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Molecular data delineate four genera of "*Thryothorus*" wrens

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Abstract

Wrens of the genus *Thryothorus* comprise over a third of the species diversity in the family Troglodytidae. In addition to this species diversity, these wrens vary in a number of behavioral characteristics, in particular in the presence and structure of vocal duets, which makes them an interesting target for comparative evolutionary ecological and behavioral study. However, no phylogenetic hypothesis for this group—which would provide a sound basis for comparative analysis—is currently available. While previous molecular phylogenetic work established conclusively that the type of this genus, *Thryothorus ludovicianus* (Latham), was not part of a monophyletic group with other *Thryothorus*, the exact limits of the genus could not be established due to limited taxon sampling. Here, we present molecular data from all but four currently recognized species of *Thryothorus*. These data confirm that *Thryothorus* is paraphyletic, and that the type *T. ludovicianus* does not form a monophyletic group with any other member of the genus. Based on analyses of our data, we resurrect two previously recognized wren genera, *Pheugopedius* and *Thryophilus*, and erect a new genus—*Cantorchilus*—to house the remaining ex-*Thryothorus* species. Our hypothesis of relationships will provide a firm basis for future behavioral and morphological analyses of these species.

Keywords: Cytochrome *b*; β-Fibrinogen; Intron; Duetting

1. Introduction

The wrens (family Troglodytidae) are a primarily New World radiation of insectivorous passerine birds, known in particular for their often complex, melodious vocalizations. Wren song has long been the subject of scientific study (e.g., Armstrong, 1963), as this group exhibits impressive diversity in such features as song structure, repertoire size, presence of female song, and sex-specific patterns of song use (Farabaugh, 1983; Kroodsma, 1975; Kroodsma, 1977; Kroodsma et al., 2001; Leger et al., 2000; Mann et al., 2005). The species richness of this group is concentrated in one genus of the fifteen currently recognized—*Thryothorus*—which comprises 27 of approximately 76 wren species (Dickinson, 2003). Species of this genus range from southern Canada (*T. ludovicianus*) through southern Brazil (*T. longirostris*). More significantly, these species exhibit variation in behavioral characteristics that make the family as a whole of particular interest, perhaps most strikingly in the occurrence and nature of female song (Brown and Lemon, 1979; Farabaugh, 1983; Levin, 1996a; Levin, 1996b; Logue and Gammon, 2004; Mann et al., 2005; Mann et al., 2003; Molles and Vehrencamp, 1999). Although comparative analyses of these species may provide important insights into song evolution (Brown and Lemon, 1979; Farabaugh, 1983), no phylogenetic hypothesis to inform such comparisons is currently available.

Barker (2004) provided the first data on relationships of *Thryothorus* wrens. One of the main conclusions of that

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study was that the genus *Thryothorus* was paraphyletic, with the type species of the genus *T. ludovicianus* being sister to *Thryomanes bewickii*, and the two together sister to the genus *Campylorhynchus*. The remaining sampled *Thryothorus* (only four species) fell in an unresolved but well-supported clade that also contained the genera *Cinnycerthia*, *Cyphorhinus*, and *Henicorhina*. Given the poor sampling of *Thryothorus* in that study, as well as the absence of another potential closely related genus (*Uropsila*), few conclusions could be drawn regarding the phylogeny and taxonomy of the genus as a whole, other than the fact that the latter would have to be significantly revised.

In this paper, we report sequence data obtained from all but four species of the genus *Thryothorus*, as well as from the previously unsampled genus *Uropsila*. Based upon these data, we infer relationships among *Thryothorus* species and their close relatives, providing the first comprehensive test of relationships in this group. Finally, we offer recommendations for a revised taxonomy that incorporate these phylogenetic data, including resurrection of two previously-recognized genera. To our knowledge, we also provide the first DNA sequence-based definition and diagnosis of a new avian genus.

2. Methods

2.1. Taxon sampling

We obtained data from 23 species of *Thryothorus*, including multiple exemplars (individuals and/or subspecies) for eight species (Table 1). Where possible systematic work should be based on material vouchered in publicly accessible collections (e.g., Ruedas et al., 2000; Winker et al., 1996); however, the majority of *Thryothorus* samples included in this study were aliquots of blood obtained by NIM in the course of banding for behavioral fieldwork requiring individual identification, and our results should be interepreted in this light. At least, given the congruence of our current results (see below) with previously recognized taxonomic divisions and with analyses based entirely on vouchered samples (Barker, 2004), we doubt that they have been affected by sample misidentification. In addition to the new data from these samples, we collected sequences from samples of *Henicorhina*, *Uropsila*, *Campylorhynchus*, and *Troglodytes* (Table 1), and included previously obtained wren data (Barker, 2004). This sample comprised all wren genera save two (the monotypic *Thryorchilus* and *Ferminia*), allowing a comprehensive test of monophyly for *Thryothorus* (the two unsampled genera have clear affinities with the well-supported *Troglodytes*/*Cistothorus* clade; Rice et al., 1999; Barker, unpublished data). Based on previous analyses (Barker, 2004), we restricted our analyses of *Thryothorus* relationships to members of the Troglodytidae (*sensu stricto*), and included a single member of its sister group (*Polioptila caerulea*) as an unambiguous outgroup.

2.2. Data collection

We obtained novel sequences from two gene regions, the mitochondrial cytochrome *b* gene, and the fourth intron of the nuclear-encoded β-fibrinogen gene (FGB-I4), previously used in phylogenetic analysis of wren relationships (Barker, 2004). Data collection was primarily as described by Barker (2004). However, a new 5′ primer (L14857, 5′-AGG ATC ATT CGC CCT ATC CAT-3′) was used to obtain the cytochrome *b* sequences from some individuals (samples of *T. genibarbis* and *T. longirostris*). In addition, cycle sequencing was performed using ABI BigDye v3.1 reactions, with electrophoresis on an ABI PRISM 3700 DNA Analyzer. Contig alignments were performed in Sequencher (GeneCodes, Ann Arbor, MI), and sequences were aligned by eye. Alignment of new FGB-I4 sequences to the previously constructed alignment (Barker, 2004) was trivial, and required no novel indel events. All sequences have been submitted to GenBank (accessions DQ415680–DQ415713 and DQ415713–DQ415716).

2.3. Phylogenetic analyses

Two data sets were analyzed. The first comprised all available wren cytochrome *b* sequences (Table 1; Barker, 2004), rooted with a single outgroup (*Polioptila*). The second data set comprised a subset of taxa for which both cytochrome *b* and FGB-I4 were available (Table 1; Barker, 2004), again with *Polioptila* as an outgroup. In three cases sequences from the two gene regions were available from different individuals of the same species, and these were analyzed as individual-level chimeras (Table 1). Only one of these cases involved a *Thryothorus* wren (the subspecies *albinucha* of *T. ludovicianus*).

The data sets were analyzed using parsimony, maximum likelihood, and Bayesian methods, as implemented in PAUP* v4.0b10 (Swofford, 2000) and MrBayes v3.1 (Altekar et al., 2004; Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). However, separate likelihood analyses of the second data set were not performed, and the combined data were only analyzed using partitioned Bayesian methods. Prior to combined analysis, support for nodes in separate analyses were compared for evidence of conflict: congruence of wren cytochrome *b* and β-fibrinogen intron 4 sequences has been discussed extensively elsewhere (Barker 2004). Model selection for likelihood and Bayesian analyses was performed using decision theory as implemented in DT_ModSel (Minin et al., 2003). For the second data set, separate optimal models were chosen for the two gene regions (Barker, 2004). Heuristic searches were performed in PAUP* with multiple random taxon addition sequences (50 and 10 for parsimony and likelihood, respectively). Support for recovered nodes in optimization methods was estimated by the bootstrap (Felsenstein, 1985; 1000 and 200 replicates for parsimony and likelihood, respectively). Optimal trees under maximum likelihood were compared to selected alternatives (e.g., trees from constrained analyses)

Table 1
List of all *Thryothorus* wrens (primarily following Dickinson, 2003) and allies, with specimen information for species sampled in this study: information is also given for selected taxa of wrens for which new sequence data were obtained

Genus	Species	Subspecies	Voucher or Locality[a]	Prior Genus[b]
Campylorhynchus	*turdinus*	*hypostictus*	Tiputini Biodiversity Field Station, Napo, Ecuador	
Cinnycerthia	*peruana*	*olivascens*	MZUC (O2450; NK13)	
Thryomanes	*bewickii*	*eremophilus*	MZAH 9734 (BEHB43)	
Thryothorus	*atrogularis*	monotypic	La Suerte Biological Field Station, Limón, Costa Rica	*Pheugopedius*[2]
	spadix	monotypic	Not sampled	*Pheugopedius*[1]
	fasciatoventris	*melanogaster*	Manuel Antonio National Park, Puntarenas, Costa Rica	*Pheugopedius*[3]
	euophrys	*longipes*	Pasochoa, Pichincha, Ecuador	*Pheugopedius*[4]
	eisenmanni		Not sampled	None
	mystacalis	*mystacalis*	Rio Palenque Scientific Station, Pichincha, Ecuador	*Pheugopedius*[5]
	genibarbis	*bolivianus*	FMNH 433732	***Pheugopedius***[2]
		genibarbis	FMNH 427189	
	coraya	*ridgwayi*	FMNH 339666 (SML88-345)	*Pheugopedius*[4]
		griseipectus	Tiputini Biodiversity Station, Napo, Ecuador	
	felix	*felix*	Estación de Biología Chamela, Jalisco, México	*Pheugopedius*[3]
	maculipectus	*maculipectus*	MZAH 7828 (MEX127)†	*Pheugopedius*[3]
		canobrunneus	Reserva Ecologica El Edén, Quintana Roo, México	
	rutilus	*hyperthrus*	Carara National Park, Puntarenas, Costa Rica	*Pheugopedius*[3]
	sclateri	*paucimaculatus*	Cerro Blanco, Guayas, Ecuador	*Pheugopedius*[5]
	semibadius	monotypic	Manuel Antonio National Park, Puntarenas, Costa Rica	*Thryophilus*[6]
	nigricapillus	*costaricensis*	La Suerte Biological Field Station, Limón, Costa Rica	*Thryophilus*[3]
		schotti	Cana, Darién, Panama	
		connectens	Playa de Oro, Esmeraldas, Ecuador	
		nigricapillus	Rio Palenque Scientific Station, Pichincha, Ecuador	
	thoracicus	monotypic	La Suerte Biological Field Station, Limón, Costa Rica	*Thryophilus*[6]
	leucopogon	*leucopogon*	Cana, Darién, Panama	*Thryophilus*[1]
	pleurostictus	*nisorius*	Quilamula, Morelos, México	*Thryophilus*[6]
	ludovicianus	*ludovicianus*	AMNH 20929 (PRS063)†	***Thryothorus***[7]
		albinucha	Reserva Ecologica El Edén, Quintana Roo, México [MTCYB]†	
			KUMNH 89472 (B-538) [FGB-I4]†	
	rufalbus	*castanotus*	Carara National Park, Puntarenas, Costa Rica	***Thryophilus***[3]
	nicefori		Not sampled	None
	sinaloa	*sinaloa*	Estación de Biología Chamela, Jalisco, México [MTCYB]†	*Thryophilus*[1]
		sinaloa	FMNH 343272 (MEX210) [FGB-I4]†	
	modestus	*modestus*	El Rodeo Protection Zone, San Jose, Costa Rica	*Thryophilus*[3]
		zeledoni	La Suerte Biological Field Station, Limón, Costa Rica	
	leucotis	*galbraithii*	Summit Gardens, Panamá, Panamá	*Thryophilus*[3]
		albipectus	MUSP 73431 (DFS92-103)†	
	superciliaris	*superciliaris*	Cerro Blanco, Guayas, Ecuador	*Thryophilus*[6]
	guarayanus	monotypic	FMNH 334541 (DW3915)†	*Thryophilus*[6]
	longirostris	*bahiae*	FMNH 392512	*Thryophilus*[3]
		bahiae	FMNH 392954	
	griseus		Not sampled	*Thryophilus*[1]
Uropsila	*leucogastra*	*leucogastra*	Estación de Biología Chamela, Jalisco, México [MTCYB]†	
		brachyuran	KUMNH 89473 (B-549) [FGB-I4]†	
Henicorhina	*leucosticta*	*prostheleuca*	FMNH 343285 (MEX102)†	
		costaricensis	La Suerte Biological Field Station, Limón, Costa Rica	
	leucophrys	*leucophrys*	Maquipucuna, Pichincha, Ecuador	
Cyphorhinus	*arada*	*arada*	FMNH (1775; ATP86-142)†	
Troglodytes	*troglodytes*		AY156507 [MTCYB]†	
	troglodytes	*hiemalis*	AMNH (PRS309) [FGB-I4]†	
Troglodytes	*musculus*	*intermedius*	La Suerte Biological Field Station, Limón, Costa Rica	

Previous generic names for species currently in the genus *Thryothorus* (Paynter and Vaurie, 1960) are given (the types of these genera have the genus in boldface). Samples marked with daggers were included in a combined analysis of mtDNA and nuclear data (see Methods).

[a] All samples with locality rather than voucher data are blood collected by NIM and stored in the lab of JAG at the University of St. Andrews. For some samples where voucher data could not be obtained (e.g., some FMNH samples with Brazilian vouchers), the tissue number and associated collector's number are given in parentheses: numbers in parentheses after vouchers refer to collector's numbers). Samples that are the sources for chimeric sequences (separate mtDNA and nuclear data) have the gene sequenced indicated in brackets. AMNH = American Museum of Natural History; FMNH = Field Museum; KUMNH = University of Kansas Museum of Natural History; MUSP = Museu de la Universidad de Saõ Polo; MZAH = Museo de Zoología "Alfonso L. Herrera", Universidad Nacional Autónoma de México; MZUC = Zoological Museum, University of Copenhagen.

[b] Superscripts on former genera indicate sources for generic assignment: 1. original description (see Paynter and Vaurie, 1960), 2. Ridgway (1904), 3. Baird (1874), 4. Chapman (1926), 5. Chapman (1917), 6. Sharpe (1881), and 7. Vieillot (1816).

using the test of Shimodaira and Hasegawa (Shimodaira and Hasegawa, 1999). Bayesian analyses of the cytochrome *b* data were performed recognizing a single partition, using default priors for all parameters, excepting the state transition frequencies, which were constrained by a non-uniform Dirichlet distribution (see Results). Bayesian analyses of the combined mitochondrial and nuclear data were performed using optimal models for each of two partitions (cytochrome *b* and FGB-I4), allowing all parameters their default priors (excepting cytochrome *b* transition rates, as above), and enforcing branch length proportionality between the two partitions. In both cases, at least two replications were performed of two simultaneous runs (nruns = 2), each with four incrementally heated chains, sampling every 100th generation of $2 \cdot 10^6$ total generations. The effectiveness of MCMC runs in posterior estimation was evaluated by examining convergence of partition posterior probabilities, the distributions of parameter values, and comparisons of values from multiple runs.

3. Results

Analysis of the cytochrome *b* data yielded similar results with all three methods used. Equally-weighted parsimony analysis recovered 11 most parsimonious trees, the strict consensus of which was resolved at 45 out of 54 possible nodes (Table 2, Fig. 1). Conflict among trees was focused on the deeper relationships, such that only three polytomies appear in the consensus tree (one seven clade polytomy and two three clade polytomies). Model selection for the complete cytochrome *b* data set yielded the transversional model with invariant sites and rates at variable sites following a Γ distribution (TVM+I+Γ, Table 2; Rodríguez et al., 1990) as the best fit. Likelihood analysis of the cytochrome *b* data yielded one maximum likelihood tree, which contained one polytomy with branches of effectively zero length (Fig. 2). As for the parsimony analysis, support for basal relationships in this tree was poor. As the TVM model of sequence evolution (which recognizes four separate transversion rates and a single transition rate) is not available in MrBayes, the character transition probabilities were constrained by entering a non-uniform Dirichlet prior, which had as its parameters 10X the maximum likelihood estimates of the transition probabilities. This places stronger weight on parameter values with the same proportionality as in the TVM model, with variance from this proportionality determined by the magnitude of the values used in the prior (with higher magnitudes translating to lower variance). Bayesian analyses of the data converged after approximately 2×10^5 generations, as estimated by among-run variance in clade credibility values (e.g., s.d. <0.01 with the first 25% of generations discarded). These analyses yielded posterior partition probability estimates that largely mirrored bootstrap results from parsimony and likelihood (Fig. 2). No partition that was not present in the maximum likelihood tree received an estimated probability

Table 2
Data set characteristics, analytical summaries (MP and ML refer to parsimony and likelihood, respectively), and parameter estimates for the two data sets analyzed. The column headings "All Taxa" and "Combined Data Subset" refer to analyses of cytochrome *b* alone for all wrens, and of the combined cytochrome *b* (MT-CYB) and β-fibrinogen intron 4 (FGB-I4) data for a subset of species

	All Taxa	Combined Data Subset	
	MT-CYB	MT-CYB	FGB-I4
# characters	1045	1045	663
# variable	445	406	174
# informative	389	319	66
# MP Trees	11	3	1169
# nodes resolved	45	13	12
Tree Length (MP)	2612	1519	223
CI	0.269	0.394	0.839
RI	0.416	0.303	0.836
Model	TVM+I+G	TVM+I+G	HKY+G
Tree Length (ML)	3.774 (4.051, 6.527)	2.661 (3.003, 3.953)	0.418 (0.357, 0.452)
π_A	0.311 (0.297, 0.342)	0.293 (0.017, 0.040)	0.321 (0.293, 0.347)
π_C	0.428 (0.405, 0.451)	0.414 (0.415, 0.458)	0.175 (0.151, 0.194)
π_G	0.105 (0.090, 0.115)	0.117 (0.096, 0.121)	0.182 (0.163, 0.207)
π_T	0.156 (0.135, 0.170)	0.176 (0.145, 0.173)	0.322 (0.297, 0.351)
r_{AC}	0.959 (0.533, 2.177)	1.654 (0.740, 1.999)	NA
r_{AG}	14.588 (9.190, 36.641)	15.763 (10.045, 24.527)	NA
r_{AT}	1.594 (1.020, 4.498)	1.961 (1.287, 3.471)	NA
r_{CG}	0.321 (0.113, 0.938)	0.326 (0.100, 0.566)	NA
r_{CT}	14.588 (10.654, 41.778)	15.763 (11.209, 27.192)	NA
κ	NA	NA	1.737 (3.002, 4.742)
p_{IV}	0.557 (0.512, 0.573)	0.582 (0.542, 0.599)	NA
α	1.319 (0.950, 1.424)	1.456 (0.988, 1.584)	1.049 (0.971, 18.449)

Parameter estimates for the optimal model chosen for each gene by DT_ModSel are shown, as estimated on an initial MP tree: 95% Bayesian credibility intervals for these same parameters are shown in parentheses. CI = Ensemble consistency index, RI = ensemble retention index, π_i = base frequencies, r_{ij} = base substitution rates, κ = transition/transversion ratio, p_{IV} = proportion of invariant sites, α = parameter of Γ distribution.

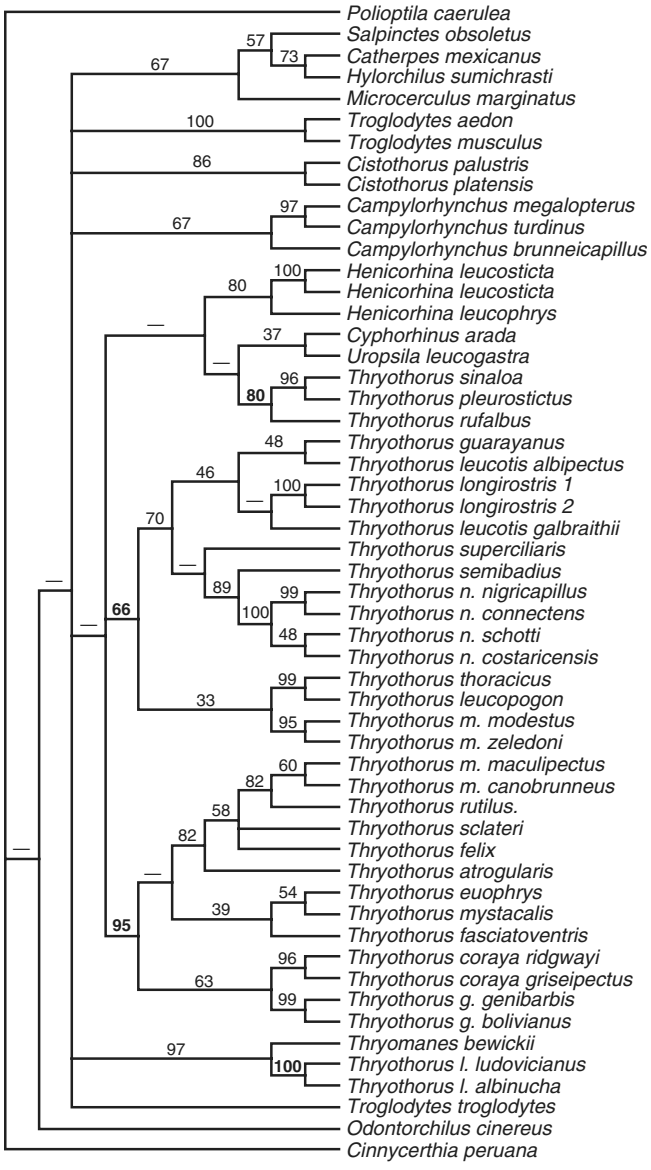

Fig. 1. Results of equally-weighted parsimony analysis of cytochrome *b* data for *Thryothorus* wrens and allies. Shown is the strict consensus of 11 equally-parsimonious trees (L = 2612, CI = 0.269, RI = 0.416). Numbers near branches are the percentage recovery under non-parametric bootstrap (1000 replicates; numbers less than 50 shown as dashes).

$\geqslant$0.95, although a number of nodes with bootstrap percentages between 50 and 75 had high posterior probability estimates.

All of the analyses recovered four well-supported clades containing members of the genus *Thryothorus*. First, two subspecies of *Thryothorus ludovicianus* appeared as a well-supported monophyletic group very strongly supported as sister to the species *Thryomanes bewickii* (bootstrap percentages from parsimony and likelihood of 97 and 98, respectively, estimated posterior probability = 1.00). Second, sequences derived from ten species of *Thryothorus* that have been classified in the genus *Pheugopedius* (Table 1) form a well-supported group (95 and 99 percent bootstrap percentages, estimated posterior = 1.00). Finally, sequences from the remaining species fell into two groups, one containing three species (*T. rufalbus*, *pleurostictus*, and *sinaloa*; bootstrap values of 80 and 93 percent, estimated posterior = 1.00), and a second with the remaining nine species (66 and 81 percent bootstrap, estimated posterior = 1.00). Under maximum likelihood and Bayesian analysis, these last two groups are recovered as sister taxa with very low support (bootstrap <5%, estimated posterior = 0.27). Most species in this cluster have been recognized previously under the generic name *Thryophilus* (Table 1). We performed two constrained analyses, one imposing monophyly of *Thryothorus* in the strict sense, and a second only enforcing monophyly of *Thryothorus* plus *Thryomanes*. Comparison of trees recovered from these constrained analyses with the maximum likelihood tree using the Shimodaira-Hasegawa test indicated that, while monophyly of *Thryothorus* in the strict sense could be strongly rejected ($\delta = 39.7$, $p = 0.003$), inclusion of *Thryomanes* as part of a monophyletic *Thryothorus* could not be rejected ($\delta = 19.9$, $p = 0.119$). Similarly, Bayesian MCMC analyses of the data never accepted a tree in which *Thryothorus* was monophyletic; however, these analyses also sampled a *Thryothorus* + *Thryomanes* clade very infrequently (estimated posterior probability bpp = 0.04). The bulk of sampled trees were nearly evenly split between finding three (as in Fig. 2) and four independent (i.e., separated by members of other genera) clades of *Thryothorus* (bpp = 0.45 and bpp = 0.52). Aside from the association of *Thryomanes bewickii* and *Thryothorus ludovicianus*, monophyly of these clades of *Thryothorus* wrens was violated by their association with four other genera: *Cinnycerthia*, *Cyphorhinus*, *Uropsila*, and *Henicorhina*. In likelihood and Bayesian analyses, these genera were supported as part of a large clade that included all *Thryothorus* except *T. ludovicianus* (Fig. 2).

Novel sequences of *Campylorhynchus*, *Henicorhina*, and *Troglodytes* fell as expected based on taxonomy and previous results (Barker, 2004), although *T. troglodytes* was not clearly the sister taxon to the other two species of *Troglodytes* (see also Martínez Gómez et al., 2005; Rice et al., 1999). In addition, all species with multiple exemplars (individuals and/or subspecies) were recovered as monophyletic, except *Thryothorus leucotis*, which was recovered as paraphyletic with respect to *T. guarayanus* and *longirostris*, albeit with weak support. This case aside, intraspecific divergence ranged from 0% (two individuals of a single population of *T. longirostris*), to 6.8% uncorrected sequence divergence *p* (two subspecies of *T. coraya*; Table 3). Some differences between recognized species were on the same order: *p* = 4.0%, *Troglodytes aedon* and *musculus*; 4.7%, *Thryothorus thoracicus* and *leucopogon*; 6.0%, *T. maculipectus* and *rutilus* (Table 3; see Discussion).

Analysis of the combined mitochondrial and nuclear data set was performed using a Bayesian approach only. Model selection for the two partitions based on maximum

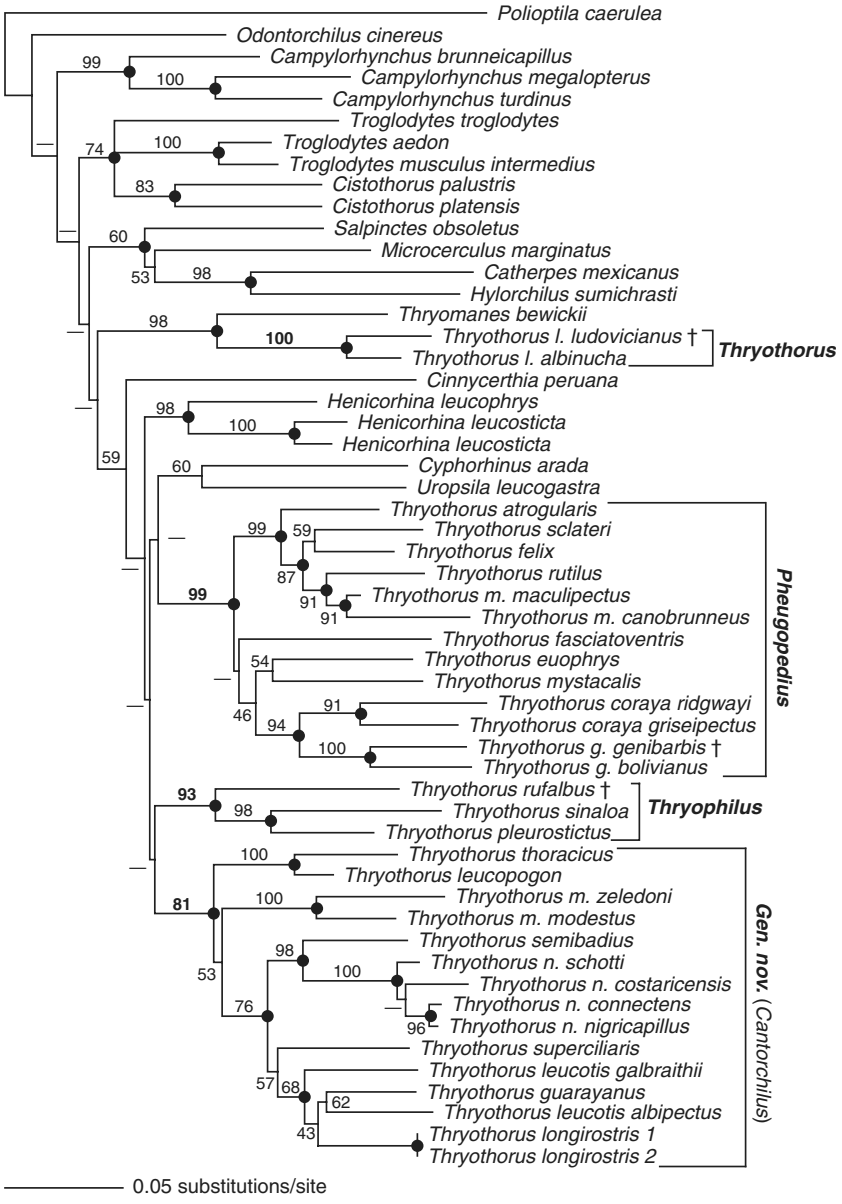

Fig. 2. Results of maximum likelihood and Bayesian analyses of cytochrome *b* data for *Thryothorus* wrens and allies. Shown is one of four trees recovered in likelihood analysis of the data under the TVM+I+Γ model of sequence evolution (-ln L = 12,491, $r_{AC} = 1.654$, $r_{AG} = 15.763$, $r_{AT} = 1.961$, $r_{CG} = 0.326$, $r_{CT} = 15.763$, $\pi_A = 0.293$, $\pi_C = 0.414$, $\pi_G = 0.167$, $\pi_T = 0.126$, $p_{IV} = 0.582$, $\alpha = 1.456$). Numbers near branches are the percentage recovery under non-parametric bootstrap (200 replicates; numbers less than 50 shown as dashes). Nodes receiving $\geqslant 0.95$ estimated Bayesian posterior probability are highlighted with filled circles. Alternative generic designations are shown, and samples of type species of previously recognized genera are highlighted by daggers.

likelihood optimizations yielded the TVM+I+Γ model for cytochrome *b* (as for the full cytochrome *b* analysis), and the HKY+Γ model (Hasegawa et al., 1985) for FGB-I4 (Table 2). As indicated by among-run variance in clade credibility levels, partitioned analyses of the data converged after approximately $2 \cdot 10^5$ generations. After discarding these as burn-in, consensus of the remainder yielded strong support for two relationships not well resolved with the mitochondrial data alone (Fig. 3). First, the combined data strongly supported a sister-group relationship between the *Thryothorus ludovicianus*/*Thryomanes bewickii* clade and two representatives of the genus *Campylorhynchus*. Second, the combined data strongly supported this group as sister to a clade containing all the remaining *Thryothorus* wrens sampled, plus representatives of the genera *Cinnycerthia*, *Henicorhina*, *Uropsila*, and *Cyphorhinus*. Within this latter group, the five remaining *Thryothorus* wrens did not form a monophyletic group, although support for most relationships in the clade was poor. Trees in which the five sampled *Thryothorus* in this clade formed a monophyletic group were never sampled (bpp < 0.001), although the *T. guarayanus*/*T. leucotis* and *T. maculipectus*/*T. coraya* pairs each received high estimated posterior values (bpp = 1.00). Separate

Table 3
Divergence at the mitochondrial cytochrome *b* gene between selected taxa of *Thryothorus*

Current Taxonomy	Comparison	Divergence (uncorrected *p*)
Subspecies	Within *nigricapillus*[a]	0.026
Subspecies	Within *ludovicianus*	0.031
Species	*thoracicus*/*leucopogon*	0.047
Subspecies	Within *maculipectus*	0.050
Subspecies	Within *genibarbis*	0.060
Subspecies	Within *modestus*	0.060
Species	*rutilus*/*maculipectus*	0.060
Species	*leucotis albipectus*/*guarayanus*	0.060
Species	*semibadius*/*nigricapillus*	0.068
Subspecies	Within *coraya*	0.068
Subspecies	Within *leucotis*	0.070
Species	*genibarbis*/*mystacalis*	0.091

[a] Average of 4 comparisons.

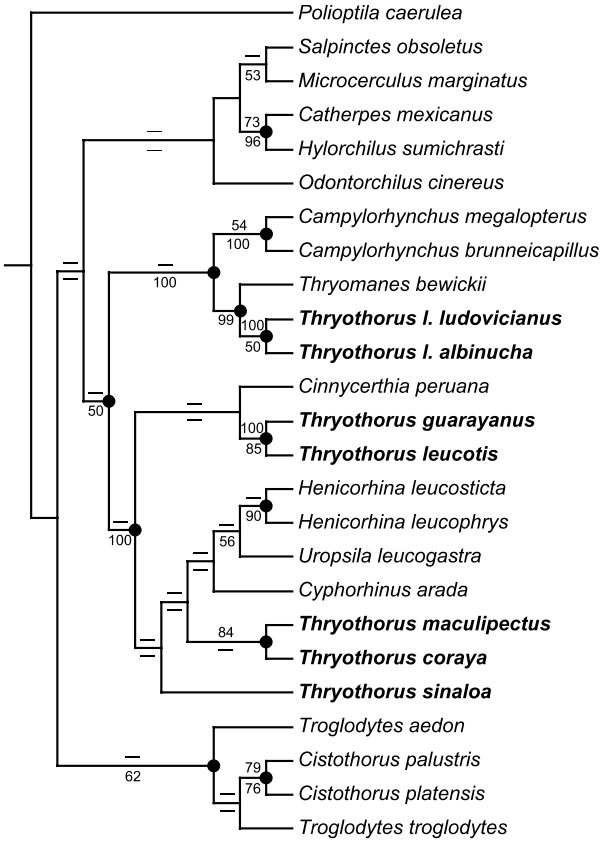

Fig. 3. Results of partitioned Bayesian analysis of combined cytochrome *b* and FGB-I4 data. Shown is the 50% majority rule consensus of 36000 trees derived from two parallel runs of $2 \cdot 10^6$ generations, with the first $2 \cdot 10^5$ of each discarded as burn-in. Nodes receiving $\geqslant 0.95$ estimated Bayesian posterior probability are lighted with filled circles. Also shown at each node are parsimony bootstrap support from separate analyses of cytochrome *b* (above) and FGB-I4 (below). Members of *Thryothorus* as currently delineated are shown in bold.

parsimony analyses of the two data sets indicated that support for most relationships was derived primarily from the nuclear FGB-I4 data (Fig. 3), and that there were no strongly supported conflicts (e.g., with bootstrap support $\geqslant 75\%$; Barker 2004) between the two data sets (not shown).

4. Discussion

4.1. Relationships among Thryothorus wrens

The assignment of *Thryothorus* forms to specific versus subspecific status has been controversial. Currently, some species have been split (e.g., American Ornithologists' Union, 1998) from previously recognized (e.g., Hellmayr, 1934; Paynter and Vaurie, 1960) polytypic species, whereas others remain unrecognized at the specific level. Essentially all hypotheses of relationship among *Thryothorus* wren species are attributable to this sometimes complex taxonomic history. Thus, *T. atrogularis* and *T. spadix* (unsampled), *T. euophrys* and *T. eisenmanni* (unsampled), *T. genibarbis* and *T. mystacalis*, *T. nigricapillus* and *T. semibadius*, *T. thoracicus* and *T. leucopogon*, and *T. nicefori* (unsampled) and *T. rufalbus* are all species pairs split from polytypic species (although in many cases currently recognized species themselves remain polytypic). Of the three species pairs for which we have samples of both members, two do in fact appear as sister taxa in our analyses, both with strong support (Figs. 1 and 2). Our results for *T. nigricapillus* and *T. semibadius* echo those of a previous study (Gonzalez et al., 2003) showing substantial differentiation of the two. The two putative sister species that did not form a monophyletic group in our analyses are *T. genibarbis* and *T. mystacalis*, formerly parts of a polytypic *T. genibarbis* (e.g., Meyer de Schauensee, 1970; Paynter and Vaurie, 1960). In our analyses, *T. genibarbis* is recovered as sister to *T. coraya*, with strong support in ML and Bayesian analyses, while *T. mystacalis* is recovered with weak support as sister to *T. euophrys* (Figs. 1 and 2). Mitochondrial divergence among these forms ranges from uncorrected divergences $p = 0.047$ to 0.091 (Table 3).

We have also sampled a number of forms currently assigned to polytypic species. Mitochondrial divergence among these broadly overlaps that observed for recognized species, with only two forms (*T. ludovicianus* and *T. nigricapillus*) showing lower divergence than the smallest interspecific value, and one value (two forms of *T. leucotis* at $p = 0.070$) exceeding that observed for all other sister species pairs save one (Table 3). Although we do not advocate distance-based species definitions (see Moritz and Cicero, 2004) this strongly suggests that current species-level taxonomy underestimates the actual diversity within the genus. Two cases are of particular note. The type species of *Thryothorus*—*T. ludovicianus*—occurs in at least four apparently allopatric populations in southern North America and in the Yucatán peninsula, Guatemala, and Nicaragua, with one disjunction including the entire Mexican state of Veracruz and half of Tabasco. Phillips (1986) recognized the southernmost forms as a species *T. albinucha*, distinct from *T. ludovicianus* (although in the same work he entertained the notion that *T. albinucha* might belong in the genus *Troglodytes* rather than *Thryothorus*). This species-level treatment has been subsequently adopted by some authors (Brewer, 2001; Howell and Webb, 1995; Navarro-Sigüenza and Peterson, 2004). The southern forms are

significantly differentiated in plumage, with less rufescent upperparts, buff rather than cinnamon underparts, and less distinct or absent barring of the flanks (Howell and Webb, 1995). The vocalizations of the two groups appear similar, and it is reported that individuals of the southern forms respond to playback of northern songs (Brewer, 2001). However, many *Thryothorus* wrens appear to respond aggressively to playback of song from other species of *Thryothorus*, or even from other bird families (NIM, pers. obs.), suggesting that this may not be a useful indicator of differentiation. Similarly, some recent authors have recognized *T. modestus zeledoni* as a species distinct from *T. modestus* (Brewer, 2001). This subspecies was synonymized by Hellmayr (1934), an action adopted by subsequent works, primarily on his authority (e.g., Paynter and Vaurie, 1960). Wetmore (in Wetmore et al., 1984; p. 74) felt that *T. zeledoni* deserved recognition due to its "larger size and darker, distinctly gray coloration," and questioned its assignment to subspecies rank. Observations of eggs and nesting behavior tentatively supported this distinction (Marshall-Ball and Slater, 2003), and studies of vocal behavior have suggested differentiation in several characteristics (Mann et al., 2003; NIM, unpublished data). Unfortunately, we do not have extensive genetic sampling of either species, as should be obtained for a rigorous assessment of the status of these forms. However, we note here that genetic divergence in both cases is substantial (Table 3), and that both cases involve allopatric populations with distinctive morphological characteristics. Based on these observations, we predict that recognition of both currently subsumed forms at the species level will be substantiated in the future.

In addition to the species and subspecies pairs discussed above, three species (*T. maculipectus*, *rutilus* and *sclateri*) have been split from a single polytypic species (*T. rutilus*; e.g., a "*formenkreis*" in Hellmayr, 1934) into a superspecies (American Ornithologists' Union, 1998), and five other species (*T. leucotis*, *modestus*, *guarayanus*, *longirostris*, and *superciliaris*) form a second superspecies (American Ornithologists' Union, 1998; Sibley and Monroe, 1990), although some authors (e.g., Brewer, 2001) exclude *T. modestus*. Components of this superspecies, particularly *T. leucotis* and *T. guarayanus*, have been merged into a single species (e.g., Carriker, 1935). Of the two previously recognized superspecies, we recover neither as generally recognized. We do recognize a core segment of the *T.* [*longirostris*] superspecies (including *T. superciliaris*, *T. leucotis*, *T. guarayanus*, and *T. longirostris*) in likelihood and Bayesian analyses alone, with weak support for association of *T. superciliaris* with the remaining species. However, monophyly of the superspecies as a whole is violated in that we find support for exclusion of *T. modestus* from the remaining species (as in Brewer, 2001). In particular, the "core" *T.* [*longirostris*] species are recovered as part of a clade including *T. nigricapillus* and *T. semibadius* (recovered in 70 and 76 percent of parsimony and likelihood bootstrap replicates, estimated Bayesian posterior of 1.00), with *T. modestus* diverged from the remaining species at $p = 0.091$. One additional point of interest regarding relationships within this group is the fact that the two samples of *T. leucotis*—one each from two disjunct populations of the species in Panamá and northern Brazil—are not recovered as sister taxa (Figs. 1 and 2). Support for their separation is weak, but the significant divergence between these samples ($p = 0.070$), and their non-monophyly reemphasizes previous observations that species limits in this group are in need of revision (American Ornithologists' Union, 1998; Ridgely and Tudor, 1989). In contrast to the previous case, we do recover the second superspecies (*T.* [*rutilus*]) in one analysis; however, only as one of several equally-parsimonious solutions (Fig. 1). This configuration was not preferred by likelihood or Bayesian analyses of the data, which placed *T. sclateri* as sister to *T. felix* (Fig. 2). However, all four of these species form a well-supported group in all analyses (Figs. 1 and 2). Although conflicting in detail, association of *T. felix* with the *T.* [*rutilus*] superspecies is consistent with the suggestion by Phillips (1986) that *T. felix* might be conspecific with *T. maculipectus*.

4.2. Paraphyly of Thryothorus

Species currently in the genus *Thryothorus* have in the past been assigned to as many as three different genera: *Thryothorus*, *Pheugopedius*, and *Thryophilus* (Table 1). These genera were delineated primarily by variations in the structure of the nasal operculum and associated membranes. Cabanis described *Pheugopedius* in a footnote to his listing of *P. genibarbis* (the type of that genus), noting in particular its similarity to *Cyphorhinus* (Cabanis, 1850; p. 79). Baird described *Thryophilus* in his listing of birds in the collections of the Smithsonian Institution (Baird, 1874; p. 127), citing a more oval form of the nostril and lack of a membranous scale in species he included in the genus. Baird (1874; pp. 91–95, 120–123, 127–128, 134) in particular gave quite a thorough discussion of all three groups and their characteristics. These distinctions were abandoned by Hellmayr (1934; p. 153), who argued in a footnote on *Thryothorus* that "… the difference between *Thryophilus*, with open nostrils, and *Pheugopedius*, with partly operculate nasal groove, is so completely bridged by intermediate species that no dividing line can be drawn …. If *Pheugopedius* and *Thryophilus* be merged, there is no valid ground for the retention of *Thryothorus*, since a good many species of so-called '*Thryophilus*' agree with the Carolina wren in the lesser graduation of the tail." In support of his contention, Hellmayr cited the comments of van Rossem (1930), who noted that variation within individual populations of *T. modestus* appeared on the same order as the differences between *Thryophilus* and *Pheugopedius*. Fusion of the three genera has been followed in all subsequent works (Paynter and Vaurie, 1960; American Ornithologists' Union, 1998; Sibley and Monroe, 1990; Dickinson, 2003), without additional comment or revision.

Our data indicate that the genus *Thryothorus*, as currently recognized, is paraphyletic. As discussed above, the type species of *Thryothorus* (Vieillot, 1816), the Carolina wren *T. ludovicianus*, is strongly supported as sister to Bewick's wren (*Thryomanes bewickii*). Furthermore, analyses of combined nuclear and mitochondrial data strongly reject association of this *T. ludovicianus*/*Thryomanes* clade with all other *Thryothorus*, to the exclusion of five other genera of wrens: *Campylorhynchus*, *Cinnycerthia*, *Cyphorhinus*, *Henicorhina*, and *Uropsila* (Fig. 3; Barker, 2004). In contrast, the available data do offer substantial support for three species groups of *Thryothorus* other than the type (Figs. 1, 2). The species in one of these groups have been previously classified as members of the genus *Pheugopedius* (Cabanis, 1850), whereas members of the other two groups were formerly classified as *Thryophilus* (Baird, 1874; Table 1, Figs. 2 and 3). Available data suggest that the two groups of *Thryophilus* form a monophyletic group (Fig. 2); however, statistical support for this relationship is virtually nonexistent.

Given that the type of *Thryothorus* can reliably be excluded from relationship with all other *Thryothorus* species, it is clear that taxonomic revision is necessary. We therefore restrict use of *Thryothorus* to *T. ludovicianus* and *T.* [*ludovicianus*] *albinucha*. Thus, there remain three well-supported clades of *Thryothorus*, for which two previously recognized names are available. Statistically, we cannot distinguish among three possible relationships for these remaining three clades: 1) monophyly, 2) diphyly, or 3) triphyly. Therefore, several possible taxonomic alternatives should be considered. If one placed a premium on minimizing the number of names being resurrected, then all ex-*Thryothorus* species would be reassigned to the genus *Pheugopedius*. Alternatively, if one read relationships directly as illustrated in Fig. 2, these species could be placed in two genera *Pheugopedius* and *Thryophilus*. However, either of these assignments could immediately be overturned by little additional evidence, as the relationships among the three groups and the genera *Cinnycerthia*, *Cyphorhinus*, *Uropsila*, and *Henicorhina* are poorly supported. A third alternative would be to recognize the three well-supported clades with generic names, such that any future rearrangement would be unlikely to disrupt taxonomy further. We endorse the latter option. Therefore, we recommend resurrection of the genera *Pheugopedius* and *Thryophilus* as outlined in Fig. 2. As the type of *Thryophilus* is *T. rufalbus*, this name is applied only to three species, leaving an additional nine species in our sample without a generic name. We propose that these species be assigned to a new genus:

4.3. Cantorchilus, gen. nov.

Type: *Thryothorus longirostris* (Vieillot).

Etymology: *cantus*, song; *orchilos*, wren.

Definition: We define this genus phylogenetically as the clade comprising the descendants of the common ancestor of [*Thryothorus*] *leucopogon* and [*Thryothorus*] *longirostris*.

Diagnosis: Currently, no known uniquely derived morphological characteristics diagnose the genus *Cantorchilus*, as defined here. Given current taxonomic and character sampling, the genus is diagnosable by 9 unreversed synapomorphies in cytochrome *b* (including: A150C, A156G, C297T, A876C, C903A, C924A, A948G, C960A and C1116A, where aNb refers to the ancestral state a and derived state b at position N), all at third codon positions, including 6 transitions and 3 transversions, one of which results in an amino acid replacement (I372M).

All of the species unsampled in this study save one have clear affinities with these groups as we have defined them (*T. spadix* and *T. eisenmanni* with *Pheugopedius*, and *T. nicefori* with *Thryophilus*). The remaining species, [*Thryothorus*] *griseus*, has been allied with *Thryophilus* (*sensu lato*) by Hellmayr (1934), but we consider its affinities uncertain, and leave it *incertae sedis*, to follow the remaining four genera. The only candidate for relationship with members of these genera remaining unsampled is the Cuban endemic *Ferminia cerverai*, which is commonly listed adjacent to *Thryothorus* in linear taxonomies (e.g., Paynter and Vaurie, 1960). However, genetic data (in prep.) clearly indicate that the relationships of this species lie within the *Troglodytes*/*Cistothorus* clade.

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