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Molecular systematics of a speciose, cosmopolitan songbird genus: Defining the limits of, and relationships among, the *Turdus* thrushes

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Abstract

The avian genus *Turdus* is one of the most speciose and widespread of passerine genera. We investigated phylogenetic relationships within this genus using mitochondrial DNA sequence data from the ND3, ND2 and cytochrome *b* genes. Our sampling of *Turdus* included 60 of the 65 extant species currently recognized, as well as all four species from three genera previously shown to fall inside *Turdus* (*Platycichla*, *Nesocichla*, and *Cichlherminia*). Phylogenetic trees based on maximum likelihood and maximum parsimony algorithms were congruent. Most of the *Turdus* taxa sampled fall into one of four clades: an African clade, a Central American-Caribbean clade, a largely South American clade, and a Eurasian clade. Still other taxa are placed either at the base of *Turdus*, or as links between clades. In no instance is any continent reciprocally monophyletic for the species distributed on it. A general lack of nodal support near the base of the phylogeny seems related to a rapid intercontinental establishment of the major clades within *Turdus* very early in the history of the genus. The monotypic genus *Psophocichla* is distantly related to, but clearly the sister of, *Turdus* rather than a constituent member of it.

Keywords: Turdinae; *Turdus*; Systematics; Bayesian methods

1. Introduction

The avian genus *Turdus* is one of the largest and most widely distributed passerine genera, with 65 recognized extant species occurring throughout South America, Central and North America, Africa, and Eurasia; one species (*merula*) has been introduced to Australia. Despite being cosmopolitan, relationships among most *Turdus* species remain virtually undefined. Presumed relationships are largely limited to the recognition of a handful of superspecies groups (Sibley and Monroe, 1990; Clement, 2000; Collar, 2005).

The number of species belonging to *Turdus* is also in flux. Some taxonomic treatments have recently increased the number of recognized species by elevating described races based on plumage or song differences, even when widespread intergradations of relevant taxa are present (e.g., Collar, 2005). Other studies which have focused on several African *Turdus* species have shown that some taxa previously considered subspecies clearly deserve species status (Bowie et al., 2003, 2005). The validity of *Turdus* as a whole, the validity of presumed superspecies, and the determination of species relationships throughout the genus have received little attention from molecular systematists.

Establishing a phylogeny for *Turdus* will facilitate studies of broader evolutionary interest. For example, of the 65 extant species (*sensu* Sibley and Monroe, 1990), over half are found in the New World, yet just one (*migratorius*) is widely distributed in North America. Four species are

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endemic to Caribbean islands, and within South America, some species have cis- or trans-Andean distributions while others are restricted to the Andes. In the Old World, at least eight species are found in Africa; some of these species are broadly distributed, whereas others are restricted to the Eastern Arc Mountains or volcanic islands in the Atlantic or Indian Oceans. Roughly 20 species occur in Eurasia, and one species (*poliocephalus*) is found throughout Southeast Asian islands. Thus, resolution of relationships within *Turdus* should provide interesting insights into speciation mechanisms and timing, and biogeography at multiple taxonomic levels; those results would in turn allow for broad comparisons with other widely distributed avian genera (e.g., Voelker, 1999, 2002).

Turdus species are also morphologically diverse in plumage. With 52 described subspecies (Ripley, 1964; Clement, 2000), *Turdus poliocephalus* epitomizes the plumage diversity evident across the rest of the genus. For example, entirely black plumage has evolved multiple times not only in *poliocephalus* subspecies, but across *Turdus* species as well. Further insight into the validity of *poliocephalus* as an umbrella species uniting its described races is also needed. Collar (2005) for example has suggested that the Taiwanese race (*niveiceps*) might be recognized as a distinct species based on sexual plumage dimorphism. Jones and Kennedy (in press) found the Philippine subspecies to be monophyletic, but additional sampling from across the range of *poliocephalus* is needed, as is comprehensive sampling of *Turdus* species to determine if many of the races of *poliocephalus* are monophyletic.

Beyond species relationships within the genus, need for systematic treatment of *Turdus* is evident from confusion over the limits of the genus. Both White (1962) and Hall and Moreau (1970) placed the African bar-winged forest thrushes in *Turdus*. This placement was not recognized by either Irwin (1984) or Dowsett and Dowsett-Lemaire (1993), who maintained bar-winged thrushes in the genus *Zoothera*. For Dowsett and Dowsett-Lemaire this appears to have been more for convenience than for systematic reasons, as they state that their decision to retain *Zoothera* for bar-winged thrushes was "to reduce to manageable size the large genus *Turdus*" (1993; p. 353). Klicka et al. (2005) have subsequently shown that bar-winged thrushes (*Zoothera*) and *Turdus* are distinct from one another, but they were unable to assess the monophyly of *Turdus*. Given the large number of species and the plumage diversity found within *Turdus*, it is possible that *Turdus* could prove to be polyphyletic when additional species are included in molecular studies. Recent works on thrush genera have clearly provided evidence that generic limits need reassessment (e.g., Voelker and Spellman, 2004; Klicka et al., 2005; Outlaw et al. 2007).

Additional issues with delimiting *Turdus* have been evident. The Groundscraper Thrush (*litsipsirupa*) has alternatively been placed in *Turdus*, in *Zoothera*, or in the monotypic genus *Psophocichla* (Ripley, 1964; Hall and Moreau, 1970; Irwin, 1984). Klicka et al. (2005) found this species to fall between *Turdus* and a clade of Afro-Asian *Zoothera*, which is consistent with its morphological intermediacy between those groups. However, the limited number of *Turdus* species included in that study (10) could not reject the possibility that *litsipsirupa* is more appropriately considered as a member of *Turdus*.

Ripley (1952) felt that the monotypic genera *Nesocichla* (Tristan Thrush) and *Cichlherminia* (Forest Thrush) were primitive thrush genera likely close to *Turdus*, and he also questioned the validity of the genus *Platycichla*. Ridgley and Tudor (1989) have also questioned this treatment, noting that *Platycichla* was named solely because it is smaller than most *Turdus*. All three of these genera have clearly been shown to be invalid as they fall within *Turdus* (Klicka et al., 2005), but their relationships within the genus remain unclear.

Our goals in this paper are threefold. First, we provide a molecular assessment of the relationships of 92% of the described species of *Turdus* (Sibley and Monroe, 1990), using mitochondrial (mtDNA) sequence data from the ND3, ND2, and cytochrome *b* genes. Second, our sampling allowed us to determine the systematic positions of *Platycichla*, *Nesocichla*, *Cichlherminia*, and *Psophocichla*. Third, we assessed the validity of previously described relationships within *Turdus*, and we offer preliminary insights into the monophyly of *poliocephalus*.

2. Materials and methods

2.1. Sampling strategy and outgroup taxa

Our sampling of *Turdus* species represents sequence data from 60 of the 65 extant species recognized by Sibley and Monroe (1990) (Table 1). Based on recent molecular studies, we also include *Turdus smithi* (Bowie et al., 2003) and as well as *abyssinicus* and *helleri* (Bowie et al., 2005). We further include all four species from three genera (*Nesocichla*, *Platycichla*, and *Cichlherminia*) shown to fall inside *Turdus* (Klicka et al., 2005). We sequenced multiple samples for species when possible (Table 1).

Of the five species of *Turdus* missing from this study, one (*graysoni*) is restricted to Tres Marias Island (Mexico), one is from South America (*subalaris*), two have highly restricted ranges in northeastern Africa and Arabia (*tephronotus* and *menachensis*), and one is isolated on a few small Japanese islands (*celaenops*).

As outgroup taxa we initially used *Zoothera gurneyi*, *Z. piaggiae*, and *Psophocichla litsipsirupa*; the latter was previously determined to be the closest extant relative of *Turdus* (Klicka et al., 2005). Following an initial analysis with these outgroups we subsequently used the basal-most *Turdus* species as outgroups (see below) to improve estimates of gene evolution rates in subsequent analyses.

2.2. Laboratory protocols

DNA was extracted using the DNeasy Kit according to the manufacturer's instructions (Qiagen Inc., Valencia,

Table 1
Species, museum voucher specimen or tissue number, and collecting localities for specimens examined

Species	Sample source[a]	Collection locality
Turdus		
[*libonyanus*] *pelios*	AMNH DOT-2038	Liberia
	LSU B27170	Cameroon
[*libonyanus*] *libonyanus*[b]	UWBM 52923	South Africa: KwaZulu Natal
[*olivaceus*] *olivaceofuscus*[b]	PFI[c]	Sao Tome
[*olivaceus*] *smithi*[b]	MBM 5877	South Africa: Free State
[*olivaceus*] *abyssinicus*[b]	RB 294[c]	Kenya: Ngong Hills
[*olivaceus*] *helleri*[b]	UG TT20[c]	Kenya: Taita Hills
[*olivaceus*] *bewsheri*[b]	RMCA	Comoro Islands
[*unicolor*] *hortulorum*[b]	UWBM 51161	Russia: Primorskiy Kray
[*unicolor*] *unicolor*[b]	AMNH 831316	Nepal: Malde, NW of Betrabati
[*unicolor*] *dissimilis*	USNM 585844	India: Arunachal Pradesh
cardis[b]	OMNH A2672	Japan
albocinctus	USNM 536210	Nepal
torquatus[b]	ZMUC MFJ1[c]	Denmark: Christiansoe Island
boulboul	AMNH 831319	Nepal: Malde, NW of Betrabati
merula	LSU B1335	Denmark: Vestjaelland
poliocephalus[b]	1: FMNH 357456	Philippines: Mindanao
	2: UWBM 58814	Solomon Islands: Rennell
	3: AMNH DOT-264	Solomon Islands: Kolombangara
	4: LSU B45769	Vanuatu: Santo (FLMNH voucher)
rubrocanus	UMMZ 182199	India: Assam
kessleri	ANSP 182082	China: Szechwan
feae	MICH 182284	India: Manipur
obscurus	CMNH 37056	Philippines: Negros
[*pallidus*] *pallidus*[b]	UWBM 47110	Russia: Khabarovskiy Kray
[*pallidus*] *chrysolaus*[b]	LSU B16992	Japan: Nagano Prefecture
ruficollis[b]	UWBM 46282	Russia: Respublika Gorno-Altay
naumanni[b]	UWBM 59779	Mongolia: Dornod Aymag
pilaris[b]	LSU B1330	Denmark: Vestjaelland
iliacus	LSU B13478	Germany: Schleswig-Holstein
philomelos[b]	LSU B13468	Germany: Schleswig-Holstein
mupensis	ANSP 174093	China: Tseo-Jia-Keo
viscivorus[b]	UWBM 46429	Kazakhstan: Almaty Oblysy
aurantius	FMNH 331094	Jamaica
plumbeus[b]	LSU B11518	Puerto Rico
chiguanco[b]	MBM 5431	Argentina: Prov. Jujuy
nigrescens[b]	LSU B19929	Costa Rica: Cartago Province
fuscater	LSU B7678	Peru: Huanuco Department
[*serranus*] *infuscatus*	MBM 13588	Guatemala: Dept. Quezaltenango
[*serranus*] *serranus*	LSU B22823	Bolivia: La Paz Department
[*serranus*] *nigriceps*[b]	MBM 6562	Argentina: Prov. Tucuman
reevei[b]	LSU B5258	Peru: Lambayeque Department
olivater	LSU B7448	Venezuela: Amazonas Territory
maranonicus[b]	ANSP 1705	Ecuador: Zamora Chinchipe
fulviventris[b]	ZMUC NK12[c]	Ecuador/Peru border
rufiventris	LSU B25910	Paraguay: Caaguazú Department
falcklandii	LSU B14010	Chile: Mag. y Antartica Chilena
leucomelas	LSU B14719	Bolivia: Santa Cruz Department
amaurochalinus[b]	LSU B13004	Bolivia: Santa Cruz Department
plebejus	MBM 4322	Nicaragua: Matagalpa
ignobilis	LSU B7255	Peru: Loreto Department
lawrencii	LSU B27886	Peru: Loreto Department
[*fumigatus*] *obsoletus*[b]	LSU B12002	Ecuador: Esmeraldas Province
[*fumigatus*] *fumigatus*	STRI SV-TFU1[c]	St. Vincent: Cumberland Valley
[*fumigatus*] *hauxwelli*	LSU B18551	Bolivia: Santa Cruz Department
grayi[b]	MBM 6620	Honduras: Departamento Copan
[*nudigenis*] *nudigenis*[b]	STRI MA-TNU1[c]	Martinique: Vendredi
[*nudigenis*] *maculirostris*	LSU B7740	Ecuador: Bolivar Province
haplochrous	LSU B7620	Bolivia: Beni Department
jamaicensis	FMNH 331099	Jamaica
[*albicollis*] *assimilis*[b]	MBM 7017	Honduras: Departamento Copan
[*albicollis*] *albicollis*	LSU B22690	Bolivia: La Paz Department

Table 1 (*continued*)

Species	Sample source[a]	Collection locality
[*rufopalliatus*] *rufopalliatus*	UNAM	Mexico
swalesi[b]	AMNH 832872	Dominican Republic
[*migratorius*] *migratorius*	MBM 5137	United States: Colorado
[*migratorius*] *rufitorques*	MBM 10754	Guatemala: Dept. Quezaltenango
Nesocichla eremita[b]	PFI[c]	Tristan da Cunha
Platycichla leucops	ZMUC NK4-110291	Ecuador: Loja
Platycichla flavipes	AMNH DOT-2943	Venezuela: Bolivar
Cichlherminia lherminieri	STRI DO-CLH1[c]	Dominica
Psophocichla litsipsirupa	MBM 5853	South Africa: Northwest Province
Zoothera gurneyi	FMNH 356762	Tanzania: Tanga, Korogwe Dist.
Zoothera piaggiae	FMNH 355649	Uganda: Nyabitaba

Species taxonomy follows Sibley and Monroe (1990). Brackets indicate members of presumed superspecies complexes.

[a] Sample sources, abbreviations as follows: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences, Philadelphia; CMNH, Cincinnati Museum of Natural History; ZMUC, Zoologisk Museum Copenhagen; FLMNH, University of Florida Museum of Natural History; FMNH, Field Museum of Natural History; LSU, Louisiana State University Museum of Natural Science; MBM, Marjorie Barrick Museum of Natural History, UNLV; OMNH, Osaka Museum of Natural History; PFI, Percy FitzPatrick Institute of African Ornithology, Cape Town; RMCA, Royal Museum for Central Africa, Belgium; STRI, Smithsonian Tropical Research Institute; UG, University of Ghent; UMMZ, University of Michigan Museum of Zoology; UNAM, Universidad Nacional Autónoma de México; UWBM, University of Washington Burke Museum; USNM, U. S. National Museum.

[b] Species for which multiple samples were sequenced to confirm species identity or monophyly.

[c] Unvouchered samples consisting of blood or purified DNA.

California), or via cesium chloride gradient (Dowling et al., 1990). Toepad samples were also extracted with the DNeasy Kit, but with the following modifications: initial incubation at 55 °C for 2–4 days, with 20 μl of proteinase K added each 24 h period; two elution steps were carried out with 50 μl of elution buffer. Toepad samples were extracted either in a separate laboratory, or under a fume hood.

Following typical protocols and PCR conditions, the cytochrome *b* gene was in general amplified and sequenced with primers described in Voelker (1999, 2002). The ND2 gene was amplified and sequenced with primers described in Hackett (1996) and Johnson and Sorenson (1998). The ND3 gene was amplified and sequenced following the methodology described in Bowie et al. (2005). In most cases where frozen tissue was available, genes were amplified as single units; toepad samples were amplified in smaller pieces. In general, fragments were amplified in 50 μl reactions under the following conditions: denaturation at 94 °C followed by 40 cycles of 94 °C for 45 s, 50 °C for 45 s, and 72 °C for 1 min. Cycles were followed by a 10 min extension at 72 °C and a 4 °C soak. Exact reaction conditions and primers used in obtaining gene sequences varied across individuals, particularly for toepad samples; specific conditions and primers for individuals are available upon request. Products were purified using a Qiagen PCR purification kit following manufacturer's instructions. Standard 20 μl sequencing reactions were performed using 3 μl of BigDye (ABI). Products of these reactions were run out on Long Ranger (BMA) acrylamide gels on ABI 377 automated sequencers.

Complementary strands of each gene were sequenced. Sequences were aligned unambiguously using Sequencher 4.2.2 (GeneCodes Corporation, Madison, Wisconsin). No gaps, insertions, or deletions were apparent in the sequence alignments, and all data readily translated to amino acids. Sample preparation and sequencing was conducted in the Barrick Museum DNA Laboratory and at the University of Memphis. All analyses were performed at the University of Memphis.

We analyzed 1000 base pairs (bp) of cytochrome *b*, 333 bp of ND3 and 1035 bp of ND2 (2368 total bp) for all taxa except *dissimilis* and *albocinctus* (lacking complete cytochrome *b* and ND2), *mupinensis* and *rubrocanus* (represented by partial cytochrome *b* only) and *feae* (represented by partial ND2 only) due to amplification difficulty. These five taxa were represented by DNA extracted from museum study skins. Sequences are available on GenBank under Accession Nos. DQ910930–DQ911121.

2.3. Phylogenetic protocols

We conducted three sets of analyses. In the first, we used *Zoothera* and *Psophocichla* as outgroup taxa to establish which species or clade of species were at the base of *Turdus*, and their relative phylogenetic positions. *Psophocichla* is the sister to *Turdus*, but it is rather distant from *Turdus* in sequence divergence (Klicka et al., 2005). Our goals for this set of analyses were first, to establish the relationships of the basal members, or basal clade, of *Turdus* and then use these basal members as outgroups to the remaining species (see below), and second to establish the clades to which *mupinensis*, *feae*, *albocinctus*, and *rubrocanus* belonged. Modeltest 3.04 (Posada and Crandall, 1998) was used to select the most appropriate model of sequence evolution for all ML analyses. Hierarchical likelihood ratio tests (LRTs) and the Akaike Information Criteria identified GTR+I+Γ as the model that best fit our data.

Due to the size of our dataset, we used a successive approximations approach (Swofford, 2000; Voelker and Edwards, 1998) to obtain a ML estimate of phylogeny. An initial likelihood search was started from a LogDet Neighbor-joining topology and the parameters indicated by Modeltest. After over 25,000 rearrangements without a change in likelihood score, parameters were re-estimated on

the resulting tree, and a subsequent search was initiated using this topology and the re-estimated parameters as a starting point. This process was repeated a second time, running over 40,000 rearrangements without a change in likelihood score or parameters. We reran this same analysis but excluded the data-poor species *mupinensis*, *feae*, *albocinctus*, and *rubrocanus*; removing these species did not otherwise change relationships on the tree (see Section 3).

Support for individual nodes in our estimate of relationships was conducted using three methodologies; due to the limited amount of sequence data for *mupinensis*, *feae*, *albocinctus*, and *rubrocanus*, we removed these taxa from these analyses. In our first analysis assessing support we used Bayesian inference (Rannala and Yang, 1996) as implemented in the program MRBAYES 3.0 (Huelsenbeck and Ronquist, 2001). In Bayesian analysis the GTR+I+Γ model of sequence evolution was again employed, and genes were allowed to vary in parameter estimates. All Bayesian analyses were initiated from random starting trees. Four Markov chain Monte Carlo chains were run for two million generations and sampled every 100 generations, yielding 20,000 trees. The first 500,000 generations (=5000 trees) were discarded to ensure that chain stationarity had been reached. To ensure that the Markov chain was sampling from the posterior distribution, this procedure was repeated two more times. Because all three runs converged on the same distribution, all trees (excluding those sampled before burn-in) were combined yielding a total of 45,000 topologies from which a 50% majority rule consensus tree was reconstructed. Nodes having posterior probability values of 95% or greater on this tree were deemed significantly supported.

Our second assessment of support relied on maximum likelihood bootstrap analysis implemented in TREEFINDER (Jobb, 2005). We used the GTR+I+Γ model with 500 pseudoreplicates. Finally, we used MP heuristic bootstrap (PAUP*), and employed both codon specific, and gene specific transition/transversion ratio weighting schemes. Both MP analyses employed 100 pseudoreplicates, each with 10 random addition sequence replicates.

In the second set of analyses, we used *Turdus philomelos* and *viscivorous* (see Section 3) as outgroups relative to the remaining *Turdus* species and again performed all tests and analyses described above. After initial analysis, we again removed *mupinensis*, *feae*, *albocinctus*, and *rubrocanus* as their positions in the resulting trees matched their positions from the previous analysis. This pruning allowed us to better estimate sequence evolution rates for *Turdus*, thereby contributing the least amount of homoplasy to the dataset. For this reduced dataset, Modeltest 3.04 (Posada and Crandall, 1998) again identified the GTR+I+Γ model of nucleotide evolution as the best fit, which we incorporated into our ML analysis. We again performed all measures assessing internal support on this reduced dataset. We used the Shimodaira and Hasegawa (1999, S-H test) test to assess all previous hypotheses of relationships among taxa, relative to our results from this set of analyses (see below).

Finally, we repeated all above described analyses to resolve the positions of *feae*, *albocinctus*, and *rubrocanus* within the Eurasian clade. For this analysis, we used six species from other clades as outgroups (see Section 3).

3. Results

3.1. Sequence characteristics

As expected, the ND2 and ND3 genes were more variable than cyt-*b* (Table 2). Over the combined sequence, 1120 sites were variable (47%), and of these 918 (39%) were parsimony informative. Overall, 94% of third position sites varied. For cyt-*b*, uncorrected percent sequence divergence ranged from 0.6% between *migratorius* and *rufitorques* to 12.5% between *philomelos* and *fuscator*. Corresponding values from ND2 and ND3 are greater in all comparisons.

Table 2
Overall and codon-position specific dynamics of the ND3, ND2 and cyt-*b* genes

Position	Number of sites	Variable sites	Parsimony informative	%A	%C	%G	%T	χ^2	Ts/Tv	α
ND3										
1st	111	47	36	20.0	36.0	23.0	21.0	$P=1.0$	14.69	0.341
2nd	111	17	13	17.0	28.0	13.0	42.0	$P=1.0$	5.17	0.169
3rd	111	108	100	40.0	45.0	5.0	10.0	$P=0.99$	11.24	1.847
All	333	172	149	20.0	36.0	23.0	21.0	$P=1.0$	7.98	0.907
ND2										
1st	345	130	92	33.0	30.0	18.0	19.0	$P=1.00$	12.3	0.564
2nd	345	74	40	16.0	34.0	11.0	39.0	$P=1.00$	9.47	0.411
3rd	345	327	299	37.0	43.0	8.0	12.0	$P=1.00$	14.73	2.091
All	1035	531	431	29.0	35.0	13.0	23.0	$P=1.00$	14.44	0.836
Cyt-*b*										
1st	334	79	49	23.0	30.0	25.0	22.0	$P=1.00$	6.27	0.673
2nd	333	35	11	20.0	27.0	13.0	40.0	$P=1.00$	1.68	0.648
3rd	333	303	278	41.0	46.0	4.0	9.0	$P=0.99$	10.75	1.70
All	1000	417	338	28.0	34.0	14.0	24.0	$P=1.00$	7.87	0.800

Mean base composition was averaged over all sequences, and χ^2 tests of nucleotide homogeneity were performed. Transition–transversion ratio (Ts/Tv) and α (among-site rate variation) values were estimated simultaneously for each partition.

Nucleotide composition and bias varies only slightly across genes. All display an excess of cytosine, and a deficiency of guanine (Table 2). Tests of homogeneity of base frequencies across ingroup taxa were not significant for any gene, or codon position within each gene region (Table 2).

Codon position-specific alpha shape parameter (α) estimates indicate, not surprisingly, that among-site rate heterogeneity is a likely problem in this dataset. However, rate heterogeneity across genes are surprisingly similar to one another (Table 2) suggesting that analyses might not be overly biased by using a single rate under maximum likelihood criteria (as PAUP* currently does).

3.2. Taxonomic position of Psophocichla, philomelos, mupinensis, and viscivorous

Because the GTR+I+Γ model is more resistant to error caused by homoplasy than are MP analyses (Kuhner and Felsenstein, 1994; Huelsenbeck, 1995; Swofford, 2000), we had a priori considered our ML topology (Fig. 1) to be our best estimate of phylogenetic relationships. *Psophocichla litsipsirupa* is clearly basal to *Turdus*, and it differs substantially in sequence divergence from both basal *Turdus* members (10.1–12.0% uncorrected cytochrome *b*) and *Zoothera* (see Klicka et al., 2005).

Turdus philomelos, *mupinensis*, and *viscivorous* are clearly the basal extant members of *Turdus*, and therefore not members of the larger Eurasian clade. Bayesian analysis indicates posterior probabilities of 1.0 for the position of these taxa relative both to other *Turdus*, and to outgroup taxa (Fig. 1). An alternative topology forcing *philomelos* and *viscivorous* to be sister to the co-distributed Eurasian clade (see below) was rejected as a significantly worse estimate of relationships ($P = 0.007$).

3.3. Systematics of the Central American-Caribbean clade, and the position of Cichlherminia and plebejus

The largely Central American-Caribbean clade contains 10 species (Fig. 1). Four species (*infuscatus*, *nigrescens*, *rufitorques*, and *rufopalliatus*) are found in Central America and four (*aurantius*, *plumbeus*, *jamaicensis*, and *swalesi*) are found on Caribbean islands. Additionally, *migratorius*, the only widespread species found in North America north of Mexico is part of this clade, as is *iliacus*, a Eurasian-distributed species (Fig. 1).

The Caribbean species are not reciprocally monophyletic. *Turdus aurantius* and *plumbeus* are instead sister to the Central American clade, which also includes *migratorius* (Fig. 1). Forcing the Caribbean taxa to be monophyletic just fails to be a significantly worse estimate of relationships ($P = 0.056$).

Maximum likelihood analysis clearly places *Turdus iliacus* in this otherwise New World clade, rather than in the large Eurasian clade, or at the base of the genus with other Eurasian distributed species. A tree forcing *iliacus* to be part of the Eurasian clade is rejected as a significantly worse estimate of topology ($P = 0.035$).

Cichlherminia lherminieri, a Caribbean endemic, is clearly a member of *Turdus*. Our analyses place this species near *plebejus* (Central America), at the base of the South American-Eurasian clade divergence. Forcing these two species to be part of the Central American-Caribbean clade is a significantly worse estimate of topology ($P < 0.001$).

3.4. Systematic relationships of African taxa

Six of the African species that we included in this study have historically been considered subspecies of *Turdus olivaceus*, *libonyanus* or *pelios* (e.g., Hall and Moreau, 1970). In our analyses, five of these species do form a clade, although this association is not strongly supported (Fig. 1). Within the clade, sister relationships for *abysinnicus* and *helleri*, as well as *olivaceus* and *smithi* are strongly supported. *Turdus olivaceofuscus*, endemic to the islands of São Tomé and Príncipe in the Gulf of Guinea, is clearly part of this clade.

The sixth member of the "*olivaceus*" complex included in our analyses is *bewsheri* (Comoro Islands). Our results indicate that this species is not associated with other members of the "*olivaceus*" complex, and that it is instead sister to *libonyanus*. Our samples of *libonyanus*, representing the subspecies *peripheris* and *tropicalis* were sisters, as were our samples of *pelios*, representing the subspecies *saturatus* and *chiguancoides* (not shown). Thus, while we continue to pursue subspecies relationships and boundaries in these and other African thrush taxa (Voelker and Bowie, unpublished data), it appears that the placement of *libonyanus* and *pelios* here (Fig. 1) is not simply a function of misidentified samples. It further appears that at least the above subspecies may be properly ascribed to species in recent taxonomic treatments (see Clement, 2000).

3.5. Systematics of the Eurasian clade

All analyses resulted in virtually identical topologies for this clade (Figs. 1 and 2).

Although ML analyses place *Turdus merula* at the base of the Eurasian clade, Bayesian analysis does not support this placement (Figs. 1 and 2). Maximum likelihood and MP bootstrap analysis similarly failed to provide support for this placement. However, an alternative topology forcing *merula* to be sister to *viscivorous* and *philomelos* was rejected as a significantly worse estimate of relationships ($P = 0.005$).

Our reanalysis of the Eurasian clade (Fig. 2) to determine the relationships of the data-poor species *rubrocanus* and *feae*, and somewhat data-poor *albocinctus* was highly congruent with our overall estimate of *Turdus* relationships (Fig. 1). The only topological change was a sister relationship indicated for *kessleri* and *pilaris*. This relationship is moderately supported by ML bootstrap (Fig. 2), whereas in the overall analysis the systematic position of both species was unsupported by any measure (Fig. 1). Given the reduced number of species with concomitant reduction in

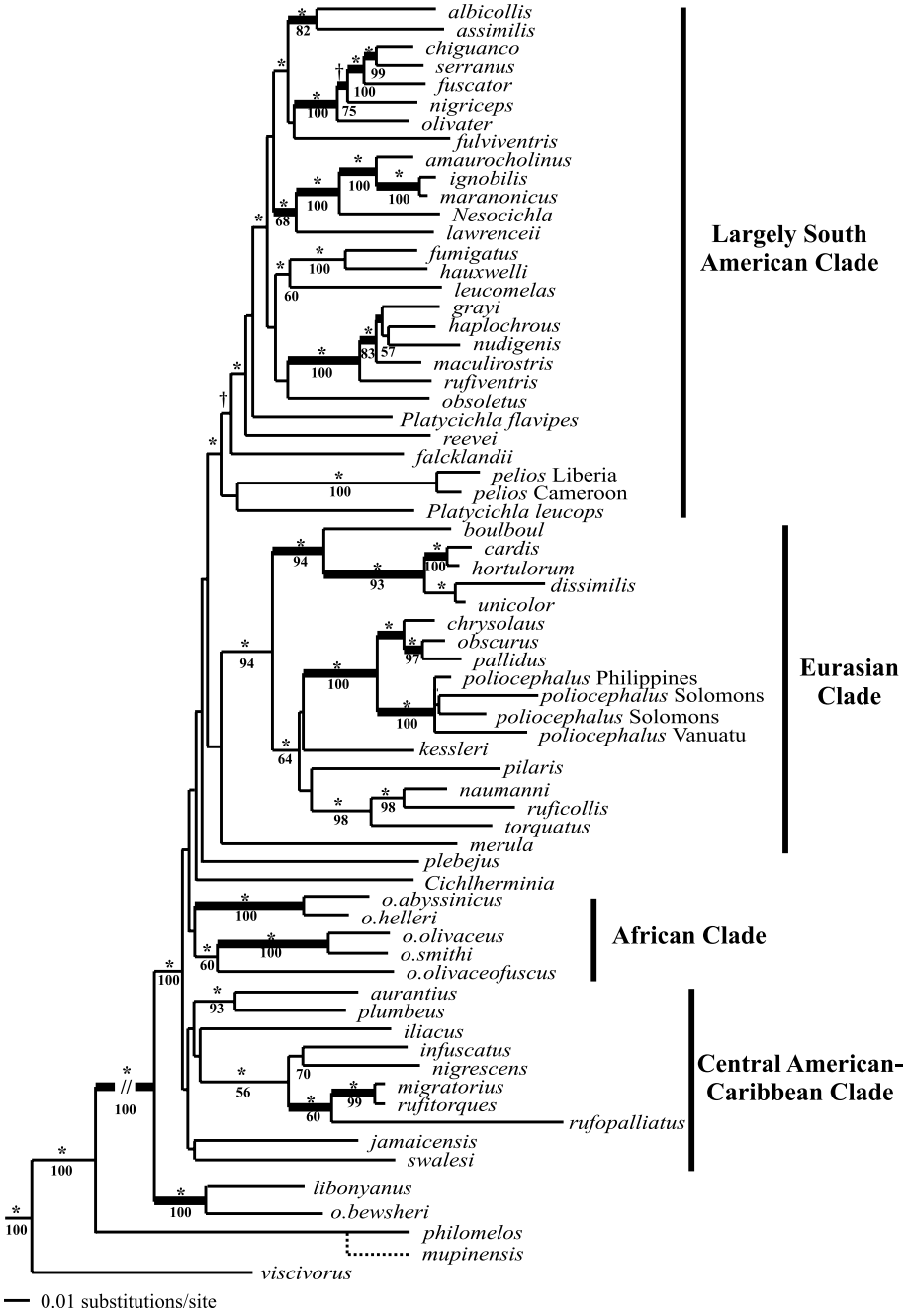

Fig. 1. ML phylogeny of *Turdus* thrushes, based on combined analysis of the ND3, ND2, and cytochrome *b* genes. Outgroups include several *Zoothera* species, and *Psophocichla*. Asterisks above nodes indicate Bayesian posterior probability support of 0.95 or greater based on the GTR+I+Γ model of nucleotide evolution; a dagger indicates support between 0.90 and 0.94. Thickened nodes indicate maximum parsimony bootstrap support of >50%, based on 100 repetitions with 10 random additions and weighted by gene specific parameters. Numbers below nodes indicate maximum likelihood bootstrap support (>50%), based on the GTR+I+Γ model of nucleotide evolution. *Turdus mupensis*, represented by just 300 bp of data, is attached to the phylogeny by a dashed line to indicate its position based on initial searches only. The node leading to the basal three taxa is substantially reduced in length (indicated by"//").

parameter variability, we feel that a sister relationship for *kessleri* and *pilaris* is probably a better estimate of relationships than that depicted in Fig. 1.

Turdus rubrocanus and *albocinctus* are placed as sisters in the phylogeny, with posterior probability support of 0.91; several posterior probability support values in the sister clade also approach significance. However, if *rubrocanus* (only 300 bp of cyt-*b*) is removed from Bayesian analysis, posterior probability values reach significance (see also Fig. 1). *Turdus feae* is sister to *pallidus* in this analysis, with *obscurus* basal to them (Fig. 2).

Our MP trees differed only in placing *rubrocanus* and *albocinctus* at the base of the Eurasian clade (consensus of nine equally parsimonious trees); this is likely due to the reduced number of base pairs associated with those taxa.

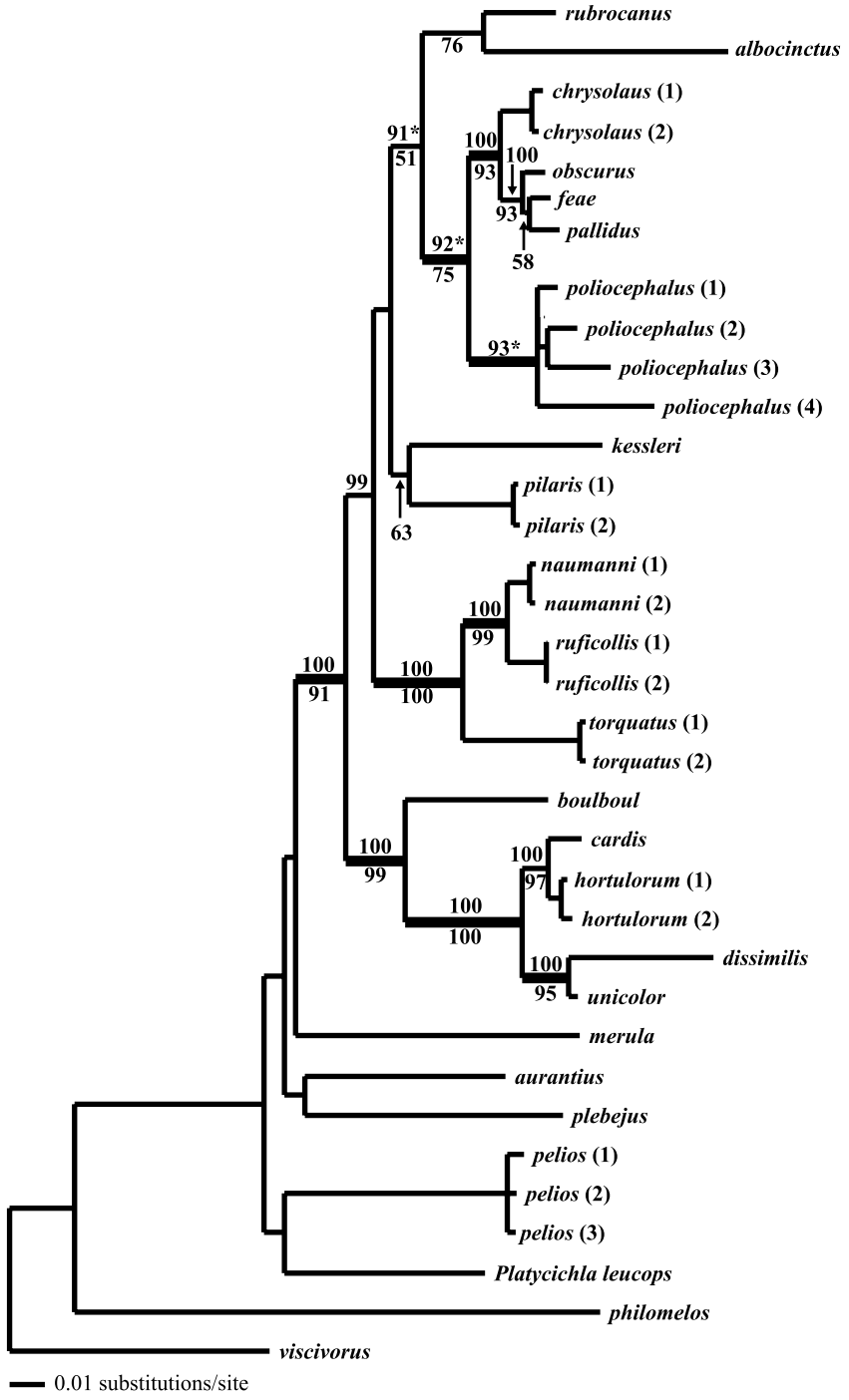

Fig. 2. ML phylogeny of the Eurasian *Turdus* clade, rooted with *viscivorous* and *philomelos*, and representatives of other major clades. Numbers above nodes are Bayesian posterior probability values. Numbers followed by (∗) denote posterior probability values that increase to a value of 95% or greater if *rubrocanus* (represented by just 300 bp of sequence data) is removed from analyses. Thickened nodes indicate maximum parsimony bootstrap support of >80%, except the *cardis-unicolor* node (73%) and *dissimilis-unicolor* node (60%). Numbers below nodes indicate maximum likelihood bootstrap support (>50%), based on the GTR+I+Γ model of nucleotide evolution. With the exception of *poliocephalus*, nodes joining multiple exemplars of a given species were supported with a posterior probability value of 1.0, and bootstrap values greater than 92%.

Over 50 morphologically distinct and geographically isolated subspecies are ascribed to *Turdus poliocephalus* (Island Thrush; Clement, 2000). We included four morphologically diverse and geographically disjunct subspecies of *poliocephalus* in this study (Table 1), and they did form a monophyletic clade (Fig. 1). However, uncorrected cyt-*b* sequence divergence ranged from 1.1% (between *katanglad* (Philippines) and *rennellianus* (Solomons)) to 3.0% (between *vanikorensis* (Vanuatu) and *kulambangrae* (Solomons)), indicating degrees of separation as great as between other species in our analyses.

Tests of competing topologies could not reject the possibility of a monophyletic *pallidus* ($P = 0.62$) or that of a

monophyletic *unicolor* ($P = 0.46$) (see Table 1 for relevant taxa). However, both Bayesian posterior probabilities and ML and MP bootstrap analysis suggest that these taxa are not sister to one another (Figs. 1 and 2).

3.6. Systematics of the largely South American clade

Both levels of analysis identified a largely South American clade with Bayesian support of 1.0, and most nodes within the clade received strong Bayesian, ML bootstrap or MP bootstrap support (Fig. 1). Unsupported nodes in this clade generally appear to be the result of rapid speciation following colonization of South America, and species relationships throughout the clade are recovered in all of our analyses.

Turdus pelios from Africa is clearly part of this clade, as is *Nesocichla eremita* which is endemic to Tristan da Cunha in the central South Atlantic. Three Central American species (*grayi*, *assimilis*, and *obsoletus*) are constituent members of this clade as well, and each represents an independent colonization of Central America from South America (Fig. 1).

Tests of competing topologies generally failed to reject traditional taxonomic arrangements (Sibley and Monroe, 1990). Again, this is not surprising given the conservative nature of this test, and the short branch lengths separating the taxa involved in the competing arrangements. We could not reject a monophyletic *fumigatus* (*fumigatus* + *hauxwelli* + *obsoletus*; $P = 0.75$) or a monophyletic *nudigenis* (to include *maculirostris*; $P = 0.91$). A monophyletic *serranus* (to include *infuscatus*) is clearly rejected; *infuscatus* is in a distinctly different clade and simply moving *serranus* to the base of the South American clade results in a significantly worse estimate of topology ($P < 0.001$). Not only do they clearly not define a valid genus, the two "*Platycichla*" species can be rejected as being sisters ($P = 0.047$).

4. Discussion

4.1. Taxonomic overview and the basal Turdus assemblage

In this study, we sampled 92% (60 of 65) of the species suggested by Sibley and Monroe (1990) to comprise the genus *Turdus*. We additionally included several former subspecies of the *Turdus olivaceus* complex that have recently been recognized as warranting specific status based on molecular systematic studies (Bowie et al., 2003, 2005). We further included all four members of the genera *Nesocichla*, *Platycichla*, and *Cichlherminia*. Previous molecular analyses placed these "genera" within *Turdus* (Klicka et al., 2005); relationships of the constituent members are identified here for the first time.

We included *Psophocichla litsipsirupa* to determine whether this species is in fact a member of *Turdus*, based on our more comprehensive sampling of *Turdus* relative to that of Klicka et al. (2005). Our molecular results clearly suggest that *litsipsirupa* is not a *Turdus*. Given this result we suggest that it should remain in the monotypic genus *Psophocichla* which provides a link between *Turdus* and Afro-Asian *Zoothera* (see also Klicka et al., 2005).

One interesting feature of the placement of *philomelos*, *mupinensis*, and *viscivorous* at the base of *Turdus* is that they are morphologically very similar in plumage. Based on this similarity, Klicka et al. (2005) had predicted that *philomelos* and *mupinensis* would fall out near *viscivorous* at the base of *Turdus*. Our results confirm that prediction (Fig. 1; Klicka et al., 2005). Morphology throughout the rest of *Turdus* may not to be evolutionarily informative (Voelker et al., unpublished).

The distant relationship of *philomelos*, *mupinensis*, and *viscivorous* to all other members of *Turdus* could be interpreted as sufficient reason to assign them a different generic name. However, *viscivorous* is the type for the genus (Ripley, 1964), therefore given the shape of the tree, only this species would remain in *Turdus*. Other genus names, now synonymies of *Turdus*, would be available to encompass at least some of the clades discussed below. For example, *Merula* could serve as the generic name of the Eurasian clade (type *Merula nigra* = *Turdus merula*), *Planesticus* for the Central American-Caribbean clade (type = *Turdus jamaicensis*), *Cossyphopsis* for the largely South American clade (type = *Turdus reevei*), and *Afrocichla* for the African clade (type = *Turdus olivaceus*) (Ripley, 1964). Recognizing these names would, we argue, add unnecessary taxonomic complexity to a biologically cohesive group. Therefore, we recommend maintaining all currently designated *Turdus* species in that genus.

Our results therefore suggest at least two Eurasian radiations of *Turdus* thrushes: a basal assemblage of three species, and a larger clade of at least 18 species. In addition, our analyses clearly indicate that the Eurasian distributed *Turdus iliacus* is not part of either of these clades but belongs instead to a New World clade.

4.2. Central American-Caribbean clade, and the position of Cichlherminia and plebejus

The Central American subclade itself falls inside two radiations of Caribbean taxa, *aurantius* + *plumbeus* and *jamaicensis* + *swalesi* (Fig. 1). Although the latter relationship is not well supported, the two species endemic to Jamaica (*aurantius* and *jamaicensis*) are clearly not sisters. The Caribbean taxa are probably not reciprocally monophyletic (Fig. 1), and forcing them to be monophyletic is very nearly rejected as a significantly worse estimate of topology.

Until very recently, confusion was evident as to where the monotypic genus *Cichlherminia* (Caribbean) belonged within true thrushes. Ripley (1952) depicted the genus as being basal to a *Turdus*-*Catharus* split, whereas Sibley and Monroe (1990) placed *Cichlherminia* between *Zoothera* and *Myadestes* in their linear classification. In a molecular study of true thrush genera, Klicka et al. (2005) clearly showed

that *Cichlherminia* belongs in *Turdus*, and our results place it near *plebejus* at the base of a major divergence resulting in the largely South American clade and a Eurasian clade. A somewhat surprising result from our study is that *Cichlherminia* and *plebejus* (Central America) were not part of the Central American-Caribbean clade. The overall lack of monophyly among all the Central American (several are included in the South American clade) or all the Caribbean taxa is clearly indicative of complex speciation patterns in this geographic region.

Turdus migratorius, the only *Turdus* species occurring widely throughout North America north of Mexico, falls within a subclade containing four Central American species. A sister relationship between *migratorius* and *rufitorques* is highly supported (Fig. 1), and these two species have been considered to constitute a superspecies based on behavioral and vocal (but not plumage) similarities (Collar, 2005). Indeed, uncorrected sequence divergence between *migratorius* and *rufitorques* is just 0.6% for each gene, which is plainly indicative of recent speciation, and therefore a recent colonization of North America by *migratorius*.

Turdus iliacus (western Eurasia) is part of the Central American-Caribbean clade, although this relationship is not well supported. Irrespective of this lack of support, *iliacus* is clearly not a member of either the basal Eurasian radiation, or the more recently derived and speciose Eurasian clade.

4.3. African taxa

Our results indicate that the "*olivaceus*" complex is not monophyletic. These results are consistent with previous molecular analyses of the "*olivaceus*" complex (Bowie et al., 2005). Our results also reject a superspecies relationship between *olivaceus*, *pelios*, *libonyanus*, *bewsheri*, and *olivaceofuscus* (Hall and Moreau, 1970), and the possibility of a *pelios*, *libonyanus*, and *tephronotus* superspecies (Collar, 2005), despite not having *tephronotus* represented in our study.

In general, authors have and continue to recognize the species status of each of these "superspecies" members (e.g., Ripley, 1952, 1964; Clement, 2000; Collar, 2005). However, Ripley (1952, 1964) had recognized *pelios* as a race of *olivaceus*, despite its initial description as a species (Bonaparte, 1851 in Ripley, 1964). Based on song, Dowsett and Dowsett-Lemaire (1980) recognized *Turdus pelios* as a distinct species. Habitat associations further serve to draw a distinction between *pelios* and *olivaceus* (Urban et al., 1997). Our analyses strongly reject *pelios* being related to any other African taxa, and instead show it to be a well-supported member of the largely South American clade.

Our analyses strongly support a sister relationship between *libonyanus* and *bewsheri*. To the best of our knowledge, a close relationship between these species has not been suggested historically; a recent molecular study (Bowie et al., 2005) did suggest this relationship. Although they are morphologically quite different, *libonyanus* is the only *Turdus* species that is distributed along the coast of Mozambique, which is directly west of the Comoro Islands on which *bewsheri* is endemic.

4.4. The Eurasian clade

With the exception of four species, all Eurasian *Turdus* species included in our analyses formed a clade (Figs. 1 and 2). Overall, relationships within this clade were strongly supported. There is no evidence that subclades within the Eurasian clade are the product of within-region speciation events. For example, Himalayan species are scattered throughout the clade (*albocinctus*, *boulboul*, *dissimilis*, and *kessleri*) rather than being a monophyletic assemblage. By extension, western and eastern Palearctic species also do not form monophyletic clades.

We were unable to reject the validity of several superspecies designations using the Shimodaira-Hasegawa test (see Section 3). However given the conservative nature of this test, and the proximity of relevant species to one another in phylogeny, this was not surprising. We note that various support measures suggest that these superspecies are not valid. Our results clearly suggest that *dissimilis* is not a race of *hortulorum*, which is in line with the conclusions of Sibley and Monroe (1990) and Clement (2000). Neither Vaurie (1959) nor Ripley (1964) had recognized *dissimilis* as specifically distinct. These results, along with results from other studies (e.g., Voelker, 2002) suggest that the taxonomic rank of superspecies is often misleading and probably superfluous.

In all analyses, *Turdus merula* was placed as the basal member of the Eurasian clade. While this placement did not receive strong support, *merula* is clearly not related to the basal assemblage of Eurasian species. The lack of support may be a function of what appears to be a very rapid radiation in this part of the phylogeny, which in turn appears to be a function of major intercontinental movements (Voelker et al. in preparation). Collar (2005) has recently suggested that several *merula* subspecies be considered species based on differences in song (*maximus*; Tibetan Blackbird) or plumage and vocalizations (*simillimus*; Indian Blackbird). Inclusion of these forms may serve to provide stronger support for the placement of *merula*, should they in fact be close relatives or at least nearer to *merula* than are the other members of the Eurasian clade.

Our limited sampling of the Island Thrush (*poliocephalus*) suggests that this species is monophyletic. Collar (2005) had predicted this, and had suggested that this taxon would likely prove of recent origin. Our results support his suggestion of recent origin, but fail to support his suggestion that *poliocephalus* was close to *merula* (Collar, 2005). A larger sampling of taxa, focused on Philippine races and based on ND2 data, supports monophyly of *poliocephalus* (Jones and Kennedy, in press). Even wider geographic sampling of races using both ND2 and cyt-*b* data further supports this monophyly relative to other described *Turdus* species (Voelker, unpublished data).

The *poliocephalus* race *niveiceps* (Taiwan) may be the most obvious candidate for species status, as it is generally thought to be the only race with pronounced sexual dimorphism (Collar, 2005; at least one other exists (Peterson, unpublished data)); this race is not yet represented in our analyses. In a broad reassessment of morphology across *poliocephalus* races, Peterson (unpublished data) has defined 12 major plumage types, and 38 distinct diagnosable forms. This is lower than the roughly 50 described subspecies, but clearly supportive of extreme morphological variation in a single species. Given the morphological diversity, disjunct nature of subspecies (islands), lack of migratory behavior and sequence variation, *Turdus poliocephalus* should arguably be split into multiple species.

Based on several different phenotypic characters and vocal differences, Collar (2005) has recognized *Turdus atrogularis* as being a distinct species, rather than retaining it as a subspecies of *ruficollis*. Of the two *ruficollis* samples that we included in our analyses, one is from well within the Russian range of *atrogularis* (UWBM 56813, Tyumenskaya Oblast'), while the other is from just west of the westernmost edge of the range defined for *ruficollis* (UWBM 46282, Avtonomnaya Respublika Gorno-Altay). These two individuals, both of which are males with greatly enlarged testes, have zero differentiation for the genes we sequenced. Collar (2005) noted that the two forms intergrade over a wide area (which would include Gorno-Altay), and suggested that further study is warranted; we agree with this suggestion, and feel that a formal split was premature. We were unable to assess similar splits made for taxa previously considered part of *naumanni* with the samples included in this study. These splits are also based on morphology or song, and at least with respect to *naumanni*, broad intergradation of forms exists (Collar, 2005).

4.5. The largely South American clade

All South American *Turdus* species fall into to a large, almost entirely New World clade. The African species *pelios* and several Central American taxa are included in this clade, as are several species formerly considered to belong to different genera (see below). This largely South American clade is well supported, as are most nodes within the clade. While biogeography is not a focus of this study, we point out that within this clade there is a subclade composed entirely of Andean species (the *fulviventris* clade; Fig. 1). These Andean species overlap to varying degrees in geographic distribution, but tend to differ in elevational distribution or habitat. The potential role of these factors in driving speciation in *Turdus* is being explored elsewhere (Voelker et al., in preparation).

We were not able to reject a monophyletic *fumigatus* or a monophyletic *nudigenis* superspecies group. However we note that there is strong Bayesian support for the nodes separating *fumigatus* "lineages" (Fig. 1, Table 1). Thus, we feel that *obsoletus* is clearly not part of *fumigatus*, a separation recognized by Meyer de Schauensee (1966, 1970), but not Ripley (1964). We have followed Sibley and Monroe (1990) in recognizing *fumigatus* and *hauxwelli* as distinct but, given their sister relationship in our phylogeny (Fig. 1) they could also be conspecific, as suggested by Hellmayr (1934). However, we note that they are genetically quite divergent (6.5% uncorrected cyt-*b*), and that they are sympatric in Brazil which Gyldenstolpe (1945 in Clement, 2000) felt was sufficient to warrant their separation. A monophyletic *serranus* superspecies is clearly rejected, as *infuscatus* is clearly part of the Central American-Caribbean clade.

Platycichla clearly belongs in *Turdus*, and the two "*Platycichla*" species are not sisters (Fig. 1). *Platycichla* was originally erected due to differences in morphology relative to *Turdus*. Goodwin (1957) had argued that the differentiation was sufficient to warrant continued recognition of *Platycichla*. Ridgley and Tudor (1989) however noted that the morphological differentiation was very weak, and suggested the genus was not valid. Ripley (1952) had similarly rejected the validity of *Platycichla*. The nests of the two *Platycichla* species differ from one another, but the nest shape and materials as well as egg coloration of *leucops* is very similar to several *Turdus* species (Londoño, 2005). We recommend that *Platycichla* be subsumed into *Turdus* and that the two species retain their specific epithets.

While *Nesocichla eremita* is generally similar to *Turdus* in shape and structure (see Clement, 2000), it also has short rounded wings and a reduced keel typical of island species (Rand, 1955; Ryan and Moloney, 1991). One notable exception to the overall similarity is an unusual brush-tipped tongue which it uses to extract egg contents (Lowe, 1923). *Nesocichla* has been considered a primitive relative of *Turdus*, with probable origins in the New World (Rand, 1955). A New World origin is supported here, as *eremita* is clearly part of a largely South American *Turdus* radiation (Fig. 1). Therefore, we suggest that this species be renamed *Turdus eremita*.

5. Conclusion

The speciose genus *Turdus* is clearly paraphyletic as currently described. The genera *Platycichla*, *Cichlherminia*, and *Nesocichla* are not valid, and should be subsumed into *Turdus*. To the best of our knowledge, the specific epithet and common name of each of these species would be available under *Turdus*. Although we did not have all *Turdus* species (*sensu* Sibley and Monroe, 1990) represented in our study, we feel it highly unlikely that inclusion of the five missing species, or other *Turdus* taxa (see Collar, 2005) will change this conclusion. We also feel it unlikely that including these species will change the relationships of the major clades and groups discussed here.

What are the likely placements of the five species missing from our analyses? Based solely on geography, we would predict that *subalaris* (South America) will fall within the largely South American clade, that *graysoni* (Mexico) will be part of the Central American-Caribbean clade, that

celaenops (Japan) will be part of the Eurasian clade, and that *tephronotus* (northeast Africa) will be part of the African clade. Given that interchange between Africa and Eurasia has occurred multiple times within other genera (Voelker, 1999, 2002), the position of *menachensis* is more difficult to predict, as its distribution (southwest Arabia) makes it a candidate for membership in either the African clade or the Eurasian clade. Due to the general lack of morphological cohesiveness within clades, we refrain from more specific predictions regarding sister relationships of these missing species.

This study may be one of just a very few cases where a passerine genus has actually increased in size as the result of molecular systematic studies. The overwhelming trend has been documentation of polyphyly (and thus genus-level splitting) for genera that are large (e.g., *Nectarinia*, Irwin, 1999; Bowie, 2003), medium (e.g., *Francolinus*, Bloomer and Crowe, 1998; *Phylloscopus*, Olsson et al., 2005; *Zoothera*, Klicka et al., 2005) and even rather small (e.g., *Alethe*, Beresford, 2003).

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