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Source: The Auk, 126(4) : 915-921

Published By: American Ornithological Society

URL: <https://doi.org/10.1525/auk.2009.91009>

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The Auk 126(4):915–921, 2009
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Printed in USA.

CONSTRUCTING CHECK-LISTS AND AVIFAUNA-WIDE REVIEWS: MEXICAN BIRD TAXONOMY REVISITED

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SUMMARIZING TAXONOMIC AND distributional information of regional avifaunas has been an important task of the American Ornithologists' Union (AOU) from early in its history up to the present day (AOU 1998). The North American *Check-list* is updated by yearly supplements (e.g., Banks et al. 2008), and taxonomic changes are incorporated on the basis of a self-described “conservative and cautious” system of consensus among committee members regarding recently published proposals of changes (AOU 1998). The newer South American *Check-list* follows similar procedures (Remsen et al. 2008). Because many communities depend on these regional taxonomies as baseline summaries for diverse applications (e.g., in conservation, biodiversity studies, and systematic studies), consideration of the system employed and its implications is paramount, particularly given the statement that the decisions are made following a “time-honored tradition,” which—as we will argue—may not constitute the optimal strategy for 21st-century taxonomy. An alternative approach is that of regional “sweeps” and broad taxonomic reviews (e.g., Christidis and Boles 2008). This approach may, in the end, base decisions on less-complete information for establishing species limits, but it has the advantage of producing an internally consistent list.

In our ongoing efforts to understand and summarize the Mexican avifauna (Escalante-Pliego et al. 1993, Peterson and Navarro-Sigüenza 2000b), we have become aware of numerous species taxa that merit full recognition as species, under both the biological species concept and the evolutionary species concept (Navarro-Sigüenza et al. 1992, Peterson and Navarro-Sigüenza 2000a, Puebla-Olivares et al. 2008). This realization led to the development of a new, country-wide taxonomic treatment under the evolutionary species concept (Navarro-Sigüenza and Peterson 2004), which was subsequently criticized as cursory and unscientific by Remsen (2005). Instead of miring the discourse in more opinion, the purpose of this commentary is to briefly review new evidence, published after our original analysis, to establish how

well that first-pass analysis fares in light of much more detailed evidence. We then reflect on how the process of assembling regional “avifaunas” might be optimized.

REVIEW OF RECENT EVIDENCE REGARDING SPECIES LIMITS IN MEXICAN BIRDS

Our original taxonomic revision covered all Mexican birds and recommended emendations to species limits in 135 biological species (*sensu* AOU 1998), recognizing an additional 198 species taxa in the country. Here, we have reviewed literature published after 2003 (when we concluded our original studies) for treatment of any of the 135 complexes that we addressed (see appendix in Navarro-Sigüenza and Peterson 2004) using molecular systematic approaches (note that we include one earlier publication [Kirchman et al. 2000] of which we had been unaware). We included only studies that sampled multiple populations of the taxon in question that span multiple evolutionary species from our recommendations; we excluded all species for which molecular evidence was published at the time of our previous analyses (Navarro-Sigüenza and Peterson 2004). We evaluated phylogenetic trees or haplotype networks presented in each study to establish (1) whether our overall portrayal of species limits within the complex had been correct, (2) whether we had missed any distinct forms, and (3) whether each evolutionary species was indeed distinct from other such forms. The latter question was answered in terms of strong differentiation and reciprocal monophyly versus genetic differentiation, which could be incomplete and might not, as yet, include establishment of reciprocal monophyly.

We found recent studies treating 28 of the 135 biological species and 72 of the 323 evolutionary species treated in our previous summary (see Appendix). Our portrayal of species limits in 22 of these 28 complexes was completely correct. For the other six complexes, relationships were not as we had hypothesized—for

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example, Kirchner et al. (2000) showed that northern populations of Cave Swallow (*Petrochelidon fulva*) are not a lineage distinct from Caribbean and Yucatan Peninsula populations, but rather that they are nested within those populations phylogenetically, contrary to our hypothesis. On the other hand, and most dramatically, for Common Bush-Tanager (*Chlorospingus ophthalmicus*), our hypothesis of five differentiated forms in Mexico was confirmed fully by further in-depth analyses (Bonaccorso et al. 2008). In six cases, our proposed “splits” were not sufficient, and additional distinct lineages were revealed by detailed molecular study (e.g., Mexican Jay [*Aphelocoma ultramarina*]; e.g., McCormack et al. 2008). Eight of nine biological species complexes (treated in less detail in our original analysis; tables 1 and 2 in Navarro-Sigüenza and Peterson 2004) that included splits outside Mexico or taxa for which we were unable to make conclusive recommendations were confirmed in subsequent analyses (Appendix).

At the level of individually proposed evolutionary species, of the 72 for which recent molecular evidence was available, 41 were confirmed by those studies as strongly differentiated and reciprocally monophyletic, as compared with related taxa—for example, Wagler’s Toucanet (*Aulacorhynchus wagleri*) of western Mexico was confirmed as differing by 3.68% in mitochondrial DNA sequence composition from the more broadly distributed Emerald Toucanet (*A. prasinus*), in addition to numerous phenotypic differences (Puebla-Olivares et al. 2008). More broadly, 52 of the 72 species were differentiated from related taxa, albeit not always with reciprocal monophyly (e.g., the Baja California Sur form of Acorn Woodpecker (*Melanerpes formicivorus*; Honey-Escandón et al. 2008). Of the 19 additional evolutionary species proposed in less detail in our original publication (tables 1 and 2 in Navarro-Sigüenza and Peterson 2004), 17 were amply supported as distinct (e.g., Brown Schiffornis [*Schiffornis veraepacis*; Nyári 2007] and Ridgway’s Pygmy-Owl [*Glaucidium ridgwayi*; Proudfoot et al. 2006]).

IMPLICATIONS FOR ASSEMBLY OF MODERN REGIONAL BIRD TAXONOMIES

The idea of broad reviews and regional treatments, although originally very common (Ridgway 1880, Hellmayr 1925, Peters 1931), has certainly passed from its original grace. Indeed, our earlier analysis (Navarro-Sigüenza and Peterson 2004) was criticized for its “lack of rigor . . . which recalls the heyday of the antiquated ‘Peters Checklist’ method” (Remsen 2005). More “modern” approaches depend on detailed analyses of molecular and phenotypic characters published on a case-by-case basis.

The conservative approach advocated by the AOU checklist committees, although less likely to result in incorrect decisions based on preliminary or incomplete evidence, has serious drawbacks. Species concepts themselves evolve (e.g., compare the treatments of Baltimore Oriole [*Icterus galbula*] in the 1983 and 1998 editions of the North American *Check-list*), and new species concepts are introduced (Zink and McKittrick 1995). Check-lists assembled by the “time-honored methods” (AOU 1998) respond only very slowly to these shifts, and—worse still—their response is uneven: for example, the Least Pygmy-Owl (*Glaucidium minutissimum*) complex has been split into three species in North America and several more in South America in recent years, thanks to

recent detailed analyses (Howell and Robbins 1995, Robbins and Howell 1995), yet related taxa (e.g., *Megascops* spp.) remain little examined and certainly undersplit. As such, inconsistency and uneven treatment come to permeate such check-lists.

We argue that the “antiquated” methods of taxonomic reviews and regional treatments are not as useless and outdated as has been suggested. Our admittedly preliminary and incomplete revision of Mexican bird taxonomy based on the evolutionary species concept was correct in 52 of 72 evolutionary species-level recommendations and 22 of 28 biological species-level recommendations, with only a few genuine failures (e.g., Cave Swallow, Red-winged Blackbird [*Agelaius phoeniceus*], and Margaret’s Hummingbird *Lampornis “margaritae”*), and produced a taxonomic arrangement that is much more consistent across taxa, and closer to the biological reality of bird diversity in the region, than any earlier check-list. Current national-scale efforts to prioritize biodiversity conservation in Mexico being developed by the Comisión Nacional para el Uso y Conocimiento de la Biodiversidad require such a consistent taxonomic base for rigorous science and decision making. Thus, we challenge our colleagues who are attempting to assemble such check-lists to take on the task at the broadest of levels—to produce region-wide reviews and consistent treatments of all taxa, regardless of the varying amounts of evidence available by which to judge. When the available information is truly minimal and insufficient to permit conclusions, a category of “uncertain status” should be allowed—authority lists can become more authoritative by acknowledging the gaps in their information.

ACKNOWLEDGMENTS

We thank our many colleagues in the field of systematic ornithology for years of fruitful debate and discussion of these ideas. Financial support for this study was provided via a grant from the Secretaría del Medio Ambiente y Recursos Naturales and the Consejo Nacional de Ciencia y Tecnología (SEMARNAT-CONACYT Sectorial Fund, C01-0265) for developing systematic studies of Mexican birds.

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Received 26 January 2009, accepted 7 April 2009

Associate Editor: R. M. Zink

APPENDIX. Summary of studies that have used molecular characters to treat biological species complexes included in a recent revision of species limits in Mexican birds (Navarro-Sigüenza and Peterson 2004). "Complex right" indicates that the entire biological species complex was treated in a way consistent with the molecular results. "Missed a species" indicates that a differentiated form was not detected in the phenotypic studies. "Species distinct" indicates that the particular evolutionary species form was reciprocally monophyletic with respect to other such groups. "Species at least differentiated" indicates that the evolutionary species was differentiated, although perhaps not dramatically, or perhaps without reciprocal monophyly. Abbreviations: mtDNA = mitochondrial DNA, microsat = microsatellites, AFLPs = amplified fragment length polymorphisms, nucDNA = nuclear DNA, 1 = correct, 0 = incorrect, and + = partially correct (see notes in far right column).

Species group See appendix in Navarro-Sigüenza and Peterson (2004):	Proposed species (Navarro-Sigüenza and Peterson 2004)	Complex right	Missed a species	Species distinct	Species at least differentiated	Genes	References and notes
<i>Agelaius phoeniceus</i>	<i>gubernator</i> <i>phoeniceus</i> <i>graysoni</i>	0	0	0	0	mtDNA mtDNA mtDNA	Form <i>gubernator</i> not differentiated (Barker et al. 2008) Missed the differentiated population of the Yucatan peninsula (B. E. Hernández et al. unpubl. data)
<i>Amazonia rutila</i>	<i>rutila</i> <i>villadai</i> <i>viridifrons</i> <i>wagneri</i> <i>oratrix</i> <i>tresmariae</i> <i>californica</i> <i>sumichrasti</i> <i>woodhouseii</i> <i>potosina</i>	1	0	1	1	mtDNA	G. García-Deras et al. unpubl. data
<i>A. viridifrons</i>	<i>rutila</i> <i>villadai</i> <i>viridifrons</i> <i>wagneri</i> <i>oratrix</i> <i>tresmariae</i> <i>californica</i> <i>sumichrasti</i> <i>woodhouseii</i> <i>potosina</i>	1	0	0	1	mtDNA	C. García-Deras et al. unpubl. data
<i>Amazona oratrix</i>	<i>rutila</i> <i>villadai</i> <i>viridifrons</i> <i>wagneri</i> <i>oratrix</i> <i>tresmariae</i> <i>californica</i> <i>sumichrasti</i> <i>woodhouseii</i> <i>potosina</i>	1	0	0	1	mtDNA	Eberhard and Bermingham 2004
<i>Apelocoma californica</i>	<i>rutila</i> <i>villadai</i> <i>viridifrons</i> <i>wagneri</i> <i>oratrix</i> <i>tresmariae</i> <i>californica</i> <i>sumichrasti</i> <i>woodhouseii</i> <i>potosina</i>	1	0	1	1	mtDNA	Delaney et al. 2008
<i>A. ultramarina</i>	<i>rutila</i> <i>villadai</i> <i>viridifrons</i> <i>wagneri</i> <i>oratrix</i> <i>tresmariae</i> <i>californica</i> <i>sumichrasti</i> <i>woodhouseii</i> <i>potosina</i>	+	1	1	1	mtDNA	Missed a differentiated form in the southern Sierra Madre Oriental (McCormack et al. 2008)
<i>Aulacorhynchus prasinus</i>	<i>ultramarina</i> <i>wollweberi</i> <i>prasinus</i> <i>wagleri</i> <i>canadensis</i>	1	0	1	1	mtDNA	Puebla-Olivares et al. 2008
<i>Branta canadensis</i>	<i>leucopareia</i> <i>minima</i> <i>elegans</i>	+	0	1	1	mtDNA	Forms <i>leucopareia</i> and <i>minima</i> not differentiated from <i>hutchinsii</i> (Scribner et al. 2003)
<i>Buteo lineatus</i>	<i>leucopareia</i> <i>minima</i> <i>elegans</i>	1	0	0	1	mtDNA, microsat	Hull et al. 2008
<i>Campylopterus curvipennis</i>	<i>lineatus</i> <i>curvipennis</i> <i>pampa</i> <i>capistratus</i> <i>humilis</i> <i>rufinucha</i> <i>albifrons</i> <i>dwighti</i> <i>ophthalmicus</i> <i>postocularis</i> <i>wetmorei</i>	1	0	0	1	mtDNA	I. Sarmiento et al. unpubl. data
<i>Campylorhynchus rufinucha</i>	<i>lineatus</i> <i>curvipennis</i> <i>pampa</i> <i>capistratus</i> <i>humilis</i> <i>rufinucha</i> <i>albifrons</i> <i>dwighti</i> <i>ophthalmicus</i> <i>postocularis</i> <i>wetmorei</i>	1	0	1	1	mtDNA	Vázquez-Miranda et al. 2009
<i>Chlorospingus ophthalmicus</i>	<i>lineatus</i> <i>curvipennis</i> <i>pampa</i> <i>capistratus</i> <i>humilis</i> <i>rufinucha</i> <i>albifrons</i> <i>dwighti</i> <i>ophthalmicus</i> <i>postocularis</i> <i>wetmorei</i>	1	0	1	1	mtDNA	Bonaccorso et al. 2008

(continued)

APPENDIX. Continued.

Species group See appendix in Navarro- Sigüenza and Peterson (2004):	Proposed species (Navarro-Sigüenza and Peterson 2004)	Complex right	Missed a species	Species distinct	Species at least differentiated	Genes	References and notes
<i>Coereba flaveola</i>	<i>caboti</i>	1	0	1	1	mtDNA, nucDNA	Bellemain et al. 2008
<i>Cyananthus latirostris</i>	<i>mexicana</i>	1	0	1	1	mtDNA	García-Deras et al. 2008
	<i>latirostris</i>	+	1	+	+	mtDNA	Missed form <i>nigrifrons</i> as differentiated; <i>coronata</i> and <i>auduboni</i> not differentiated (Milá et al. 2007b)
<i>Dendroica coronata</i>	<i>coronata</i>	0	0	1	1	mtDNA	Forms <i>pustulatus</i> and <i>sclateri</i> not differentiated (Cortés-Rodríguez et al. 2008a)
<i>Icterus pustulatus</i>	<i>goldmani</i>	1	0	0	+	mtDNA	Baker et al. 2003
	<i>graysonii</i>	0	0	1	1	mtDNA	No differentiation among forms (Milá et al. 2007a)
<i>I. spurius</i>	<i>pustulatus</i>	1	0	0	+	mtDNA	
	<i>sclateri</i>	0	0	0	+	mtDNA	
<i>Junco hyemalis</i>	<i>fuertesii</i>	1	0	0	1	mtDNA	
	<i>spurius</i>	0	0	0	1	mtDNA, AFLPs	
<i>J. phaeonotus</i>	<i>caniceps</i>	0	0	0	0	mtDNA	
	<i>hyemalis</i>	1	0	0	0	mtDNA	
<i>Lampornis amethystinus</i>	<i>oreganus</i>	1	0	0	0	mtDNA	
	<i>alticola</i>	0	0	1	1	mtDNA	Milá et al. 2006
<i>Melanerpes aurifrons</i>	<i>phaeonotus</i>	1	0	1	1	mtDNA	Form <i>margaritae</i> not different from <i>amethystinus</i> (Cortés-Rodríguez et al. 2008b)
	<i>amethystinus</i>	0	0	+	+	mtDNA	
<i>M. formicivorus</i>	<i>margaritae</i>	+	0	+	+	mtDNA	Forms <i>grateloupensis</i> and <i>polygrammus</i> not differentiated from <i>santacruzii</i> (García-Trejo et al. 2009)
	<i>salvini</i>	+	0	1	1	mtDNA	
<i>M. formicivorus</i>	<i>aurifrons</i>	+	0	1	1	mtDNA	
	<i>grateloupensis</i>	+	0	+	+	mtDNA	Forms <i>bairdi</i> and <i>formicivorus</i> not differentiated (Honey-Escandón et al. 2008)
<i>Momotus momota</i>	<i>polygrammus</i>	+	0	+	+	mtDNA	
	<i>santacruzii</i>	+	0	+	+	mtDNA	
<i>Passerculus sandwichensis</i>	<i>angustifrons</i>	+	1	0	1	mtDNA	
	<i>coeruliceps</i>	1	0	0	1	mtDNA	C. Witt et al. unpubl. data
<i>Petrochelidon fulva</i>	<i>lessonii</i>	0	0	1	1	mtDNA	Forms <i>rostratus</i> and <i>beldingi</i> not differentiated (Zink et al. 2005)
	<i>beldingi</i>	0	0	+	+	mtDNA	
<i>Petrochelidon fulva</i>	<i>rostratus</i>	0	0	+	+	mtDNA, microsat	Forms <i>pelodoma</i> and <i>fulva</i> not differentiated (Kirchman et al. 2000)
	<i>sandwichensis</i>	0	0	1	1	mtDNA, microsat	
<i>Petrochelidon fulva</i>	<i>fulva</i>	0	0	0	0	mtDNA, microsat	
	<i>pelodoma</i>	0	0	0	0	mtDNA, microsat	

(continued)

APPENDIX. Continued.

Species group See appendix in Navarro-Sigüenza and Peterson (2004):	Proposed species (Navarro-Sigüenza and Peterson 2004)	Complex right	Missed a species	Species distinct	Species at least differentiated	Genes	References and notes
<i>Stelgidopteryx serripennis</i>	<i>ridgwayi</i> <i>serripennis</i> <i>curvirostre</i>	1	0	1	1	mtDNA	Babin 2005
<i>Toxostoma curvirostre</i>	<i>palmeri</i>	+	1	1	1	mtDNA	Missed the differentiated population in Oaxaca (Rojas-Soto et al. 2007)
See appendix and table 1 in Navarro-Sigüenza and Peterson (2004):	<i>apertus</i>	1	1	1	1	mtDNA	Missed differentiated population in Guerrero (Navarro-Sigüenza et al. 2008)
<i>Buarremon brunneinucha</i>	<i>brunneinucha</i> <i>macrourus</i> sp. nov.			+	+		
See table 1 in Navarro-Sigüenza and Peterson (2004):	<i>paludicola</i> <i>palustris</i> <i>intermedius</i> <i>miniatus</i>	1	0	1	1	mtDNA	Hebert et al. 2004
<i>Cistothorus palustris</i>		1	0	1	1	mtDNA	Pérez-Ernán 2005
<i>Myioborus miniatus</i>		1	0	1	1	mtDNA	
See table 2 in Navarro-Sigüenza and Peterson (2004):	<i>brasilianum</i> <i>ridgwayi</i> <i>leucosticta</i> <i>mexicana</i> <i>assimilis</i> <i>oleagineus</i> <i>magister</i> <i>tyrannulus</i> <i>turdinus</i> <i>veraepacis</i> <i>collaris</i> <i>puella</i>	1	0	1	1	mtDNA	Proudfoot et al. 2006
<i>Glaucidium brasilianum</i>		1	0	1	1	mtDNA	Dingle et al. 2006
<i>Henicorhina leucosticta</i>		1	0	1	1	mtDNA	Miller et al. 2008
<i>Mionectes oleagineus</i>		1	0	1	1	mtDNA	Joseph et al. 2004
<i>Myiarchus tyrannulus</i>		1	0	1	1	mtDNA	Nyári 2007
<i>Schiffornis turdinus</i>		1	0	1	1	mtDNA	DaCosta and Klicka 2008
<i>Trogon collaris</i>		1	0	1	1	mtDNA	