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Phylogenetic relationships between *Turdus* species: Mitochondrial cytochrome *b* gene analysis

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The phylogeny of the widespread *Turdus* genus (Passeriformes, Muscicapidae, Turdinae) still remain controversial. We investigated phylogenetic relationships within the *Turdus* assemblage using the mitochondrial cytochrome *b* gene, with an emphasis of the taxomomic status of *T. mupinensis*. Nineteen species from *Turdus* were analyzed as ingroups, and *Myiophoneus caeruleus* and *Monticola cinclorhynchus* were selected as outgroups. Altogether 991bp gene fragments from these species were obtained, in which 368 variable sites and 278 parsimony informative sites were identified. Phylogenetic analyses indicated that the genus *Turdus* is paraphyletic and that it forms a well supported clade including three mostly monotypic genera (*Cichlherminia*, *Platycichla* and *Nesocichla*). Three types of phylogenetic tree (MP, ML and Bayesian) support two steady clades (Europe–Asia clade and South America clade) in *Turdus*. Species from the Europe–Asia clade include *T. rubrocanus*, *T. pallidus*, *T. obscurus*, *T. naumanni*, *T. torquatus*, *T. boulboul* and *T. cardis,* while species from the South America clade include *P. leucops*, *N. eremita*, *T. chiguanco*, *T. fuscater*, *T. rufiventris* and *T. grayi*. Applying a substitution rate of 2% per million years, the divergence of the Europe–Asia clade was estimated to have occurred approximately 0.95–3.30 Mya, the South America clade divergence occurring at around 1.2–3.7 Mya. Our results also revealed that *T. mupinensis* was located at the base of all three phylogenetic trees, which suggested that *T. mupinensis* might be the most primitive taxon among all ingroup clades. The divergent time between *T. mupinensis* and other *Turdus* species was estimated at occurring 3.6–5.7 Mya. The high divergence in mtDNA and obvious differences in morphology suggest that *T. mupinensis* may be considered as a species in a distinctive genus from *Turdus*.

1. Introduction

The genus *Turdus* covering 65 species is the largest group in Turdinae. It is widespread, being distributed across most of the world (Sibley & Monroe 1993). Recent studies about relationships among *Turdus* species are based mostly on morphological and ecological characters. Many taxa are clearly identifiable from these approaches only with great difficulty. Very few molecular studies have been done on the phylogenetic relationships within *Turdus* species, although some studies that attempted to work out the relationships at higher taxonomic levels (such as subfamily, family or order) included some of turdid species (Sibley & Monroe 1990, Voelker & Spellman 2004). Klicka *et al*. (2005) used the cyt *b* and ND2 mitochondrial (mtDNA) sequence data to investigate the phylogenetic relationships within the true thrushes (Turdinae), but 10 species included in *Turdus* were not adequate for relationship analysis. Therefore, studies on phylogeny and relationship of *Turdus* species are still necessary. In addition, there is a question about the taxonomic status of *Turdus mupinensis* (Eastern Song Thrush), which is an endemic species to China (Lei *et al*. 2002). When the cyt *b* gene was used to reconstruct the 16 genera phylogenetic tree within the Turdinae, an unexpected finding was that *T. mupinensis* does not lie within the genus *Turdus*, but instead it forms a single clade (Pan *et al*. 2006).

The mitochondrial cytochrome *b* gene is the most widely used gene for phylogenetic research, and has been the most prevalent source of sequence data in avian studies (Johnson 2001, Klicka *et al*. 2001, Thomassen *et al*. 2003, Sheldon *et al*. 2005). In this study, we use DNA sequences from a segment of mitochondrial cytochrome *b* gene to: (1), Test the monophyly of the genus *Turdus*. (2), Reconstruct a phylogenetic hypothesis for the constituents of this group. (3), Explore the origin and time of divergence of some major groups in *Turdus*. (4), Assess the validity of taxonomic status of *T. mupinensis*.

2. Materials and methods

2.1. Sampling strategy

Nineteen species in *Turdus* were collected in the study. In attempting to better view the phylogenetic relationships of *Turdus* species, we also included some species from other genera (*Zoothera*, *Cochoa*, *Cichlherminia*, *Catharus*, *Platycichla* and *Nesocichla*). *Myiophoneus caeruleus* and *Monticola cinclorhynchus* were used to root the phylogenetic trees. Ten species were sampled in our lab and the other sequences were downloaded from GenBank (Table 1).

2.2. DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from tissue, blood, feather or toe-pad using BS424 or DNeasy Tissue Kit (the latter was used to extract toe-pad) following the manufacturer's protocol and prepared for subsequent polymerase chain reaction (PCR).

The primers used for amplification are H15299 (Hackett 1996) and L14841 (Kocher *et al*. 1989); H4A (Harshman 1996) and L14838 (5-GCTTCCATCCAACATCTCAGCATGATG-3, derived from L14841). Amplification products were sequenced with the same primers as used for PCR amplification. PCR reactions were carried out in a 50µl reaction volume containing 10× PCR buffer 5 µl, 25 mmol/l $MgCl_2$ 5µl, 10 µM of each primer 5 µl, 2 mmol/l dNTP 5 µl, 2.5 U Taq polymerase 0.5 µl and 100 ng DNA template. The regions to be analyzed were amplified using standard PCR approaches under the following conditions: an initial denaturation at 94°C for 4 min; 36 cycles of 94°C for 30 s, 54 °C for 45 s, and 72°C for 2 min; followed by a final extension of 10 min at 72°C. To toe-pad, the conditions were performed in: 1 cycle of 94°C for 3 min, 50°C for 1 min, and 72°C for 1 min. 33 cycles of 94°C for 1 min, 50°C for 1 min, and 72°C for 1 min. PCR amplification was terminated with a post extension of 10 min at 72 °C. Both strands of DNA for all taxa were sequenced using an ABI3730 automated sequencer. The DNA sequences are deposited at GenBank (accession number from DQ 263751 to DQ 263760).

Table 1. List of taxonomic samples and sequences used in this study.

Taxa	Code	Collection locality	GenBank accession No.
Turdus migratorius	Tmig	Klicka et al., 2005	AY752395
Turdus chiguanco	Tchi	Klicka et al., 2005	AY752394
Turdus rufiventris	Truf	Klicka et al., 2005	AY752393
Turdus pallidus	Tpal	Klicka et al., 2005	AY752392
Turdus olivaceus	Toli	Klicka et al., 2005	AY752391
Turdus libonyanus	Tlib	Klicka et al., 2005	AY752389
Turdus grayi	Tgra	Klicka et al., 2005	AY752388
Turdus fuscater	Tfus	Klicka et al., 2005	AY752387
Turdus abyssinicus	Taby	Bowie et al., 2003	AY251583
Turdus philomelos	Tphi	Van der Meij et al., 2005	AY495411
Turdus torquatus	Ttor	Europe: Slovakia	DQ263751
Turdus rubrocanus	Trub	China: Gansu Prov.	DQ263752
Turdus naumanni	Tnau	China: Hubei Prov.	DQ263753
Turdus obscurus	Tobs	China: Fujian Prov.	DQ263754
Turdus cardis	Tcar	China: Fujian Prov.	DQ263755
Turdus viscivorus	Tvis	China: Xinjiang Uygur Aut. Reg.	DQ263756
Turdus merula	Tmer	China: Hunan Prov.	DQ263757
Turdus mupinensis	Tmup	China: Sichuan Prov	DQ263758
Turdus boulboul	Tbou	China: Gansu Prov.	DQ263759
Cochoa viridis	Cvir	Klicka et al., 2005	AY752378
Zoothera marginata	Zmar	Klicka et al., 2005	AY752367
Zoothera dixoni	Zdix	Klicka et al., 2005	AY752362
Cichlherminia lherminieri	Clhe	Voelker and Spellman, 2004	AY329453
Platycichla leucops	Pleu	Winker and Pruett, 2001, unpublished	AY049486
Catharus ustulatus	Cust	Winker and Pruett, 2001, unpublished	AY049507
Catharus minimus	Cmin	Winker and Pruett, 2001, unpublished	AY049503
Nesocichla eremita	Nere	Klicka et al., 2005	AY752384
Myiophoneus caeruleus	Mcae	China: Shaanxi Prov.	DQ263760
Monticola cinclorhynchus	Mcin	Goodman and Weigt, 2000, unpublished	AF276777

DNA sequences of the cytochrome *b* gene were edited using DNASTAR package (SeqMan), and the sequences datasets were aligned using Clustal W1.83 (Thompson *et al*. 1997). No gaps, insertions, or deletions were found in the aligned sequences, and all sequences were translated into amino acid sequences to verify the alignments. The final sequences included most of the cyt *b* gene (991 bp).

2.3. Phylogenetic protocols

Base frequencies, sequence variation and divergence values were determined using MEGA3.0 (Kumer *et al*. 2004). The sequence data were analyzed using maximum parsimony (MP), maximum likelihood (ML) in PAUP v4.0b10 (Swofford 2000), and Bayesian inference as implemented in MrBayes v3.1b (Huelsenbeck & Ronquist 2003).

Maximum parsimony analysis was performed with TBR branch swapping and 100 random taxa addition replicates were obtained by a heuristic search. 1,000 bootstrap pseudo-replicates were analyzed. All characters were treated as unordered and used an unweighted parsimony analysis.

Prior to the maximum likelihood phylogenetic analysis, Modeltest 3.06 (Posada & Crandall 1998) was used to find the optimal model of DNA substitution. The phylogenetic reconstruction for maximum likelihood was based on the best-fit model selected by AIC (Posada & Buckley 2004). Furthermore, the TVM + I + G model was identified as the best fit model to our data using AIC criteria in Modeltest. 10 heuristic searches with random addition of taxa and TBR branch swapping were performed in PAUP v4.0b10 (Swofford 2000). ML nodal support was restricted to 300

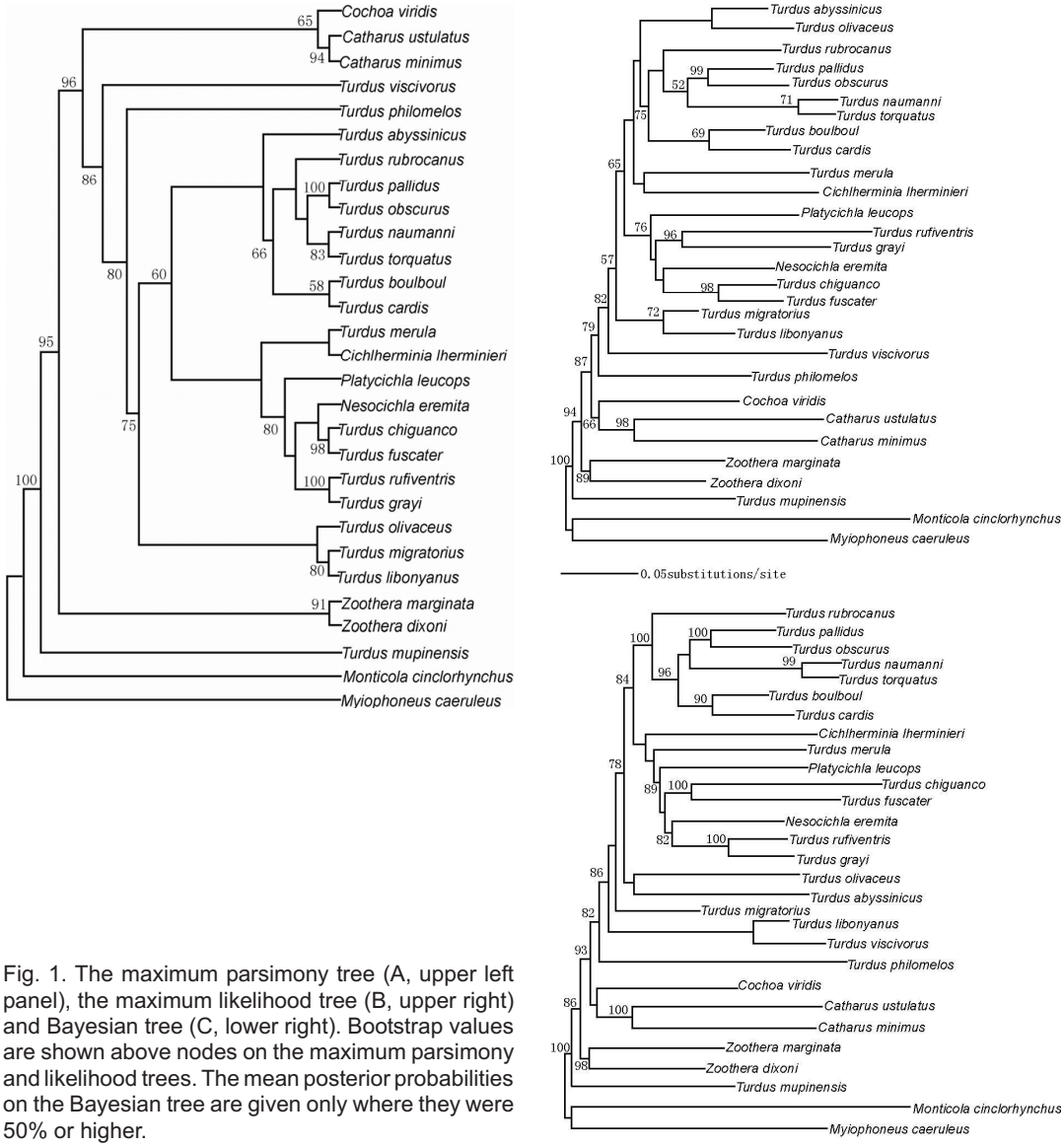

Fig. 1. The maximum parsimony tree (A, upper left panel), the maximum likelihood tree (B, upper right) and Bayesian tree (C, lower right). Bootstrap values are shown above nodes on the maximum parsimony and likelihood trees. The mean posterior probabilities on the Bayesian tree are given only where they were 50% or higher.

pseudo-replicates. Bayesian analyses began with random starting trees and ran for 5 million generations, with Markov chains sampled every 100 generations. One cold and three heated Markov chains were used in the analysis.

The burn-in generations (random points generated prior to stationarity) were defined according to the plot of an x-y graph between generations and likelihood values, and then subsequent generations were used to form the posterior probability distribution. The remaining trees from both analyses (produced in MrBayes v3.1b automatically) were used to create a majority rule consensus tree. Posterior probabilities greater or equal to 95% were considered significant (Leache & Reeder 2002).

3. Results

3.1. Sequence divergence

Among the 991bp datasets, there were 368 variable and 278 parsimony informative sites. Aver-

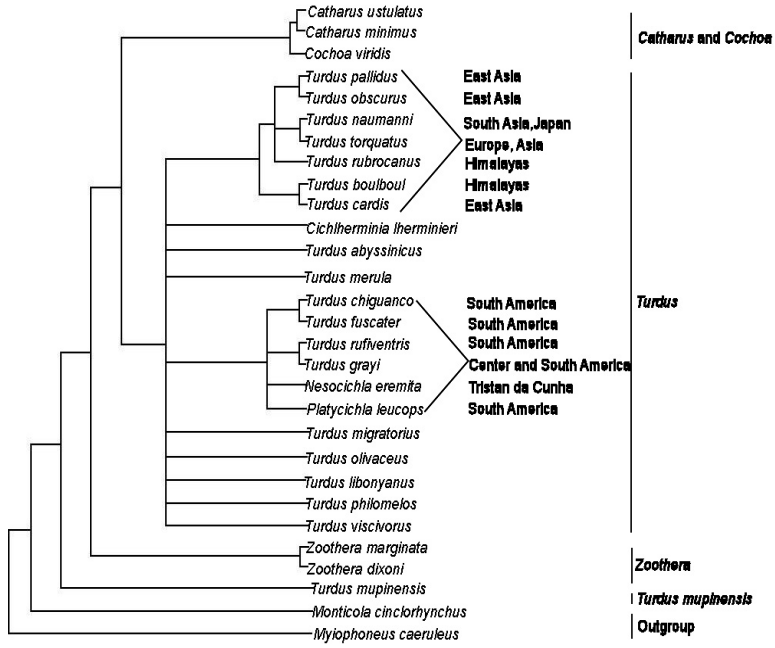

Fig. 2. The 50%consensus tree based on the maximum parsimony, maximum likelihood and Bayesian trees at Figs 1A–C.

age nucleotide composition for the sequences was as follows: A = 27.9%, T = 23.9%, C = 34.2%, G=14.0%. Pairwise distances and numbers of substitution (transitions / transversions) among the 27 ingroups and 2 outgroups are summarized in Table 2. Uncorrected cyt *b* divergence among intrageneric ranged from 0.059 (*Zoothera marginata* and *Z. dixoni*) to 0.106 (*T. libonyanus* and *T. viscivorus*). Intergeneric cyt *b* comparisons ranged from 0.051 (*Nesocichla eremita* and *T. fuscater*) to 0.128 (*Cichlherminia lherminieri* and *Catharus ustulatus*).

3.2. Phylogenetic analysis

The topologies of some clades to be discussed are basically identical in MP, ML and Bayesian trees (Fig. 1). The genus *Turdus*, as presently recognized, is paraphyletic including three mostly monotypic genera (*Cichlherminia*, *Platycichla* and *Nesocichla*). *T. viscivorus* and *T. philomelos* are located at the base of this clade. The node supports on this clade of three phylogenetic trees are as follows: 86% for MP tree, 79% for ML tree and 82% for Bayesian tree. There are two basal clades in *Turdus*, Europe–Asian clade and South American clade. *T. mupinensis* is out of the genera *Turdus*, *Cochoa*, *Zoothera* and *Catharus*, forming a single clade.

However, the MP, ML and Bayesian trees differ in the placement of *Cichlherminia lherminieri*, *T. abyssinicus*, *T. merula* and *T. olivaceus*. The taxonomic status and relationships of these taxa are not well supported.

4. Discussion

Klicka *et al*. (2005) previously investigated the phylogenetic relationships of 10 species in *Turdus* using cyt *b* and ND genes, and draw a preliminary conclusion concerning relationships within these taxa. In this study, nearly 30% (19 of 65) of the species in *Turdus* were analysed. The topologies shown in MP, ML and Bayesian trees gave some more explicable results compared to Klicka *et al*. (2005).

4.1. *Cichlherminia lherminieri, Platycichla leucops* and *Nesocichla eremita*

Our results support the view that the genus *Turdus* is not monophyletic, which should include *Cichlherminia lherminieri*, *Platycichla leucops*

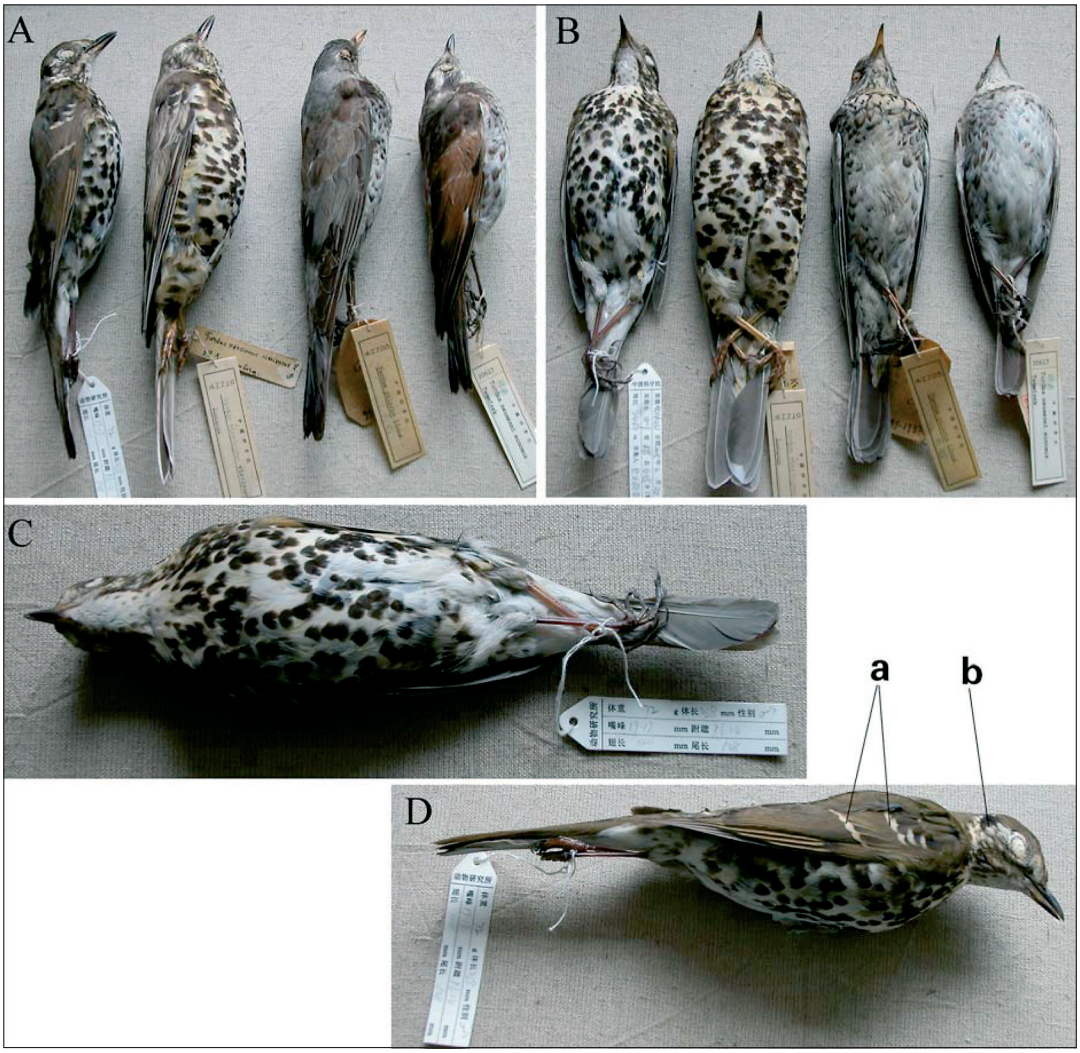

Fig.3. Comparison of specimens of *Turdus mupinensis* with some morphologically similar species: A and B, from left to right, *T. mupinensis, T. viscivorus, T. pilaris* and *T. naumanni*, respectively; C and D, ventral and lateral aspects of *T. mupinensis*, a and b representing the distinct characters of *T. mupinensis*. (Note: This picture is presented in colour in the online version of this article.)

and *Nesocichla eremita*. This finding is in accordance with the conclusion drawn by Klicka *et al*. (2005). The genus *Platycichla* comprises two species distributed in South America (Sibley & Monroe 1993). *Cichlherminia* and *Nesocichla* are all monotypic, and respectively distributed in Lesser Antilles and Tristan da Cunha (Sibley & Monroe 1993). There are insufficient morphological characteristics to support their distinct generic position (Groodwin 1957, Klicka *et al*. 2005). With respect to the relationships of the three genera, and to the phylogeny among the three genera as applying to other species in *Turdus*, previous studies have not shown consensus (Ripley 1952, Sibley & Monroe 1990, Voelker & Spellman 2004, Klicka *et al*. 2005). In this study, our results show first of all that *Platycichla*, *Cichlherminia* and *Nesocichla* are merged into the genus *Turdus*. However, further relationships studies are still needed. Our results (Fig. 1) also show that *Nesocichla eremita* is sister to the clade composed of *T. chiguanco* and *T. fuscater*.

4.2. The Europe–Asia clade and the South America clade occurring in *Turdus*

Two distinct clades are observed in all three trees (Fig. 1). One clade includes *T. rubrocanus*, *T. pallidus*, *T. obscurus*, *T. naumanni*, *T. torquatus*, *T. boulboul* and *T. cardis*. The other clade comprises *Platycichla leucops*, *Nesocichla eremita*, *T. chiguanco*, *T. fuscater*, *T. rufiventris* and *T. grayi*. The distribution of the two clades are geographically distinctive, as shown in Fig. 2 (Sibley & Monroe 1993), the first clade being composed of species from Europe–Asia and the second clade of species from South America. In this study, if we assumed a substitution rate of 2% per million years (Shields & Wilson 1987, Fleischer *et al*. 1998, Lovette & Bermingham 1999, Warren *et al*. 2003), the uncorrected P distances within the Europe–Asia *Turdus* clade range from 1.9% to 6.6% (Table 2) and suggest a divergence time at approximately 0.95~3.30 Mya. Similarly, the South America *Turdus* clade (range 2.4~7.4%) corresponds to an estimated data range of 1.2~3.7 Mya.

4.3. Taxonomic status of *Turdus mupinensis*

T. mupinensis is endemic in central China, distributed in Neimenggu, Beijing, Hebei, Gansu, Guizhou, Sichuan and Yunnan provinces. *T. mupinensis* shows almost no sexual dimorphism. It is almost the same size as *T. naumanni*. Its diagnostic characteristics are: olive brown above, with a black spot near the ear, and whitish below with a large blackish spots on the abdomen (Fig. 3) (Cheng *et al*. 1995). Vaurie (1955) thought that *T. mupinensis* appears to be monotypic and seems to be most closely related to *T. philomelos* based on morphological characteristics. He also implied that *T. mupinensis* would be promoted from a distinct species level if further study were done.

The phylogenetic relationship and the taxonomic status of *T. mupinensis* in the three phylogenetic trees (Fig. 1) are strictly identical. *Turdus* species are clustered with a sister group comprising *Catharus* and *Cochoa* in a terminal branch, and then clustered with *Zoothera*, forming a large clade. In the final analysis, *T. mupinensis* is sister to this clade. The bootstrap values supporting the *T. mupinensis* clade are high, with 95% for MP tree and 94% for ML tree. The posterior probability in Bayesian tree is 86%. Due to a relatively basal position (Fig. 1), *T. mupinensis* represents a primitive taxon compared to other *Turdus* species. The sequence divergence between *T. mupinensis* and other taxa in *Turdus* is from 7.2% (*T. mupinensis* and *T. naumanni*) to 11.4% (*T. mupinensis* and *T. philomelos*) (Appendix). Assuming a substitution rate of 2% per million years in each case, *T. mupinensis* may be estimated as diverging from its most recent common ancestor with *Turdus* at 3.6~5.7 Mya. We suggest that it would be more appropriate to elevate *T. mupinensis* to a distinct monotypic genus.

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Turdus-rastaslajien väliset fylogeneettiset suhteet mitokondriaalisen sytokromi *b*-geeniin perustuvan analyysin pohjalta

Laajalle levinneen *Turdus*-suvun fylogenia on edelleen kiistanalainen. Tarkastelimme kyseisen suvun rastaiden sukulaisuussuhteita *T. mupinensis*-lajin taksonomian kannalta käyttäen sytokromi *b*-geeniä. Käytimme 19 *Turdus*-lajia sisäryhmänä sekä *Myiophoneus caeruleus* ja *Monticola cinclorhynchus* lajeja ulkoryhmänä. Kaikenkaikkiaan tutkitusta geenistä eristettiin 991 fragmenttia, joista 368:ssa oli vaihtelua ja 278 oli parsimonisesti informatiivisia.

Fylogeneettiset analyysit osoittivat, että *Turdus*-suku on parafyleetinen muodostaen ryhmän, johon kuuluu kolme enimmäkseen yhteneväistä sukua (*Cichlherminia, Platycichla, Nesocichla*). Kolme eri fylogeneettistä puuta (MP, ML, Baye-

sialainen) puoltavat kahta ryhmää (Euraasialainen ja Etelä-Amerikkalainen ryhmä) *Turdus*-suvulle. Euraasian ryhmään kuuluivat *T. rubrocanus, T. pallidus, T. obscurus, T. naumanni, T. torquatus, T. boulboul* ja *T. cardis,* kun taas Etelä-Amerikan ryhmään kuuluivat *P.leucops, N. eremita, T. chiguanco, T. fuscater, T. rufiventris,* ja *T. grayi*.

Käyttämällä 2 % korvautuvuusnopeutta miljoonaa vuotta kohden, arvioimme, että Euraasian ryhmä on eriytynyt 0.95–3.3 milj. vuotta sitten. Etelä-Amerikan ryhmä on eriytynyt vastaavasti 1.2–3.7 milj. vuotta sitten. *T. mupinensis* sijoittuu kaikkien kolmen fylogeneettisen puun juureen, mikä viittaa siihen, että *T. mupinensis* on sisäryhmän alkukantaisin laji. *T. mupinensis* on arviolta eriytynyt muista rastaslajeista 3.6–5.7 milj. vuotta sitten. Suuret erot morfologiassa ja mitokondriaalisessa DNA:ssa viittavat siihen, että *T. mupinensis* ei kuulu *Turdus*-sukuun, jonka luokittelua tulisi täten uudistaa.

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Appendix. Genetic distance (uncorrected P distance, upper triangle) and numbers of substitution (transitions/ transversions, lower triangle) for *cyt* b gene of 29 species from Turdinae in the study. The abbreviated species names in column 2 are given in full in Table 1.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Tpal	–	0.019	0.053	0.056	0.066	0.056	0.059	0.098	0.098	0.080	0.074	0.074	0.082	0.088
2	Tobs	6/1	–	0.051	0.061	0.059	0.053	0.056	0.096	0.093	0.077	0.072	0.077	0.085	0.090
3	Tnau	18/2	18/1	–	0.027	0.027	0.032	0.048	0.074	0.074	0.056	0.056	0.061	0.069	0.069
4	Tbou	20/1	23/0	9/1	–	0.053	0.045	0.035	0.088	0.082	0.074	0.064	0.069	0.064	0.069
5	Ttor	20/5	18/4	7/3	16/4	–	0.051	0.059	0.085	0.085	0.061	0.066	0.074	0.077	0.082
6	Trub	19/2	19/1	10/2	16/1	14/5	–	0.037	0.074	0.074	0.066	0.056	0.061	0.069	0.082
7	Tcar	19/3	19/2	15/3	11/2	16/6	11/3	–	0.082	0.088	0.066	0.069	0.080	0.066	0.074
8	Tmig	35/2	35/1	26/2	32/1	27/5	26/2	28/3	–	0.088	0.061	0.074	0.072	0.082	0.090
9	Tlib	35/2	32/3	24/4	28/3	25/7	24/4	28/5	29/4	–	0.080	0.072	0.074	0.093	0.101
10	Toli	29/1	29/0	20/1	28/0	19/4	24/1	23/2	22/1	27/3	–	0.066	0.059	0.064	0.072
11	Tchi	25/3	25/2	18/3	22/2	19/6	18/3	24/2	25/3	22/5	23/2	–	0.029	0.056	0.072
12	Tfus	26/2	28/1	21/2	25/1	23/5	21/2	29/1	25/2	24/4	21/1	10/1	–	0.051	0.074
13	Nere	27/4	29/3	22/4	21/3	24/5	22/4	22/3	27/4	29/6	21/3	18/3	17/2	–	0.059
14	Truf	28/5	30/4	21/5	22/4	23/8	26/5	24/4	29/5	31/7	23/4	23/4	25/3	19/3	–
15	Tgra	25/3	29/2	19/3	22/2	21/6	24/3	26/2	28/3	31/5	20/2	20/2	22/1	23/1	7/2
16	Pleu	32/2	34/1	22/2	25/1	25/5	29/2	28/3	27/2	30/2	23/1	22/3	20/2	19/4	19/5
17	Clhe	29/3	29/2	24/3	25/2	27/6	27/3	28/4	27/3	26/5	27/2	21/4	23/3	20/3	25/4
18	Tmer	34/3	36/2	27/3	31/2	28/6	29/3	30/4	29/3	33/3	23/2	24/4	24/3	23/5	24/6
19	Taby	26/3	26/2	17/3	18/2	19/6	14/3	17/4	24/3	22/5	22/2	17/4	23/3	16/5	19/6
20	Tvis	33/6	35/5	25/6	30/5	25/9	27/6	26/7	28/6	23/6	26/5	26/7	24/6	25/6	27/5
21	Cust	31/12	30/11	26/10	30/11	26/13	26/12	27/11	29/12	32/12	29/11	32/9	33/10	29/10	33/9
22	Cmin	30/11	28/10	29/11	35/10	30/14	26/11	34/12	28/11	29/11	31/10	27/10	23/11	27/11	32/10
23	Cvir	26/10	27/9	21/10	27/9	23/13	22/10	28/11	27/10	27/10	22/9	22/9	22/10	20/10	27/9
24	Zmar	33/11	33/10	23/9	31/10	25/10	31/11	32/12	25/11	34/11	22/10	26/10	26/11	26/11	25/10
25	Zdix	26/13	28/12	20/11	28/12	22/12	23/13	28/14	25/13	27/13	20/12	22/12	19/13	23/11	26/12
26	Tphi	37/8	38/7	29/8	38/7	30/11	31/8	35/9	32/8	39/8	26/7	36/9	38/8	32/10	37/11
27	Tmup	29/10	30/9	19/8	23/9	23/9	25/10	25/9	23/10	32/10	20/9	24/9	25/8	19/8	25/9
28	Mcae	36/15	34/14	28/13	34/14	32/16	31/15	34/14	36/15	36/15	32/14	37/16	34/15	38/15	37/12
29	Mcin	33/16	35/15	29/16	35/15	30/15	31/16	36/15	31/16	40/16	30/15	34/15	32/16	31/14	35/13

15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
0.074	0.090	0.085	0.098	0.077	0.106	0.114	0.109	0.096	0.117	0.104	0.120	0.104	0.136	0.130
0.082	0.093	0.082	0.101	0.074	0.104	0.109	0.101	0.096	0.114	0.106	0.120	0.104	0.128	0.133
0.059	0.064	0.072	0.080	0.053	0.080	0.096	0.106	0.082	0.085	0.082	0.098	0.072	0.109	0.120
0.064	0.069	0.072	0.088	0.053	0.090	0.109	0.120	0.096	0.109	0.106	0.120	0.085	0.128	0.133
0.072	0.080	0.088	0.090	0.066	0.088	0.104	0.117	0.096	0.093	0.090	0.109	0.085	0.128	0.120
0.072	0.082	0.080	0.085	0.045	0.085	0.101	0.098	0.085	0.112	0.096	0.104	0.093	0.122	0.125
0.074	0.082	0.085	0.090	0.056	0.085	0.101	0.122	0.104	0.117	0.112	0.117	0.090	0.128	0.136
0.082	0.077	0.080	0.085	0.072	0.088	0.109	0.104	0.098	0.096	0.101	0.106	0.088	0.136	0.125
0.096	0.085	0.082	0.096	0.072	0.074	0.117	0.106	0.098	0.120	0.106	0.125	0.112	0.136	0.149
0.059	0.064	0.077	0.066	0.064	0.080	0.106	0.109	0.082	0.085	0.085	0.088	0.077	0.122	0.120
0.059	0.066	0.066	0.074	0.056	0.085	0.109	0.098	0.082	0.096	0.090	0.120	0.088	0.141	0.130
0.061	0.059	0.069	0.072	0.069	0.082	0.114	0.090	0.085	0.098	0.085	0.122	0.088	0.130	0.128
0.064	0.061	0.061	0.074	0.056	0.080	0.104	0.101	0.080	0.098	0.090	0.112	0.073	0.141	0.120
0.024	0.064	0.077	0.080	0.066	0.082	0.112	0.112	0.096	0.093	0.101	0.128	0.090	0.130	0.128
–	0.066	0.074	0.074	0.061	0.080	0.109	0.104	0.088	0.093	0.093	0.114	0.085	0.144	0.130
22/3	–	0.069	0.082	0.069	0.077	0.114	0.117	0.085	0.096	0.090	0.120	0.082	0.141	0.125
26/2	23/3	–	0.077	0.069	0.088	0.128	0.090	0.085	0.098	0.098	0.117	0.093	0.136	0.125
24/4	30/1	25/4	–	0.082	0.098	0.122	0.112	0.104	0.101	0.112	0.128	0.106	0.160	0.141
19/4	23/3	24/2	27/4	–	0.077	0.098	0.104	0.080	0.098	0.088	0.109	0.090	0.128	0.114
26/5	24/6	29/5	31/7	23/7	–	0.101	0.104	0.069	0.088	0.082	0.104	0.096	0.141	0.114
32/9	31/12	37/11	33/13	24/13	29/8	–	0.085	0.088	0.098	0.104	0.114	0.077	0.136	0.117
29/10	33/11	24/10	30/12	27/12	31/7	25/7	–	0.080	0.101	0.106	0.117	0.106	0.133	0.133
24/8	22/10	23/9	28/11	19/11	17/8	25/8	21/9	–	0.074	0.072	0.104	0.088	0.133	0.098
25/10	25/11	27/10	26/12	27/10	23/9	28/9	28/10	19/9	–	0.059	0.109	0.090	0.120	0.098
23/12	21/13	27/10	30/12	23/10	19/11	28/11	28/12	16/11	16/6	–	0.101	0.090	0.106	0.101
34/9	37/8	35/9	39/9	32/9	30/8	29/14	33/11	29/10	28/13	23/15	–	0.114	0.125	0.136
25/7	21/10	26/9	29/11	23/11	27/8	21/8	27/13	23/10	25/9	21/13	31/12	–	0.120	0.114
40/14	38/15	39/12	44/16	36/12	41/11	36/15	34/16	35/15	33/12	30/10	30/17	30/15	–	0.133
34/15	31/16	32/15	36/17	28/15	30/12	28/16	35/15	25/12	26/11	25/13	35/16	29/14	37/13	–