



Short Communication

Systematics of *Zoothera* thrushes, and a synthesis of true thrush molecular systematic relationshipsGary Voelker^{a,*}, John Klicka^b^a Department of Biology, University of Memphis, 3700 Walker Avenue, Memphis, TN 38152, USA^b Barrick Museum of Natural History, Box 454012, University of Nevada Las Vegas, 4504 Maryland Parkway, Las Vegas, NV 89154-4012, USA

1. Introduction

The true thrushes (Turdinae; Sibley and Monroe, 1990) are a speciose lineage of songbirds, with a near-cosmopolitan distribution. Following the systematic placement of true thrushes as a close relative of Old World flycatchers and chats (Muscicapinae) by the DNA–DNA hybridization work of Sibley and Ahlquist (1990), a number of molecular systematic studies have focused on various aspects of true thrush relationships. These studies have included phylogenetic assessments of genera membership in true thrushes, assessments of relationships among and within true thrush genera, and the recognition of “new” species (Bowie et al., 2003, 2005; Outlaw et al., 2003; Voelker and Spellman, 2004; Klicka et al., 2005; Miller et al., 2007; Voelker et al., 2007).

Despite improved hypotheses of true thrush relationships, several problems remain. One problem involves several genera that are either monotypic (*Hylocichla*, *Ridgwayia*, *Chlamydocaera*), that contain just a few species (*Cochoa*, *Sialia*, *Neocossyphus*), or that appear to be distantly related to other genera (*Sialia*, *Myadestes*, *Neocossyphus*). While each of these genera have been phylogenetically placed within well supported true thrush subclades (Klicka et al., 2005), their sister relationships are not well supported within those clades. This issue might be attributable to a lack of dense taxon sampling across true thrush species, in previous analyses.

Another problem involves the use of improper or “too distant” outgroups, which can affect resolution within single genera. For example, in a study of species relationships within the genus *Catharus*, Outlaw et al. (2003) used as outgroups two species each from the genera *Turdus* and *Zoothera*. It has subsequently been shown that neither was an appropriate genus to root *Catharus*, as both are distantly related (Klicka et al., 2005). More recently, Miller et al. (2007) used a single member of the genus *Sialia* to root their analyses of the genus *Myadestes*, despite both morphological and molecular analyses which suggested that *Neocossyphus* is probably a close relative, if not the sister taxon to *Myadestes* (Ames, 1975; Olson, 1989; Pasquet et al., 1999; Klicka et al., 2005).

Questions regarding inter-specific relationships remain within both *Catharus* and *Myadestes*. At the inter-generic level, Klicka et al. (2005) conducted analyses of true thrush relationships, using the *Sialia*–*Myadestes*–*Neocossyphus* clade (hereafter referred to as the “*Sialia* clade”) as the outgroup. While clearly a true thrush lineage, the *Sialia* clade is very divergent from other true thrush lineages. Homoplasy caused by the use of this divergent clade as a root could explain at least some of the as yet unresolved inter-generic relationships within true thrushes.

Our main objective in this study is to use dense taxon sampling across true thrushes to resolve inter- and intra-generic relationships that remain unclear. We also hope to determine the extent of “*Zoothera*” polyphyly and identify a core clade of true *Zoothera* species. To accomplish these goals, we include new and existing sequence data from true thrush species, and use as outgroups true thrush genera that are clearly sister-groups to those groups containing unresolved nodes.

2. Materials and methods

2.1. Taxon sampling and molecular methods

For inclusion in our analyses, we sequenced the following species: *Zoothera everetti* (Borneo; American Museum 648434, toepad), *Z. margaretae* (Makira Island; University of Kansas, CEF 996, tissue), *Z. monticola* (India; Academy of Natural Sciences 174641, toepad), and *Cochoa purpurea* (Vietnam; Moscow State Museum Zoological Museum, 5(#9), tissue). We extracted whole genomic DNA from each sample using DNeasy (Qiagen, Valencia, CA) following manufacturer’s protocols for tissue and blood.

The ND2 and cytochrome *b* mitochondrial genes were isolated and amplified using standard PCR protocols. Primers designed for other thrushes were used for PCR and sequencing (Voelker and Spellman, 2004; Outlaw et al., 2007) and the following thermocycling parameters were used: an initial 2 min denaturation at 94 °C followed by 35–40 cycles of: 94 °C for 45 s (denature), 50–54 °C for 45 s (anneal), and 72 °C for 2 min (extension). A final extension of 72 °C for 10 min and a 4 °C soak was used to insure reaction termination. Products were purified using the Qiaquick PCR purification kit (Qiagen, Valencia, CA). We performed 20 µl cycle sequencing reactions on purified PCR product using BigDye dye-labeled terminators (ABI). Reactions were purified and target DNA precipitated

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using Isopropanol precipitation. Cycle sequencing reactions were run out on an ABI377 automated sequencer. Each sample was sequenced for light and heavy strands.

All sequence data (1041 bp ND2 and 998 bp *cyt b*) were aligned using Sequencher v. 4.5 (Gene Codes, Ann Arbor, MI) and by eye. For toepad samples, no fewer than two separate DNA extractions and sequencing reactions were performed, at intervals up to several months apart. Repeated toepad extractions yielded identical sequences. Relevant sequences are deposited in GenBank: EU862262–EU862265.

In addition to those species listed above, we included in our analyses previously published true thrush sequence data (Outlaw et al., 2003; Voelker and Spellman, 2004; Klicka et al., 2005; Voelker et al., 2007; Miller et al., 2007; and Voelker and Outlaw, in press). In total, these studies along with the species included here represent 88% (129/147) of all true thrush species recognized by Sibley and Monroe (1990).

2.2. Phylogenetic analysis

Several analyses were conducted on the combined ND2 and cytochrome *b* dataset. Modeltest 3.04 (Posada and Crandall, 1998) was used to select the most appropriate model of sequence evolution in each analysis. Hierarchical likelihood ratio tests (LRTs) and the Akaike Information Criterion identified GTR + I + Γ as the best fit model for our data. PAUP* (Swofford, 2000) was used for all ML searches.

For each analysis discussed below, Bayesian inference was implemented using MRBAYES 3.0 (Huelsenbeck and Ronquist, 2001) to assess nodal support. We used the GTR + I + Γ model of sequence evolution, and genes were partitioned to allow each to vary in parameter estimates. Three Bayesian analyses were initiated from random starting trees, with four MCMC chains running for two million generations and sampled every 100 generations, yielding 20,000 trees. The first 5000 trees from each analysis were discarded to ensure chain stationarity. Remaining trees 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 were deemed significantly supported. We further assessed node support using maximum likelihood bootstrap analysis in TREEFINDER (Jobb, 2005), using the GTR + I + Γ model with 500 pseudo-replicates.

Our first analysis was to determine to which clade each species we sequenced belonged. For this analysis, we used the *Sialia* clade as an outgroup as it is the sister clade to all other true thrush taxa (Klicka et al., 2005), and thus a more appropriate outgroup than any songbird genus outside the true thrushes. An initial ML search using estimated parameters was started from a HKY-85 neighbor-joining topology. This search was allowed to run for 5000 rearrangements without a change in likelihood score. Parameters were then re-estimated on the resulting tree, and a subsequent search was begun from that tree. After an additional 10,000 rearrangements without change, the search was stopped. This analysis succeeded in placing all newly sequenced species into the overall true thrush phylogeny; subsequent analyses placed these species in the same positions.

We then conducted analyses aimed at better resolving intra-generic relationships within the focal *Zoothera* clade, and within *Catharus*. To resolve *Zoothera* relationships, we used all or part of the *Sialia* clade as an outgroup and excluded all other thrush genera. To examine relationships within *Catharus*, we used *Ixoreus* as an outgroup to root all other members of its clade (*Entomodestes*, *Cichlopsis*, *Ridgwayia*, *Hylocichla*, and *Catharus*; Fig. 1) while excluding all other thrush genera. Alternatively, we excluded the *Sialia*

clade and used the basal *Zoothera* clade to root the phylogeny (all remaining taxa as the ingroup), allowing another perspective on both ingroup and *Zoothera* relationships. In a final analysis we used the clade with *Ixoreus* in a basal position to root its sister clade (*Turdus*, *Geokichla*, *Cochoa*, and *Chlamydochaera*).

3. Results and discussion

3.1. *Zoothera* systematics and biogeographic comments

We define here relationships among a core group of true *Zoothera* thrushes, and further clarify relationships among other true thrush genera. Our results confirm previous studies which suggest that “*Zoothera*” as currently defined is polyphyletic (Fig. 1).

Klicka et al. (2005) had suggested that as many as three groups could be involved, and subsequently Voelker and Outlaw (in press) have demonstrated that just two well resolved clades should be recognized. Including the present study, analyses of these two clades encompass 29 of 35 (83%) taxa currently designated as “*Zoothera*” species, with the Afro-Asian clade (Klicka et al., 2005) being best defined as *Geokichla* (Voelker and Outlaw, in press; Fig. 1). Retention here of *Zoothera* for our focal clade of Austral-Asian thrushes is based on the position of *monticola*, the type species, within it (Fig. 1; Mayr et al., 1964). Given the strong basal support for *Zoothera* (Fig. 1), we do not anticipate any further division of this genus.

Phylogenetic analyses strongly support the placement of all three newly sequenced *Zoothera* (*everetti*, *margaritae*, *monticola*) in a clade of Asian *Zoothera* species, which falls between the basal *Sialia* clade and all other true thrush lineages (Fig. 1). We were unable to increase basal support for *Zoothera* by using *Neocossyphus* and *Myadestes* as outgroups, while excluding the more distantly related *Sialia* and all other genera in ML analyses. However, using this methodology did provide increased support for relationships in the *dauma* subclade (Fig. 1). Phylogenetic analyses confirm that the morphological characteristic of scaly-appearing body plumage appears to be a unifying feature of *Zoothera*. Based on this feature, we suspect that the species we were unable to sample (*turipavae*, *machiki*, *horsfieldi*, and *major*) are part of *Zoothera*, and not *Geokichla* or any other true thrush genus. Using all other genera (exclusive of the *Sialia* clade) to root *Zoothera* did not improve support for relationships within *Zoothera*.

Despite extensively overlapping distributions and generally similar appearance of the basal-most *Zoothera* species (*mollissima* + *dixonii* and *marginata* + *monticola*), linear classification schemes (Ripley, 1952; Mayr et al., 1964) have not placed them near each other. Instead, they have been separated by the widespread Asian species *dauma* (Ripley, 1952; Mayr et al., 1964), and the island species *talaseae* and *margaretae* (Mayr et al., 1964), all three of which differ substantially in plumage appearance (Clement, 2000). The latter two are highly isolated geographically (Fig. 2).

Zoothera everetti is placed between the four basal taxa and the strongly supported *andromedae* clade (Fig. 1). However, this placement is not well supported, and we expect that such support will be difficult to obtain. This species has an extremely limited distribution (northern Borneo), and thus a small population size. Rapid genetic divergence following colonization of an island should be expected (Clegg et al., 2002) and that, along with small population size, generates comparatively short internodes that are generally difficult to support.

Zoothera andromedae is distributed across Southeast Asian Islands. It occurs from Sumatra to Timor, with a major disjunction between those islands and its secondary distributional area in the Philippines (Clement, 2000). Our samples of this species (one

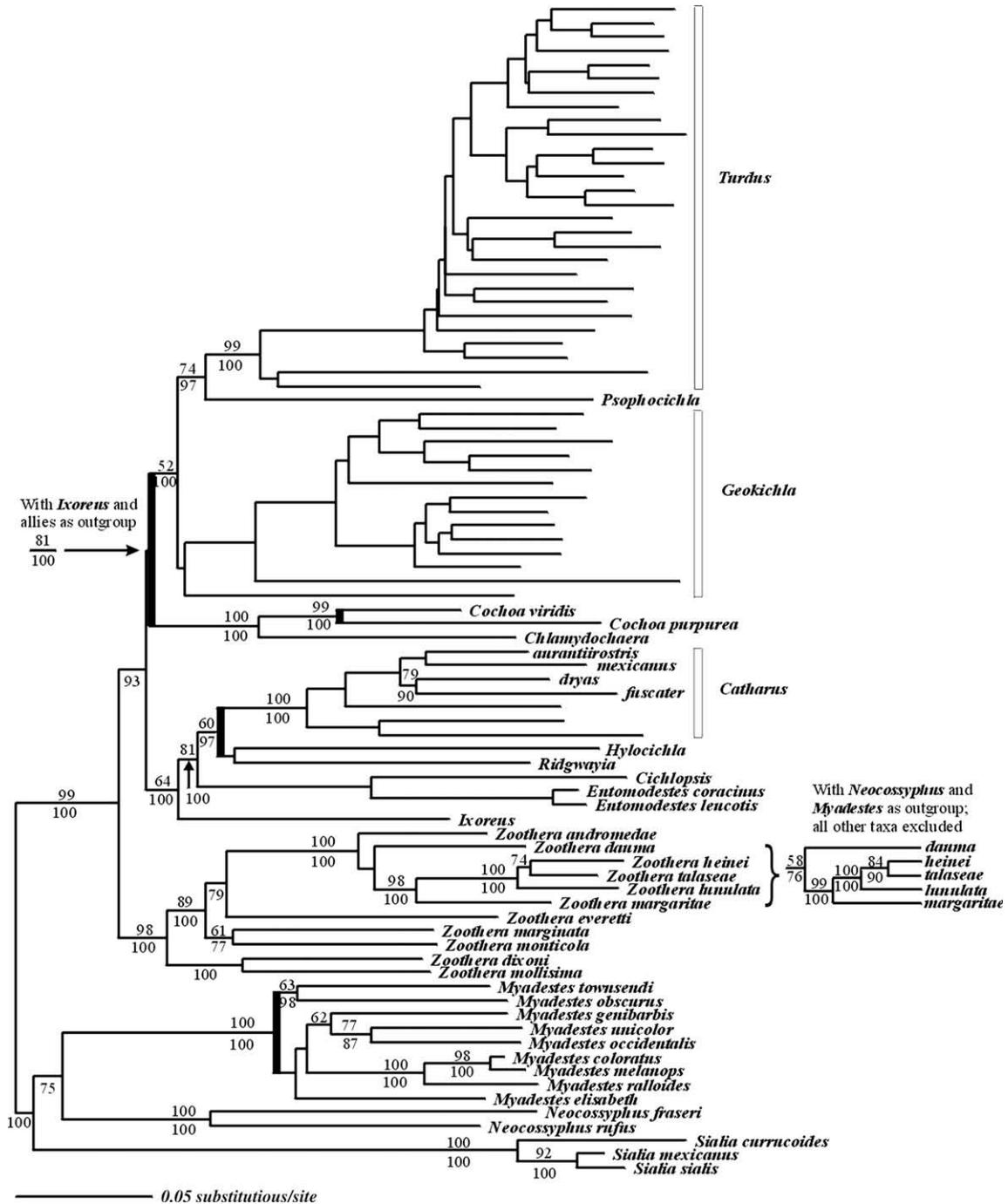


Fig. 1. Maximum likelihood estimate of true thrush relationships. Numbers at nodes indicate ML bootstrap support values >60% (top) and Bayesian posterior probability values >75% (below). Thick bars indicate nodes that were not supported in Klicka et al. (2005), or where the addition of species indicates that those species are here systematically placed in the genus to which they are taxonomically assigned.

Philippines, one Timor) were virtually identical genetically (0.008% uncorrected distance overall). This would suggest a recent range expansion by *andromedae*.

Although the position of *Zoothera dauma* is not strongly supported (Fig. 1), our results indicate that it is not sister to taxa that have at times been considered subspecies of it (*lunulata* and *heinei*; Ripley, 1952; Mayr et al., 1964). Instead, *margaritae* is placed between *dauma* and these “subspecies”, with *talaseae* falling between *lunulata* and *heinei* (although support is marginal). This result is somewhat surprising given the strong morphological similarity between *dauma*, *lunulata*, and *heinei* (Clement, 2000).

Our results indicate a Himalayan origin for *Zoothera*, as the four basal-most species in the genus all have ranges centered there (Fig. 2). Both *marginata* and *monticola* have ranges that extend east to Vietnam. Distributions across the tree generally suggest a Himalayan to southeast-most Asia to Southeast Asian Island to Australian pattern of colonization in the genus (Fig. 2). However, colonization does not proceed in a simple downstream pattern from continent to islands. The phylogenetic position of *dauma* suggests a recolonization of mainland Asia (Fig. 2), and because *dauma* is the only long-distance migrant in the genus (Clement, 2000), further suggests that this is another example of long-distance migra-

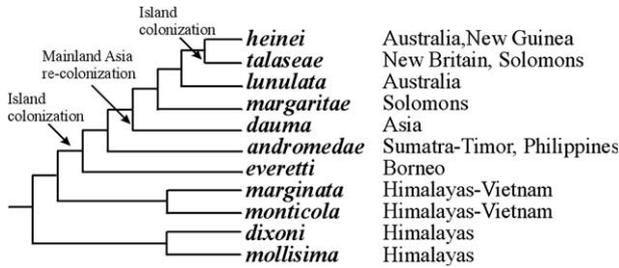


Fig. 2. Distribution of *Zoothera* species, which suggest a Himalayan origin for the genus. Southeast Asian Islands were colonized from mainland Asia, and secondarily from Australia. Mainland Asia was recolonized once.

tion evolving from sedentary ancestors. The alternative explanation for this result, that subsequent lineage divergences and distributions (*margaretae*, *lunulata*, *talaseae*, *heinei*) are the result of migratory dropoff(s) of ancestral *Zoothera* is unlikely, as *dauma* does not winter across the Southeast Asian Islands (except the Philippines).

As further evidence of a complex biogeographic history across the islands, there have been several colonizations of the Solomons. The first of these followed initial colonization of Southeast Asian islands, but the other is the result of colonization from Australia (Fig. 2). Similarly complex patterns of colonization in this region have been reported in diverse avian lineages (Filardi and Moyle, 2005; Outlaw and Voelker, 2008; Voelker and Outlaw, in press), and all have shown mainland recolonizations following initial colonization of Southeast Asian Islands.

3.2. *Cochoa*

All analyses strongly support the placement of *Cochoa purpurea* as sister to *viridis* (Fig. 1). Although they do share a few morphological features (e.g., tail color), there is otherwise little to unite *Cochoa* species, except that *beccarii* (not sampled) looks like a morphological cross between them (Collar, 2005). Inclusion of *beccarii*, and *azurea* are clearly needed to confirm the monophyly of *Cochoa* as currently defined; *azurea* is morphologically distinct from other *Cochoa* in both size and plumage (Collar, 2005). Our results further serve to support the position of *Cochoa* as a true thrush genus (Voelker and Spellman, 2004), rather than a chat (Saxicolini) genus where they have historically been taxonomically placed (Collar, 2005).

3.3. *Catharus*

Several relationships within *Catharus* remain somewhat speculative. Our analyses did suggest marginal ML bootstrap support for a sister relationship between *dryas* and *fuscater* (Fig. 1), and between *bicknelli* and *minimus* (62% ML bootstrap) (not shown). Both of these relationships have been recovered previously, but were not well supported (see Klicka et al., 2005). A *dryas*–*fuscater* relationship conflicts with the results of Outlaw et al. (2003), but we note that this earlier study did not use the closest relatives of *Catharus* as outgroups.

3.4. *Sialia* and *Myadestes*

Our results differ from previous works with regard to relationships within both *Sialia* and *Myadestes*. Here, we have shown a strong sister relationship between *Sialia mexicanus* and *sialis*; Klicka et al. (2005) had suggested that *sialis* was sister to *currucoides*. We suspect that this change is the result of increased numbers of *Myadestes* species in this study as compared to Klicka et al. (who used just one species), and that this increased sampling limited potential long-branch attraction issues.

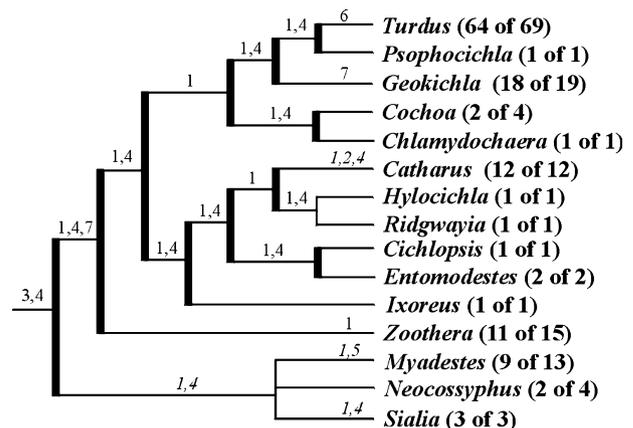
Within *Myadestes*, our results indicate a different set of relationships than those recently presented by Miller et al. (2007) (Fig. 1). Most important of these is a strong basal sister relationship between *townsendi* and *obscurus*; Miller et al. identified *townsendi* alone as the sister to all other *Myadestes*. We acknowledge that Miller et al. used additional data, which should increase the reliability of their tree over ours. Indeed, we are unable to provide support for many relationships within the genus. However, our results suggest that *Neocossyphus* is possibly sister genus to *Myadestes* (Fig. 1), and this possibility has been reported elsewhere (Pasquet et al., 1999). In defining *Myadestes* relationships, Miller et al. relied on a single *Sialia* species as an outgroup, most likely due to our previous study which suggested, but could not support, a *Sialia*–*Myadestes* sister relationship. Thus, long-branch attraction issues could be confounding species relationships in *Myadestes*.

Overall, and despite increased taxon sampling, the relationships among genera in the *Sialia* clade remain unclear. Neither the study of Klicka et al. (2005), which suggested a sister relationship between *Sialia* and *Myadestes*, or our analyses, which suggests a *Neocossyphus*–*Myadestes* sister relationship, were successful in providing significant support values for those relationships. Thus, relationships among these genera are best recognized as a polytomy for the time being (Fig. 3).

3.5. An overview of true thrush relationships

A number of recent studies have dealt with the systematic relationships among and within true thrush genera (summarized in Fig. 3). Overall, few questions remain regarding relationships among genera included herein.

Our results generally agree with those of Klicka et al. (2005), with two important exceptions. First, we show strong support for a clade comprised of *Catharus*, *Hylocichla*, and *Ridgwayia* (Fig. 1), which had not been previously established (see Klicka et al., 2005). We remain unable to resolve the relationships among these



1. This study
2. Outlaw et al. 2003
3. Voelker and Spellman 2004
4. Klicka et al. 2005
5. Miller et al. 2007
6. Voelker et al. 2007
7. Voelker and Outlaw submitted

Fig. 3. Summary of true thrush relationships, based on recent mtDNA molecular systematic studies. Numbers at nodes refer to individual studies (see legend), and numbers on terminal branches indicate studies dealing with intra-generic relationships. Italicized numbers indicate conflict between the studies listed. Thick bars indicate nodes that are strongly supported by at least one of the reference(s) listed. For each genus, the current number of recognized species is listed, followed by the number included in systematic study to date. Three genera (*Platycichla*, *Nesocichla*, and *Cichlherminia*) have been subsumed into *Turdus* (Klicka et al., 2005; Voelker et al., 2007), and *Geokichla* has been split from *Zoothera* (Voelker and Outlaw, in press).

three genera, yet feel that the issue of *Hylocichla* as *Catharus* can be laid to rest. *Hylocichla* is sister to *Ridgwayia* (Klicka et al., 2005; this study), and while nodal support is lacking for this relationship, *Catharus* species clearly form a cohesive strongly supported clade that is genetically distant.

Second, we were able to establish the position of the *Cochoa–Chlamydochaera* clade. We accomplished this by excluding the more distantly related lineages of *Sialia*, *Myadestes*, *Neocossyphus*, and *Zoothera*, and by using *Ixoreus* as an outgroup (Fig. 1). Our results strongly support the placement of *Cochoa–Chlamydochaera* between the New World radiation of *Ixoreus* and allies, and the Old World based radiations of *Geokichla*, *Turdus*, and *Psophocichla* (Figs. 1 and 3).

It is clear that little else can be done to resolve relationships with the genes we, and others, have used to resolve relationships in the true thrush clade thus far. The deep divergences within the *Sialia* clade suggest that nuclear genes might be relevant to resolving both genus relationships, and relationships within each genus (but see Nylander et al. 2008). Additional sampling could also prove useful in cementing relationships: we note that we were unable to obtain reliable sequence for *Cataponera* and *Geomalia* (both monotypic) and *Heinrichia* (several species), all of which are presumed true thrush genera (Clement, 2000). However, as all three of the latter genera are from Southeast Asia, we think it unlikely that their inclusion will resolve the issues that remain, as those issues generally involve relationships among New World genera (Fig. 3).

Acknowledgments

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