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PHYLOGEOGRAPHY OF THE *ROBSONIUS* GROUND-WARBLEDERS (PASSERIFORMES: LOCUSTELLIDAE) REVEALS AN UNDESCRIBED SPECIES FROM NORTHEASTERN LUZON, PHILIPPINES

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Abstract. The *Robsonius* ground-warblers are forest birds endemic to the Luzon Island complex in the Philippine archipelago. Their systematic relationships have long remained ambiguous; until recently they were included in the timaliid genus *Napothera*. Two *Robsonius* species are currently recognized on the basis of plumage differences: *R. rabori* from northern Luzon in the Cordillera Central and the northern Sierra Madre, and *R. sorsogonensis* from southern Luzon and Catanduanes Island. Recent specimen collections, including the first adult specimen from the Cordillera Central, establish plumage differences between populations of *R. rabori* in the Cordillera Central and Sierra Madre and reveal a third diagnosable population within Luzon. These differences have gone unnoticed because *R. rabori* (sensu stricto) had been known only from the juvenile holotype. Molecular phylogenetic data further support the hypothesis that three highly divergent taxa occur across the Luzon Island complex: *Robsonius rabori* is known only from the northern Cordillera Central in Ilocos Norte; an undescribed taxon (formerly included in *R. rabori*) occurs in the northern Sierra Madre in Cagayan, Isabela, Aurora, and Nueva Vizcaya provinces; and *R. sorsogonensis* occurs in southern Luzon (Bulacan and Laguna provinces), the Bicol Peninsula, and on Catanduanes Island. The existence of three putatively allopatric species within the Luzon island complex highlights the role of *in situ* diversification in island systems, and brings attention to the need for forest conservation to protect geographically restricted populations throughout the Luzon Island complex.

Key words: *endemism, Napothera, Philippines, phylogeography, diversification.*

La Filogeografía de *Robsonius* (Passeriformes: Locustellidae) Revela una Especie No Descripta del Noreste de Luzón, Filipinas

Resumen. Las aves del género *Robsonius* son endémicas de los bosques de la geológicamente compleja isla Luzon en el archipiélago de Filipinas. Sus relaciones sistemáticas han permanecido ambiguas por mucho tiempo; hasta hace poco, estuvieron incluidas en el género *Napothera*. Actualmente se reconocen dos especies de *Robsonius* con base en diferencias de plumaje: *R. rabori* del norte de Luzon en la Cordillera Central y el norte de Sierra Madre, y *R. sorsogonensis* del sur de Luzón y la isla Catanduanes. Colecciones recientes de especímenes, incluyendo el primer espécimen adulto de la Cordillera Central, permitieron diferencias de plumaje entre las poblaciones de *R. rabori* en la Cordillera Central y Sierra Madre y revelaron una tercera población diagnosticable. Estas diferencias han pasado inadvertidas debido a que *R. rabori* (sensu stricto) ha sido conocida solo por el holotipo juvenil. Datos moleculares filogenéticos refuerzan el apoyo a la hipótesis de que tres taxones altamente divergentes se encuentran a lo largo del complejo de la isla Luzón: *R. rabori* es conocida sólo del norte de la Cordillera Central en Ilocos Norte; un taxón no descrito (anteriormente incluido en *R. rabori*) se encuentra en el norte de Sierra Madre en las provincias de Cagayan, Isabela, Aurora y Nueva Vizcaya; y *R. sorsogonensis*, que se encuentra en el sur de Luzón (provincias de Bulacan y Laguna), la península Bicol y en la isla Catanduanes. La existencia de tres especies alopátricas putativas dentro Luzón destaca del papel de la diversificación *in situ* en los sistemas de islas y resalta la necesidad de conservar el bosque para proteger poblaciones geográficamente restringidas a través de la compleja isla de Luzón.

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INTRODUCTION

In 1959, D. S. Rabor led an expedition to Ilocos Norte Province in northwestern Luzon Island, Philippines. Inland from the small coastal village of Pagudpud, the team collected a single juvenile of a long-legged, long-tailed, medium-sized passerine that differed strikingly from any known species. Rand (1960) described the species as *Napothera rabori*, believing it was related to southeast Asian *Napothera* babblers (Timaliidae). Rabor secured two more juveniles at Mt. Cagua in Cagayan Province, northeastern Luzon, the following year, and four more specimens (adults and juveniles) from Sorsogon Province at the southern end of Luzon in 1961. The southern birds differed from the northern birds in lacking the rusty tinge on the head present in the juvenile northern specimens. Rand and Rabor (1967) named the southern birds *N. sorsogonensis*, after the type locality. Thus, within two years, two species of a group of unique and enigmatic passerines were discovered from the opposite ends of Luzon Island.

Approximately a decade after the initial discoveries, DuPont (1971a, b) received an adult specimen from Laguna, in central Luzon, and declared that it was intermediate between *N. rabori* and *N. sorsogonensis*, notwithstanding that he was comparing adults and juveniles. He lumped *N. rabori* and *N. sorsogonensis* into a single species and named the Laguna specimen as a new subspecies, *N. r. mesoluzonica*.

Ornithological exploration in the 1980s and 1990s began to clarify the natural history and distribution of the *rabori* complex, until then virtually unknown in life, which led to questions about its phylogenetic relationships. Goodman and Gonzales (1990) observed an individual flipping leaf litter and wood debris while walking on the ground, presumably foraging for insects. De Roeber (1990) observed an individual walking and running with its tail cocked and likened it to a small rail or a neotropical anthrush. Lambert (1993) observed a pair walking and foraging on the forest floor, noted that this behavior would be unusual for *Napothera* (other species of *Napothera* hop), and suggested that the species may belong in another genus. Harrap and Mitchell (1994) described the song—high-pitched phrases given from a horizontal branch or log—as similar to those of warblers of the genera *Bradypterus* or *Urosphena*, and, on the basis of song and behavior, advocated placing the complex in its own genus.

Collar (2006) synthesized the natural history observations and morphological evidence and proposed for the *rabori* complex a new genus, *Robsonius*, within the Timaliidae. On the basis of four distinctive plumage differences between the two taxa, he also returned to Rand and Rabor's (1967) treatment of two species, *R. rabori* and *R. sorsogonensis* (the later including *R. s. mesoluzonica*). In a comprehensive molecular phylogeny of the babblers, Moyle et al. (2012) found that *Robsonius* fell far outside of the main babbler lineages, further justifying its removal from *Napothera*. Most recently, Oliveros et al. (2012)

reported that *Robsonius* is sister to the grassbirds and allies (Locustellidae), and they coined a new English name for the genus, the ground-warblers.

In June 2011, a field team from the University of Kansas Biodiversity Institute, Philippine National Museum, and University of Utah visited the forests of Ilocos Norte to survey terrestrial vertebrates and their parasites. The team surveyed two localities south of the small village of Adams, only 5–10 km from where Rabor and his team collected the unique juvenile holotype of *R. rabori*. We collected an adult, salvaged from a mammal trap, which differed in several plumage characters from all other adult specimens of *Robsonius* (Appendix 1, available at <http://dx.doi.org/10.1525/cond.2013.120124>). Because of these plumage differences, we investigated the molecular phylogeographic structure within the genus to assess whether the differences reflect individual variation within a poorly known species or a suite of distinct, diagnosable taxa. Analysis of the data revealed (Fig. 1) that populations from the southern, northeastern, and northwestern sectors of Luzon are genetically (on the basis of mitochondrial DNA and nuclear introns) and morphologically distinct, and that an unnamed lineage of ground-warbler is present in the northern Sierra Madre of northeastern Luzon Island (Fig. 2). Because the name *R. rabori* applies to the species occurring in the Cordillera Central in Ilocos Norte (northwestern Luzon), the northern Sierra Madre birds, long attributed to *R. rabori*, remain undescribed, long hidden from taxonomic recognition because the adult plumage of *R. rabori* sensu stricto was unknown. We proudly name this species

***Robsonius thompsoni* sp. nov.**

Sierra Madre Ground-Warbler

Holotype. Philippine National Museum (PNM) 20006; originally catalogued as University of Kansas Biodiversity Institute (KU) 114678, adult female (skull 100% pneumatized, no bursa), KU tissue number 19632, collected on 18 June 2009 in the Philippines, Luzon Island, Aurora Province, San Luis Municipality, 12 km SW Baler (15.680° N, 121.529° E, elevation 525 m). This individual was net-captured in secondary lowland forest and prepared as a study skin by Jameson B. Reynon.

Description of holotype. Adult female; ovary 6 × 3 mm; light fat; mass 63 g; molt on wing, breast, and nape; stomach contents insect parts; maxilla dark brown, mandible pale gray; iris dark brown; legs and feet light brown. Colors in the following description of the plumage are those of Smithe (1975). Crown and nape amber, the feathers tipped with dusky brown; auriculars amber. Loes white, the feathers tipped with black. Thin eye ring whitish; small area of bare gray skin behind eye. Throat white, the feathers tipped with black; malar stripe black, formed of feathers with white bases; submoustachial stripe white with black feather edging. Black feather tips on the lower throat and upper breast form a necklace of spots, which separates the primarily white

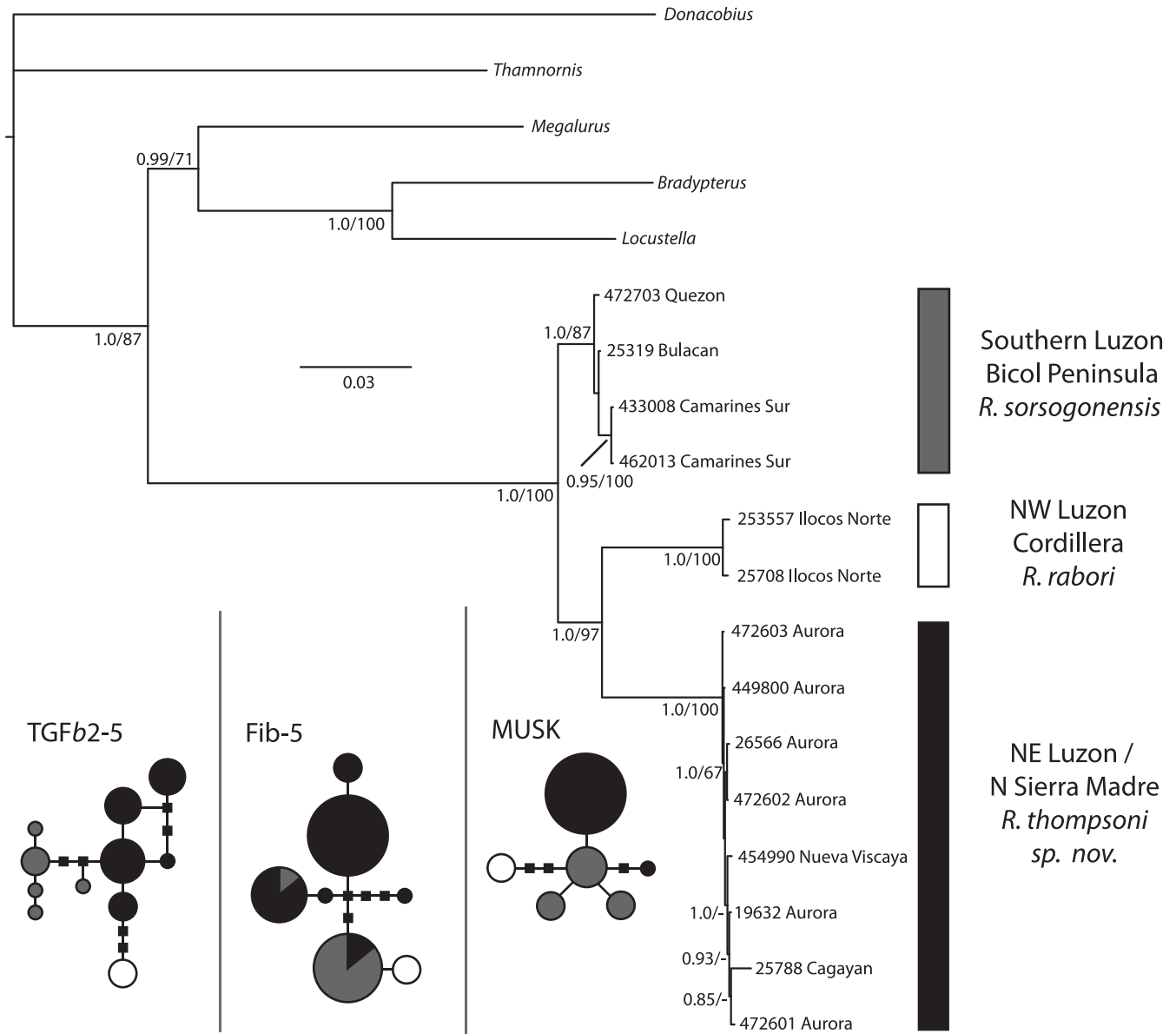


FIGURE 1. Bayesian consensus tree of the concatenated dataset of six genes (cytochrome *b*, ND2, ND3, TGFb2-5, Fib-5, MUSK) and networks of phased haplotypes of three nuclear introns. Each shade in the haplotype networks corresponds to one of the three clades of *Robsonius*; black squares represent unsampled haplotypes. Values at nodes indicate support by Bayesian posterior probability/maximum-likelihood bootstrap; scale bar indicates 0.03 substitutions per site.

throat from the gray breast. Breast medium neutral gray, with feather shafts slightly paler; belly whitish; flanks dusky brown, with cinnamon-brown to chestnut tinge. Back cinnamon-brown with dusky brown tips to individual feathers. Long fluffy rump feathers form a thick mat and are dusky brown with a chestnut tinge; white feather tips form a concealed white rump band; uppertail and undertail coverts and tail dusky brown with chestnut tinge. Wings chestnut to dusky brown, each feather dusky brown with a broad chestnut edge, so that the wing appears mostly chestnut when folded. Alula and wing coverts broadly tipped with white,

so that the folded wing has several bars of white spots. Outer three primaries also tipped with white, although not visible in the folded wing.

Diagnosis. Adult plumage: *Robsonius thompsoni* (cover; Fig. 3C) is most similar to *R. rabori* (Fig. 3A) but differs in three plumage characters: presence of a necklace of black spots (lacking in *R. rabori*), black feather tips on the throat and submoustachial area (pale gray in *R. rabori*), and a uniform gray breast with pale feather shafts and faint darker edging (in *R. rabori*, breast feathers have broad white bases and centers and gray edges, lending the breast a scaled appearance). *Robsonius*

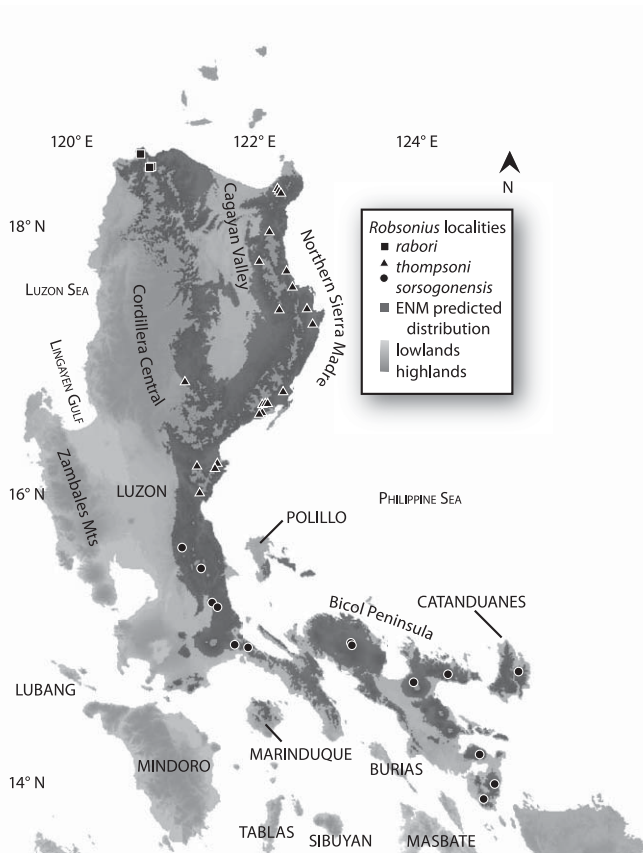


FIGURE 2. Distribution of *Robsonius* in the Luzon Island complex, which includes Luzon, Catanduanes, Polillo, and Marinduque. Areas of environmental conditions suitable for *Robsonius* (as inferred from ecological niche models) are shown in dark gray. All localities known for *Robsonius* (specimens and observations), used to train models, are displayed on top of the modeled distribution.

thompsoni differs from *R. sorsogonensis* (Fig 3E) in four plumage characters: amber crown, nape, and auriculars (uniform dark gray with white feather shafts on the auriculars in *R. sorsogonensis*), dark gray to blackish tips on throat feathers (unmarked white in *R. sorsogonensis*), and pale feather shafts in the gray breast band (uniform gray without pale feather shafts or feather bases in *R. sorsogonensis*). Juvenile plumage: from a limited number of specimens, *R. thompsoni* ($n = 4$) and *R. rabori* ($n = 1$) are not distinguishable (Fig. 3B and 3D). Overall the juvenile plumage is similar to the adult plumage, but the throat, back, and underparts are variably cinnamon brown to olive brown with paler feather bases; crown, nape, and auriculars similar to those of the adult but lores and eye ring uniform amber. The juvenile of *R. sorsogonensis* (Fig 3F; $n = 4$) is similar to that of *R. rabori* and *R. thompsoni* except that the underparts (especially flanks) are richer chestnut brown and the crown, nape, auriculars, lores, and eye ring are cinnamon brown.

Vocalizations. All three species of *Robsonius* sing similar extremely high-pitched (7.5–10.0 kHz) songs, from the ground or an elevated perch. Each song bout is approximately 1.6–2.2 sec in duration and generally consists of three or four variable

phrases with ascending and descending notes. Each phrase is separated by a brief (0.1–0.2 sec) pause. Individuals give song bouts approximately every 5–10 sec when singing regularly. Because of small sample sizes (*rabori*, $n = 1$; *thompsoni*, $n = 10$; *sorsogonensis*, $n = 2$), it is currently unclear whether slight differences in songs represent geographic or individual variation. More recordings are needed from additional localities to assess whether or not each species may be identified solely by vocalizations. In addition to the song, a rapid trill, thought to be an alarm call, has been recorded from one of a group of *R. thompsoni* (P. Noakes, Xeno-canto [XC] 40990).

Designation of paratypes. Field Museum of Natural History (FMNH) 472602; adult male (skull pneumatized, no bursa) captured 10 April 2010, Philippines, Luzon Island, Aurora Province, Dunalungan Municipality, 1.9 km S, 4.0 km E Mt. Anacua (16.237° N, 121.927° E; 1300 m), in primary lower montane forest. This specimen was originally prepared as a fluid specimen in formalin (DSB 7110) but re-prepared as a skin by PAH: mass 57 g; fat moderate; stomach with sclerotized insect fragments; molt on wing and body; testes 5×4 mm. KU 119893; juvenile male (skull not pneumatized, bursa 10×8 mm), tissue number KU 25788. This individual was net-captured on 7 July 2011 in the Philippines, Luzon Island, Cagayan Province, Gonzaga Municipality, Mt. Cagua crater (13. 219° N, 122.111° E; 780 m) and prepared as a study skin by PAH: fat light; mass 52.5 g; stomach empty; iris dark brown; legs dusky; maxilla dusky with yellow tomiom; mandible yellow with dusky tomiom; molt on body; mouth lining yellow.

Variation within Robsonius. We found no apparent significant differences in size (Baldwin 1931, Winker 1998) among the three species of *Robsonius* (Table 1; ANOVA, $P > 0.01$) or between the sexes (t -test, $P > 0.01$). Juveniles tend to have bills shorter (mean 12.3 mm) than those of adults (mean 13.8 mm; t -test $P = 0.0007$); no other differences in measurements were significant (t -test, $P > 0.01$). Most plumage variation in adults of *Robsonius* results from variation in the amount of dark feather edging on the back, throat, and breast, which is strongly affected by feather wear. Overall, *R. sorsogonensis* has the least dusky feather edging; some specimens show faint dusky scalloping on the back, but none has scalloping on the throat and upper breast as in *R. rabori* and *R. thompsoni*. The malar stripe, formed from grayish or blackish feather tips, is reduced in *R. sorsogonensis* and *R. rabori* in comparison to *R. thompsoni*. The distinctive necklace of black spots in *R. thompsoni* is variable and influenced by feather wear; in some specimens, the throat is clean white and only a few black spots on the upper breast form the necklace, whereas other specimens have spotted or scalloped throats and prominent black necklaces. The size of the white throat patch, thickness of the breast band, and amount of white on the belly are also variable within species, apparently mostly as a function of feather wear and style of specimen preparation, so the biological significance of this variation remains unclear.

In our examination of specimens of *Robsonius*, we found no diagnosable differences between *R. s. sorsogonensis* and

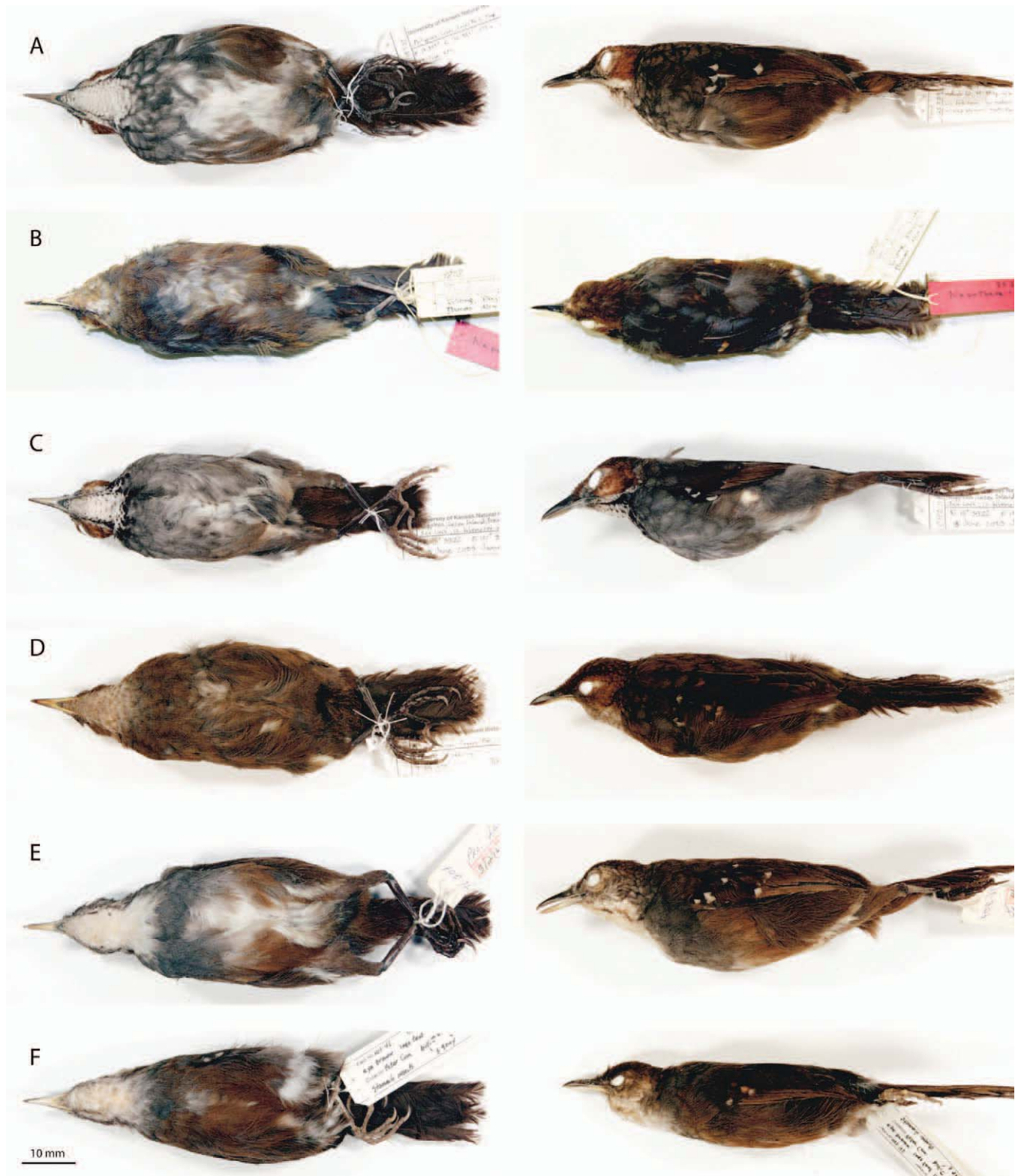


FIGURE 3. Representative specimens of adult and juvenile plumages of all three species of *Robsonius*, viewed ventrally (first column) and laterally (second column). (A) adult *R. rabori* KU 119500); (B) juvenile *R. rabori* (FMNH 253557, holotype); (C) adult *R. thompsoni* (PNM 20144, holotype); (D) juvenile *R. thompsoni* (KU 119893); (E) adult *R. sorsogonensis* (DMNH 37276); (F) juvenile *R. sorsogonensis* (CM 153961).

TABLE 1. Mean measurements of specimens of the three species of *Robsonius*, with sample size (in parentheses) and ranges of measurements. We found no significant differences between the species or sexes, although juveniles had significantly shorter bills than adults. Sample sizes varied because some measurements were not possible on some specimens.

	Bill length	Bill depth	Bill width	Wing chord	Tail	Tarsus
<i>Robsonius rabori</i>	13.5 (2) 12.7–14.3	5.3 (1) 5.3	4.5 (2) 4.1–4.8	78.6 (2) 76.6–80.5	75.8 (2) 70.7–80.8	29.9 (2) 29.8–30.0
<i>R. sorsogonensis</i>	13.7 (21) 10.0–15.6	5.5 (17) 4.7–6.2	5.0 (19) 4.1–6.2	85.3 (21) 71.5–96.0	74.6 (17) 67.0–87.7	30.2 (21) 28.0–31.8
<i>R. thompsoni</i>	12.9 (9) 12.1–14.5	5.1 (8) 4.3–5.8	5.0 (10) 4.6–5.7	79.8 (10) 71.0–87.0	73.3 (9) 64.3–81.7	29.7 (10) 27.4–32.3

R. s. mesoluzonica. Each of Dupont's (1971a) characters varies from individual to individual and are influenced strongly by preparation style and feather wear. The holotype of *sorsogonensis* is heavily worn, in contrast to the holotype of *mesoluzonica*. Topotypes (Pakil, Laguna) of *mesoluzonica* are variable, with fresh-plumaged birds similar to the holotype of *mesoluzonica*, worn birds more similar to that of *sorsogonensis*. Our DNA-sequence data, which include two samples from central Luzon within the geographic range of *mesoluzonica*, also suggest no population structure within *R. sorsogonensis*. As a consequence, we suggest that *R. s. mesoluzonica* is not a diagnosable subspecies and recommend treating *R. sorsogonensis* as monotypic, with the name *mesoluzonica* DuPont as a junior synonym.

Etymology. We name this species in honor of Max C. Thompson, for his decades of contributions to natural history collections and ornithology in particular. Long employed as a professor of biology at Southwestern College, in Winfield, Kansas, his involvement in diverse initiatives has produced scientific insights and extensive specimen collections not only from the Philippines, but also from Africa, Asia, Australia, the southwestern Pacific, and numerous sites in the New World. His collections are deposited at the University of Kansas, Smithsonian Institution, Bernice P. Bishop Museum, and American Museum of Natural History (AMNH), and have provided an invaluable resource for the ornithological community.

The English names currently and recently used for *Robsonius* are misleading because they refer to previous taxonomic treatments when *Robsonius* was considered a babbler (Rabor's Wren-Babbler/Luzon Wren-Babbler), or because they refer to plumage characters that, in light of new specimen evidence, do not diagnose the species (Rusty-headed Babbler/Gray-banded Babbler; two species have a rusty head, all three have a gray breast band, albeit with slight differences between each species). We suggest new English names that highlight the restricted distributions and geographic areas of endemism occupied by each species within Luzon: *Robsonius rabori*, Cordillera Ground-Warbler; *R. thompsoni*, Sierra Madre Ground-Warbler; and *R. sorsogonensis*, Bicol Ground-Warbler.

Specimen material examined. ***Robsonius rabori***: FMNH 253557 (holotype); KU 119500. ***Robsonius sorsogonensis***: AMNH 807095 (photos only); British Museum of Natural

History (BMNH) 1977.16.65–6 (photos only); Carnegie Museum (CM) 151227, 153961; Delaware Museum of Natural History (DMNH) 10800 (holotype of *mesoluzonica*, photos only) 17443, 21812, 37275–6, 37928–33, 43771, 55857; FMNH 275745 (holotype), 399710, 462013, 472703; PNM 16656, 16795, 17532, 20144; Rijksmuseum van Natuurlijke Histoire (RMNH) 99810 (photos only, from Collar 2006), University of the Philippines Los Baños (UPLB) 3554; United States National Museum (USNM) 608086 (photos only). ***Robsonius thompsoni***: Cincinnati Museum of Natural History (CMNH) 37710–1; FMNH 259385, 449800, 454990, 472601–3; KU 114634, 119893; PNM 16801, 19167, 20006 (holotype), University of Michigan Museum of Zoology (UMMZ) 226770 (photos only), USNM 607458, Yale Peabody Museum (YPM) 39989.

Audio records examined. ***Robsonius rabori***: Macaulay Library, Cornell University (ML) 166395. ***Robsonius thompsoni***: Xeno-Canto (XC) 23080, 35259–61, 40988–92, 57572–3. ***Robsonius sorsogonensis***: 2 recordings (Scharringa 2005).

REMARKS

SYSTEMATICS

We used an initial molecular phylogenetic framework from recent higher-level systematic studies that included *Robsonius* (Moyle et al. 2012, Oliveros et al. 2012) to clarify the phylogenetic relationships among the populations. Character sampling (4092 bp) included three mitochondrial genes (1143 bp cytochrome *b*, 1041 bp ND2, 351 bp ND3) and three nuclear introns (544 bp TGF β 2-5, 570 bp Fib-5, 443 bp MUSK). Sequences of 13 individuals (Appendix 1; GenBank accession numbers KC603622–KC603686) were derived from fresh tissue samples, whereas the sequence of the juvenile type specimen of *R. rabori* was derived from DNA extracted from a toepad clip. Outgroups included *Donacobius*, *Thamnornis*, *Megalurus*, *Locustella*, and *Bradypterus* (Oliveros et al. 2012). We inferred trees by Bayesian (MrBayes 3.1, Ronquist and Huelsenbeck 2003; 20 million generations) and maximum-likelihood (RAxML, Stamatakis 2006; 1000 bootstrap replicates) analysis of the concatenated dataset. Preliminary analyses of individual loci indicated no strongly supported conflicts in phylogenetic

signal between loci, justifying concatenation. See Moyle et al. (2012) and Oliveros et al. (2012) for descriptions of gene regions sequenced, laboratory protocols, and details of analysis. In addition to analyses described by Moyle et al. (2012), we reconstructed phased (Stephens et al. 2001) haplotype networks for each nuclear locus with TCS (Clement et al. 2000).

Bayesian and maximum-likelihood analyses recovered three strongly supported geographic clades within *Robsonius* (Fig. 1). One clade comprised samples from southern Luzon, including the Bicol Peninsula and Bulacan Province (1.0 Bayesian posterior probability [BP], 87% maximum-likelihood bootstraps [BS]); a second clade comprised samples from the northern Sierra Madre in northeastern Luzon, including Aurora, Nueva Vizcaya, and Cagayan provinces (1.0 BP, 100% BS); and a third clade comprised samples from the Cordillera Central in Ilocos Norte Province, northwestern Luzon (1.0 BP, 100% BS). The northwestern clade (Cordillera Central, including the type specimen of *R. rabori*) and the northeastern clade (northern Sierra Madre, *R. thompsoni*) were strongly supported as sister taxa (1.0 BP, 97% BS), which together were sister to the southern Luzon clade (*R. sorsogonensis*).

Mitochondrial haplotypes of the three clades were highly divergent; in ND2, uncorrected pairwise distances between the three populations ranged from 7.4 to 8.7% (*rabori*–*thompsoni*, 8.3–8.7%; *rabori*–*sorsogonensis*, 7.9–8.2%; *thompsoni*–*sorsogonensis*, 7.4–8.1%). In cytochrome *b*, uncorrected pairwise distances between populations ranged from 5.2 to 7.4%. For comparison, divergences in mtDNA of most recently described species have been less than 5% (Voelker et al. 2010, Pyle et al. 2011, Lara et al. 2012), and many are less than 2% (O'Neill et al. 2011, Carneiro et al. 2012, Seeholzer et al. 2012). Haplotype networks of nuclear genes (Fig. 1) showed no haplotype sharing among species, except in Fib-5, of which *R. sorsogonensis* and *R. thompsoni* shared two haplotypes. The ND3 sequence amplified from a toepad of the type specimen of *R. rabori* was the same haplotype as that from sample KU 25708 and included no stop codons or heterozygous sites, lending additional confidence that the DNA amplified is of true mitochondrial origin.

Molecular data and plumage independently indicate three diagnosable lineages of *Robsonius* within Luzon, consistent with treatment of three species under the phylogenetic, evolutionary, and general-lineage species concepts (de Queiroz 2007). Distributions of the three taxa are currently not known to overlap, precluding direct evaluation of reproductive isolation and determination of species status under the biological species concept. However, indirect evidence strongly suggests reproductive isolation between the three species. First, deep genetic divergences between lineages support a long independent history with no evidence of hybridization. For example, specimens of *R. thompsoni* and *R. sorsogonensis* collected from southern Aurora and northern Bulacan provinces show no evidence of phenotypic or genetic intergradation, despite a separation of only 60 km and no intervening break in continuous lowland forest. Second, all

plumage differences between the lineages are 100% diagnosable, discrete, and fixed, no specimens being intermediate.

DISTRIBUTION

We used ecological niche modeling to produce a model of environmental requirements of *Robsonius* as a clade, a model with which we could assess distributional patterns and whether phylogenetic breaks coincide with zones of low environmental suitability. Occurrence data (Appendix 1) consisted of specimen records (data accessed via the Global Biodiversity Information Facility or museum collection managers), supplemented with observations from the literature (de Roeber 1990, Lambert 1993, Harrap and Mitchell 1994, Poulsen 1995, Collar 2006), web-reported sightings (eBird; Wood et al. 2011), and data associated with vocal archives (XC, ML). The occurrence data thus included 26 unique localities with voucher specimens and 12 additional unique localities based on observations and audio recordings, for a total of 38 occurrence points, adequate for producing robust models (Pearson et al. 2007). We chose to model *Robsonius* at the genus level in light of the small sample size and because ecological niches of allopatric replacement species tend to be similar (Peterson et al. 1999, Peterson 2011). Climate data (30" spatial resolution, or about 1 km) were drawn from the WorldClim climate archive (Hijmans et al. 2005); we used the following data layers: annual mean temperature, mean diurnal temperature range, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, and precipitation of the wettest and driest months. We developed niche models with GARP (Stockwell and Peters 1999) and Maxent (Phillips et al. 2006).

Suitable areas identified by the niche models (Fig. 2) suggest that the distribution of *Robsonius* is limited by environmental factors within Luzon. Analysis of the contributions of variables in Maxent indicates that precipitation in the driest month (62.5%), minimum temperature in the coldest month (18.8%), and annual mean temperature (11.9%) explain the most variance; all other variables contributed less than 5% of the variance. Thus niche models suggest that *Robsonius* is confined to wetter rainforest and submontane forest and absent from seasonally dry monsoon forest in western Luzon and the Cagayan Valley and from montane forest above ~1500 m. The environmentally unsuitable Cagayan Valley may isolate *R. rabori* and *R. thompsoni*, whereas *R. thompsoni* and *R. sorsogonensis* do not appear to be isolated currently by gaps in suitable environmental conditions.

DISCUSSION

SYSTEMATIC RELATIONSHIPS, BIOGEOGRAPHY, AND DISTRIBUTION

Two scenarios may explain the diversification of *Robsonius* within the Luzon island complex. First, the three species may

constitute a case of intra-island diversification in a lowland forest bird. Generally, birds are not thought to speciate readily within the confines of islands (Diamond 1977, Coyne and Price 2000), although recent molecular genetic studies suggest that this phenomenon may be more widespread than previously appreciated (e.g., Ryan et al. 2007, Hosner et al. 2013). Alternatively, three ancient taxa could have evolved on separate proto-islands that constitute the current Luzon (Hall 2002, Sly et al. 2011).

Robsonius is limited to the Luzon Pleistocene aggregate island complex (Heaney 1986, Brown and Diesmos 2002; Appendix 1), with records from Catanduanes Island as well as Luzon itself. Ecological niche models suggest that climatically suitable areas also exist on the smaller satellite islands Polillo and Marinduque (Fig. 2), to which the complex evidently had access during the low sea levels of the Pleistocene. Recent surveys on Polillo have not encountered *Robsonius*; however, Marinduque has received little ornithological attention since the voice of *Robsonius* was described (Harrap and Mitchell 1994), so its presence there could have been overlooked.

Robsonius thompsoni replaces *R. rabori* east of the Cagayan Valley in forests associated with the northern Sierra Madre and has been recorded in Cagayan, Isabela, Aurora, and Nueva Vizcaya provinces; niche models indicate potential for occurrence in Quirino Province also (Fig. 2). *Robsonius sorsogonensis* replaces *R. thompsoni* south of the Mid-Sierra Madre Filter Zone, a region that has been hypothesized as an important isolating barrier in birds (e.g., *Sterrhoptilus nigrocapitatus* and *S. dennistouni*; Kennedy et al. 2000) and other vertebrates (Welton et al. 2010). *Robsonius sorsogonensis* has been recorded in Bulacan, Laguna, Quezon, Camarines Norte, Camarines Sur, and Sorsogon provinces; ecological niche models suggest it may also occur in Rizal, Marinduque, and Albay provinces.

Robsonius rabori has been recorded at only three localities (the type locality and two localities explored near Adams in 2011) in northernmost Ilocos Norte Province, hence the first species of this genus to be described is by far the least well known. Ecological niche models identify broader environmental suitability in northwestern Luzon (Fig. 2), including parts of Apayao, Kalinga, Mountain, and Ifugao provinces. This block of lowland forest in the northern Cordillera Central is presumably occupied by *R. rabori* but is poorly known by biologists and requires further surveys. Alternatively, the distribution of *R. thompsoni* may extend into the southern Cordillera Central. It is known from Mt. Palali, an outlying peak of the Sierra Madre just east of the Magat River (the largest tributary of the Cagayan River, which separates the Sierra Madre from the Cordillera Central). We encourage researchers working in Apayao, Kalinga, Mountain, and Ifugao provinces to search for *Robsonius* to clarify the range limits of each species and determine whether contact zones exist.

HABITAT

Limited data indicate that the three species of *Robsonius* have similar habitat requirements. They have been collected and observed in broad-leaved lowland and lower montane forest, including primary forest, secondary forest, forest edge, logged second growth, and forest on karst, from sea level to at least 1300 m. In these habitats, *Robsonius* seems to prefer areas of dark, thick undergrowth, including level areas with limestone rocks, outcrops, and fallen logs; steep slopes with bamboo and moss-covered boulders (de Roeber 1990, Lambert 1993, Harrap and Mitchell 1994, Poulsen 1995, Kennedy et al. 2000, Collar and Robson 2007); tree-fall gaps; and steep, shrub-filled ravines (PAH, pers. obs.). Occasionally, it has been found in tall, thick grass near the edge of secondary forests (Poulsen 1995; PAH, pers. obs. at Mt. Cagua, Cagayan Prov.). In areas of mixed primary and secondary habitats, our limited observations suggest that *Robsonius* may be more frequent in younger second growth. For example, at Adams, Ilocos Norte, we heard *R. rabori* only twice in 10 days of survey effort at the tall-forest site on Mt. Pao but heard up to five birds in a single day in secondary forest on nearby Mt. Cabacan. Greater abundance in secondary forest may be a function of suitable dense undergrowth rather than preference for secondary habitats per se; we are unaware of records of *Robsonius* populations in isolated patches of secondary forest away from large tracts of tall forest.

ECOLOGY AND BEHAVIOR

Because of the birds' secretive habits and occurrence in dense undergrowth, the ecology and behavior of *Robsonius* remain poorly understood. Most sightings are of individuals or family groups (adults with juveniles) walking slowly on the ground, flipping over leaves and woody debris in search of invertebrates (Goodman and Gonzales 1990, de Roeber 1990, Lambert 1993, Harrap and Mitchell 1994, Poulsen 1995, Collar and Robson 2007). Stomach contents ($n = 4$) included primarily sclerotized insect parts. *Robsonius* walks or runs across the forest floor, with the tail held straight out or cocked at a 30–60° angle, occasionally to 90° when startled or agitated (de Roeber 1990). In addition to its typical ground-walking habits, in response to playback, an agitated *R. sorsogonensis* made short wing-assisted jumps between several small vertical stems and perched vertically in a posture similar to that of many wrens (Troglodytidae) and neotropical antbirds (i.e., *Pithys* or *Gymnopithys*; PAH, pers. obs. at Mt. Labo, Camarines Norte Prov.).

Collar and Robson (2007) and Sánchez-González et al. (2010) described the nest of *Robsonius sorsogonensis* and *thompsoni* as a large ball structure with a side entrance and placed in understory vegetation, reminiscent of nests of *Pitta* and some species of *Bradypterus* and *Megalurus*. Sánchez-González et al. (2010) referred to the northern Sierra Madre populations as *R. rabori*, consistent with past taxonomic treatments, but the nest actually belonged to *R. thompsoni*, so the nest was described before the species had a name. The

nest of *R. rabori* remains undescribed. The clutch size in each described nest was two, and the eggs were white with reddish-brown speckles.

CONSERVATION

In the most recent conservation assessments, *R. "rabori"* (including both *R. rabori* and *R. thompsoni*) and *R. sorsogonensis* have each been treated as vulnerable on the basis of limited range (<6000 km²), small number of known localities, and suspected population declines from forest fragmentation (BirdLife International 2012). The species of *Robsonius* are now known from more localities and a larger area than previously reported (Appendix 1): 3, 21, and 14 localities for *R. rabori*, *thompsoni*, and *R. sorsogonensis*, respectively. Recognizing *R. thompsoni* as a species results in smaller distributions; on the basis of this information and revised taxonomy, we recommend elevating *R. rabori* to endangered, but treating *R. thompsoni* and *R. sorsogonensis* as vulnerable, in each case following the criteria of the IUCN (2013).

In recent years, the forests of the northern Sierra Madre have rightfully received a great deal of attention from the conservation community. They are the largest within Luzon and protect large numbers of endemic, endangered, and threatened species (Mallari and Jensen 1993, Poulsen 1995). However, the discovery we report here illustrates that conserving small portions of species' ranges may leave differentiated populations unprotected, particularly in a landscape whose beta diversity is as great as the Philippines' (Peterson 2006, Welton et al. 2010). We hope that *R. rabori*, now the only bird known to be endemic to the lowland forests around the Cordillera Central, can become a flagship species for forest conservation in the region. Tracts of lowland forest persist in Ilocos Norte, Apayao, Kalinga, and Mountain provinces. Compared with the northern Sierra Madre region, the lowland avifauna of the Cordillera Central is poorly known, and renewed interest in the area will likely result in discovery of other bird populations important for conservation.

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