

Janice M. Hughes
Department of Biology,
Lakehead University, 955 Oliver
Road, Thunder Bay, Ontario
Canada P7B 5E1
Email: janice.hughes
@lakeheadu.ca

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Phylogeny of the cuckoo genus *Coccyzus* (Aves: Cuculidae): a test of monophyly

Abstract *Coccyzus* comprises nine species of New World cuckoos (Aves: Cuculidae) that breed from southern Canada to central South America. The phylogeny of this genus was reconstructed using 2490 base pairs of the mitochondrial genes cytochrome oxidase II and III, and cytochrome *b*. Maximum likelihood, maximum parsimony, and Bayesian inference approaches produced similar topologies in which *Coccyzus*, as currently classified, is polyphyletic. Topological-constraint analyses demonstrated that trees resulting from this study were significantly better than those derived from conventional classifications. Furthermore, results support paraphyly of *Piaya*, another genus of New World cuckoos. These conclusions reflect some early classifications of these genera and support the resurrection of *Micrococcyx* to house the ash-coloured (*Coccyzus cinereus*) and dwarf (*C. pumilus*) cuckoos, and *Coccyca* for the little cuckoo (*Piaya minuta*).

Key words Cuculidae, New World cuckoos, *Coccyzus*, phylogeny, monophyly, *Piaya*, *Micrococcyx*

Introduction

The genus *Coccyzus* comprises nine species of New World cuckoos that breed from central North America south to Argentina. Five species – the dwarf (*C. pumilus*), ash-coloured (*C. cinereus*), grey-capped (*C. lansbergi*), dark-billed (*C. melacoryphus*) and pearly-breasted (*C. euleri*) cuckoos – are endemic to South America. Mangrove (*C. minor*) and Cocos (*C. ferrugineus*) cuckoos occur predominantly at Central American latitudes. Yellow-billed (*C. americanus*) and black-billed (*C. erythrophthalmus*) cuckoos are long-distance migrants that maintain winter distributions in the Neotropics (Sibley & Monroe, 1990; Hughes, 1997, 1999, 2001).

Coccyzus was first established to include only *C. cinereus* and *C. melacoryphus* (Vieillot, 1817). Although described earlier, *C. americanus*, *C. minor* and *C. erythrophthalmus* had been placed in *Cuculus*, a genus now restricted to Old World obligately brood parasitic cuckoos. Brood parasites lay their eggs in other birds' nests, thus, relinquishing the responsibilities of rearing young (Hughes, 2000). In the following decades, four more *Coccyzus* species were described – *C. ferrugineus*, *C. lansbergi*, *C. pumilus* and *C. euleri* – and those previously included in *Cuculus* were moved to *Coccyzus* (Gray, 1846). The composition of *Coccyzus* remained intact for many decades, albeit with some differences of opinion regarding the taxonomic rank of a few species (Bouchard, 1876; Dubois, 1902).

Ridgway (1912) erected the genus *Micrococcyx* to house *C. pumilus* [= *M. pumilus*] and *C. cinereus* [= *M. cinereus*] cuckoos based on differences in tail and wing shape. Although recognized in some older publications (e.g. Ridgway, 1916;

Cory, 1919; Wetmore, 1926; Pinto, 1938), *Micrococcyx* has not been maintained in more recent classifications (Peters, 1940; Sibley & Monroe, 1990; American Ornithologists' Union, 1998). Some authors have suggested that *C. melacoryphus* and *C. minor* comprise a superspecies (Stiles & Skutch, 1989; Sibley & Monroe, 1990) most probably based on similarities in appearance, behaviour, vocalizations and partial sympatry (Hilty & Brown, 1986; Ridgely & Gwynne, 1989; French, 1991). *C. euleri* (= *C. julieni*; Banks, 1988; but see Sibley and Monroe, 1993) was considered a subspecies (southern yellow-billed cuckoo; Ridgway, 1916; Cory, 1919; Gyldenstolpe, 1945) or junior synonym (Shelley, 1891; Dubois, 1902) of *C. americanus* by some earlier authors. However, more recent classifications uphold its species status (Peters, 1940; Morony *et al.*, 1975; see Banks, 1988).

The evolutionary relationships within *Coccyzus* have not been previously examined. Earlier phylogenetic analyses of cuckoos using osteological characters (Seibel, 1988; Hughes, 2000) or nucleotide sequences (Aragón *et al.*, 1999) to assay evolutionary relationships above the generic level were limited to a few representative species from each included taxon. Moreover, the monophyly of *Coccyzus* has not been questioned since early in the 20th century. Given the morphological disparity of some species – *C. pumilus* and *C. cinereus*, in particular – further investigation is justified.

Materials and methods

Eight *Coccyzus* species were recognized in this study: *C. pumilus*, *C. cinereus*, *C. erythrophthalmus*, *C. lansbergi*,

C. melacoryphus, *C. minor*, *C. euleri* and *C. americanus*. This follows conventional taxonomy with one possible exception. Some classifications give species status to *C. ferrugineus*, an endemic of Cocos Island off the Pacific Coast of Costa Rica (Sclater, 1870; Ridgway, 1916; American Ornithologists' Union, 1998; Sibley & Monroe, 1990); others consider it a subspecies of *C. minor* (Peters, 1940; Morony *et al.*, 1975).

Traditionally, *Coccyzus* has been classified with nonparasitic cuckoos in the Phaenicophaeinae (Peters, 1940) or Coccyzinae (Sibley & Monroe, 1990; American Ornithologists' Union, 1998), implying that a nonparasitic New World genus, such as *Piaya* or *Saurothera*, is sister to *Coccyzus*. However, three phylogenetic analyses based on behaviour and osteology indicate that *Coccyzus* may be placed with obligate parasites in the Cuculinae (Seibel, 1988; Hughes, 1996, 2000). Hence an obligate brood parasite would be a more appropriate outgroup choice. Consequently, individuals from both purported sister taxa – common cuckoo (*Cuculus canorus*), squirrel cuckoo (*Piaya cayana*), black-bellied cuckoo (*P. melanogaster*), little cuckoo (*P. minuta*) and Puerto Rican lizard-cuckoo (*Saurothera vieilloti*) – were used as outgroups.

Two specimens were sequenced for all species except *C. minor*, *C. euleri* and *Piaya* cuckoos for which only one individual was used. Voucher specimens for material studied are listed in the Appendix, apart from those already published by Hughes & Baker (1999). Tissue was not available for *C. pumilus*. Extraction, amplification and sequencing protocols follow Hughes & Baker (1999). Sequences 2490 base pairs (bp) in length comprising portions of the mitochondrial genes cytochrome oxidase II (684 bp) and III (783 bp), and cytochrome *b* (1023 bp) were obtained by amplifying via the polymerase chain reaction using the following primer pairs: L8205, LYSH; A5REV, GLYH; and *b*₁, *b*₆. Aligned sequences were assembled using SE-AL v2.0 (Rambaut, 2000) and verified through amino acid alignment to homologous genes in the chicken (*Gallus gallus*). Taxa represented by only one specimen were sequenced twice for all genes to insure accuracy. All sequences have been deposited with Genbank (www.ncbi.nlm.nih.gov/Genbank/).

The data were subjected to three different methods of phylogenetic reconstruction – Maximum Likelihood (ML), Bayesian Inference (BI) and Maximum Parsimony (MP). I performed separate analyses on concatenated and individual gene sequences using all inference approaches, and compared the results for consistency.

Prior to the ML and BI analyses, Modeltest 3.06 (Posada & Crandall, 1998) was used to determine the appropriate model of nucleotide substitution under the Akaike Information Criterion, and estimate the gamma distribution parameter of rate heterogeneity and proportion of invariant sites. The ML analyses employed PAUP* 4.0b10 (Swofford, 2002) with heuristic searches based on tree bisection and reconnection (TBR) branch swapping and 10 random stepwise additions of taxa. The BI approach by Markov chain Monte Carlo (MCMC) used MrBayes 3.0b.4 (Huelsenbeck & Ronquist, 2001) running four simultaneous chains for 1×10^6 generations, sampling every 100 generations for a total of 10 000 trees. Trees were visualized using 50% majority rule consensus. The general-

time-reversible (GTR) model of nucleotide substitution (Yang, 1994), incorporating proportion of invariant sites (I) and four gamma distribution (G) values, was used in all cases except for cytochrome *b*, in which the HKY model (Hasegawa *et al.*, 1985) better approximated the molecular evolution of this gene. The MP analysis was implemented using PAUP*. Tree searches were exhaustive.

Clade support was evaluated by non-parametric bootstrapping of 1000 pseudoreplicates (ML and MP), Bayesian posterior probabilities (BI) and decay indices (MP). All tests were performed using PAUP*, with the exception of Bayesian posterior probabilities that were implemented in MrBayes. To test the hypotheses of *Coccyzus* monophyly, I used MacClade 4.03 (Maddison & Maddison, 2000) to construct monophyly constraint trees that simulated traditional classifications. The ML tree search analyses were repeated while enforcing topological constraints that kept only those trees that were compatible with constraint trees. I calculated log-likelihood scores (-lnL) for optimal and constrained trees using PAUP, and compared these values for significance (Kinshino & Hasegawa, 1989).

Results

Aligned sequences had a transition/transversion ratio of 3.90 and a composition of 29.7% A, 32.3% C, 13.5% G and 24.5% T. There were 548 variable informative sites (22.0%) and 243 variable uninformative positions. No insertions or deletions, frameshift mutations, or unexpected stop codons were found. Genetic distances across all positions of same-species individuals were low – *C. cinereus* (0.0%), *C. erythrophthalmus* (0.003%), *C. lansbergi* (0.003%), *C. melacoryphus* (0.001%), *C. americanus* (0.004%) and *Saurothera* (0.0%) – suggesting that sequences do not represent pseudogenes or nuclear inserts. Average sequence divergence among *Coccyzus* species was 11.7% and ranged from 1.00 to 22.6% (Table 1).

Figure 1 depicts the 50% majority-rule consensus tree resulting from the Bayesian inference analysis; the single optimal MP tree (length = 1367 steps; CI = 0.6547; g1 = -0.807300, $P < 0.01$; Hillis & Huelsenbeck, 1992) is identical to Fig. 1. Furthermore, the optimal ML tree is similar to Fig. 1 differing only in *C. cinereus* and *Piaya minuta* forming a clade basal to all other species aside from *Cuculus canorus*. The analyses of genes separately yielded slightly less-well resolved topologies that were otherwise similar to Fig. 1; in general, the incomplete resolution involved the position of *Saurothera*.

These reconstructions imply that *Coccyzus* is polyphyletic with *C. cinereus* placed among outgroup taxa. *Coccyzus americanus* and *C. euleri* form the internal clade, with *C. minor* sister to this pair. *Coccyzus melacoryphus* is sister to this assemblage. Interestingly, *C. lansbergi* forms a clade with *Saurothera*; *C. erythrophthalmus* is basal to this pair. The study also implies that *Piaya* may be paraphyletic; *P. minuta* does not cluster with *P. cayana* and *P. melanogaster*, as traditionally classified.

Clade support values – bootstrap, posterior probabilities, and decay indices – are indicated on internodes. In general, nodal support is strong within clades of *Coccyzus* cuckoos

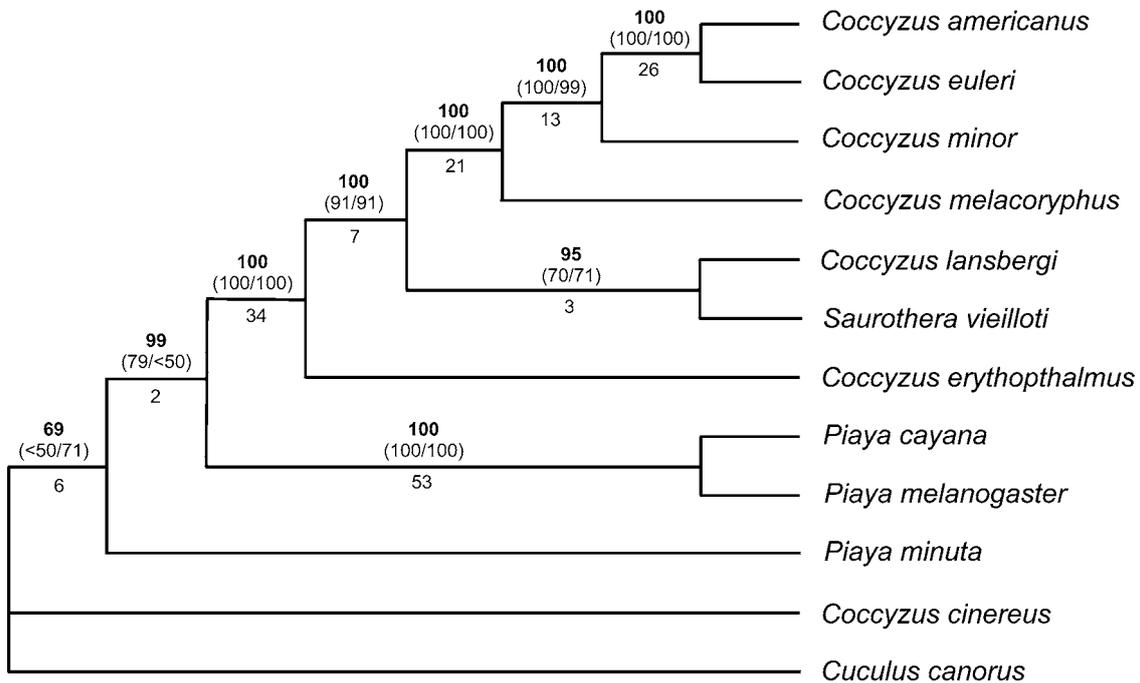


Figure 1 BI consensus tree for seven *Coccyzus* species and five outgroup species, based on 2490 base pairs of the mitochondrial genes cytochrome oxidase II, III and cytochrome *b*. MP tree is identical to this reconstruction; ML tree differs only in that *P. minuta* and *C. cinereus* form a clade. Support values – posterior probabilities (bold), bootstrap values (parentheses: ML/MP) and decay indices (below branch) – are indicated.

(excluding *C. cinereus*) and *Piaya* cuckoos (excluding *P. minuta*), ranging from 91–100% with decay indices of 13–53. Lower support values are in evidence for the *C. lansbergi*/*Saurothera* clade and two basal internodes, reflecting the lack of resolution of these taxa in some reconstructions.

Constraint-tree analyses further supported the non-monophyly of *Coccyzus* (Fig. 2). In all cases, the -lnL score for the optimal ML tree (9463.2657; $df = 10$) was significantly different from scores resulting from constraint tree analysis: monophyletic *Piaya* and *Saurothera* in polytomy basal to monophyletic *Coccyzus* (Fig. 2a; 9574.9561; $P < 0.0001$); *Saurothera* and all *Piaya* species in polytomy basal to monophyletic *Coccyzus* (Fig. 2b; 9573.6843; $P < 0.0001$). However, the placement of *Saurothera* in a polytomy with paraphyletic *Piaya* basal to *Coccyzus* (without *C. cinereus*; Fig. 2c) was not significant (9471.3099), suggesting that *Saurothera* should not necessarily be classified among *Coccyzus* cuckoos. When this analysis was repeated, forcing a monophyletic *Piaya* (Fig. 2d), the results were significant (9476.4620; $P < 0.001$); thus, supporting the conclusion of *Piaya* paraphyly.

Discussion

Ridgway (1912, 1916) and others (e.g., Wetmore, 1926; Pinto, 1938) suggested that *C. pumilus* and *C. cinereus* were sufficiently different in morphology from their congeners to warrant classification in their own genus *Micrococcyx*. Unlike typical *Coccyzus* cuckoos, these species have short bills; red irides; short rounded wings with diminished 1st, 2nd, 9th, and 10th primary feathers; and short tails that are much less roun-

ded at the tip, being ungraduated or only slightly so (Ridgway, 1916; Payne, 1997). Likewise, my study suggests that *Coccyzus* is monophyletic with the exclusion of *C. cinereus*. Although *C. pumilus* was not included in my study, there is no taxonomic evidence to separate these two species. Indeed, Sibley & Monroe (1990) suggested that they may be conspecific. Furthermore, my study places *C. cinereus* basal to some outgroup taxa; therefore, I suggest that the resurrection of *Micrococcyx* is warranted for these two species.

My study sheds additional light on *Coccyzus* taxonomy. For example, some workers have proposed that *C. melacoryphus* and *C. minor* comprise a superspecies (e.g., Stiles & Skutch, 1989; Sibley & Monroe, 1990). This classification is not supported by my results because these two species are paraphyletic in all reconstructions. In addition, earlier authors considered *C. euleri* to be a subspecies (Ridgway, 1916; Cory, 1919; Gyldenstolpe, 1945) or junior synonym (Shelley, 1891; Dubois, 1902) of *C. americanus*. My hypothesis of phylogeny supports a sister relationship between these taxa, but they are sufficiently divergent genetically (Table 1) to be recognized as separate species.

Unlike other *Coccyzus* species, *C. erythrophthalmus* and *C. americanus* are long-distance migrants that breed in North America and winter in South America (Hughes, 1999, 2001). They are not sister taxa, however, suggesting that their breeding distributions – which are sympatric throughout much of their range – resulted from independent invasions. Furthermore, they are likely to be derived from tropical species that migrated into temperate North America to establish new breeding grounds. This is akin to the southern-ancestral-home theory, which states that many migratory species were originally

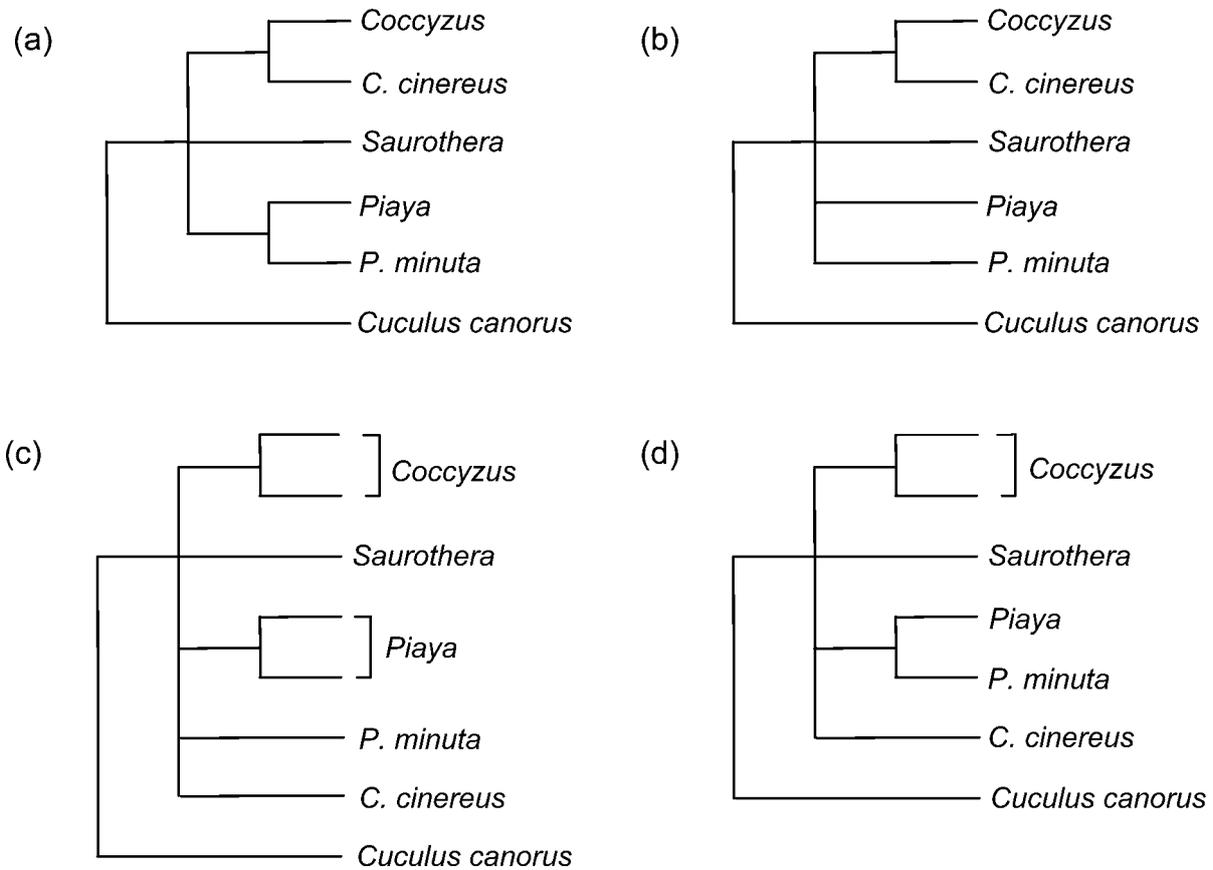


Figure 2 Constraint-tree hypotheses of phylogenetic relationships for study taxa based on traditional classifications: (2a) monophyletic *Piaya* and *Saurothera* in polytomy basal to monophyletic *Coccyzus*; (2b) *Saurothera* and all *Piaya* species in polytomy basal to monophyletic *Coccyzus*; (2c) *Saurothera* in a polytomy with paraphyletic *Piaya* basal to *Coccyzus*; and (2d) *Saurothera* in a polytomy with paraphyletic monophyletic *Piaya*.

Species	1	2	3	4	5	6	7	8	9	10	11	12
1 <i>Cuculus canorus</i>	–											
2 <i>Piaya melanogaster</i>	0.141	–										
3 <i>P. cayana</i>	0.137	0.051	–									
4 <i>P. minuta</i>	0.139	0.108	0.109	–								
5 <i>Saurothera vieilloti</i>	0.146	0.114	0.113	0.115	–							
6 <i>Coccyzus cinereus</i>	0.135	0.110	0.112	0.100	0.114	–						
7 <i>C. erythroptalmus</i>	0.134	0.106	0.106	0.107	0.078	0.105	–					
8 <i>C. lansbergi</i>	0.301	0.184	0.189	0.201	0.102	0.205	0.100	–				
9 <i>C. melacoryphus</i>	0.265	0.237	0.246	0.209	0.120	0.226	0.113	0.115	–			
10 <i>C. minor</i>	0.246	0.200	0.210	0.199	0.110	0.208	0.110	0.120	0.062	–		
11 <i>C. euleri</i>	0.245	0.205	0.200	0.196	0.106	0.200	0.115	0.111	0.056	0.042	–	
12 <i>C. americanus</i>	0.253	0.224	0.220	0.205	0.115	0.222	0.120	0.119	0.062	0.044	0.010	–

Table 1 Pairwise estimates of genetic distance for *Coccyzus* and outgroups based on uncorrected “p” distance.

permanent residents in southern latitudes with distributions approximating their present winter ranges; these species subsequently invaded seasonally favourable northern breeding sites (Cox, 1968). Cox (1985) used a regression analysis to determine the origin location of paruline warblers (Parulinae) based on observed migration patterns. I followed his methodology by plotting the individual midpoint latitudes (latitudinal centre) of breeding and non-breeding ranges for five

migratory *Coccyzus* species (*C. erythroptalmus*, *C. melacoryphus*, *C. lansbergi*, *C. euleri*, and *C. americanus*; Payne, 1997) against the latitudinal interval (latitudinal distance) between their ranges. The intercept of the regression of midpoint latitude on latitude span (latitudinal difference between northerly and southerly limits of range) was 0.4°N and 6.0°S for breeding and non-breeding ranges, respectively. These intercepts were not significantly different from a latitude midway between the

equator and Tropic of Capricorn (breeding: $t = 0.475$; non-breeding: $t = 1.216$; $df = 4$), thereby, supporting a hypothesis of a tropical centre of origin in the Southern Hemisphere for migratory *Coccyzus* cuckoos.

The position of *Saurothera vieillotii* among *Coccyzus* is perplexing. Although this species superficially resembles typical *Coccyzus* cuckoos, albeit being much larger in size and somewhat terrestrial in habits, the two genera (*Saurothera* and *Coccyzus*) have not been merged in the past. Furthermore, my topological constraint analysis failed to find significant difference in $-lnL$ scores between trees that placed *S. vieillotii* within or without *Coccyzus*. Inclusion of additional *Saurothera* taxa in future studies may resolve this enigma.

My study also calls into question the monophyly of *Piaya* with placement of *P. minuta* outside the clade. This three-species genus – *P. cayana*, *P. melanogaster* and *P. minuta* – ranges from Mexico south through Central America into north-central South America (Sibley & Monroe, 1990). First described by Lesson (1831), *Piaya* comprised only *P. cayana* and *C. erythrophthalmus*; Lesson established an additional genus, *Coccyua*, with *P. minuta* [= *Coccyua minuta*] as sole member. Morphological differences cited for the exclusion of *P. minuta* from *Piaya* include its substantially shorter tail and 10th primary wing feather, and much smaller size overall (Ridgway, 1916). Prior to the origin of *Coccyua*, *P. minuta* was considered to be a member of *Coccyzus* (*C. minutus*; Vieillot, 1817). Sclater (1860) subsequently moved the species to *Piaya* (*P. rutila* 1860; *P. minuta* Sclater, 1862) where it is currently classified (American Ornithologists' Union, 1998). Some authors, however, have upheld the assignment of *P. minuta* in *Coccyua* (e.g. Cabanis & Heine, 1862; Ridgway, 1916; Hughes, 2000; Kruger & Davies, 2002).

My evidence to support *Coccyzus* polyphyly is compelling. Furthermore, the additional suggestion that *Piaya* is paraphyletic favours a complete review of New World cuckoo systematics, particularly that of the Coccyzinae. It is likely that future analyses will support the resurrection of the genera *Micrococcyx* and *Coccyua* to explain morphological anomalies observed by earlier taxonomists.

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Appendix. List of specimens used in the analysis

Taxa	Locality	Voucher Number
<i>Coccyzus americanus</i>	Canada: Ontario	ROM IB2291
	United States: Kansas	ROM MPK881
<i>Coccyzus euleri</i>	Ecuador	ANSP 4661
<i>Coccyzus minor</i>	Puerto Rico	LSUMZ B11517
<i>Coccyzus melacoryphus</i>	Ecuador	ANSP 5958
	Paraguay	MVZ 20036
<i>Coccyzus lansbergi</i>	Ecuador	ANSP 5233
	Peru: Lambayeque	LSUMZ B5126
<i>Coccyzus erythrophthalmus</i>	Canada: Ontario	ROM IB2004
	Canada: Ontario	ROM IB2703
<i>Coccyzus cinereus</i>	Bolivia: Beni	LSUMZ B6833
	Argentina: Entre Rios	USNM 2716
<i>Saurothera vieilloti</i>	Puerto Rico	LSUMZ B11323
	Puerto Rico	LSUMZ B13358
<i>Piaya melanogaster</i>	Guyana: Potaro-Siparuni	ANSP 8348
	Guyana: Potaro-Siparuni	ANSP 8603
<i>Piaya cayana</i>	Bolivia: Santa Cruz	LSUMZ 15093
<i>Coccyua minuta</i>	Ecuador: Morona-Santiago	ANSP 1466
	Bolivia: Santa Cruz	LSUMZ 15136

Appendix 1 Prefixes indicate voucher specimens deposited in the following museums: ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; LSUMZ, Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana, USA; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; USNM, United States National Museum, Washington, DC, USA.