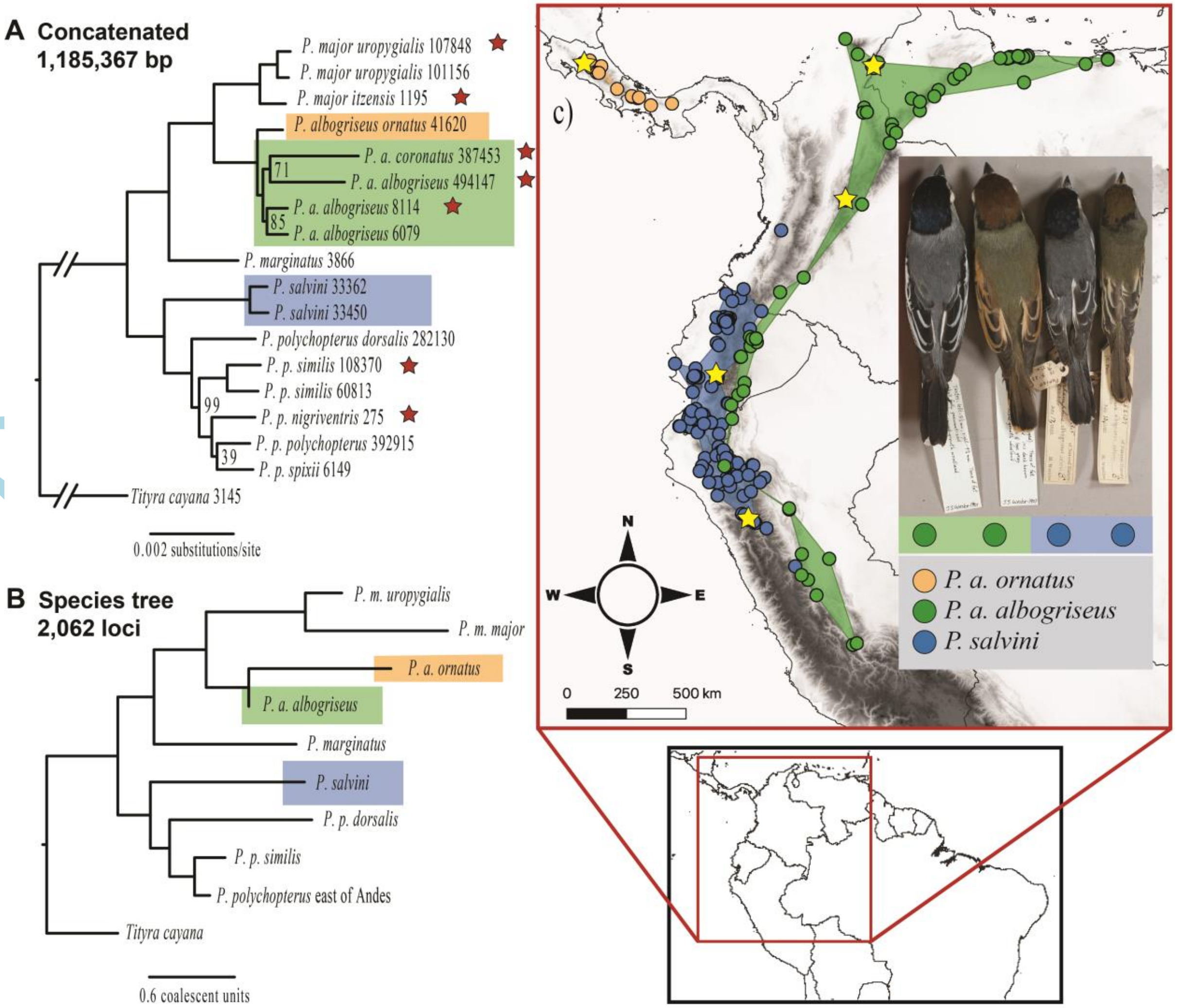

A Concatenated
1,185,367 bp
P. major uropygialis 107848
P. major uropygialis 101156
P. major itzensis 1195
P. albogriseus ornatus 41620
P. a. coronatus 387453
71
P. a. albogriseus 494147
P. a. albogriseus 8114
85
P. a. albogriseus 6079
P. marginatus 3866
P. salvini 33362
P. salvini 33450
P. polychopterus dorsalis 282130
P. p. similis 108370
P. p. similis 60813
99
P. p. nigriventris 275
P. p. polychopterus 392915
39
P. p. spixii 6149
Tityra cayana 3145
0.002 substitutions/site
B Species tree
2,062 loci
P. m. uropygialis
P. m. major
P. a. ornatus
P. a. albogriseus
P. marginatus
P. salvini
P. p. dorsalis
P. p. similis
P. polychopterus east of Andes
Tityra cayana
0.6 coalescent units
c)
N
W
E
S
0
250
500 km
P. a. ornatus
P. a. albogriseus
P. salvini

Figure 3

Figure 4

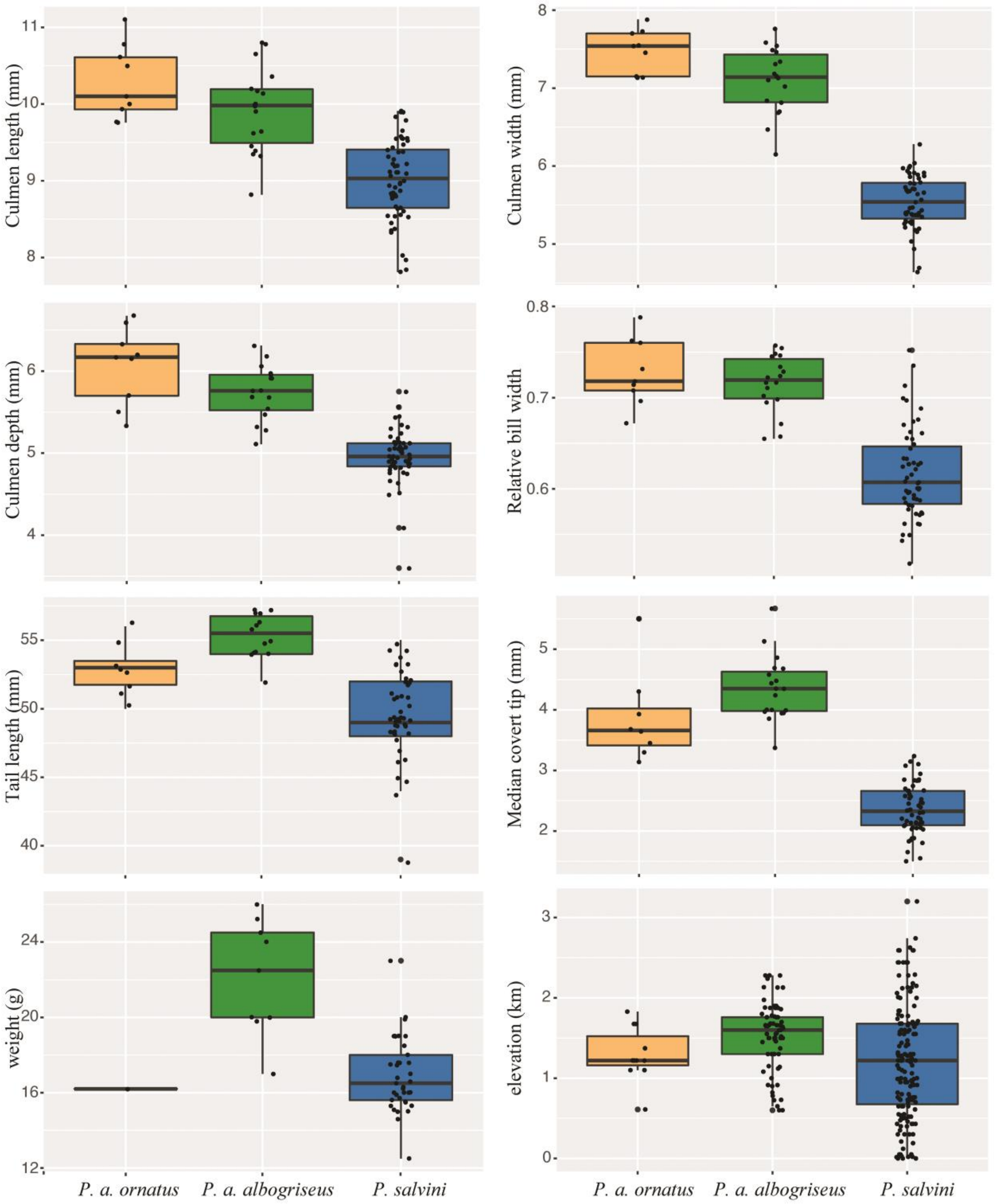

Culmen length (mm)
8
9
10
11
Culmen width (mm)
5
6
7
8
Culmen depth (mm)
4
5
6
Relative bill width
0.6
0.7
0.8
Tail length (mm)
40
45
50
55
Median covert tip (mm)
2
3
4
5
weight (g)
12
16
20
24
elevation (km)
0
1
2
3
P. a. ornatus
P. a. albogriseus
P. salvini
P. a. ornatus
P. a. albogriseus
P. salvini

Figure 5

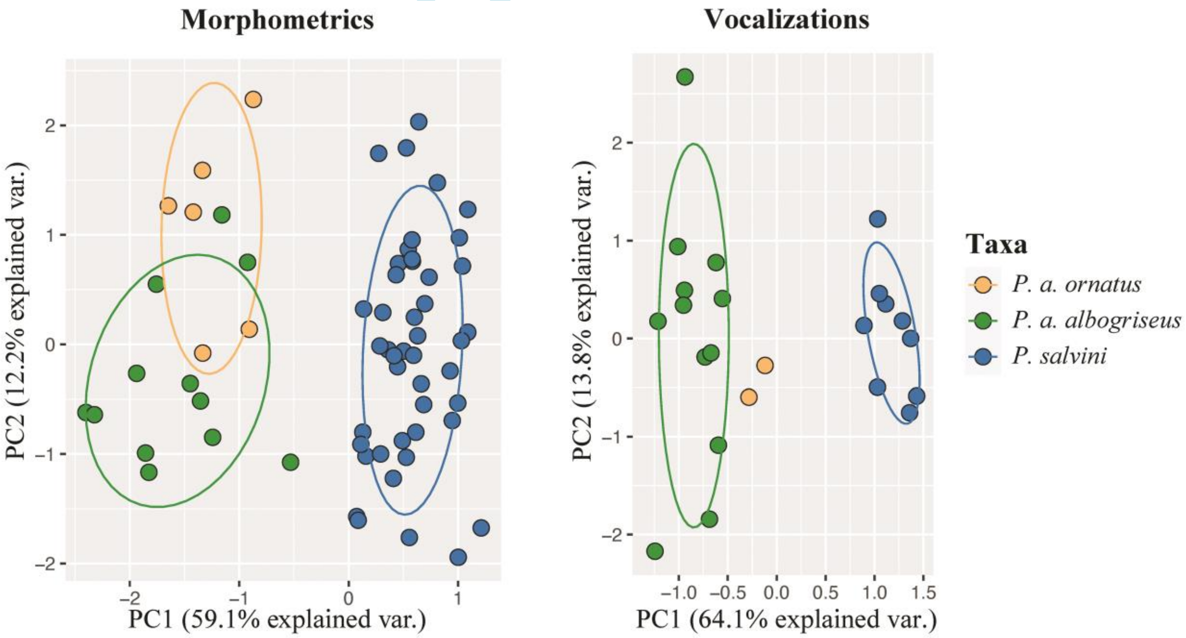

Morphometrics
PC2 (12.2% explained var.)
2
1
0
−1
−2
−2
−1
0
1
PC1 (59.1% explained var.)
Vocalizations
PC2 (13.8% explained var.)
2
1
0
−1
−2
−1.0
−0.5
0.0
0.5
1.0
1.5
PC1 (64.1% explained var.)
Taxa
P. a. ornatus
P. a. albogriseus
P. salvini

Figure 6

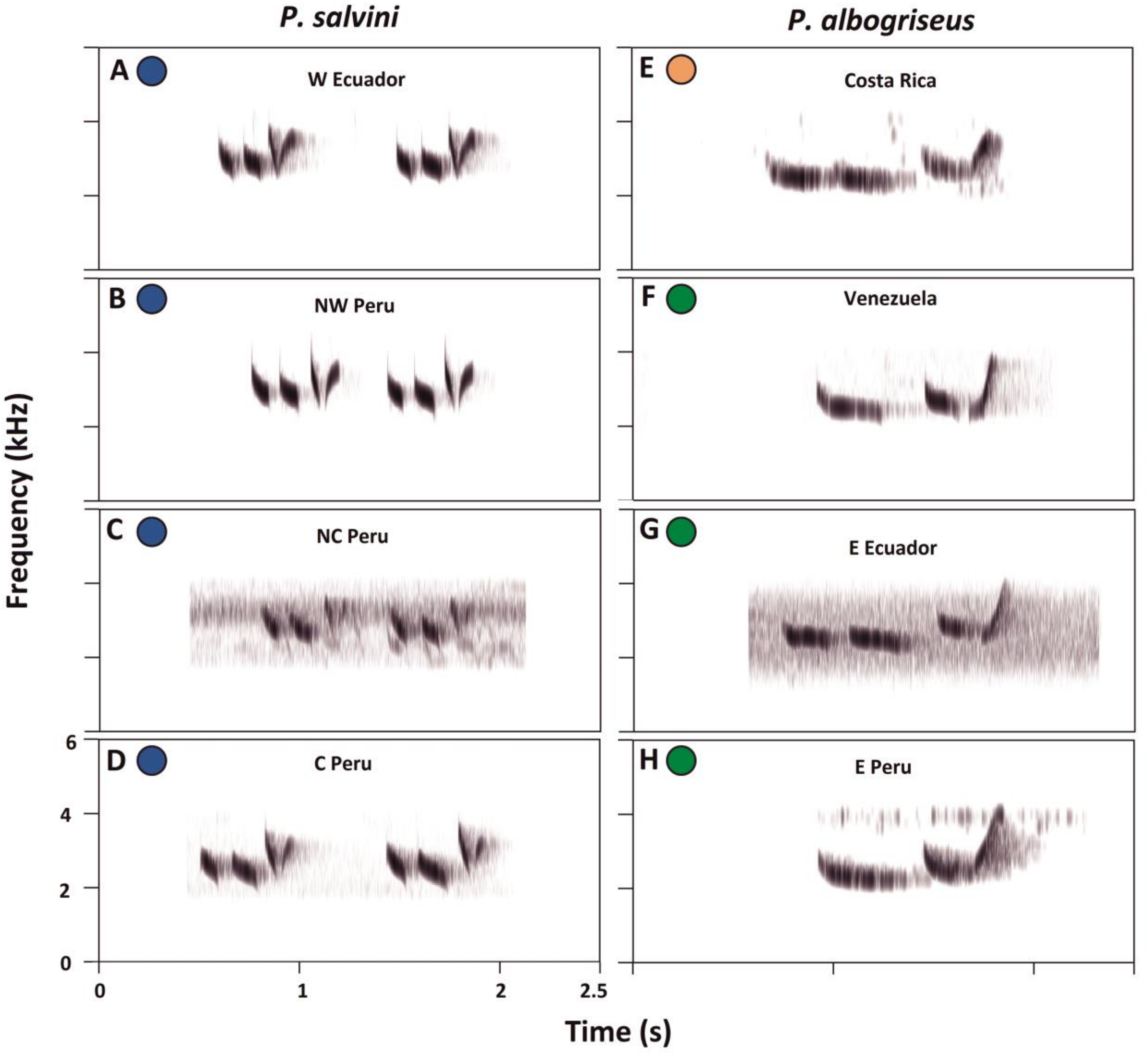
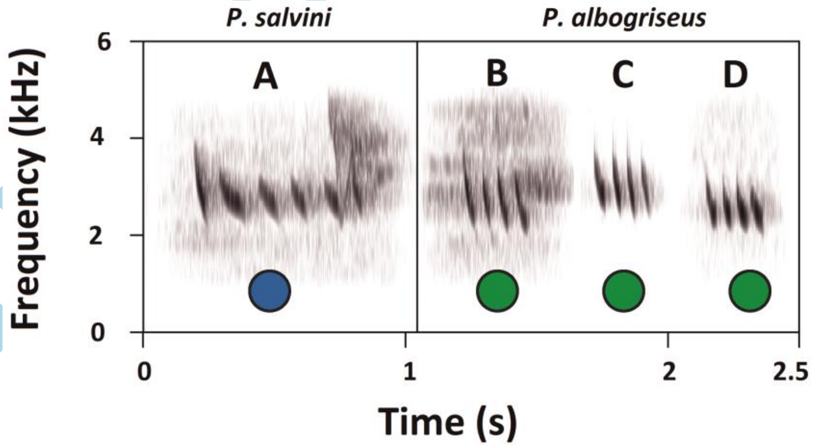

P. salvini
P. albogriseus
A
W Ecuador
B
NW Peru
C
NC Peru
D
C Peru
E
Costa Rica
F
Venezuela
G
E Ecuador
H
E Peru
Frequency (kHz)
6
4
2
0
0
1
2
2.5
Time (s)

Figure 7


P. salvini
P. albogriseus
A
B
C
D
Frequency (kHz)
6
4
2
0
0
1
2
2.5
Time (s)