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PHYLOGENETIC POSITION AND GENERIC PLACEMENT OF THE SOCORRO WREN (*THRYOMANES SISSONII*)

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Abstract.—Since early in its taxonomic history, placement of the Socorro Wren (*Thryomanes sissonii*) has been an object of contention. Of particular interest is its current placement in the genus *Thryomanes*, which makes that genus ditypic and leads to an odd biogeographic scenario for the Socorro Wren's colonization of Socorro Island. We assessed its phylogenetic position by analyzing 516 base pairs of mitochondrial DNA sequences from the ND2 gene of this species and 14 additional wren taxa. Contrary to its present placement, the Socorro Wren is nested phylogenetically within the House Wren species complex, being placed as sister to the clade *Troglodytes aedon* + *T. musculus*. The current hypothesis (i.e. sister to *Thryomanes bewickii*) is strongly invalidated by our analysis. Our analyses indicate that the most appropriate taxonomic classification for the Socorro Wren is *Troglodytes sissonii*. *Received 29 January 2003, accepted 20 July 2004.*

Key words: Revillagigedo Archipelago, Socorro Island, Socorro Wren, *Thryomanes sissonii*, *Troglodytes sissonii*.

Posición Filogenética y Ubicación Genérica de *Thryomanes sissonii*

Resumen.—Desde el comienzo de su historia taxonómica, la ubicación de *Thryomanes sissonii,* una especie de troglodítido endémica de la isla Socorro, ha sido objeto de controversia. De particular interés es su ubicación actual en el género *Thryomanes*, la cual hace que este género sea ditípico y plantea un escenario biogeográfico extraño en cuanto a la colonización de Socorro por parte de esta especie. En este estudio determinamos la posición filogenética de *T. sissonii* analizando secuencias de 516 pares de bases del gen mitocondrial ND2 para esta especie y para 14 taxa adicionales de la famila Troglodytidae. En contraste con su ubicación actual, *T. sissonii* se encuentra anidado filogenéticamente al interior del complejo de *Troglodytes aedon*, como la especie hermana del clado formado por *T. aedon* y *T. musculus*. La hipótesis actual (i.e. que la especie es hermana de *Thryomanes bewickii*) es fuertemente invalidada por nuestros análisis. Nuestros resultados indican que la clasificación taxonómica más adecuada para esta especie es *Troglodytes sissonii*.

The Socorro Wren (*Thryomanes sissonii*) is an endemic taxon of Socorro Island, an island off the west coast of Mexico (18°47′N, 110°59′W). The taxonomic affinities of this species have remained unclear for more than a century, and its placement in either *Thryomanes* or *Troglodytes* remains unresolved. The Socorro Wren was first collected by Andrew Jackson Grayson during his expedition to Socorro Island in 1865. Upon arrival in mainland Mexico, he sent all of his specimens to the Smithsonian Institution and granted permission to S. F. Baird to classify the new taxa (Bryant 1891). Later, he decided to

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describe them himself and classified the Socorro Wren as *Thryothorus sissonii* (Grayson 1868). Although uncertain of his generic allocation (for lack of comparative specimen material), he considered it the most appropriate at the time.

His description published in *The California Farmer* went unnoticed by ornithologists, including Grayson's most sincere admirers (e.g. Lawrence 1871, Bryant 1891). Contrary to Phillips (1986), Grayson never admitted that his descriptions were improperly published. After he died in 1869, G. N. Lawrence's posthumous publication of Grayson (1871) led to the misunderstanding.

Unaware of Grayson's earlier description, Lawrence (1871) described the Socorro Wren as *Troglodytes insularis*. He noted a striking similarity between the Socorro Wren and *T. aedon* [= *musculus*] *inquietus* from Panama. Oberholser (1898) moved the species to the genus *Thryomanes* solely on the basis of bill depth and shape of the nares. That generic placement soon became firmly established (e.g. Ridgway 1904, McLellan 1926). Thus, the Socorro Wren was set as *Thryomanes insularis*, in spite of Lawrence's (1871) original placement in the genus *Troglodytes*.

Taylor (1951) concurred with Oberholser's placement of the species in *Thryomanes*, and that placement was followed by taxonomic authorities (e.g. Mayr and Short 1970, American Ornithologists' Union [AOU] 1998), though a few workers have since voiced doubts (Phillips 1986, Howell and Webb 1995). Taylor (1951), however, challenged the priority of Lawrence's (1871) description, providing evidence of Grayson's original work. Hence, Grayson's original specific epithet *sissonii* was revived for the taxon, and has been maintained since (Banks and Browning 1995).

The objective of the present study is to re-evaluate the case in the light of new evidence. On the basis of newly available tissue specimens of the species, and prior phylogenetic studies of the Troglodytidae, we performed additional analyses using mitochondrial DNA (mtDNA) sequences to elucidate the relationships of this enigmatic species. Below, we provide taxonomic recommendations for the Socorro Wren.

METHODS

To determine the phylogenetic position of the Socorro Wren, we obtained partial mtDNA sequences from this species, five additional wren taxa, and one outgroup (Table 1) and combined them with sequences from GenBank (deposited by Rice et al. 1999). We used *Certhia americana* as a more appropriate outgroup than Rice et al.'s (1999) *Gymnorhinus cyanocephalus* (a very distant taxon) and *Henicorhina leucosticta* (a taxon appearing as sister to *Troglodytes* [*Nannus*] *troglodytes* in their phylogeny). Thus, the mtDNA sequence data set consisted of 516 base pairs (bp) of the ND2 gene for 15 wren taxa, plus 1 outgroup taxon.

We extracted whole-genomic DNA from muscle tissues and a blood sample of the Socorro Wren using QIAmp tissue extraction kit, following manufacturer's protocols (Qiagen, Valencia, California). We obtained sequences via polymerase chain reactions (PCR) using *TAQ* DNA polymerase (Promega, Madison, Wisconsin) for the entire ND2 gene, using the primers L5215 (5′-TATCGGGCCCATACCCCGAATAT-3′), developed by Hackett (1996), and H1064 (5′-CTTTGAAGGCCTTCGGTTTA-3′), equivalent to position 6,297 in the Desjardins and Morais (1990) nomenclature and developed by Drovetski et al. (2004). Amplification was carried out for 35 cycles under the following profile: an initial 94°C hotstart for 150 s, 94°C denaturing for 30 s, 55°C annealing for 30 s, extension at 72°C for 70 s, and terminal extension at 72°C for 10 min. We purified PCR products using QIAquick PCR purification (Qiagen).

We sequenced PCR products for both primers on an ABI 3700 automated sequencer (Applied Biosystems, Foster, California), following manufacturer's protocols. We aligned and edited sequences with SEQUENCHER, version 3.1.1 (Gene Code Corporation, Ann Arbor, Michigan). All sequences were deposited in GenBank (AY465888–AY465894). Although we obtained the entire ND2 gene sequence, we used only that portion of the gene available from Rice et al. (1999); their data set contained 534 bp, of which 18 were beyond the 3′ end of the ND2 gene and were not included in our analyses.

To ensure that the sequences used were of mitochondrial origin, we examined them for insertions, deletions (indels), and internal stop codons: indels and internal stop codons would be observed if sequences did not code for proteins. We observed no indels or internal stop codons, and so we are confident that we obtained mitochondrial sequence data.

Table 1. Taxa used in the study.

Name	Taxa	Locality	Collection	Tissue number	GenBank accession number
White-browed Wren[a]	*Thryothorus (ludovicianus) albinucha*	Campeche, Mexico	KU	2174	AY465893
Carolina Wren[a]	*T. ludovicianus*	Kansas, USA	KU	2781	AY465894
Socorro Wren[a]	*Thryomanes (Troglodytes) sissonii*	Socorro Island, Mexico	Mist-netted	blood	AY465888
Bewick's Wren[a]	*T. bewickii*	Missouri, USA	KU	2470	AY465891
Sedge Wren[a]	*Cistothorus platensis*	Minnesota, USA	BMNH	41546	AY465889
Winter Wren[a]	*Troglodytes (Nannus) troglodytes*	Maine, USA	BMNH	68256	AY465892
Winter Wren	*T. (Nannus) troglodytes*	Illinois, USA	FMNH	1778	AF104976
Northern House Wren	*T. aedon*	Illinois, USA	FMNH	1815	AF104979
Southern House Wren	*T. musculus*	Oaxaca, Mexico	FCUNAM	Uncategorized	AF104978
Brown-throated Wren	*T. brunneicollis*	Oaxaca, Mexico	FCUNAM	OMVP213	AF104973
Rufous-browed Wren	*T. rufociliatus*	Chiapas, Mexico	FCUNAM	BMM607	AF104977
Ochraceous Wren	*T. ochraceus*	Cartago, Costa Rica	LSU	19926	AF104982
Mountain Wren	*T. solstitialis*	Pasco, Peru	LSU	8178	AF104981
Tepui Wren	*T. rufulus*	Amazonas, Venezuela	LSU	7395	AF104983
Timberline Wren	*Thryorchilus browni*	Cartago, Costa Rica	LSU	19924	AF104974
White-breasted Wood-Wren	*Henicorhina leucosticta*	Loreto, Peru	KU	814	AF104972
Brown Creeper[a]	*Certhia americana*	Minnesota, USA	BMNH	Uncategorized	AY465894

[a] Sequences obtained by authors; all others are from Rice et al. (1999), obtained from GenBank.

Abbreviations: KU = University of Kansas Natural History Museum; BMNH = Bell Museum of Natural History, University of Minnesota; FMNH = Field Museum of Natural History,; FCUNAM = Museo de Zoología Facultad de Ciencias, Universidad Nacional Autónoma de México; LSU = Lousiana State University Museum of Natural Science.

We conducted parsimony analyses in PAUP*, version 4.0b.10 (Swofford 2002), using a branch-and-bound search with all positions and transversions–transitions weighted equally (tree bisection reconnection [TBR] is an option only in heuristic searches). Additional analyses were carried out under the following transversion–transition weighting schemes: 2/1, 4/1, 8/1, and 10/1. We determined support for each node via heuristic bootstraps (1,000 replicates; Felsenstein 1985). We calculated Bremer support values for the equally weighted parsimony tree (Bremer 1988) using TREEROT (Sorenson 1999).

For maximum likelihood (ML), we used MODELTEST, version 3.06 (Posada and Crandall 1998) to determine the model that best explained the data, using a hierarchical likelihood ratio test. We determined nodal support for the maximum likelihood analysis via branch-and-bound bootstraps with 100 replicates. Bayesian analyses were implemented in MRBAYES, version 2.01 (Huelsenbeck and Ronquist 2001).

In the Bayesian analyses, the gamma-shape parameter and base frequencies were not defined *a priori*; instead, those parameters were treated as unknowns to be estimated during the analysis. Markov chain Monte Carlo (MCMC) simulations via four chains were run for 2,000,000 generations; for every 100 generations, a data point was saved for subsequent analysis. Random swapping between chains decreases the likelihood that an individual chain will be trapped in a local optima. A plot (not shown) of likelihood values versus generation determined that the likelihood values leveled off at ~50,000 generations.

To ensure that subsequent analyses were not biased by "burn-in" trees, we removed the first 99,900 generations, or the first 999 trees; we retained the remaining 19,001 trees for additional analysis. ("Burn-in" trees are those trees obtained before the log-likelihood values reach stationarity and are discarded before posterior probabilities are calculated.) We obtained a 50% majority rule consensus tree from those remaining trees. Percentage of times a given node appears in the posterior distribution of retained trees is interpreted as the posterior probability of that node (Huelsenbeck and Ronquist 2001). We examined alternative phylogenetic hypotheses by creating user-determined trees and comparing that topology with the equally weighted parsimony tree using a Shimodaira and Hasegawa (1999) test.

RESULTS

Of 516 bp of the ND2 gene analyzed, 245 were variable and 157 were phylogenetically informative; of those 157 bp, 34 were in first-codon positions, 16 in second-codon positions, and 107 in third-codon positions. Parsimony analysis using a branch-and-bound search resulted in a single most-parsimonious tree of 519 steps (consistency index [CI] = 0.6243, retention index [RI] = 0.5768; Fig. 1). The CI, with uninformative characters excluded, was 0.5301.

The critical node for our analyses is that linking *Thryomanes sissonii*, *Troglodytes aedon*, and *T. musculus*. That clade received unequivocal bootstrap support in all analyses, including a posterior probability of 1.0 in the Bayesian analysis (Fig. 1). Those taxa, together with *T. brunneicollis*, are part of a larger clade that makes up the House Wren complex; all parsimony analyses (not shown) using the different transversion–transition weighting schemes recovered this clade (clade A; Fig. 1). That is, in combination with the strong support for a node with *Thryomanes bewickii* + *Thryothorus ludovicianus*, the preceding results confirm that the Socorro Wren is not related to Bewick's Wren, and is in fact nested within *Troglodytes*. A Shimodaira and Hasegawa (1999) test significantly ($P < 0.05$) rejected the user-defined tree that placed *Thryomanes sissonii* as sister to *T. bewickii* as a better explanation of the data versus the equally weighted parsimony tree.

DISCUSSION

Thryomanes sissonii was placed with high support as a lineage basal to *Troglodytes aedon* and *T. musculus* under three distinct optimality criteria and numerous models of molecular evolution (Fig. 1). Moreover, the Socorro Wren is part of the House Wren complex and of a larger clade containing members of *Troglodytes*. Although the topology of those clades might change with the addition of other taxa (e.g. other insular forms of *Troglodytes*), it should be expected that the monophyly of *Troglodytes* would be supported, with the exception of *Troglodytes* [= *Nannus*] *troglodytes*.

Rice et al. (1999) observed that *T. troglodytes* did not appear within the clade containing the

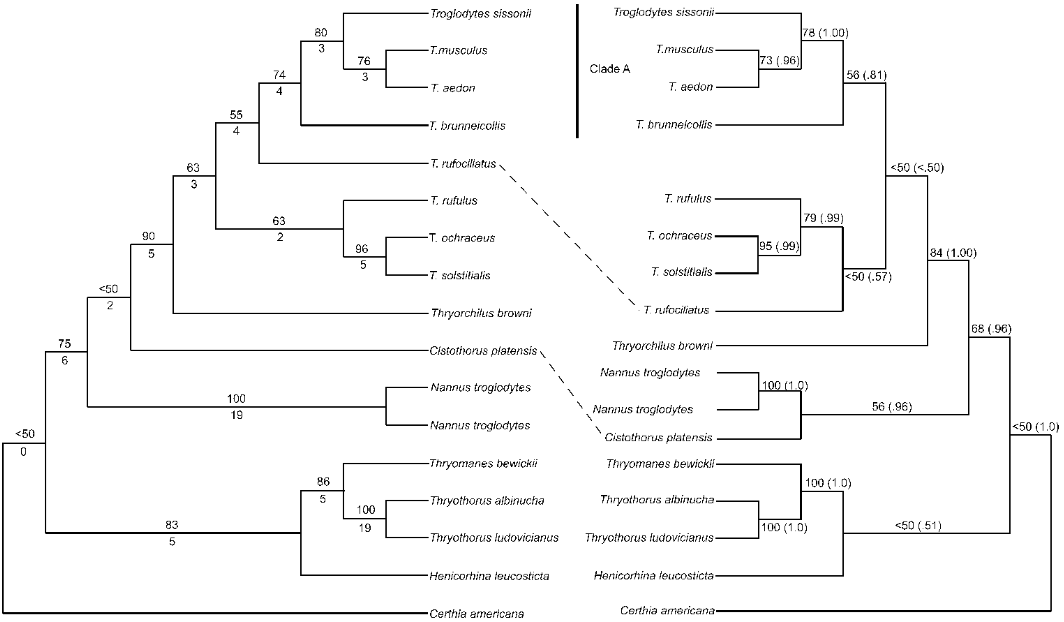

FIG. 1. Phylogenetic hypotheses suggested via maximum parsimony (MP), maximum likelihood (ML), and Bayesian analyses of ND2 mitochondrial DNA sequences. (Left) Topology resulting from equally weighted parsimony analysis. Numbers above lines are bootstrap values; numbers below are Bremer support values. (Right) Topology resulting from ML and Bayesian analyses. Numbers outside of parentheses are bootstrap values for the ML topology, numbers inside are Bayesian posterior probabilities. Bootstrap values for clade A were relatively high in each analysis (ML = 56, MP equal weights = 74, MP 2× tv/ts = 72, MP 4× tv/ts = 71, MP 8× tv/ts = 67, MP 10× tv/ts = 65, Bayesian = 0.81). For ML analysis, the following model (–lnL = 2991.5352; base frequencies: A = 0.3076, C = 0.3794, G = 0.0890, T = 0.2240; rate matrix: AC = 1.0, AG = 20.88, AT = 0.8990, CG = 0.8990, CT = 6.7244, GT = 1.0; proportion of invariable sites = 0; and gamma-shape parameter = 0.3834) was selected by MODELTEST, version 3.06 as the most appropriate model of evolution that explains the data set. The estimated Bayesian parameters were –ln = –3015.12 ± 23.22, A = 0.312 ± 0.0003, C = 0.386 ± 0.0004, G = 0.087 ± 0.00009, T = 0.215 ± 0.003, $\propto$ = 0.360 ± 0.002 (parameters that were not fixed in the Bayesian analysis and differ from those obtained with MODELTEST). Incongruences between alternative topologies are highlighted with dashed lines. For clarity, branch lengths are not shown.

other members of the genus *Troglodytes*. Here, using a different outgroup and adding five new taxa to the analysis resulted in the placement of *T. troglodytes* basal to *Thryorchilus browni* and the other *Troglodytes* (and to *Cistothorus platensis* in one tree). This pattern supports Rice et al.'s (1999) placement of *Troglodytes troglodytes* as *Nannus troglodytes*, though its definitive placement will depend on the final position of *Cistothorus* and *Thryorchilus* in relation to *Troglodytes*; the alternative to treatment as *Nannus* would be a very inclusive *Troglodytes*.

The phylogenetic hypothesis for *Troglodytes* in our analysis suggests that the House Wren complex as currently conceived is paraphyletic (clade A, Fig. 1). The House Wren of montane Mexico and the extreme southwestern United States, which has been recognized at the specific level (as *T. brunneicollis*), is basal to the clade containing the Northern and Southern house wrens (*T. aedon* and *T. musculus*; AOU 1998), and the Socorro Wren (*Thryomanes sissonii*). Hence, to avoid nonmonophyly in a species-level taxonomy, two options are available: (1) lump the entire *Thryomanes sissonii* + house wren clade into a single inclusive species, *Troglodytes aedon*, or (2) split the clade provisionally into lowland (*T. aedon, T.*

musculus) and highland (*T. brunneicollis*) species and recognize *Troglodytes sissonii*.

It has been suggested that the insular forms of house wrens scattered throughout the Caribbean and Pacific islands probably descended from continental lowland forms (Rice et al. 1999), but many aspects of their evolution remain intriguing. The Clarion Wren (*T. tanneri*) and the Socorro Wren, the only members of the genus in the Revillagigedo Archipelago, may prove to be sister species. However, they differ markedly in size, and their songs have different structures and do not elicit responses in the other species (Howell and Webb 1995, Baptista and Martínez-Gómez 2002). The Cozumel Wren (*T. beani*), thought to be a close relative of the Northern House Wren by some authors but considered closely related to the Caribbean house wrens by others (AOU 1998), represents another case that awaits revision. Wrens in the Caribbean are certainly house wrens on the basis of morphology and behavior, but their origins and species limits remain controversial: subspecies of *T. aedon* of recent origin versus distinct species representing much older lineages.

We believe that the most parsimonious course of action at this time is to recognize *Troglodytes sissonii*, even if disagreement prevails regarding other members of the complex. Several lines of evidence argue for the latter arrangement under both the phylogenetic species concept (PSC) and the biological species concept (BSC). Phenotypic differences between *T. aedon*, *T. musculus*, and *T. sissonii* are marked, making each form a separate entity clearly diagnosable and recognizable under PSC. Moreover, *T. brunneicollis* and *T. aedon* exist in broad parapatry across most of Mexico without apparent intergradation (BSC; but see Lanyon 1960).

Moving *Thryomanes sissonii* to *Troglodytes* makes interpretation of biogeography much simpler (Rice et al. 1999). If *Thryomanes* were to include two species (*T. bewickii* and *T. sissonii*), the biogeographic interpretation becomes extremely complex; in Mexico, *T. bewickii* is found primarily in the central highlands; only in Baja California are there lowland populations close to the Pacific coast from which to colonize Socorro Island (Howell and Webb 1995). In *Troglodytes*, however, the widespread lowland forms (mainly migratory) are well known as excellent colonizers. Hence, the corrected placement of *Troglodytes sissonii* provides a much more parsimonious biogeographic interpretation of the biogeography of the Islas Revillagigedo (Brattstrom 1990).

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