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GEOGRAPHICAL VARIATION, TAXONOMY AND DISTRIBUTION OF SOME AMAZONIAN *PYRRHURA* PARAKEETS

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Resumen. – Variación geográfica, taxonomía y distribución de algunas especies de perico del género *Pyrrhura*. – Se evalúa la variación geográfica dentro y entre poblaciones de los pericos Amazónicos frecuentemente clasificados como subespecies *lucianii*, *roseifrons* y *amazonum* de *P. picta*. Se examinaron 231 especímenes correspondientes a siete grupos geográficos. Se ofrece una taxonomía revisada como base para estudios sistemáticos completos. *P. lucianii* (Deville, 1851) se restringe a las poblaciones Amazónicas centrales de la localidad tipo de Tefé en el Río Solimões y a lo largo del Río Purús. *P. lucianii* carece de rojo brillante en el plumaje, el plumaje azul de la frente es de una extensión mínima o está completamente ausente, y el pecho está marcado con escamado en forma de “V.” *P. roseifrons* (G. R. Gray, 1859) se restringe a poblaciones variables de la Amazonía oeste, donde los ejemplares adultos poseen plumaje rojo en la frente y corona anterior, y en cierta medida también en la corona posterior, así como en el plumaje de los hombros, y los bordes carpal y crural (tibial). *P. roseifrons* abarca dos poblaciones disjuntas. Adicionalmente, se identifica un nuevo taxón de la zona oeste cuyos caracteres diagnósticos son anchas bandas subterminales en el plumaje del pecho y garganta, una débil pero discernible coloración azul en la frente, y la falta de coloración roja brillante en el plumaje. Los datos disponibles sugieren que este taxón a su vez también posee dos poblaciones disjuntas, una al norte de una población de *P. roseifrons* en el noroeste de la Amazonía peruana, y otra en el centro del Perú, entre dos poblaciones de *P. roseifrons*. Ciertas poblaciones de la zona angosta entre Shanusi y el Río Maní se distinguen por poseer una estrecha frente escarlata, por lo que anteriormente se han considerado parte de *P. lucianii* o ejemplares juveniles de *P. roseifrons*. Aunque se considera que definitivamente no forman parte de ninguno de estos taxones, se pospone una decisión con respecto a su taxonomía, hasta realizar análisis genéticos. Las poblaciones de la cuenca del Río Madeira en la Amazonía central (Brasil y Bolivia) se distinguen claramente por las marcas “en punta” que posee el plumaje del pecho y garganta, únicas dentro de *Pyrrhura*. La singularidad de estas poblaciones fue reconocida ya en 1914, y se les asigna aquí finalmente un nombre. Por último, *P. amazonum* Hellmayr, 1906 se considera válida para todas las poblaciones restantes de la Amazonía este y sureste. *P. amazonum* posee tres rasgos distintivos: coloración azul prominente en la frente y corona anterior, ausencia de rojo en la plumaje, y pecho con un diseño escamado. Aunque este taxón posee una variación significativa de tamaño, la misma no se incorpora a su taxonomía por el momento.

Abstract. – Geographical variation within and among populations of the Amazonian *Pyrrhura* parakeets that are often treated as the subspecies *lucianii*, *roseifrons* and *amazonum* of *P. picta* is assessed. Two hundred and thirty-one specimens were examined from seven geographical groupings. A revised taxonomic basis is developed as a platform for full systematic study. *P. lucianii* (Deville, 1851) is restricted to central Amazonian populations from the type locality Tefé on the Rio Solimões and along the Rio Purús. *P. lucianii* has no bright red in the plumage and blue in the forehead is minimal or absent; its breast is marked with chevrons. *P. roseifrons* (G. R. Gray, 1859) is restricted to variable western Amazonian populations in which adults have red in the forehead and forecrown and usually to some extent in the hindcrown, as well as in the shoulder, carpal edge and crural (tibial) feathering. *P. roseifrons* comprises two disjunct populations. Additionally, a new western Amazonian taxon is diagnosable by broad subterminal bands on the breast and throat, and weak but readily discernible blue in the forehead. There is no bright red in its plumage. Present evidence suggests that this new taxon has two disjunct populations, one to the north of a population of *P. roseifrons* in far northwestern Amazonian Peru, the other in central Peru between the two populations of *P. roseifrons*. Populations in a narrow zone between the Rio Maniti and Shanusi are diagnosable by a narrow scarlet frons. They have previously been considered to be *P. lucianii* or the juvenile of *P. roseifrons*. Although definitely neither of these taxa, a decision on their taxonomic status is deferred pending genetic analysis. Populations of the Rio Madeira drainage in central Amazonia (Brazil and Bolivia) are most easily diagnosable by the “pointed” markings of the breast and throat feathers, utterly unlike any other *Pyrrhura* parakeet. Recognized as distinct in 1914, they are named. Finally, *P. amazonum* Hellmayr, 1906 is recognized for all remaining populations of eastern and south-eastern Amazonia. *P. amazonum* is diagnosable by the combination of prominent blue in the forehead and forecrown, no red in the plumage, and chevroned breast. Significant size variation within this taxon is provisionally not recognized taxonomically. Accepted 30 April 2002.

Key words: *Pyrrhura*, taxonomy, geographical variation, systematics, parrots, Amazonia.

INTRODUCTION

Pyrrhura comprises approximately 25–30 species of Neotropical parakeets (Forshaw & Cooper 1989, Collar 1997, Juniper & Parr 1998). Geographical variation and taxonomy in the species and subspecies often considered to comprise the Painted Parakeet (*Pyrrhura picta*)/White-eared Parakeet (*P. leucotis*) complex have long been problematic. Joseph (2000) tentatively concluded that the complex comprises 12 valid taxa and that the two species/multiple subspecies taxonomy, which traces to Peters (1937), should be abandoned. The present paper examines more closely geographical variation and taxonomy of this group’s Amazonian populations.

Amazonia is here defined as the drainage of the Marañon, Ucayali, Huallaga, Solimões and Amazonas rivers. Recently, Amazonian

populations discussed here have usually been treated as three subspecies of *P. picta*: *P. p. amazonum*, *P. p. lucianii* and *P. p. roseifrons* (Forshaw & Cooper 1989, Juniper & Parr 1998, Collar 1997). *P. p. picta sensu stricto* occurs from the Guianas west to southern Venezuela and northern Brazil (Joseph 2000; Fig. 1). The first aim of this paper is to report a study of variation in plumage and size in the Amazonian populations to which the epithets *amazonum*, *lucianii*, and *roseifrons* have been applied. The literature surrounding application of these names is extraordinarily confused. The second aim of this paper is to bring the literature to order. Clarification of the literature provides the extra, albeit tedious, detail necessary for the final aim, integration of the new results presented here with the literature to derive a taxonomic framework for phylogenetic study.

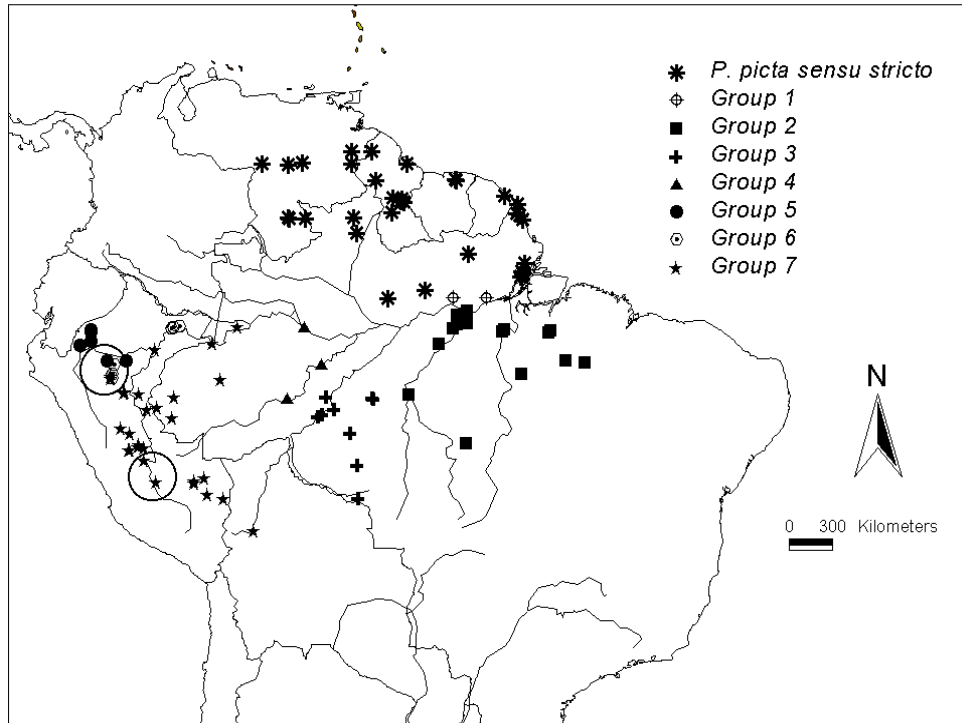


FIG. 1. Map of northern South America showing specimen locations for groups 1-7 and *P. picta sensu stricto*. The upper circle encloses specimen locations of groups 5, 6 and 7 where they approach each other closely (see text for details); the lower circle shows the two locations of three anomalous group 7 specimens, which are identified in the text as of the same unnamed taxon as group 5. Locations of *P. picta* are derived from Joseph (2000) and additional specimens held in the collections of MPEG, Belém and INPA, Manaus.

METHODS

Two hundred and thirty-one specimens (Appendix 1) were examined from the following collections: Academy of Natural Sciences, Philadelphia (ANSP), American Museum of Natural History, New York (AMNH), Field Museum of Natural History, Chicago (FMNH), United States National Museum, Washington (USNM), Carnegie Museum, Pittsburgh (CM), Natural History Museum of Los Angeles County, Los Angeles (NHMLAC), Louisiana State University Museum of Natural Science, Baton Rouge

(LSUMZ), Peabody Museum, Yale University, New Haven (YPM), Museum of Comparative Zoology, Harvard University, Cambridge (MCZ), Swedish Museum of Natural History, Stockholm (NRM), Natural History Museum, Tring (NHM), and Musée National d'Histoire Naturelle, Paris (MNHN). Of the 231, 191 were scored and measured, and 40 were examined as digital images showing ventral, dorsal and lateral views. General data (localities, descriptions of key characters) were also obtained from 110 specimens in the Museu Goeldi, Belém (MPEG), and two in the Instituto Nacional de Pesquisas da Amazonia,

Manaus (INPA), respectively. A gazetteer (Appendix 2) gives latitudes and longitudes for localities mentioned in the text. To avoid the circularity of applying names to populations the geographical variation and taxonomy of which are to be clarified, the specimens (Appendix 1) were divided into groups based on earlier work, e.g., that populations in a narrow part of northern Amazonian Peru uniquely have a narrow scarlet-red frons (Joseph 2000), and obvious distributional disjunctions in specimen locations (>200 km) (Fig. 1). They also reflected previous taxonomy to be tested (e.g., separation of eastern Amazonian populations north and south of the Rio Amazonas). The groups were:

Group 1: Eastern Amazonia east of Manaus, north bank of the Rio Amazonas.

Group 2: Eastern Amazonia east of Manaus, south bank of the Rio Amazonas but excluding the drainage of the Rio Madeira.

Group 3: Drainage of the Rio Madeira.

Group 4: Tefé and the Rio Purús.

Group 5: Northwestern Amazonian Peru north and west of the Marañón and Amazonas rivers.

Group 6: Populations distinguished by their narrow red frons and known only in a narrow northeast to southwest zone in northern Amazonian Peru along the Huallaga, Marañón and Amazonas rivers from the mouth of the Rio Orosa to Shanusi (Joseph 2000).

Group 7: Remainder of southwestern Amazonia essentially comprising that part of Peru south of the range of group 6, La Paz

province in western Bolivia, and southwestern Brazil.

Colors with capitalized initials and numbers in parentheses are from Smithe (1975). Plumage variation was quantified with a Character Index (CI). Each specimen examined by hand ($n = 191$) was scored for seven characters, which earlier had been found to vary geographically not individually (Joseph 2000). The coding system was:

Pileum: Blue forehead and forecrown readily visible – 0; blue in forehead and forecrown not readily visible – 1; blue absent or almost so, no red – 2; narrow scarlet-red frons – 3; orange-red only in anterior pileum – 4; forecrown orange-red; hindcrown patchy orange-red – 5; whole pileum orange-red or nearly so – 6.

Face, subocular ring and cheeks: No orange-red subocular ring; bicolored cheeks – 0; orange-red in subocular ring narrow, cheeks maroon or bicolored – 1; orange-red in subocular ring; cheeks blue – 2; subocular ring and cheeks extensively orange-red – 3.

Ear-coverts: Color could not be discerned with further precision due to the mode of preparation of specimens, wear, or both: Off white – 0; whitish/some yellow visible – 1; yellow – 2.

Patterning of underparts: “*picta*” chevrons – subterminal band narrow and grayish – 0; broader yellow subterminal band to chevrons – 1; yellow margin almost covering entire feather – 2; subterminal band semi-circular \pm greenish yellow barring or scaling – 3.

Shoulder: Green – 0; green and orange-red – 1; orange-red – 2.

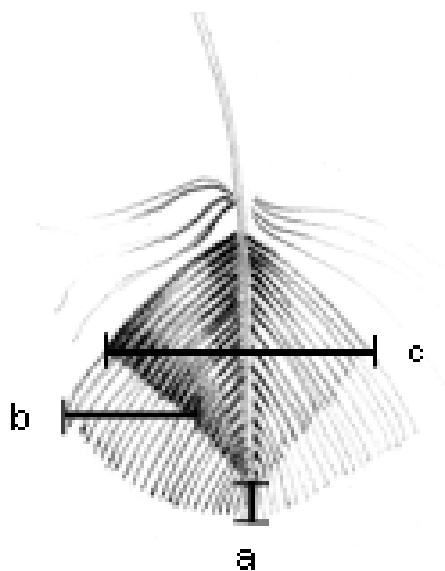


FIG. 2. Diagram illustrating how three shape variables were measured on breast and throat feathers: a) the distance between the distal tip of the dark central mark of the feather and the distal tip of the pale subterminal band; b) the width of the subterminal band taken between the outermost lateral tip of the subterminal band itself and the point on the dark central mark directly opposite and, c) the maximum width of the dark central mark of each feather. Measurement c was used - see text. Artwork by D. Cohen.

Crural (tibial) feathering: Green – 0; green and orange-red – 1; orange-red – 2.

Carpal edge: Green – 0; green and orange-red – 1; orange-red – 2.

Scores for each character were standardized to a value between 0 and 1 and then summed. The total for each specimen was divided by 7.83, which was the maximum assigned to any specimen. Thus the final CI was also between 0 and 1. Two specimens with different phenotypes can sum across all

characters to similar total CIs. Interpretation is then based on description of variation in individual characters. Inspection of specimens suggested the need to quantify variation in the shape of markings on the feathers of the breast and throat. Due to concerns of feather wear and measurement repeatability, measurements are only used for one variable, the maximum width of the dark central mark of each feather (Fig. 2). A simple measure of repeatability was made by measuring the central mark up to eleven times on a total of five individually identified breast feathers on one specimen, CM 86548. Measurements, given in centimeters, were taken with calipers in two sessions over two days and each session was broken into shorter periods of 20–30 minutes. A coefficient of variation (CV, mean/standard deviation) was calculated for each feather. The mean CV for width of the central black mark of the feather across the five feathers was 0.06 ± 0.02 cm. Two lower breast and two upper breast/throat feathers were measured on at least ten specimens of each group. Measurements in millimeters of wing (flattened chord) and maxilla (anterior tip of the cere to tip of maxilla) were measured with calipers; obviously damaged or molting birds were excluded. Wear on tails was so often obvious that tail measurements, although taken, have not been used. Mann-Whitney *U*-tests were used for univariate comparisons between groups and done with Statistica (StatSoft 1994). Latitudes, longitudes and altitudes of localities were taken from Stephens & Traylor (1983), Paynter & Traylor (1991), Paynter (1992), Killeen & Schulenberg (1998), and specimen tags. Localities were plotted using ArcView[®]GIS 3.2a (ESRI 1999).

RESULTS

Table 1 summarizes the morphometric statistics for the seven groups. Three clusters of CI

TABLE 1. Descriptive morphometric statistics for the seven groups highlight the small size of group 2 relative to all other groups.

Population	Males	Females	Unsexed	n*	Wing length			n*	Maxilla length			n*	Tail length		
					Range	Mean	SD		Range	Mean	SD		Range	Mean	SD
Group 1	14	10	-	24	116-125	121.63	2.28	24	13.8-15.5	14.56	0.46	24	105-128	115.29	5.97
Group 2	24	27	5	55	104-120	116.64	3.49	51	12.5-15.5	13.99	0.69	55	85-115	101.64	5.93
Group 3	9	9	1	19	113-128	122.68	3.85	17	13.7-16.3	15.05	0.79	19	97-128	111.47	10.04
Group 4	11	3	-	14	112-124	119.50	2.82	14	13.5-15.9	14.59	0.75	14	100-117	111.08	5.29
Group 5	3	5	1	9	111-124	117.67	4.15	9	14.0-15.4	14.77	0.48	7	95-112	105.86	6.28
Group 6	13	5	5	23	111-128	121.48	4.13	23	13.8-15.9	15.04	0.57	23	105-122	113.67	5.02
Group 7	29	15	2	46	112-132	121.70	4.28	44	14.0-16.3	15.18	0.59	45	87-129	109.18	7.99

*Numbers measured are sometimes less than the total examined because prior damage incurred to specimens during collecting and preparation prevented them from being measured for certain traits.

scores were apparent. First, almost all group 1 and 2 specimens scored zero across all characters and their similar mean CIs (group 1: 0.00 ± 0.01 ; group 2: 0.01 ± 0.02) reflect shared character states. They differed from each other only in group 2 being significantly smaller. Group 2 was significantly smaller than other groups ($P < 0.01$ for all comparisons except $P < 0.05$ for comparison with group 4 for maxilla). Second, groups 3, 4, 5 and 6 had mean scores between 0.08 ± 0.00 (group 6) and 0.19 ± 0.20 (group 4). Variation within each of these groups was slight except group 4 (see Fig. 2). Variation in CI between these groups was mostly slight and shown by inspection to be due to different scores across all characters summing to similar totals. As one moves from east to west through the ranges of groups 2, 3 and 4, however, CI values are stepped from 0.01 ± 0.02 to 0.11 ± 0.02 to 0.19 ± 0.20 , respectively. Group 4's high variance in CI is an artifact of using whole numbers in the raw coding system: specimens with weak but discernible blue scored 1, whereas those with no blue discernible on the forehead received a higher score of 2. Thus the variance is inflated although the two character states involved are similar. Group 7 alone had a high CI of 0.44 ± 0.22 due to non-zero scores for ear-coverts and crural, carpal edge and shoulder feathering, whereas other groups consistently scored zero for these characters. Relatively high variation within group 7 is due to two factors: (1) individual variation in all characters except underparts patterning, and (2) three adult female specimens of group 7 (AMNH 820834, AMNH 819871, and AMNH 819816) that are anomalous with respect to all other group 7 specimens. Their pilea have no red, but blue is readily discernible in the forecrown, and their underparts are chevroned not scaled. The forecrown of one of these specimens was lost in preparation and could not be scored for all

characters. CIs of the other two (0.04 ± 0.03) fell outside the range of all other group 7 specimens (0.46 ± 0.21 , $n = 45$). Groups 6 and 7 closely approach each other in geographical range but show little or no overlap in CI. Thus, a group 7 specimen, USNM 108269 from Tarapoto, the closest locality to which group 7 approaches group 6, has a CI (0.11) similar to group 6 but shows the diagnostic orange-red forecrown of group 7 rather than the scarlet-red frons of group 6. Similarly, of two specimens from Requena Ucayali, AMNH 408678 and AMNH 408679 (CIs = 0.11, 0.49, respectively) the former overlaps group 6 in CI but like USNM 108269 shows group 7's diagnostic orange-red forecrown. The divergent CI scores of the two Requena Ucayali specimens stress the individual variability of group 7.

Plumage variation

Pileum. Easternmost (groups 1 and 2) and westernmost groups (group 5) have blue readily visible in the forehead and forecrown whereas in geographically intermediate groups (groups 3, 4 and 6) blue is barely discernible (group 3), absent (group 4), or weak and only on the forecrown (group 6). Group 6 is unique in having a narrow scarlet-red [= Geranium (12)] frons with some blue distal to it in the otherwise brown pileum. Some group 7 birds of both sexes and from throughout their range (e.g., LSUMZ 130085, male; LSUMZ 156185, female) have blue distal to the forecrown's orange-red. In all group 7 specimens except youngest birds (e.g., LSUMZ 161562–3) and three anomalous specimens (AMNH 820834, AMNH 819871, and AMNH 819816), orange-red [= Flame Scarlet (15)] in the pileum usually covers the frons, forehead and most of the forecrown and is often at least patchy in the hindcrown. The orange-red feathers have a yellowish wash in their centers. Again, this is in both sexes throughout the range (e.g., LSUMZ

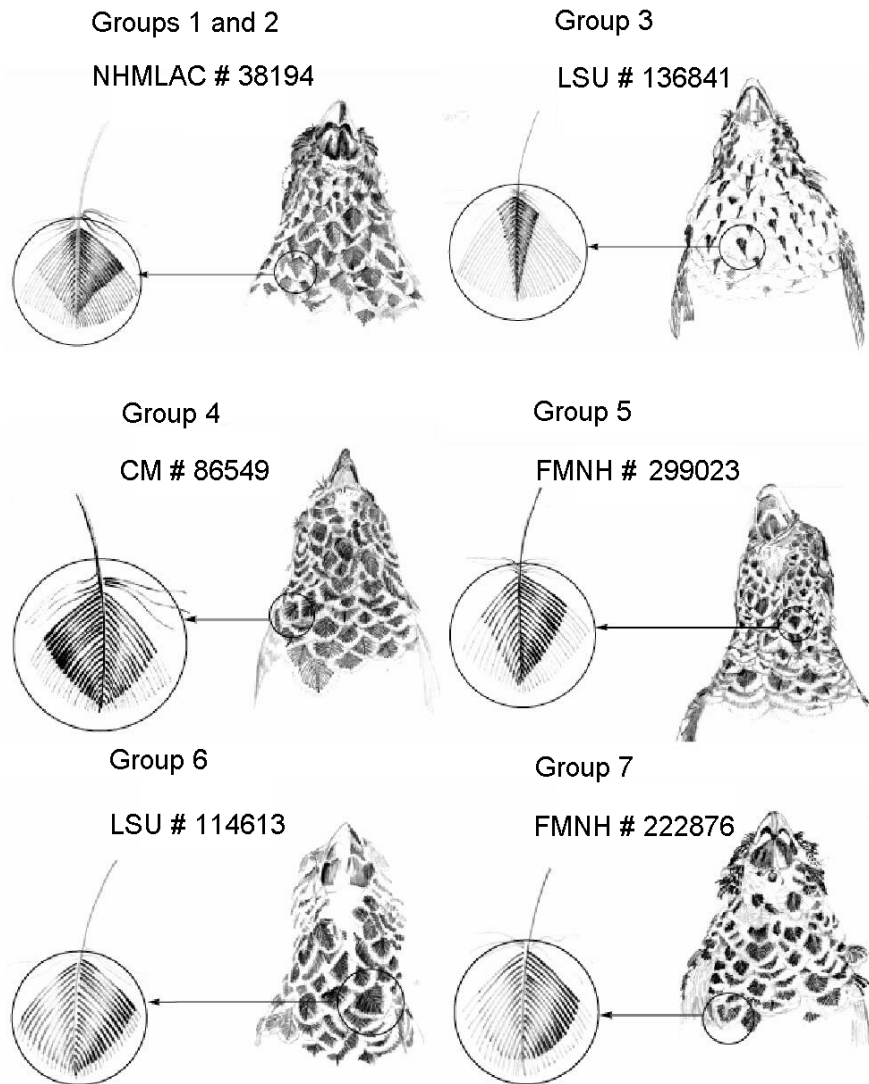


FIG. 3. The distinctiveness of groups 3, 5 and 7 in patterning of the underparts. Representative specimens of the seven groups (groups 1 and 2 are represented by one specimen) show between-group variation in patterning of individual feathers of the upper breast and throat. Artwork by D. Cohen.

156182, male; LSUMZ 156186, female). Hereafter, 'red-crowned' refers to any group 7 specimen with orange-red [= Flame Scarlet (15)] in either the forecrown, hindcrown or both but not to group 6 specimens with scar-

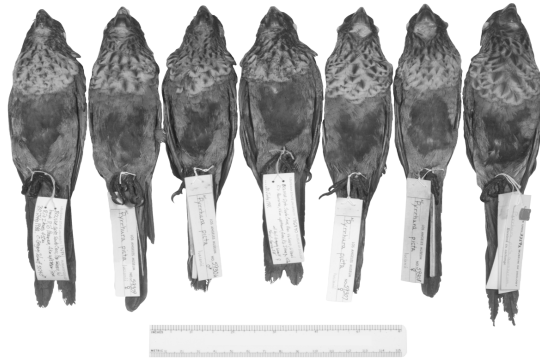
let-red (= Geranium (12)) only in the frons.

Patterning of underparts. Figures 3 and 4 illustrate the following trends, which are difficult to quantify reliably. In all groups except red-

Groups 1 and 2



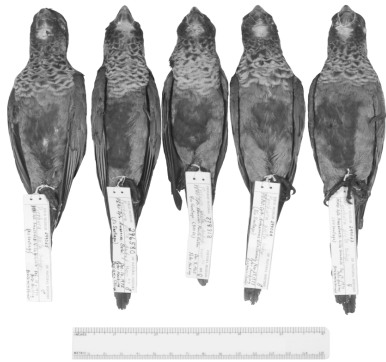
Group 3



Group 4



Group 5



Group 6



Group 7



FIG. 4. Underparts of *Pyrrhura* examined. See Figure 3 and images at <http://www.acnatsci.org/publication/appendix4.html>. Left to right, specimens are: Groups 1 and 2: CM 82986, MCZ 173435, CM 83204; group 3: LSUMZ 136841, NHMLAC 59309, NHMLAC 59306, LSUMZ 136840, NHMLAC 59307, NHMLAC 59308, LSUMZ 33592; group 4: CM 86550, CM 86547, CM 86406; group 5: FMNH 299025, FMNH 296580, FMNH 278312, FMNH 299024, FMNH 299023; group 6: ANSP 176011, ANP 176010, ANSP 176012; group 7: FMNH 222876, FMNH 300430, YPM 81446. Photography: J. Reich.

crowned group 7, feathers of the throat and upper breast generally are chevroned. This results from each feather having a dark, usually brownish, wedge-shaped central mark framed by a pale gray to creamy subterminal band the width of which is greater proximally than distally (Figs 2 and 3). In group 7 the central mark's outer border tends to be curved rather than straight, giving instead a scaled appearance (Figs 3 and 4). Inspection shows the pale subterminal band also to be no wider proximally than distally. In all groups, feathers of the lower breast are barred or scaled rather than chevroned. Variations on the basic chevroned pattern of the throat and upper breast follow.

In group 3 the central dark markings on the feathers of the upper breast and throat are significantly smaller than in all other groups (group 3, mean 0.23 ± 0.08 cm, all comparisons significant, $P < 0.01$). They are thus narrow and "pointed" and give breasts and throats a unique striated appearance. The effect is seen in specimens from throughout group 3's range, e.g., easternmost specimens (AMNH 127347–9, Rio Roosevelt) close to the westernmost specimens of group 2, two from its northern- and westernmost localities on the Rio Madeira (AMNH 474676–82), and two southernmost specimens from the Rio Paucerna, Bolivia (LSUMZ 136840–1). Further, the greatly enlarged subterminal bands of the feathers of the entire breast and throat in group 3 are uniquely pale cream-buff approaching, but lighter than, Cream Color (54) or Pale Horn Color (92).

Group 5 and the three anomalous group 7 specimens are unique in that although the dark central mark of the breast feathers is chevroned, the subterminal band is broad. The dark central mark on any one feather tends to be obscured by the extensive pale subterminal of the feather lying above it. Group 5 thus is more extensively pale-breasted than other groups (Figs 3 and 4). In

group 7, the subterminal band is more consistently curved rather than wedge-shaped. Again, reliable quantification is difficult but the effect is plain (see Figs 3 and 4).

Other plumage characters. Orange-red on the crural feathers, shoulder and carpal edge of the wing, and yellow ear-coverts appear only in group 7, although there is much individual variation within that group. For example, two males from Manu, Peru, YPM 81446 and YPM 81442, have CIs of 0.894 and 0.382, respectively. Whereas group 7 consistently scored non-zero values for these characters, other groups consistently scored zero.

Soft part colors and sex- and age variation
Label data describing the condition of gonads in recently collected specimens can establish age-related patterns of variation in groups 3, 6 and 7 (Table 2). Both the extreme "pointed" appearance of breast and throat feathers of group 3 and the narrow scarlet-red frons of group 6 are found in adult, sexually mature specimens (group 3: LSUMZ 136840–1, group 6: LSUMZ 114613–4; ANSP 176010–2). Three group 7 specimens from two localities near Contamana (LSUMZ 161562–4) comprise an adult male and two juvenal females. The male has an orange-red fore-crown, whereas the two juveniles, one of which was collected with the adult male, have no red in the forecrown. Yellow or orange-yellow facial skin has been noted in some group 7 specimens (e.g., LSUMZ 156186, 72175–6), but comparable data are unavailable for nearly all other specimens except some group 3, 6 and 7 specimens.

DISCUSSION

A taxonomic framework for later systematic study is now developed. Correct application of the two earliest names for any of the populations under study, i.e., *Conurus luciani* Dev-

TABLE 2. Label data from recently collected specimens of the Amazonian taxa under study that are of use in establishing age- and sex-related patterns of variation.

Specimens	Locality	Group	Label data
LSUMZ 161562	Peru: Loreto, NE bank upper Rio Cushabatay, 84 km WNW Contamana, 07°09'S, 75°44'W; c. 200 m above sea level (a.s.l.)	7	Female, ovary 5 x 2mm, oviduct smooth straight; iris dark brown
LSUMZ 161563-4	Peru: Loreto, c. 77 km WNW Contamana, c. 1000 m a.s.l.	7	LSUMZ 161563: Female, ovary 3 x 1.5mm, oviduct minute, smooth ovary; iris dark brown
		7	LSUMZ 161564: Male testis 6 x 3mm, 68 g, iris dark brown
LSUMZ 136840-1	Bolivia: Santa Cruz, Velasco, west bank Rio Paucerna, 4 km upstream from Rio Itenez, 450 m a.s.l.	3	LSUMZ 136840: Female, ovary 15 x 5 mm, largest ova 3 mm, oviduct 2 mm; iris brown; orbital skin tan with brown and yellow blotches
		3	LSUMZ 136841: Male, testes 6 x 19 mm; 69g, orbital skin buffy cream; irides brown
LSUMZ 114613-4	Peru: Loreto, S. Rio Amazonas, c. 10 km SSW mouth Rio Napo on E. bank Quebrada Vainilla; 03°32'S, 72°44'W, 100 m a.s.l.	6	LSUMZ 114613: Male testis 4 x 2mm; iris brown
		6	LSUMZ 114614: Male, testis 4 x 2mm; 72.5g; Iris brown; eye ring and pre maxillary skin - [LJ] strong yellow; bill blackish gray
ANSP 176010-2	Peru: Loreto, Santa Cecilia, Rio Maniti, 03°33'S, 72°53'W	6	ANSP 176010: Female, ovary 7 x 2mm, largest ovum < 1mm; 64g, irides brown
		6	ANSP 176011: Male, testes 5 x 2mm; 75g; Irides brown
		6	ANSP 176012: Female, ovary 8 x 4mm, largest ovum < 1mm; 71 g; irides brown

ille, 1851, and *Conurus roseifrons* G. R. Gray, 1859, is first examined. The present study's results are then integrated with a clarification of the confused taxonomic literature. The generic name *Pyrrhura* is used unless the argument calls for another. For simplicity, specific epithets are in places used without generic qualifiers.

Deville (1851) based *Conurus lucianii* on MNHN 1847/682 from Ega (= Tefé; locality checked on specimen – L.J), Brazil and noted: “tête et joues d’un beau rouge très-foncé” (translation: the head and cheeks are a beautiful very deep red) but Des Murs in Castelnau (1855) noted that this should have read: “d’un brun rouge très-foncé” (translation: a very dark brown-red) (see also Gyldenstolpe 1945). The holotype in fact has an entirely brown pileum lacking bright red or blue; fading with age may have lessened any reddish tinge implicit in the French “brun rouge”. It has no red on the wings. Its upper breast and throat are chevroned with pale gray to creamy subterminal bands and its lower breast has yellow subterminal bands. In each of these characters it closely resembles group 4, i.e., AMNH 308975 (collected 10 August 1928 at Santo Isidoro, Tefé) and 13 specimens from the Rio Purús, which flows into the Solimões some 350 km downstream from Tefé. No group 4 specimens resemble the geographically close group 3 from the Rio Madeira drainage with their distinct “pointed” breast markings. Note that the Rio Purús is not part of the Rio Madeira drainage but flows parallel with the Madeira some 200 km to the west. AMNH 308975 is the only other specimen that has been located from near the type locality of *C. lucianii*. Two paintings based on the holotype of *C. lucianii* were published in the 1850s and are relevant here for completion (Appendix 3 and Plate).

Todd (1947) considered the Rio Purús specimens that resemble the holotype of *C. lucianii* to be identical with Gyldenstolpe's

(1945) description of *lucianii* from Porto Velho on the Rio Madeira. Gyldenstolpe (1945), however, tentatively suggested that Porto Velho specimens were *lucianii* and gave an excellent description for them of group 3 of the Rio Madeira drainage: “the feathers of the breast and the upper breast are rather pointed and distinguished by having a dusky-brown to greenish-brown comparatively narrow central area, broadly margined and tipped pale ochraceous-buff to cream-buff.” Gyldenstolpe (1945) urged “a careful comparison between the type of *P. p. lucianii* and a series from Rio Madeira.” This has now been done and specimens from the Rio Madeira drainage (group 3) have a unique, diagnostic breast pattern utterly unlike the chevrons in the two Tefé specimens (holotype of *C. lucianii* and AMNH 308975) and the Rio Purús birds (group 4) (Figs 3 and 4). Populations at Tefé and along the Rio Purús are diagnosable by the following combination of character states: no red on the wing, crural feathers or pileum, blue absent or at best barely discernible in the pileum, and relatively narrow subterminal bands on breast and throat feathers, which also have a concomitantly broad, dark central mark in each feather. Application of the epithet *lucianii* is here restricted to group 4. Thus Todd (1947) correctly assigned the Rio Purús birds to *lucianii* for the wrong reasons.

Conurus roseifrons G. R. Gray, 1859 was based on three specimens sent to the then British Museum by H.W. Bates. The provenance of Bates's specimens cannot be determined (see Appendix 4). Gyldenstolpe (1945: 50) realized this and restricted the type locality of *C. roseifrons* G.R. Gray, 1859 to the Upper Rio Juruá but did not designate a lectotype. Gyldenstolpe's restriction of the type locality accords with Recommendation 76A.1 of ICZN (1999).

Hellmayr (1907a; 1919) synonymized red-crowned *roseifrons* (G. R. Gray, 1859) with

brown-crowned *lucianii* (Deville, 1851) under *Pyrrhura picta lucianii* because he considered brown-crowned birds (group 4) and those with a narrow scarlet-red frons (group 6) to be the immature of red-crowned birds (group 7). Thus, of adult *lucianii* (Hellmayr 1907a: 36–38), he wrote: “forehead and more or less of the pileum as well as the lores and ring around the eye clear red. Bend of the wing green, sometimes with a few scattered red feathers.” Note his reference to both the diagnostic orange-red pileum and individually variable orange-red shoulders of red-crowned group 7. When describing young *lucianii* as so construed, he cited the diagnostic narrow scarlet-red frons of some group 6 specimens from Shanusi (Hellmayr 1907a: 38): “Top of the head very dark brown, forehead with only a few small red feathers; in more advanced plumage with a distinct red frontal band.” Hellmayr (1919: 127) reiterated this conclusion: “...der Typus von *C. lucianii* das Jugendkleid der rotscheiteligen Form aus Oberamazonien darstellt” (translation: ...the type of *C. lucianii* is the immature plumage of the red-crowned bird from Upper Amazonia).

Given that no group 7 specimens have a narrow scarlet-red frons, that no red-crowned birds have been found within the range of group 6 and *vice versa*, and that group 6 has a narrow geographical range with virtually no overlap with group 7, the critical question is whether the scarlet-red frons of group 6 can possibly indicate immaturity in red-crowned group 7 as Hellmayr (1907a, 1919) supposed. Indeed, it would be remarkable if entire series of group 6 birds were all young red-crowned birds. Label data describing gonads in two juvenal group 7 specimens from Contamana with no red in their pileum (LSUMZ 161562–3) and in a plainly red-crowned adult collected with one of them (LSUMZ 161564) show that immature birds in otherwise red-crowned group 7 have no red in the pileum

but that they do have that group’s distinct breast and throat scaling or barring. Label data with adult ANSP and LSUMZ group 6 specimens (Table 2) show that the frons of group 6 birds is in adult plumage. Thus the red frons of group 6 does not indicate that they are immature group 7.

Gyldenstolpe (1945) claimed that immature *roseifrons* have reduced red in the crown. None of the specimens he examined (all in NRM), however, have label data describing the gonads or reproductive condition of the birds involved and all have some orange-red in the forecrown, i.e., not restricted to the frons. None therefore resemble group 6. Further, their underparts show the distinctive scaling of group 7, not chevrons of group 6. Application of the epithet *roseifrons* is thus restricted to group 7, except the three anomalous specimens.

With *lucianii* and *roseifrons* so restricted, group 6 with its diagnostic scarlet-red frons and its chevrons with narrow subterminal bands on the breast and throat is either undescribed or genetically and geographically intermediate between red-crowned *roseifrons* to the south and brown-crowned group 5 to the north. Three specimens from within the range of *roseifrons* (AMNH 820834, AMNH 819871 and AMNH 819816) are anomalous brown-crowned adult females with blue foreheads. Although analysed in group 7 on geographical grounds, they are now excluded from *roseifrons*. With these specimens excluded from *roseifrons*, that taxon comprises two disjunct populations (Fig. 1) between which there is no significant difference in CI ($P = 0.14$). Groups 1, 2, 3 and 5 are now addressed before returning to the identities of group 6 and the three anomalous group 7 specimens.

Variation in groups 1, 2, 3, 5 and 6, and the anomalous brown-crowned group 7 specimens. Groups 1 and 2, which are isolated in eastern and

southeastern Amazonia, are diagnosable by blue readily visible and no red in the forehead and forecrown. Breast patterning is chevroned and shoulders are green, occasionally with some red feathers. Group 2 is significantly smaller than all other populations examined, and most specimens are dark-faced, almost blackish about the cheeks. The significant morphometric distinction between groups 1 and 2, which is the only character in which they differ, is not absolute: except CM 82988 from Obidos (wing 116 mm), group 1 is longer-winged than all but four group 2 birds (AMNH 50216 and AMNH 5022 – 117 and 118 mm, respectively); AMNH 285830 – 117 mm, and NHMLAC 38194 – 120 mm). All four are from within 200 km of Obidos, the locality of all group 1 specimens examined.

Hellmayr (1906) recognized group 1 as *P. picta amazonum* (type locality Obidos, north bank of Rio Amazonas). Todd (1947) recognized group 2 as *P. picta microtera* (type locality Santarém, south bank), which he diagnosed relative to *P. p. amazonum* solely by its small size. Presumably on the basis of no clear differentiation in plumage, recent texts have considered *microtera* either doubtfully distinct (Forshaw & Cooper 1989), not valid (Juniper & Parr 1998), or as valid with no comment (Collar 1997). Obidos and Santarém are only 100 km apart on opposite sides of the Amazonas. Essentially, therefore, the four relatively long-winged group 2 birds come from the closest points at which group 2 has been recorded to group 1. Although the statistically significant difference in size between groups 1 and 2 (and, for that matter, between group 2 and all other groups) is true diversity, it can be inferred that there is gene flow between groups 1 and 2 and that they are not genetically or genealogically isolated from each other. It is provisionally concluded that they are not diagnosably distinct from each other although it is acknowledged that group 2

tends to be smaller and, perhaps, darker faced. Further NRM specimens ($n = 5$, not examined) from the north and south banks of the Amazonas come from Lagoa Cuiteuá and Patauí, respectively. Application of the epithet *amazonum* is here restricted to groups 1 and 2.

Group 3 occurs in the Rio Madeira drainage. It is diagnosable by its pale cream-buff breast with narrow dark markings to the centers of the feathers utterly unlike any other *Pyrrhura* parakeet (Figs 3 and 4). It is excluded from *P. lucianii* (Deville, 1851), which has been restricted to populations from Tefé and the Rio Purús. The literature surrounding the nomenclature of this distinctive group is especially confused but can be clarified.

Hellmayr (1907b) first discussed Rio Madeira populations based on one specimen from Humaitá (AMNH 474675) and three obtained by Natterer (not examined). He referred them to “*P. p. lucianii* and not [emphasis Hellmayr’s] to the newly described *P. p. amazonum* [from further east – LJ], although none of them have any red on the forehead.” He noted that this was proved by “the colour of the ear-coverts, which are pale buffy brownish (not clear golden buff, as in *P. p. amazonum*) and by the very small amount of bluish on the forehead.”

Hellmayr (1910) concluded that all the Rio Madeira specimens he had by then examined were referable to *P. p. amazonum*. He considered his earlier conclusion “pardonable” because all Rio Madeira specimens originally available to him were brown-crowned, which he took to indicate immaturity in *lucianii*, the adults of which he considered to be red-crowned. He felt that young *P. p. amazonum* will usually but “not always” [emphasis Hellmayr’s] have more blue on the forehead and brighter, more golden buff ear-coverts than the corresponding stage of *P. p. lucianii*, and that adults of *amazonum* “are of course easily recognizable by having no crimson whatever

on the forehead, this being replaced by a rather narrow dull, bluish band, etc., etc.” After thus concluding that Rio Madeira birds were not *lucianii*, he identified them with the only other then available name, *P. p. amazonum* Hellmayr, 1906. Label data of some group 3 specimens indicate reproductive maturity of the specimens, e.g., LSUMZ 136840 (Table 2), so the diagnostic “pointed” appearance of the breast and throat feathers does not indicate immaturity. Differentiation in color of the ear-coverts that Hellmayr (1907a, 1910) referred to cannot be scored repeatedly because of fading and the poor condition of these feathers in many specimens.

Snethlage (1914: 155) explicitly but confusingly considered Rio Madeira birds to be undescribed. Under *P. picta amazonum*, she noted the diagnostic trait of group 3: “garganta e peito côr de ocre clara, listrados de cinzenta escuro” (translation: throat and breast of a pale ochraceous colour streaked with dark grayish). She gave its distribution as the Rio Madeira. She then listed “*P. picta* conspec. nov.” in eastern Amazonia along the Tocantins, Tapajós and Amazonas rivers. In an appendix, however, she corrected the main text by interchanging headings so that *P. picta* conspec. nov. referred to Rio Madeira birds (group 3), and *P. picta amazonum* to eastern Amazonian birds (= groups 1 and 2). She reiterated that the Madeira birds differ “da maneira mencionada na nossa descrição e talvez será necessario de separalo-os como conspecie nova” (translation: [they differ] in the way mentioned in my description and perhaps it will be necessary to separate them as a new species).

Griscom & Greenway (1941) knew that Snethlage (1914) considered Rio Madeira birds to be undescribed but followed Hellmayr (1910) in recognizing them as *P. p. amazonum*. Gyldenstolpe (1945) described a series from Porto Velho on the Rio Madeira but did

not refer to Snethlage (1914), noting that they “agree closely with the current descriptions of *Conurus lucianii* Dev., as well as with the colored plate of *Maracana Luciani* in Castelnau [1855].” However, that illustration (see Plate) does not have the “pointed” breast feathers of group 3 (e.g., Fig. 4, Plate) whereas Gyldenstolpe (1945) plainly described in Rio Madeira birds the diagnostic “pointed” appearance of the breast and throat feathers of group 3. Finally, in 1989, J. M. Bates annotated the labels of two group 3 specimens (LSUMZ 136840–1) “*Pyrrhura picta* nov. subsp. JMB 89”.

Between westernmost *amazonum* from beyond the Rio Madeira drainage (CM 76340, Villa Braga, Rio Tapajós) and easternmost group 3 from within it (AMNH 127347–9, Rio Roosevelt), blue on the pileum declines from being conspicuous in all *amazonum* to barely discernible in group 3. Also, breast and throat feathers’ markings become “pointed”, the pallor and extent of the subterminal band sharply increase, and overall size increases. Thus, variation between *amazonum* and group 3 is greater and more steeply stepped than within either *amazonum* or group 3. Similarly, between westernmost group 3 specimens from the Rio Madeira drainage (e.g., AMNH 148193, Porto Velho) and easternmost *lucianii* from beyond it (CM 93531 and CM 93981, Arimã), blue on the pileum disappears altogether, breast and throat feathers’ markings “reverse” to chevrons, and color of the subterminal band darkens. Again, variation between group 3 and *lucianii* is greater than that within either. Uniqueness of group 3 is therefore not due to its being a stage in a cline between *amazonum* and *lucianii*. Group 3 is unique in *Pyrrhura* and Snethlage (1914) and J. Bates (unpubl.) correctly recognized Rio Madeira drainage populations as undescribed.

Group 5 occurs in northwestern Amazonian Peru north and west of the Marañon and

Huallaga rivers. It differs consistently from all other populations in weak but discernible blue forehead and forecrown, extensive pale subterminal bands on breast and throat feathers (although not to the extent in group 3, Figs 3 and 4), and more consistently yellowish-buff subterminal band of these feathers than in all other groups. E. Blake and P. Hocking (unpubl.) annotated labels of group 5 specimens to indicate that they considered group 5 to be an undescribed form. Joseph (2000) tentatively disagreed and considered group 5 to be *lucianii*. I now concur with Blake and Hocking (unpubl.). Also, three specimens analysed here as part of group 7 on geographical grounds (AMNH 820834, AMNH 819871, and AMNH 819816) are so different from all other specimens of that group (now assigned to *roseifrons*) that they clearly belong to a different taxon. No red is evident in any of their pilea. There is weak but clearly discernible blue in the forehead of the two undamaged birds, and all three have breast patterning typical of group 5 not *roseifrons*. They are here identified as the same unnamed taxon as group 5.

Group 6 is problematic. Its scarlet-red frons with some blue posterior to it on an otherwise brown pileum is unique. That the scarlet-red frons indicates immaturity in *roseifrons* has been dismissed. Alternatively, this same character could be expected from the geographical intermediacy of group 6 between brown-crowned group 5 to its north and red-crowned group 7 to its south. Some group 6 specimens do have individual rosy feathers scattered around the eye ring but their color as well as that of the frons is consistently closer to Geranium (12) than the Flame Scarlet (15) of *roseifrons*. It is worth noting that one group 3 specimen (AMNH 47465) has some rosy feathers about its eye ring (Hellmayr 1907b, pers. observ.) and that the pileum is entirely red in a further species of *Pyrrhura*, the Rose-crowned Parakeet (*P.*

rhodocephala) of Venezuela. Reddish feathers in the ocular ring and crown may therefore have limited, if any, taxonomic significance in these birds. Group 6's breast chevrons have consistently narrower grayish subterminal bands than group 5 and not as broad as in other chevroned groups (Fig. 3). Breast feathers are never scaled as in *roseifrons*. Group 6 is thus not intermediate with respect to breast patterning. An intergrade population is reasonably expected to be variable in all characters, i.e., breast patterning, ear-coverts, and carpal edge and shoulder feathering, not just the patterning of the pileum.

Group 6 has always been identified as *lucianii*. Berlepsch (1889) noted that none of Garlepp's Yurimaguas and Shanusi specimens had red extending beyond the frons and he supposed young birds to have little or no red on the frons. Hellmayr (1907a) considered them immature *lucianii* with which he synonymized red-crowned *roseifrons*. This study has shown that they are not immature *roseifrons* and that none have been found within the range of *roseifrons*. Robbins *et al.* (1991) listed *P. picta lucianii* for the Rio Maniti and Quebrada Vainilla, Peru on the basis of five group 6 specimens (ANSP 176010–2, LSUMZ 114613–4). Noting the scarlet-red frons, Joseph (2000) tentatively assigned 20 group 6 birds from the Orosa River, Santa Cecilia and Shanusi to *lucianii* but urged further study. With 26 group 6 specimens now examined, *lucianii* restricted to Tefé and Rio Purús populations, and group 6 not immature *roseifrons*, it is nonetheless concluded that data are still insufficient to discriminate between the following hypotheses: (1) group 6 is genetically intermediate between group 5 and *roseifrons*, and (2) it is a valid, undescribed taxon influenced by gene flow from group 5 and *roseifrons* that is mostly manifest in the frons and forecrown. Certainly, the recent description of several new bird species with restricted ranges in this part of Amazonian Peru, espe-

cially that of the Allpahuayo Antbird *Percnoscotola arenarum*, lends biogeographical feasibility to the second hypothesis (Alvarez & Whitney 2001, Isler *et al.* 2002, Whitney & Alvarez 1998).

Taxonomy. Treating the populations under study as subspecies of *P. picta* under the Biological Species Concept (BSC) perpetuates blind adherence to the arrangement Peters (1937) introduced with no justification and which is often considered unsatisfactory (e.g., Forshaw & Cooper 1989; see also Joseph 2000). Further, it predicts that the populations are all more closely related to *P. picta* than to other *Pyrrhura*. Given existing data from so few characters, even this prediction is unjustifiable. This issue aside, it is difficult to see any logic in treating two such divergent taxa as *picta* (*sensu stricto*) and *roseifrons* as conspecific when they are not connected by intermediate populations.

Given the above, an alternative taxonomy would treat *P. picta* (P. L. S. Muller, 1776) and *P. roseifrons* (G. R. Gray, 1859) as two species by all modern species concepts (e.g., de Queiroz 1998, Johnson *et al.* 1998). If group 6 is an intergrade population between *P. roseifrons* and group 5, then group 5 could be treated as a subspecies of *P. roseifrons* under the BSC. This, however, argues that group 5 is more closely related to *P. roseifrons* than to other Amazonian populations unless they, too, are subspecies of *P. roseifrons*. The point here is that relationships within the group cannot at present be determined. Therefore, a necessarily conservative taxonomy is adopted here based on the General Lineage Concept (de Queiroz 1998) and the Comprehensive Biologic [sic] Species Concept for birds (Johnson *et al.* 1998). The former recognizes that all modern species concepts equate species with segments of population level evolutionary lineages. The latter sees avian species as systems of populations represent-

ing essentially monophyletic, genetically cohesive and genealogically concordant lineages of individuals on independent evolutionary trajectories. Use of these species concepts here makes no statement about inter-relationships. If later phylogenetic analysis shows, for example, that two species recognized here are more closely related to each other than either is to a third, then one might treat them as subspecies of one species. Far from setting taxonomy back 100 years as some critics of this approach argue (see papers in Wheeler & Meier 2000), interim use of a binominal nomenclature does precisely what a taxonomy should do: summarize present understanding of relationships in the group in question. If, as here, one can do no more than identify taxa and not their inter-relationships, then there is a need not for criticism of the taxonomy but for further collecting and research, as is planned for this group. The further criticism that one or two diagnosable differences between, for example, genetic siblings can be artificially induced under laboratory conditions is negated here by consistent, steeply stepped inter-population differences involving combinations of characters found in nature over component parts of an extensive geographical region. Finally, taxa in *Pyrrhura* have been diagnosed by one or a few subtly varying characters (e.g., Ridgely & Robbins 1988). Recognition here of weakly but consistently differentiated forms thus accords with previous taxonomic treatment of *Pyrrhura*.

The following taxonomy summarizes the present study. Authorship of new names reflects the contributions of those who have studied each taxon.

***Pyrrhura lucianii* (Deville, 1851)**

Deville's Parakeet

Conurus lucianii Deville, 1851: 210; *Maracana lucianii* Castelnau, 1855: 14; *Microsittace lucianii*

Bonaparte, 1854: 150; *Pyrrhura lucianii* Souancé, 1857: plate 14; *Pyrrhura picta lucianii* Hellmayr, 1907a: 37, Todd 1947: 336.

Holotype. MNHN 1847/682; Ega (= Tefé); adult; sex?; 1847.

Diagnosis. No red in the pileum, carpal edge, shoulder or crural feathers; breast feathers marked with subterminal chevrons. Blue in forecrown absent or barely discernible.

Range. Known only from Tefé and the Rio Purús, Brazil.

Remarks. Group 4 of the present paper.

***Pyrrhura roseifrons* (G.R. Gray, 1859)**

Red-crowned Parakeet

Conurus roseifrons G.R. Gray, 1859: 42; *Pyrrhura picta lucianii* Hellmayr, 1907a: 37; Hellmayr 1919: 127; *Pyrrhura picta roseifrons* Gyldenstolpe, 1945: 50.

Type data. NHM 1858.4.27.35, NHM 1858.1.11.2, NHM 1858.1.11.3 are syntypes, precise localities of which are indeterminable. A lectotype cannot be designated from among them without over-ruling Gyldenstolpe's (1945: 50) valid restriction of the type locality to Upper Rio Juruá. See Appendix 4 for details.

Diagnosis. Adults with bright red of pileum extending to hindcrown; subterminal bars on breast feathers curved rather than chevroned. Crural feathers, carpal edge and shoulder red, sometimes with scattered green. Ear-coverts distinctly yellowish.

Range. Two populations in western Amazonia. Northern one from São Paulo de Olivença and Rio Javari, Brazil and Requena Ucayali,

Peru in the north to Yurinaqui Alto and Conchapan, Peru in the south. Southern one from Itahuania, Peru in north to Teoponte, Bolivia in south.

Remarks. Group 7 of the present paper except AMNH 820834, AMNH 819871, and AMNH 819816.

***Pyrrhura amazonum* Hellmayr, 1906**

Hellmayr's Parakeet

Pyrrhura picta amazonum Hellmayr, 1906: 8; *Pyrrhura picta microtera* Todd, 1947: 335 (holotype CM 78378, adult male, Santarém, Brazil 28 September 1920).

Holotype. AMNH 474671, Obidos; adult female, 11 March 1906.

Diagnosis. Blue in forecrown readily discernible but less intense and less extensive than in *P. picta sensu stricto*. Southern populations tending smaller and very dark-faced.

Range. Eastern Amazonia from Obidos, Lagoa Cuiteua and Pataua in the north to Imperatriz in the east, to Villa Braga along the Rio Tapajós in the west, and to Alta Floresta, Rio Teles Pires in the south.

Remarks. Groups 1 and 2 of the present paper. Subdivision is not recommended at present. Gene flow from *P. picta* is suggested in some specimens, e.g., MPEG 12998 with some red shoulder feathers. The extent of contact, if any, with *P. picta* requires study (Fig. 1).

***Pyrrhura snethlageae* sp. nov. Joseph and**

J. Bates

Madeira Parakeet

Pyrrhura picta lucianii Hellmayr 1907b: 404; Gyldenstolpe 1945: 51; *Pyrrhura picta amazonum* Hellmayr, 1910: 403.

Holotype. LSUMZ 136840, adult female, 4 km upstream from Rio Itenez, west bank of Rio Paucerna, Prov. Velasco, Depto. Santa Cruz, Bolivia, 450 m, c. 17°30'S, 61°30'W, 30 July 1988, collected by Gregory Schmitt and Mary C. Garvin.

Diagnosis. Differs from all other *Pyrrhura* parakeets in the extremely pale cream-buff breast feathers and throat finely streaked Dark Grayish Brown (20) with green centers to the feathers only on the lower breast. Each breast and throat feather has a greatly enlarged, pale subterminal band, and the dark central part of the feather is restricted to little more than a striation (Fig. 3). There is no red on the pileum and blue, although present on the forehead, is barely discernible.

Description of holotype. Head mostly brown approaching Vandyke Brown (121). Forehead darker blue than Sky Blue (66) and narrowly bordered above the cere with maroon. Broken nuchal collar of brown feathers bordered laterally with blueish-green. Maroon ocular ring ca 3 mm in width below the eye and narrower above it almost completely encircling eye. Some small blueish-green feathers in anterior cheeks. Ear-coverts off-whitish, darker than Pale Horn Color (92). Lower cheeks and throat dark brown, approaching Dark Grayish Brown (20). Throat and upper breast feathers with a similarly dark brown central mark that is either even in width or distally narrowed (giving a "pointed" appearance to the breast) and bordered by a pale cream-buff subterminal band, approaching but lighter than, Cream Color (54) or Pale Horn Color (92). Lower breast feathers patterned similarly but with dark centers greenish and the pale outer borders yellowish not off-whitish, with a green terminal band. Center of abdomen, rump, upper tail-coverts and tail maroon between Burnt Sienna (132) and Brick Red (132A). Underside of tail's outer

webs blackish and the outer webs of the tail proximally green approaching Parrot Green (260). Sides of abdomen, undertail-coverts, back and wings except primaries, primary-coverts and alular quills, green approaching Parrot Green (260). Primaries, primary-coverts and alular quills blueish-green approaching Turquoise Blue (65). Inner webs of primaries black. Tertiaries green with blackish terminal band. Underwing mostly blackish but lesser underwing-coverts green. Label data: weight 85g, ovary 15 x 5 mm, largest ova 3 mm, oviduct 2 mm, no wing or tail molt, slight molt on belly, iris brown, bill dark brown, orbital skin tan with brown and yellow blotches. Tissue sample vouchered as LSUMZ B 12781.

Measurements of holotype. Wing (flattened chord) 123 mm, maxilla (from distal edge of cere to tip) 15.7 mm, tail 97 mm.

Specimens examined. AMNH 474675, AMNH 474678, AMNH 127348, AMNH 127347, AMNH 127349, AMNH 474682, AMNH 474680, AMNH 474681, AMNH 474679, AMNH 474677, AMNH 474676, AMNH 148193, NHMLAC 59307, NHMLAC 59308, NHMLAC 59309, NHMLAC 59306, LSUMZ 33592, LSUMZ 136841.

Range. Drainage of the Rio Madeira.

Etymology. The scientific name *P. snethlageae* honors Dra Emilia Snethlage who first recognized the distinctiveness of these populations (Snethlage 1914) and who pioneered modern studies of the Amazonian avifauna. The vernacular name refers to the occurrence of this bird strictly within the drainage of the Rio Madeira.

Remarks. Group 3 of the present paper. The distinctiveness of *P. snethlageae* in the Rio Madeira's drainage, although noted in 1914,

has usually been overlooked because of confusion with *P. amazonum* and *P. lucianii*. *P. snethlageae* has been recorded from both banks of the Rio Madeira and to that extent its range is not typical of species of the Rondônia center of endemism *sensu* Cracraft (1985). That it has not been recorded west of that river's west bank, however, also indicates that it has not been recorded within the Inambari center of endemism to the west.

***Pyrrhura peruviana* sp. nov. Hocking,
Blake and Joseph**
Wavy-breasted Parakeet

Conurus cyanopterus Sclater and Salvin, 1867: 753; *Conurus lucianii* Taczanowski, 1874: 549; *Pyrrhura lucianii* Joseph, 2000: 283.

Holotype. FMNH 278312, adult female, Rio Santiago, Puerto Galilea, Depto Amazonas, Peru, (800 ft – label data), c. 03°45'S, 77°45'W, 8 December 1965, collected by Peter Hocking.

Diagnosis. Differs from all other Amazonian populations considered here by its combination of broad yellowish subterminal bands of the breast and throat feathers, and blue forehead on an otherwise brown pileum. There is no bright red in the plumage.

Description of holotype. Head mostly brown approaching Vandyke Brown (121). Forehead darker blue than Sky Blue (66) and narrowly bordered above the cere with maroon. Maroon ocular ring almost completely encircling eye and extending onto the upper cheeks. Some small blueish-green feathers in lower cheeks. Ear-coverts off-whitish darker than Pale Horn Color (92). Throat dark brown bordered laterally with pale creamy subterminal band. Breast feathers with extensive pale outer borders yellowish and dark centers becoming greener ventrally. Center of

abdomen, rump, upper tail-coverts and tail maroon between Burnt Sienna (132) and Brick Red (132A). Underside of tail's outer webs blackish and the outer webs of the tail proximally green approaching Parrot Green (260). Sides of abdomen, undertail-coverts, back and wings except primaries, primary-coverts and alular quills, green approaching Parrot Green (260). Primaries, primary-coverts and alular quills blueish-green approaching Turquoise Blue (65). Inner webs of primaries black. Tertiaries green with blackish terminal band. Underwing mostly blackish but lesser underwing-coverts green. Label data: eyes orange, bill black, feet black, ovaries enlarged.

Measurements of holotype. Wing (flattened chord) 111 mm, maxilla (from distal edge of cere to tip) 14.4 mm, tail 109 mm.

Specimens examined. FMNH 296580, FMNH 299022, FMNH 299023, FMNH 299024, FMNH 299025, LSUMZ 33996, LSUMZ 33997, LSUMZ 33998, NHM1889.1.30.151, NHM1869. 5.25.107, NHM1869.5.25.108, NHM1890. 6.1.89, AMNH 820834, AMNH 819871, AMNH 819816.

Variation in the specimens examined. Specimens from central Amazonian Peru within the range of *P. roseifrons* have less extensive distal tips to the pale subterminal band of the breast and throat feathers.

Range. Known from two disjunct regions in northwestern and central Amazonian Peru, between which occur group 6 and northern populations of *P. roseifrons* (Fig. 1). It is beyond the scope of this paper to discuss the origin of this "leapfrog" distribution pattern. The northern population corresponds to the specimens hitherto treated as group 5 from three localities on the Rio Santiago (FMNH 278312, FMNH 296580, FMNH 299022–

299025) and single localities on the Rio Cenepa (LSUMZ 33996–97) and Rio Kagka (LSUMZ 33998) and it occurs south-east to Chamicuro (NHM1869.5.25.107, NHM1869.5.25.108, NHM1890.6.1.89) and Chyavitas (NHM1889.1.30.151). Sclater & Salvin (1867, 1873) identified the NHM specimens from the latter localities as *Conurus lucianii*. The southern population has been recorded on the Rio Ene at the mouth of the Rio Quipachiari (AMNH 820834) and at 6 and 2 km E of Luisiana in the Cordillera Vilcabamba (AMNH 819871 and AMNH 819816, respectively). Taczanowski (1874) mentioned a male (not examined) from Monterico, which is within ca 40 km of the localities of AMNH 819871 and AMNH 819816. He compared it with the holotype of *Conurus lucianii* Deville, 1851 and made no reference to red in the pileum. This specimen was likely *P. peruviana*. Records of *P. picta* from Ecuador (Ridgely & Greenfield 2001) undoubtedly refer to *P. peruviana*. The disjunct range of *P. peruviana* is certainly novel in the Peruvian avifauna (T. Schulenberg, pers. comm.). P. Hocking and T. Arndt (in prep.) will give a more detailed account of the range of *P. peruviana* and *P. roseifrons*.

Etymology. The epithet *peruviana* was chosen by P. Hocking to indicate the known occurrence of this form only in Peru. The vernacular name refers to the effect created by the extensive subterminal bands on the feathers of the throat and breast.

Remarks. Group 5 and the three anomalous group 7 specimens of the present paper. The diagnostic extensive pale creamy to yellowish breast barring of *P. peruviana* recalls *P. melanura chapmani* (Ridgely & Robbins 1988: fig. 2). Further taxonomic subdivision of *P. peruviana* may be warranted after closer study of the two allopatric populations recognized here.

CONCLUDING REMARKS

Three major (> 200 km) and several smaller distributional gaps are evident in Brazil and Peru (Fig. 1). Many localities that span the larger gaps have been collected for birds (Haffer 1974) but relevant papers do not mention these *Pyrrhura* parakeets (e.g., Cohn-Haft *et al.* 1997 based on 15 years of observations; Schubart *et al.* 1965). Remarkably, only two specimens (MNHN 1847/682, AMNH 308975) are from along the Solimões and Amazonas rivers in what would otherwise be a gap of c. 1500 km between São Paulo de Olivença and Obidos in a region Oren & Guerrero (1991) felt had low priority for future bird collecting (Fig. 1). Both are from Tefé roughly midway between these localities. Hellmayr (1907c) noted no further specimens from Tefé. Nonetheless, these gaps may be sampling artifacts (see also Oren & Guerreiro 1991) because these parakeets can be notoriously difficult to collect. Competitive ecological interactions among these parakeets themselves, e.g., among *P. peruviana*, group 6 and *P. roseifrons* where they approach each other, as well as between them and Pearly Parakeets *P. perlata* and Maroon-tailed Parakeets *P. melanura* in eastern and western Amazonia, respectively, may be involved in maintaining distributional gaps. Terrain between northern and southern populations of *P. roseifrons* is probably too high for these parakeets, which have been recorded to c. 1100 m (FMNH 278311). All gaps merit further study.

Also of note is how few specimens have been sexed by dissection, with soft parts labeled, and with tissue samples vouchered for molecular study (Joseph, in prep.). For example, all but one of the *P. amazonum* specimens located from north of the Amazonas (n = 30) were collected before 1922 (one in 1988) and all except 14 of 55 examined from south of the Amazonas were collected before

1957 (four in 1957, eight in 1960, and 2 in 1988). All the *P. lucianii* specimens (n = 15) were collected before 1929. Among exceptions are recent AMNH, ANSP and LSUMZ specimens of *P. roseifrons*, *P. snethlageae*, *P. peruviana* and group 6. Soft parts and gonad data from these have been critical in separating age-related and geographical patterns of variation in *P. roseifrons* and in demonstrating that the red frons and “pointed” underparts of group 6 and *P. snethlageae*, respectively, are in adults. This emphasizes the need for freshly collected, well-labeled specimens from all the populations under study. Finally, diagnoses here of new taxa solely from existing material in museums reinforces Bates & Demos’s (2001) plea for recognition among the conservation community of the need to document and recognize evolutionary subdivisions within Amazonia.

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Haven, (J. Gauthier, P. Whitehead), Museum of Comparative Zoology, Harvard University, Cambridge (A. Pirie), Swedish Museum of Natural History, Stockholm, (P. Ericson), Natural History Museum, Tring (M. Adams, R. Prys-Jones), and Musée National d’Histoire Naturelle, Paris (E. Pasquet). Kim Goodger (Natural History Museum) helped with information about H. W. Bates in Amazonia. P. Callomon, E. Danulat, D. Fonseca, C. Jersabek, B. Parisi and C. Reimer assisted with translations of original texts not in English and A. L. Porzecanski translated the Abstract into Spanish. J. Bates and P. Hocking kindly agreed to join with me in co-authoring the names of the new taxa described herein. G. Rosenberg (International Commission on Zoological Nomenclature) advised on intricacies of the Zoological Code. P. Morris and F. G. Stiles advised on analyses. J. Bates, T. Schulenberg and J. P. O’Neill offered encouragement and made valuable comments on drafts. Two anonymous reviewers of an earlier draft made valuable comments. L. Belasco, C. Fisher, R. McNeil and N. Rice offered assistance and support. I am especially indebted to the following colleagues at ANSP for freely giving the benefit of their expertise: Julie Reich and Eileen Mathias (Albert M. Greenfield Digital Imaging Center for Collections), who prepared digital images of specimens, and Dana Cohen, who prepared line drawings. To all these people and institutions, I express my thanks.

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APPENDIX 1. Specimens examined.

Group 1/*P. amazonum*. Obidos: AMNH 474674, AMNH 474671, AMNH 474672–3, CM 82649, CM 82721, CM 82938–9, CM 82985–6, CM 82988, CM 83007, CM 83204–5, CM 83487–8, CM 83510, CM 83624, CM 83765, CM 83815, YPM 27635, YPM 27637–8, YPM 27636.

Group 2/*P. amazonum*. All localities in Brazil. Caxiracatuba, Rio Tapajós: AMNH 285833, ANSP 129260, MCZ 173435–6; Colonia do Mojuy, Santarém: CM 74546, 74548; Diamantina: USNM 121053–4; Igarape

Brabo, Rio Tapajós: AMNH 285834, 285836–9; Imperatriz: NHMLAC 42239–47; Santarém: AMNH 50216, AMNH 50222, CM 71689–91, CM 71693, CM 71851–2, CM 71962, CM 71966, CM 72247–8, CM 78379; Sao João do Araguaia: MCZ 134975; Tauari, Rio Tapajós: AMNH 285823–32; Urucuritubu, Rio Tapajós, Para: NHMLAC 38191–4; Villa Braga, Rio Tapajós: CM 76340.

Group 3/*P. smetblageae*. All localities in Brazil unless stated otherwise. Allianca, Rio Madeira, AMNH 474676; Calama: AMNH 474677–82; Humaita: AMNH 474675; Pimenta Bueno: NHMLAC 59306–9, LSUMZ 33592; Porto Velho: AMNH 148193, NRM 568474, NRM 568470, NRM 568471, NRM 568473, NRM 568472; Roosevelt River: AMNH 127347–9; Rio Paucerna, west bank, 4 km upstream from Rio Itenez, Santa Cruz, Velasco, Bolivia: LSUMZ 136840–1.

Group 4/*P. lucianii*. All localities in Brazil. Arimã, Rio Purús: CM 93531, CM 93581; Hyutanahan, Rio Purús: CM 86406, CM 86546–50, CM 86620–1, CM 86660, CM 86964, YPM 27634; Santa Isidoro, Tefé: AMNH 308975; Ega (= Tefé) (holotype): MNHN 1847/682.

Group 5/*P. peruviana*. All localities in Peru. Bashium, Rio Kagka: LSUMZ 33998; Betel, Rio Santiago: FMNH 296580; Chamicuros: NHM1869.5.25.107–8, NHM1890.6.1.89; Chyavitas: NHM1889.1.30.151; Puerto Galilea, Rio Santiago: FMNH 278312; Tutinum, Rio Cenepa: LSUMZ 33996–7; Villa Gonzalo, Rio Santiago: FMNH 299022–25; Luisiana, 2 km E, Cordillera Vilcabamba: AMNH 819816; Luisiana, 6 km E, Cordillera Vilcabamba: AMNH 819871; Rio Ene at mouth of R. Quipachiari: AMNH 820834.

Group 6. All localities in Peru. Orosa River: AMNH 230866–74; Quebrada Vainilla, east bank, ca 10 km SSW mouth Rio Napo: LSUMZ 114613–4; Santa Cecilia, Rio Maniti: ANSP 176010–12; Sarayacu, R. Ucayali: AMNH 237723; Shanusi: AMNH 474697–702, USNM 145680–1; Yurimaguas: NHM1890.6.1.78–79, NHM1889.1.30.502.

Group 7/*P. roseifrons*. All localities in Peru unless stated otherwise. Abra Aguachini, ca 30 km SW Puerto Bermudez: LSUMZ 130085–6; Altamira, Manu: YPM 81442, 81446; Cerro de Pantiacolla, above Rio Palatota: FMNH 320430; Cerro Tahauyo, SE slope, ca 65 km ENE Pucallpa: LSUMZ 156182–3; Conchapien: FMNH 285078; Contamana, ca 77 km WNW, LSUMZ 161563–4; Contamana, 84 km WNW, north-east bank of Rio Cushabatay: LSUMZ 161562; Contamana, Aguas Calientes: FMNH 320233–4; Hacienda Santa Elena, ca 35 km NE Tingo Maria: LSUMZ 72175–6; Igarape do Gordão, Rio Juruá, Brazil: NRM 552779; Itahuania: FMNH 222875–80; Joao Pessoa, Rio Juruá, Brazil: FMNH 183717; NRM 604804–9, NRM 604812–3; NRM 604802, NRM 604809, NRM 604810, NRM 604814, NRM 604803, NRM 604804, NRM 604807, NRM 604808, NRM 604818, NRM 604813, NRM 604805, NRM 604816, NRM 604806, NRM 604817, NRM 604812, NRM 604815, NRM 604811; La Pampa, Sandía: ANSP 103849, AMNH 145927; Lago Grande, Rio Juruá, Brazil: NRM 604820, NRM 604821; Nevati: FMNH 297883; Nusiniscato: FMNH 208169–70; Palcazu: AMNH 474703–4; Requena Ucayali: AMNH 40678–9; Rio Ene at mouth of Rio Shesha, west bank, ca 65 km ENE Rio Pucallpa: LSUMZ 156184–6; River Amazon: NHM 1858.1.11.2–3, NHM 1858.4.27.35; São Paulo de Olivença, Rio Solimões, Brazil: CM 96184; Tarapoto: NHM 1890.6.1.77, NHM 1889.1.30.503, USNM 108269; Teoponte, Rio Kaka, Bolivia: ANSP 121087; Tsiovenienti: FMNH 297882; Yurinaqui Alto: ANSP 176390, FMNH 278311.

APPENDIX 2. Gazetteer: Latitudes and longitudes of localities mentioned in the text.

Alta Floresta, Rio Teles Pires, Brazil, 07°21'S, 58°03'W.

Arimã, Brazil, 05°47'S, 63°38'W.

Chyavitas, Peru, (= Chayahuitas, Stephens & Traylor 1983) 5°27'S, 76°48'W .

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Chamicuros, Peru, 5°30'S, 75°30'W.
Contamana, Peru, 07°09'S, 75°44'W.
Cordillera de Vilcabamba, Peru, 12°39'S, 73°44'W.
Itahuania, Madre de Dios, Peru, 12°47'S, 71°13'W.
Jeberos, Peru, 05°17'S, 76°13'W.
Lago Cuíteuá, Brazil, (= Lago Cuípeuá Paynter & Traylor 1991) ca 01°54'S, 55°32'W.
Luisiana, 6 km E, Cordillera Vilcabamba, Peru, 12°39'S, 73°40'W.
Luisiana, 2 km E, Cordillera Vilcabamba, Peru, 12°39'S, 73°44'W.
Manaus, Brazil, 03°08'S, 60°01'W.
Manu, Peru, 12°15'S, 70°50'W.
Monterico, Peru, ca 12°28'S, 73°54'W.
Obidos, Pará, Brazil, 01°55'S, 55°31'W.
Patauá, Brazil, ca 03°05'S, 55°03'W.
Porto Velho, Brazil, 08°36'S, 63°54'W.
Quebrada Vainilla, Peru, 03°32'S, 72°44'W.
Rio Roosevelt, Brazil, 07° 35'S, 60°20'W.
Requena Ucayali, Peru, 04°58'S, 73°50'W.
Rio Cenepa, Peru, 04°33'S 78°12'W
Rio Ene, at mouth of R. Quipachiari, Junin, Peru, 11°35'S, 74°04'W.
Rio Kagka, Peru, 04°33'S 78°16'W.
Rio Madeira, Brazil, 08°03'S, 62°53'W; 08°37'S, 63° 32'W.
Rio Maniti, Peru, 03°33'S, 72°53'W.
Rio Paucerna, west bank, 4 km upstream from Rio Itenez, Santa Cruz, Velasco, Bolivia, 13°31'S, 61°06'W.
Rio Santiago, Peru, (three localities), 03°45'S, 77°45'W; 03°55'S, 77°45'W; 04°08'S, 77°45'W.
Santarém, Brazil, 02°26'S, 54°42'W.
São Paulo de Olivença, Amazonas, Brazil, 03°27'S, 68°48'W.
Shanusi, Peru, 06°07'S, 76°15'W.
Tabatinga, Brazil, 04°16'S, 69°56'W.
Tarapoto, Peru, 06°30'S, 76°25'W.
Tauri, Rio Tapajós, Brazil, 03°05'S 55°06'W.
Tefé, Amazonas, Brazil, 03°22'S, 64°42'W.
Urucuritubu, Rio Tapajós, Brazil, 03°32'S, 55°30'W.
Villa Braga, Rio Tapajós, Brazil, 4°25'S, 56°17'W.
Yurimaguas, Peru, 05°54'S, 76°05'W.

APPENDIX 3. Two 1850s paintings of *P. lucianii* (Deville, 1851).

Two paintings based on the holotype of *C. lucianii* Deville, 1851 were published in the 1850s. They warrant mention here because they contribute to confusion in the literature and because they address the argument that Rio Purús birds and the holotype of *C. lucianii* represent the same taxon. Castelnaud (1855) published a painting (see Plate, upper) that was explicitly stated to have been based on the holotype of *C. lucianii*. Red and blue are entirely absent from the brown pileum and the breast shows creamy, unrealistically evenly shaped subterminal bars unlike the chevrons actually on the holotype's upper breast. Souancé (1857) published a second painting of *P. lucianii* (see Plate, lower). No extensive red or blue are evident anywhere on the pileum, and the subterminal bars on the lower breast in this painting are yellow as are those on the *lower* breast of the holotype of *C. lucianii* and indeed all populations under discussion here. Consequently, it depicts a very different-looking bird than Castelnaud's (1855) plate and one that more closely resembles the holotype. Given the second painting's 1857 publication date, that both paintings are in French publica-

tions, and that the holotype has always been housed in the MNHN collection in Paris, I know of no specimen other than the *C. lucianii* holotype on which it could have been based. Examination of both paintings (see Plate) suggests that one artist emphasized over the entire breast the pale creamy patterning on the specimen's throat and upper breast whereas the other more accurately depicted the differentiation between upper and lower breast. Neither resembles the Rio Madeira populations *pace* Gyldenstolpe (1945) in showing the "pointed" markings of the breast feathers.

APPENDIX 4. Type specimens and type locality of *Conurus roseifrons* G. R. Gray, 1859.

In 1857, H.W. Bates traveled from Tefé in the range of *P. lucianii* to São Paulo de Olivença in the range of *P. roseifrons*. Bates wrote that while at São Paulo de Olivença, he "made a large collection" and employed a collector at nearby Tabatinga on the banks of the Rio Jaurí (= Rio Javari) for several months (Bates 1863: 408). It is not clear whether this "large collection" included many birds because Bates had earlier remarked that he was not successful in obtaining hunters to collect birds there (Bates 1858: 6162). Bates (1858: 6162) did note that he was accompanied *on his journey* [emphasis mine] by the bird collector T.C. Hauxwell. It is not known whether Hauxwell secured any of the syntypes of *C. roseifrons*. On the other hand, Sclater (1857) reported on a series of birds sent by Bates "mostly from Ega [=Tefé] or from the Rio Javari" and among these listed *Conurus guianensis* with no locality details. The name *C. guianensis* probably refers to parakeets of this complex, but it is not known whether Sclater was referring to the specimens that G. R. Gray (1859) later described as *C. roseifrons* or *P. lucianii* specimens from Tefé. Either would be of interest. Also, Sclater and Salvin (1866) remarked that an assistant collector for Bates secured birds for him at the Rio Javari. The words "Rio Javari" have been written on an early label of one of the syntypes (NHM 1858.4.27.35). Given that there are other spelling discrepancies in Bates's localities (K. Goodger, pers. comm.), this undoubtedly refers to the Rio Javari (or Jauri), close to Tabatinga. Numerous red-crowned *P. roseifrons*/group 7 specimens have been collected along the middle Rio Juruá, e.g., at João Pessoa and Lagoa Grande, but not near its mouth. Bates spent some time around the mouth of the Rio Juruá (Bates 1852), but it is unclear whether he himself ascended this river. Although the Rio Javari, Tabatinga, São Paulo de Olivença and the upper Rio Juruá are all within the range of red-crowned *P. roseifrons*/group 7 specimens (Fig. 1) and all are potential localities at which the syntypes of *C. roseifrons* may have been collected (especially Rio Javari), I conclude that the provenance of the syntypes remains unclear.

Warren (1966) cited only one of Bates's three specimens, NHM 1858.4.27.35 in a catalogue of avian type specimens in the British Museum. Presumably, she chose this specimen because of the three syntypes it has the most orange-red in the pileum. The point remains that she did not formally designate NHM 1858.4.27.35 as a lectotype. Even if NHM 1858.4.27.35 were to be designated as the lectotype, the name *C. roseifrons* G. R. Gray, 1859 has a valid type locality that can not be linked to any of the three syntypes. Thus a lectotype cannot be designated from among the syntypes without over-ruling Gyldenstolpe's (1945) designation of a type locality. Although this is unfortunate, a strong case can not be made for designating any other locality as a type locality. Further, there is no case for neotypification because the type specimens are not lost.

