



## Geographic variation and phylogenetic relationships of *Myiopagis olallai* (Aves: Passeriformes; Tyrannidae), with the description of two new taxa from the Northern Andes

ANDRÉS M. CUERVO<sup>1,2</sup>, F. GARY STILES<sup>3</sup>, MIGUEL LENTINO<sup>4</sup>, ROBB T. BRUMFIELD<sup>1</sup> & ELIZABETH P. DERRYBERRY<sup>2</sup>

<sup>1</sup>Department of Biological Sciences and Museum of Natural Science, Louisiana State University, Baton Rouge, LA 70803, USA.

E-mail: [amcuervo@gmail.com](mailto:amcuervo@gmail.com)

<sup>2</sup>Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA 70118, USA

<sup>3</sup>Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia

<sup>4</sup>Colección Ornitológica Phelps, Caracas, Venezuela.

### Abstract

Geographic variation in vocalizations, morphology and plumage patterns in New World flycatchers is little understood, particularly in rare species with disjunct distributions. We discovered a distinct new flycatcher of the genus *Myiopagis* from cloud forests of the northern Central Andes in Antioquia, Colombia. Comparisons of vocalizations and external morphology, and molecular phylogenetic analyses, demonstrate that the “Antioquia *Myiopagis*” is a unique lineage of the *M. caniceps-olallai* group. We show that three specimens collected in 1940–1951 from cloud forests of Serranía de Perijá in Venezuela, and traditionally assigned to *M. caniceps*, represent another distinct taxon that is closer to the “Antioquia *Myiopagis*” and *M. olallai*. Both new taxa, from Antioquia and Perijá, are described as subspecies of *M. olallai*. We present a phylogenetic hypothesis for the *M. caniceps-olallai* group, in which *M. olallai* and the “Antioquia *Myiopagis*” are phylogenetically nested within the polytypic *M. caniceps*, which consists of at least four distinct lineages, indicating that species diversity in this group could be underestimated.

**Key words:** Andes, Colombia, cloud forest, Foothill Elaenia, Serranía de Perijá, species tree, Venezuela, vocalizations

### Introduction

The suboscine passerines of the New World have long presented challenges for taxonomy and systematics because traditional morphological assessments are often misleading with regard to evolutionary relationships. Morphology, plumage patterns and coloration can vary subtly across species or be highly homoplasious in this diverse clade (e.g., Birdsley 2002; Ohlson *et al.* 2009; Hosner & Moyle 2012). The innate nature of vocalizations in nearly all suboscines (Kroodsma 1984; Kroodsma & Konishi 1991; Saranathan *et al.* 2007, Touchton *et al.* 2014) has been instrumental in redefining species limits (Isler *et al.* 1998; Renssen 2005), especially when combined with molecular phylogenetic data (Isler *et al.* 2012). The concordance between vocal and phylogenetic variation to elucidate species boundaries has demonstrated that diversity of Neotropical suboscines has been greatly underestimated in the past. Although the most striking example of this is found in the family Rhinocryptidae, in which the number of independent lineages and recognized biological species has increased fourfold in the past two decades (Krabbe & Schulenberg 2003; Cuervo *et al.* 2005; Mata *et al.* 2009; Krabbe & Cadena 2010; Maurício *et al.* 2014), numerous hitherto undetected species have been found in other suboscine lineages as well, e.g., Thamnophilidae (Chaves *et al.* 2010; Whitney *et al.* 2013), Grallariidae (Carantón-Ayala & Certuche-Cubillos 2010; Carneiro *et al.* 2012), Tityridae (Nyári 2007) and Tyrannidae (Rheindt *et al.* 2013; Zimmer *et al.* 2013). Often cryptic species are first detected by their vocalizations and then confirmed through more detailed examination of specimens and subsequent phylogenetic analyses. These discoveries were largely due to increasing

All field observations of *M. o. coopmansii* involved birds in mixed-species flocks foraging high in the tall canopy of primary cloud forests. The northern end of the Central Cordillera is a biogeographic hotspot where lineages of multiple biogeographic origins occur and endemic bird species like *Lipaugus weberi* are threatened (Cuervo *et al.* 2008a). The range of the newly discovered *M. o. coopmansii* might include the least explored adjacent areas of the northernmost Western Cordillera, which have suitable habitat for this taxon within its known elevational range (Fig. 10). In Serranía de Perijá, *M. o. incognita* is only known from the type series collected on the eastern slope in Venezuela, where a national park protects continuous tracts of cloud forest habitat. This bird has not been recorded since 1951; recent field work in the Colombian slope concentrated on elevations above the known records of this taxon (López-O. *et al.* 2014). Although it may well extend to the Colombian side of Perijá, vast deforestation along the west slope has left only very small habitat patches. The habitat is cleared below 1,600 m in most areas (López-O. *et al.* 2014). This enigmatic taxon might also occur in Sierra de Ocaña and the Sierra Nevada de Santa Marta.

The elevational range of *M. olallai* in Ecuador and Peru is 900–1,500 m (Coopmans & Krabbe 2000; Schulenberg & Kirwan 2012), whereas *M. o. coopmansii* occurs at slightly higher elevations, from 1,300 up to 1,850 m. The three specimens of *M. o. incognita* were taken between 1,100 and 1,200 m in Perijá. All known records of *M. olallai* occur entirely above the upper elevational limit of the distantly related *M. caniceps cinerea* (<700 m; Schulenberg & Kirwan 2012), the only *caniceps* taxon with which *M. olallai* could overlap along the Amazonian slopes from Ecuador through central Peru. The sister clade of *M. olallai* ranges as close as southern Peru (*M. c.* aff. *caniceps*) in the Amazonian lowlands and foothills of Puno, but *M. olallai* has not been recorded that far south. *Myiopagis olallai* may be one example of adaptation by an Atlantic forest ancestor to novel Andean environments, and rapid plumage evolution in geographic isolation.

## Acknowledgments

We thank fellow museum curators and collectors for facilitating our study: N. Rice (ANSP), M. Shanley, P. Sweet, and T. J. Trombone (AMNH), T. Valqui (CORBIDI), M. Salcedo (Pons), G. Mayr (SMF), J. McCormack and J. Maley (MLZ), G. R. Graves, B. K. Schmidt and C. M. Milensky (USNM), M. Mueller and R. Diesener (ZSM). E. Bonaccorso contributed photos and data of the *M. olallai* type series at MECN. We thank M. G. Harvey (MGH), A. Spencer, T. Brooks, N. Athanas, D. Geale, W.-P. Vellinga, S. L. Hilty, C. M. Wagner, R. Ahlman, C. Kinschots, V. Mouret, S. Sommazzi, and T. Seimola for discussion or for sharing their observations. For company and help during fieldwork we thank D. Bermúdez, N. Gutiérrez-Pinto, J. E. Avendaño, J. P. López, and J. Gutiérrez. This study would not have been possible without the hospitality of the people of Amalfi and Anorí, and of J. Tello in New York. CORANTIOQUIA (especially J. L. Toro and J. C. Restrepo), and other national authorities have supported us in various ways over the years. Funding was provided in part by CORANTIOQUIA, IAvH, Idea Wild, Lewis and Clark Exploration Fund, Society of Systematic Biologists, Society of Integrative and Comparative Biology, F. M. Chapman Memorial Fund, American Ornithologists' Union, Wilson Ornithological Society, by NSF grants DDIG DEB-0910285 and DEB-1146423. Special thanks go to C. E. Braun and the Wilson Ornithological Society for permission to reprint copyrighted material, M. Álvarez at the Banco de Sonidos Ambientales (IAvH-BSA), and G. Budney at the Macaulay Library, Cornell Lab of Ornithology (ML) for a sound equipment loan. AMC especially thanks feedback from J. E. Avendaño, B. Whitney, D. F. Lane, and the late P. Coopmans. The manuscript benefited from comments by G. Bravo, T. Chesser, G. R. Graves, N. Krabbe, M. Robbins, and B. Whitney.

## Literature cited

- Álvarez-Alonso, J. & Whitney, B.M. (2001) A new *Zimmerius* tyrannulet (Aves: Tyrannidae) from white sand forests of northern Amazonian Peru. *Wilson Bulletin*, 113, 1–9.  
[http://dx.doi.org/10.1676/0043-5643\(2001\)113\[0001:ANZTAT\]2.0.CO;2](http://dx.doi.org/10.1676/0043-5643(2001)113[0001:ANZTAT]2.0.CO;2)
- Arctander, P. (1995) Comparison of a mitochondrial gene and a corresponding nuclear pseudogene. *Proceedings of the Royal Society of London B*, 262, 13–19.  
<http://dx.doi.org/10.1098/rspb.1995.0170>

- Badyaev, A.V. & Hill, G.E. (2003) Avian sexual dichromatism in relation to phylogeny and ecology. *Annual Review of Ecology, Evolution, and Systematics*, 34, 27–49.  
<http://dx.doi.org/10.1146/annurev.ecolsys.34.011802.132441>
- Birdsley, J.S. (2002) Phylogeny of the tyrant flycatchers (Tyrannidae) based on morphology and behavior. *The Auk*, 119, 715–734.  
[http://dx.doi.org/10.1642/0004-8038\(2002\)119\[0715:POTTFT\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2002)119[0715:POTTFT]2.0.CO;2)
- Brumfield, R.T., Tello, J.G., Cheviron, Z.A., Carling, M.D., Crochet, N. & Rosenberg, K.V. (2007) Phylogenetic conservatism and antiquity of a tropical specialization: Army-ant-following in the typical antbirds (Thamnophilidae). *Molecular Phylogenetics and Evolution*, 45, 1–13.  
<http://dx.doi.org/10.1016/j.ympev.2007.07.019>
- Carantón-Ayala, D. & Certuche-Cubillos, K. (2010) A new species of antpitta (Grallariidae: *Grallaria*) from the northern sector of the Western Andes of Colombia. *Ornitología Colombiana*, 9, 56–70.
- Carneiro, L.S., Gonzaga, L.P., Rêgo, P.S., Sampaio, I., Schneider, H. & Aleixo, A. (2012) Systematic revision of the Spotted Antpitta (*Hylopezus macularius*: Grallariidae), with description of a cryptic new species from Brazilian Amazonia. *The Auk*, 129, 338–351.  
<http://dx.doi.org/10.1525/auk.2012.11157>
- Chakrabarty, P. (2010) Genotypes: a concept to help integrate molecular phylogenetics and taxonomy. *Zootaxa*, 2632, 67–68.
- Chaves, J.C., Cuervo, A.M., Miller, M.J. & Cadena, C.D. (2010) Revising species limits in a group of *Myrmeciza* antbirds reveals a cryptic species within *M. laemosticta* (Thamnophilidae). *The Condor*, 112, 718–730.  
<http://dx.doi.org/10.1525/cond.2010.100098>
- Coopmans, P. & Krabbe, N. (2000) A new species of flycatcher (Tyrannidae: *Myiopagis*) from eastern Ecuador and eastern Peru. *Wilson Bulletin*, 112, 305–312.  
[http://dx.doi.org/10.1676/0043-5643\(2000\)112\[0305:ansoft\]2.0.co;2](http://dx.doi.org/10.1676/0043-5643(2000)112[0305:ansoft]2.0.co;2)
- Cuervo, A.M., Cadena, C.D., Krabbe, N. & Renjifo, L.M. (2005) *Scytalopus stilesi*, a new species of tapaculo (Rhinocryptidae) from the Cordillera Central of Colombia. *The Auk*, 122, 445–463.  
[http://dx.doi.org/10.1642/0004-8038\(2005\)122\[0445:ssanso\]2.0.co;2](http://dx.doi.org/10.1642/0004-8038(2005)122[0445:ssanso]2.0.co;2)
- Cuervo, A.M., Pulgarín, P.C. & Calderón, D. (2008a) New distributional bird data from the Cordillera Central of the Colombian Andes, with implications for the biogeography of northwestern South America. *The Condor*, 110, 526–537.  
<http://dx.doi.org/10.1525/cond.2008.8555>
- Cuervo, A.M., Pulgarín, P.C., Calderón-F, D., Ochoa-Quintero, J.M., Delgado-V., C.A., Palacio, J.A., Botero, J.M. & Múnera, W.A. (2008b) Avifauna of the northern Cordillera Central of the Andes, Colombia. *Ornitología Neotropical*, 19, 495–515.
- Drummond, A.J., Ashton, B., Buxton, S., Cheung, M., Cooper, A., Duran, C., Field, M., Heled, J., Kearse, M., Markowitz, S., Moir, R., Stones-Havas, S., Sturrock, S., Thierer, T. & Wilson, A. (2011) Geneious. Geneious v5.4. (2011) Available from: <http://www.geneious.com/> (accessed 24 September 2014)
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.  
<http://dx.doi.org/10.1093/nar/gkh340>
- Fitzpatrick, J.W. (2004) Family Tyrannidae (Tyrant-Flycatchers). In: del Hoyo, J., Elliot, A. & Christie, D.A. (Eds.) *Handbook of the Birds of the World. Vol. 9*. Lynx Edicions, Barcelona.
- Ginés, H., Avelado-Hostos, R., Pons, A.R., Yépez, G. & Muñoz-Tebar, R. (1953) Lista y comentario de las aves colectadas en la región. In: Sociedad de Ciencias Naturales La Salle (Ed.), *La región de Perijá y sus habitantes*. Editorial Sucre, Caracas, Venezuela, pp. 225–277.
- Hackett, S.J. (1996) Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). *Molecular Phylogenetics and Evolution*, 5, 368–382.  
<http://dx.doi.org/10.1006/mpev.1996.0032>
- Hellmayr, C.E. (1904) Mr. C. E. Hellmayr exhibited the types of five South American birds, which he described as follows: *Serpophaga parambae*, n. sp. *Bulletin of the British Ornithologists & Apos Club*, 14, 54–55.
- Hellmayr, C.E. (1911) A contribution to the ornithology of western Colombia. *Proceedings of the Zoological Society of London*, 81, 1084–1213.
- Hilty, S.L. (2003) *Birds of Venezuela*. Princeton University Press, New Jersey, NJ, 183 pp.
- Hosner, P.A. & Moyle, R.G. (2012) A molecular phylogeny of black-tyrants (Tyrannidae: *Knipolegus*) reveals strong geographic patterns and homoplasy in plumage and display behavior. *The Auk*, 129, 156–167.  
<http://dx.doi.org/10.1525/auk.2012.11101>
- Isler, M.L., Cuervo, A.M., Bravo, G.A. & Brumfield, R.T. (2012) An integrative approach to species-level systematics reveals the depth of diversification in an Andean thamnophilid, the Long-tailed Antbird. *The Condor*, 114, 571–583.  
<http://dx.doi.org/10.1525/cond.2012.120012>
- Isler, M.L., Isler, P.R. & Whitney, B.M. (1998) Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae). *The Auk*, 115, 577–590.  
<http://dx.doi.org/10.2307/4089407>
- Johnson, K.P. & Sorenson, M.D. (1998) Comparing molecular evolution in two mitochondrial protein coding genes (cytochrome b and ND2) in the dabbling ducks (Tribe Anatini). *Molecular Phylogenetics and Evolution*, 10, 82–94.

- <http://dx.doi.org/10.1006/mpev.1997.0481>
- Kimball, R.T., Braun, E.L., Barker, F.K., Bowie, R.C.K., Braun, M.J., Chojnowski, J.L., Hackett, S.J., Han, K.-L., Harshman, J., Heimer-Torres, V., Holznagel, W., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Reddy, S., Sheldon, F.H., Smith, J.V., Witt, C.C. & Yuri, T. (2009) A well-tested set of primers to amplify regions spread across the avian genome. *Molecular Phylogenetics and Evolution*, 50, 654–660.  
<http://dx.doi.org/10.1016/j.ympev.2008.11.018>
- Krabbe, N. (2008) Birding Ecuador: A tribute to Paul Coopmans *Cotinga*, 29, 12–14.
- Krabbe, N. & Cadena, C.D. (2010) A taxonomic revision of the Paramo Tapaculo *Scytalopus canus* Chapman (Aves: Rhinocryptidae), with description of a new subspecies from Ecuador and Peru. *Zootaxa*, 2354, 56–66.
- Krabbe, N. & Nilsson, J. (2007) Birds of Ecuador 1.19. Bird Songs International, Westernieland, The Netherlands.
- Krabbe, N. & Schulenberg, T.S. (2003) Family Rhinocryptidae (Tapaculos). In: del Hoyo, J., Elliot, A. & Christie, D.A. (Eds.), *Handbook of the Birds of the World, vol. 8, Broadbills to Tapaculos*. Lynx Edicions, Barcelona, pp. 748–787.
- Kroodsma, D.E. (1984) Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. *The Auk*, 101, 13–24.  
<http://www.jstor.org/stable/4086218>
- Kroodsma, D.E. & Konishi, M. (1991) A suboscine bird (Eastern Phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. *Animal Behaviour*, 42, 477–487.  
[http://dx.doi.org/10.1016/S0003-3472\(05\)80047-8](http://dx.doi.org/10.1016/S0003-3472(05)80047-8)
- Lentino, M., Sharpe, C., Pérez-Emán, J.L. & Carreño, Y. (2004) *Aves registradas en la Serranía de Lajas, Serranía de Valledupar, Sierra de Perijá, Estado Zulia, en Abril del 2004*. Technical report. Colección Ornitológica Phelps, Caracas, Venezuela, 25 pp.
- Liu, L. (2008) BEST: Bayesian estimation of species trees under the coalescent model. *Bioinformatics*, 24, 2542–2543.  
<http://dx.doi.org/10.1093/bioinformatics/btn484>
- López-O., J.P., Avendaño, J.E., Gutiérrez-Pinto, N. & Cuervo, A.M. (2014) The birds of Serranía de Perijá: The northernmost avifauna of the Andes. *Ornitología Colombiana*, 14. [in press]
- Lysinger, M., Moore, J.V., Krabbe, N., Coopmans, P., Lane, D.F., Navarrete, L., Nilsson, J. & Ridgely, R.S. (2005) The birds of eastern Ecuador: The foothills and lower subtropics. John V. Moore Nature Recordings, San José, CA, U.S.A. [CD]
- Mata, H., Fontana, C.S., Mauricio, G.N., Bornschein, M.R., de Vasconcelos, M.F. & Bonatto, S.L. (2009) Molecular phylogeny and biogeography of the eastern tapaculos (Aves: Rhinocryptidae: *Scytalopus*, *Eleoscytalopus*): Cryptic diversification in Brazilian Atlantic Forest. *Molecular Phylogenetics and Evolution*, 53, 450–462.  
<http://dx.doi.org/10.1016/j.ympev.2009.07.017>
- Maurício, G.N., Belmonte-Lopes, R., Pacheco, J.F., Silveira, L.F., Whitney, B.M. & Bornschein, M.R. (2014) Taxonomy of “Mouse-colored Tapaculos” (II): An endangered new species from the montane Atlantic Forest of southern Bahia, Brazil (Passeriformes: Rhinocryptidae: *Scytalopus*). *The Auk*, 131, 643–659.  
<http://dx.doi.org/10.1642/auk-14-16.1>
- Mayr, E. (1942) *Systematics and the origin of species*. Columbia University Press, New York, NY, 120 pp.
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, LA, pp. 1–8.  
<http://dx.doi.org/10.1109/gce.2010.5676129>
- Nyári, Á.S. (2007) Phylogeographic patterns, molecular and vocal differentiation, and species limits in *Schiffornis turdina* (Aves). *Molecular Phylogenetics and Evolution*, 44, 154–164.  
<http://dx.doi.org/10.1016/j.ympev.2007.02.020>
- Nylander, J.A.A. (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University
- Nylander, J.A.A., Wilgenbusch, J.C., Warren, D.L. & Swofford, D.L. (2008) AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics*, 24, 581–583.  
<http://dx.doi.org/10.1093/bioinformatics/btm388>
- Ohlson, J.I., Fjeldså, J. & Ericson, P.G.P. (2009) A new genus for three species of tyrant flycatchers (Passeriformes: Tyrannidae), formerly placed in *Myiophobus*. *Zootaxa*, 2290, 36–40.
- Parker, T.A. (1991) On the use of tape recorders in avifaunal surveys. *The Auk*, 108, 443–444.
- Pelzeln, A.v. (1868) *Zur Ornithologie Brasiliens, Resultate von Johann Natterer Reisen in den Jahren 1817 bis 1835*. A. Pichler's Witwe & Sohn, Wien, 18 pp.  
<http://dx.doi.org/10.5962/bhl.title.3654>
- Phelps, W.H. (1943) Las Aves de Perijá. *Boletín de la Sociedad Venezolana de Ciencias Naturales*, 8, 265–338.
- Pitman, N., Moskovits, D.K., Alverson, W.S. & Borman A., R. (2002) *Ecuador: Serranías Cofán-Bermejo, Sinangoe*. The Field Museum, Chicago, IL, USA., 226 pp.
- Rambaut, A. & Drummond, A.J. (2007) Tracer v1.4.
- Remsen, J.V. Jr. (2005) Pattern, process, and rigor meet classification. *The Auk*, 122, 403–413.  
[http://dx.doi.org/10.1642/0004-8038\(2005\)122\[0403:PPARMC\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2005)122[0403:PPARMC]2.0.CO;2)
- Remsen, J.V. Jr. (2010) Subspecies as a meaningful taxonomic rank in avian classification. *Ornithological Monographs*, 67, 62–78.  
<http://dx.doi.org/10.1525/om.2010.67.1.62>

- Restall, R., Rodner, C. & Lentino, M. (2007) *Birds of Northern South America: An Identification Guide. Vol. 2. Plates and Maps*. Yale University Press, New Haven, 656 pp.
- Rheindt, F.E., Christidis, L., Cabanne, G.S., Miyaki, C. & Norman, J.A. (2009) The timing of Neotropical speciation dynamics: A reconstruction of *Myiopagis* flycatcher diversification using phylogenetic and paleogeographic data. *Molecular Phylogenetics and Evolution*, 53, 961–971.  
<http://dx.doi.org/10.1016/j.ympev.2009.09.001>
- Rheindt, F.E., Cuervo, A.M. & Brumfield, R.T. (2013) Rampant polyphyly indicates cryptic diversity in a clade of Neotropical flycatchers (Aves: Tyrannidae). *Biological Journal of the Linnean Society*, 108, 889–900.  
<http://dx.doi.org/10.1111/j.1095-8312.2012.02036.x>
- Rheindt, F.E., Norman, J.A. & Christidis, L. (2008) Phylogenetic relationships of tyrant-flycatchers (Aves: Tyrannidae), with an emphasis on the elaeniine assemblage. *Molecular Phylogenetics and Evolution*, 46, 88–101.  
<http://dx.doi.org/10.1016/j.ympev.2007.09.011>
- Ridgway, R. (1907) The birds of North and Middle America. Part IV. *Bulletin of the United States National Museum*, No. 50, 1–973.
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.  
<http://dx.doi.org/10.1093/bioinformatics/btg180>
- Salvin, O. & Godman, F.D. (1888) *Biologia Centrali-Americana. Aves. Vol. 2*. Privately printed, 598 pp.
- Saranathan, V., Hamilton, D., Powell, G.V.N., Kroodsma, D.E. & Prum, R.O. (2007) Genetic evidence supports song learning in the three-wattled bellbird *Procnias tricarunculata* (Cotingidae). *Molecular Ecology*, 16, 3689–3702.  
<http://dx.doi.org/10.1111/j.1365-294x.2007.03415.x>
- Schulenberg, T.-S. & Parker, T.-A. III. (1997) A new species of tyrant-flycatcher (Tyrannidae: *Tolmomyias*) from the western Amazon Basin. *Ornithological Monographs*, 48, pp. 722–731.
- Schulenberg, T.S. & Kirwan, G.M. (2012) Foothill Elaenia (*Myiopagis olallai*). Neotropical Birds Online. Available from: <http://neotropical.birds.cornell.edu> (accessed 1 May 2014)
- Smithe, F.B. (1975) *Naturalist's Color Guide. Part I. & II*. American Museum of Natural History, New York, NY, 237 pp.
- Smithe, F.B. (1981) *Naturalist's Color Guide, Part III*. American Museum of Natural History, New York, New York, 37 pp.
- Sorenson, M.D., Ast, J.C., Dimcheff, D.E., Yuri, T. & Mindell, D.P. (1999) Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. *Molecular Phylogenetics and Evolution*, 12 (2), 105–114.  
<http://dx.doi.org/10.1006/mpev.1998.0602>
- Sorenson, M.D. & Quinn, T.W. (1998) Numts: A challenge for avian systematics and population biology. *The Auk*, 115, 214–221.  
<http://dx.doi.org/10.2307/4089130>
- Stamatakis, A. (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.  
<http://dx.doi.org/10.1093/bioinformatics/btl446>
- Swofford, D.L. (2002) PAUP\*. Phylogenetic Analysis Using Parsimony *et al.* (\*and other methods) version 4.0b10. Sinauer Associates, Sunderland, MA
- Touhcton, J.M., Seddon, N. & Tobias, J.A. (2014) Rearing experiments confirm song development without learning in a tracheophone suboscine bird. *PLoS ONE*, 9, e95746.  
<http://dx.doi.org/10.1371/journal.pone.0095746>
- Traylor, M.A., Jr. (1977) A classification of the Tyrant Flycatchers (Tyrannidae). *Bulletin of the Museum of Comparative Zoology*, 148, 129–184.
- Traylor, M.A., Jr. (1979) *Checklist of the birds of the world. Vol. 8*. Cambridge, MA, Museum of Comparative Zoology, 365 pp.  
<http://dx.doi.org/10.5962/bhl.title.14581>
- Wetmore, A. (1963) Additions to records of birds known from the Republic of Panamá. *Smithsonian Miscellaneous Collections*, 145, 1–11.
- Whitney, B.M., Cohn-Haft, M., Bravo, G.A., Schunck, F. & Silveira, L.F. (2013) A new species of *Herpsilochmus* antwren from the Aripuanã-Machado interfluvium in central Amazonian Brazil. In: del Hoyo, J., Elliot, A., Sargatal, J. & Christie, D.A. (Eds.), *Handbook of the Birds of the World. Special Volume. New Species and Global Index*. Lynx Edicions, Barcelona, Spain, pp. 277–281.
- Whitney, B.M., Ferreira de Vasconcelos, M., Silveira, L.F. & Pacheco, J.F. (2010) *Scytalopus petrophilus* (Rock Tapaculo): a new species from Minas Gerais, Brazil. *Revista Brasileira de Ornitologia*, 18, 73–88.
- Zimmer, J.T. (1941) Studies of Peruvian birds. No. 36. The genera *Elaenia* and *Myiopagis*. *American Museum Novitates*, 1108, 1–24.
- Zimmer, K.J. & Whittaker, A. (2000) Species limits in Pale-tipped Tyrannulets (*Inezia*: Tyrannidae). *Wilson Bulletin*, 112, 51–66.  
[http://dx.doi.org/10.1676/0043-5643\(2000\)112\[0051:slptt\]2.0.co;2](http://dx.doi.org/10.1676/0043-5643(2000)112[0051:slptt]2.0.co;2)
- Zimmer, K.J., Whittaker, A., Sardelli, C.H., Guilherme, E. & Aleixo, A. (2013) A new species of *Hemitriccus* tody-tyrant from the state of Acre, Brazil. In: del Hoyo, J., Elliot, A., Sargatal, J. & Christie, D.A. (Eds.), *Handbook of the Birds of the World. Special Volume: New Species and Global Index*. Lynx Edicions, Barcelona, Spain, pp. 292–296.