


# Genetic confirmation of the species status of *Jabouilleia naungmungensis*

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**Abstract** Species assessment of allopatric taxa is problematic. Here we consider the case of the Naung Mung Scimitar Babbler (*Jabouilleia naungmungensis*) from northern Myanmar. This bird was recognized as a new species in its original description, but was subsequently considered to be a subspecies of *J. danjoui*. We review the procedures used to make this assessment, and consider them in light of morphological (significantly different bill and hallux claw lengths) and new genetic (7.0% genetic distance, cytochrome *b*) information. Based on this reconsideration, taking acoustic information into account, we conclude that the data unequivocally confirm the recognition of *J. naungmungensis* as a full species.

**Keywords** *Jabouilleia danjoui* · *Jabouilleia naungmungensis* · *Rimator* · *Napothera* · Species description · Taxonomy · Nomenclature · Timaliidae · Allopatric species

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## Zusammenfassung

### *Jabouilleia naungmungensis* ist eindeutig eine Art: Bestätigung durch genetische Analysen

Die Einstufung allopatrischer Taxa ist grundsätzlich problematisch. Hier betrachten wir den Fall des Naung Mung Krummschnabelsäcklers (*Jabouilleia naungmungensis*) aus dem nördlichen Myanmar. *J. naungmungensis* wurde ursprünglich als eine neue Vogelart beschrieben, basierend auf akustischen und morphologischen Unterschieden, aber nachfolgend lediglich als eine Unterart von *J. danjoui* anerkannt, letzteres ausschließlich basierend auf Unterschieden in der Gefiederfärbung. Wir analysieren hier alle bisherigen Ansätze, die zu diesen unterschiedlichen Bewertungen führten, und schließen alle zur Verfügung stehenden morphologischen (signifikante Unterschiede in Schnabel- und Klauenlänge) und neue genetische Informationen mit ein (7,0% genetische Distanz, Cytochrom-b). Unter Berücksichtigung von bioakustischen Daten bleibt als einzige Schlussfolgerung, dass *J. naungmungensis* eine vollständige Art ist.

## Introduction

*Jabouilleia naungmungensis*, the Naung Mung Scimitar Babbler, was described and recognized as a full species by Rappole et al. (2005) based mainly on acoustic and morphological differences from its closest known relative, *J. danjoui*, from Vietnam. Additional information on the behavior and general biology of the new species was provided by Rappole et al. (2008). However, in the account of *J. danjoui* provided by Collar and Robson (2007) in the

*Handbook of the Birds of the World*, the taxon was relegated to subspecific status. This difference in taxonomic treatment was subsequently debated in the literature and in online forums (Alström et al. 2013; Collar 2011; Collar and Pilgrim 2007; Eames and Mahood 2011; Moyle et al. 2012; Nyári and Reddy 2013; Oliveros et al. 2012; Rappole et al. 2005, 2008; Reddy 2008; Reddy and Moyle 2011; Renner et al. 2015). At present, taxonomic authorities appear to be following the arguments presented by Collar (2011) in treating *J. naungmungensis* as a subspecies of *J. danjoui* (Dickinson and Christidis 2014) or *Napothera danjoui* (Clements et al. 2015) (for differences between the two generic classifications, refer to Fig. 1).

The data upon which Collar and colleagues first based their conclusion regarding the status of *J. naungmungensis* rests principally on a subjective comparison of color differences and a limited morphometric analysis (Collar 2011; Collar and Pilgrim 2007). Meanwhile, del Hoyo and Collar (2016) revised the subspecific treatment of *naungmungensis* by ranking “the form provisionally to species rank” under specific preconditions on the available acoustic information.

Here we present a new analysis of the species status of the two taxa, taking into consideration all available acoustic, ecological, and morphological data, and including

new molecular genetic information, which unambiguously indicate that *J. naungmungensis* should have species status.

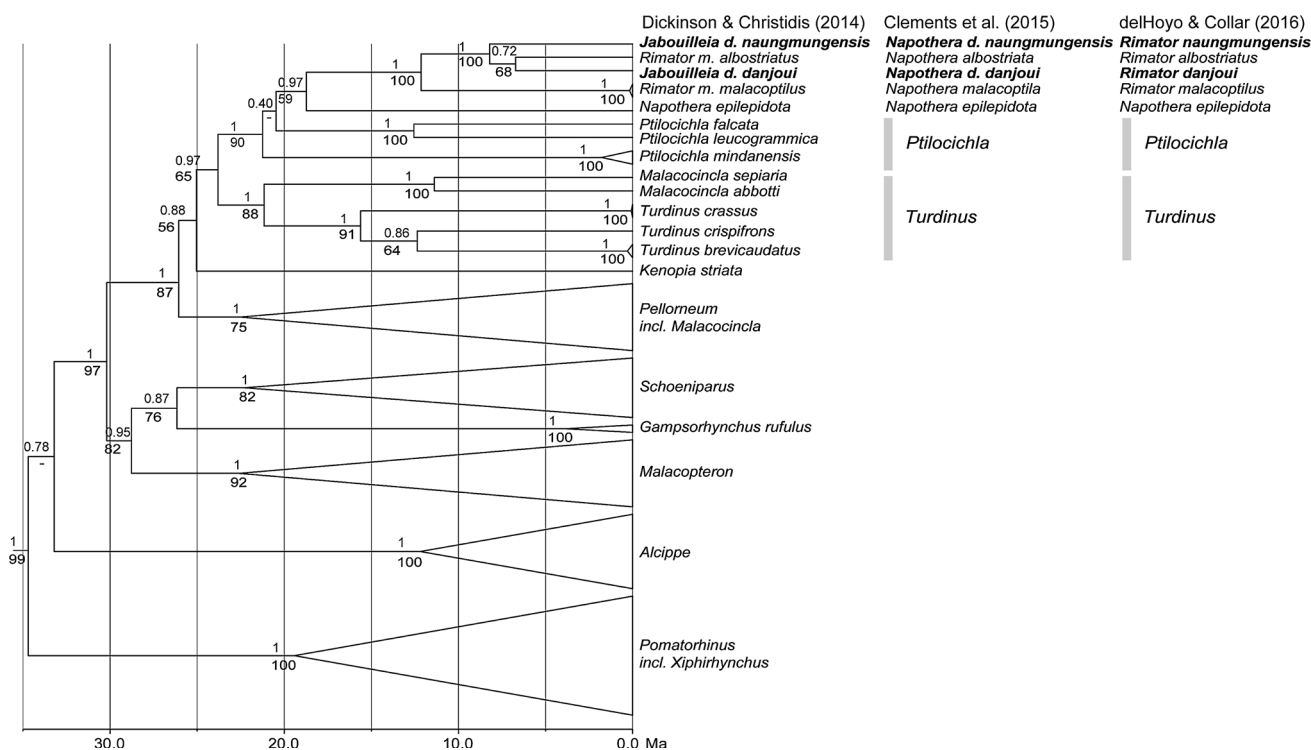
## Methods and materials

In addition to published information on plumage color, morphological traits, ecology, and acoustics (all cited where appropriate), we add new morphometric and molecular genetic data obtained via procedures described below.

### Target taxa

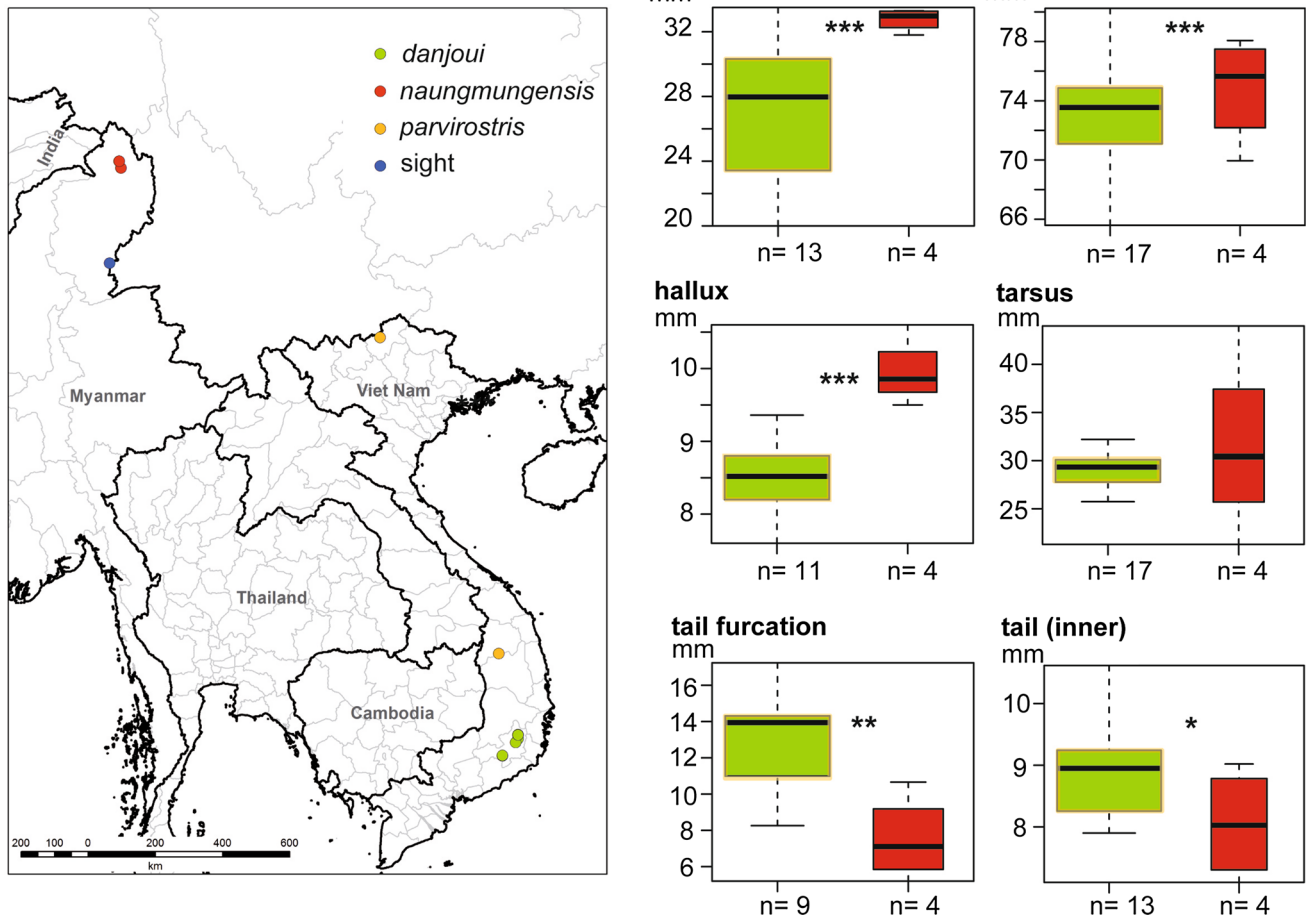
The genus *Jabouilleia* consists of two species, *Jabouilleia danjoui* and *J. naungmungensis*, each with a limited range (Fig. 2). Records for *J. danjoui* derive from two mountainous areas of Vietnam, extending into Laos (Fig. 2). Specimen records for *J. naungmungensis* come only from far-northern Myanmar, although there are sight records from the border region between China (Yunnan state) and Myanmar (Kachin) about 300 km south of the original encounter site (Renner et al. 2015).

The Short-tailed Scimitar Babbler, sometimes also called the Indochinese Wren Babbler (particularly when it is placed in the genus *Rimator*), was first described by



**Fig. 1** Phylogenetic relationships of *Jabouilleia naungmungensis*; multilocus phylogeny based on two mitochondrial genes (cytochrome *b*: 1134 bp, ND2: 1041 bp) and one nuclear intron (TGFB2: 610 bp); support from Bayesian posterior probabilities and RAXML bootstrap

analysis is indicated *above nodes* and *below nodes*, respectively; classification of target taxa according to del Hoyo and Collar (2016) and two further taxonomic authorities is indicated at the terminal clades of the crown group



**Fig. 2** Left distribution map of the *Jabouilleia* specimens analyzed. Right differences in six morphological parameters (boxplots) between *Jabouilleia naungmungensis* (red) and *J. danjoui* (green; including

Robinson and Kloss (1919) as *Jabouilleia danjoui* from Lang Bian Peaks, Vietnam (12°02'N, 108°26'E). According to Collar and Robson (2007), five subspecies are known but most are not yet considered to be valid. *J. d. parvirostris*, originally described by Delacour (1927), is the taxon known from north-central Vietnam and Central Laos (Dickinson and Christidis 2014). *J. d. parvirostris* shows a slightly darker breast band than *danjoui* does; *parvirostris* otherwise resembles *danjoui* in plumage.

**Molecular genetics**

To perform comparisons with available sequences of *Jabouilleia danjoui* and related babblers (data set for comparison from Moyle et al. 2012), we extracted DNA from one tissue sample of a *J. naungmungensis* specimen (sample number 3318, specimen currently at BOKU; Table 1), which was also included in all morphological analyses.

subspecies *danjoui* and *parvirostris*, because the latter two are not distinguishable by morphometrics); significance levels: \**p* < 0.05, \*\**p* < 0.005, \*\*\**p* < 0.001; ANOVA (color figure online)

We amplified two mitochondrial genes: cytochrome *b* (*cytb*), NADH dehydrogenase subunit 2 (ND2), and one nuclear marker: the fifth intron of the transforming growth factor β2 (TGFB2). For details on DNA extraction, primer combinations, and PCR and sequencing protocols, see Päckert et al. (2010). New sequences were deposited at GenBank under accession numbers MF563986 (COI), MF563987 (*cytb*), MF563988 (ND2), and MF563989 (TGFB2). To perform phylogenetic reconstruction, we included our sequence data in the core babbler data set of Moyle et al. (2012), available at TreeBASE (ID = MD 12,899). We furthermore included sequences of another close relative of *Jabouilleia*, the Sumatran Wren Babbler, *Rimator albobristatus* (from Reddy and Moyle 2011). Sequences were aligned with MEGA v6 (Tamura et al. 2013) and manually corrected after visual inspection.

We reconstructed a multi-locus phylogeny based on three markers (*cytb*, ND2, and TGFB2) with BEAST

**Table 1** Localities and measurements of the *Jabouilleia* specimens included in this work

Collection no.	Collection	Taxon	Sex	Country	Location	Day	Month	Year	BL	BW	BH	W	Ti	To	Tarsus	Tail furcation	Hallux nail	Remarks
AMNH	833,674	<i>Jabouilleia danjoui parvirostris</i>	F	Vietnam	Mount Tay Con Linh	11	5	2000	n/a	n/a	n/a	71.50	54.50	n/a	28.65	n/a	n/a	Not measured by Renner
ANSP	38,484	<i>Jabouilleia danjoui danjoui</i>	n/a	Vietnam	Pic de Lang Bian	3	11	1939	33.50	4.90	5.50	74.80	n/a	58.30	32.20	n/a	9.30	Topotype
BMNH	1919.12.20.280	<i>Jabouilleia danjoui danjoui</i>	F	Vietnam	Da Lat	8	4	1918	28.40	4.95	4.92	75.89	61.21	50.22	29.50	10.99	8.20	“Specimen of which the description of the ♀ was taken”
BMNH	1919.12.20.533	<i>Jabouilleia danjoui danjoui</i>	M	Vietnam	Lang Bian Plateau, Da Lat	20	4	1918	31.38	3.95	4.96	73.55	Missing	Missing	26.03	n/a	7.60	n/a
BMNH	1927.6.5.15	<i>Jabouilleia danjoui parvirostris</i>	M	Vietnam	Bana, C. Annam	14	8	1926	20.00	4.34	4.67	65.59	56.03	Moult	25.73	n/a	8.73	Holotype of <i>parvirostris</i>
BMNH	1927.6.5.890	<i>Jabouilleia danjoui danjoui</i>	M	Vietnam	Djiring, S Annam	11	3	1927	29.51	4.50	5.29	80.24	68.09	54.08	29.91	14.01	9.20	n/a
BMNH	1927.6.5.891	<i>Jabouilleia danjoui danjoui</i>	M?	Vietnam	Djiring, S Annam	11	3	1927	27.00	n/a	n/a	74.28	58.18	49.22	26.80	8.96	8.80	n/a
BMNH	1998.71.14	<i>Jabouilleia danjoui parvirostris</i>	M	Vietnam	Kon Tum Annam	26	4	1998	23.28	3.96	5.15	71.97	54.66	43.40	26.06	11.26	7.72	Specimen in suboptimal condition (breast band distorted)
BMNH	1919.12.20.279	<i>Jabouilleia danjoui danjoui</i>	M	Vietnam	Lang Bian Plateau, Da Lat	27	4	1919	31.39	5.43	4.88	75.95	59.72	45.41	30.09	14.31	8.46	Holotype
MCZ	267,847	<i>Jabouilleia danjoui danjoui</i>	F	Vietnam	Lang Bian, Da Lat	7	3	1939	n/a	n/a	n/a	74.50	60.50	n/a	29.15	n/a	n/a	Not measured by Renner
MCZ	267,848	<i>Jabouilleia danjoui danjoui</i>	M	Vietnam	Lang Bian, Da Lat	12	3	1939	n/a	n/a	n/a	79.00	64.00	n/a	31.01	n/a	n/a	Not measured by Renner
MCZ	267,849	<i>Jabouilleia danjoui danjoui</i>	n/a	Vietnam	Lang Bian, Da Lat	12	3	1939	n/a	n/a	n/a	69.00	66.50	n/a	31.31	n/a	n/a	Not measured by Renner

**Table 1** continued

Collection	Collection no.	Taxon	Sex	Country	Location	Day	Month	Year	BL	BW	BH	W	Ti	To	Tarsus	Tail furcation	Hallux nail	Remarks
MHNP	602	<i>Jabouilleia danjoui parvirostris</i>	M	Vietnam	Da Nang, Hoa Vang	14	8	1926	23.43	5.24	4.89	71.09	n/a	n/a	27.76	n/a	8.52	n/a
MHNP	603	<i>Jabouilleia danjoui danjoui</i>	M	Vietnam	Djiring, S Annam	3	3	1927	21.40	4.19	5.13	70.83	56.28	40.05	29.77	16.23	9.36	n/a
n/a	3318 <sup>a</sup>	<i>Jabouilleia naungmungensis</i>	M	Myanmar	U Ring Ga	13	3	2006	31.80	4.70	5.70	74.40	60.10	54.90	21.30	5.20	10.60	n/a
n/a	3367	<i>Jabouilleia naungmungensis</i>	n/a	Myanmar	U Ring Ga	20	3	2006	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	9.50	Only foot remains, no specimen
USNM	278,487	<i>Jabouilleia danjoui danjoui</i>	M	Vietnam	Lang Bian Plateau, Da Lat	24	4	1918	27.97	4.71	4.21	71.27	58.64	50.38	29.12	8.26	8.10	Paratype
USNM	360,907	<i>Jabouilleia danjoui danjoui</i>	M	Vietnam	Lang Bian Plateau, Da Lat	n/a	12	1939	30.32	4.86	5.11	74.86	59.78	45.84	29.44	13.94	8.20	n/a
USNM	475,738	<i>Jabouilleia danjoui danjoui</i>	F	Vietnam	Lang Bian Plateau, Da Lat	24	12	1961	26.47	4.26	5.00	69.69	60.65	43.41	31.33	17.24	8.65	n/a
USNM	633,212	<i>Jabouilleia naungmungensis</i>	F	Myanmar	Naung Mung	6	2	2004	33.30	4.20	5.30	76.90	50.50	44.00	44.00	6.50	n/a	n/a
USNM	633,213	<i>Jabouilleia naungmungensis</i>	F	Myanmar	Naung Mung	6	2	2004	33.24	4.04	4.86	78.07	57.74	47.08	30.85	10.66	9.85	Holotype
USNM	633,214	<i>Jabouilleia naungmungensis</i>	F	Myanmar	Naung Mung	8	2	2004	32.72	5.07	4.88	69.95	52.53	44.82	30.10	7.71	9.86	n/a

<sup>a</sup> Genotyped specimen

v.1.8.1 (Drummond and Rambaut 2007). We ran BEAST for 10,000,000 generations (trees sampled every 1000 generations) under the uncorrelated lognormal clock model for all loci with the “auto-optimize” option activated and a Yule process prior (speciation) applied to the tree. A GTR + I +  $\Gamma$  model was applied to each partition of the one- and two-partition schemes and the two mitochondrial genes were further partitioned by codon position. In the absence of reliable passerine fossils providing appropriate node age constraints, we estimated divergence times between clades using an empirical substitution rate of 0.0105 substitutions per site/lineage/million years for *cytb*, as evaluated by Weir and Schluter (2008). We applied this rate to the *cytb* partition, and left the rates of all other loci to be estimated relative to the *cytb* rate. The log files were examined with Tracer v.1.4.8 (Drummond and Rambaut 2007) in order to ensure effective sample sizes (ESS; which yielded reasonable values for all parameters after 10,000,000 generations). Trees were summarized with TreeAnnotator v.1.4.8 (posterior probability limit = 0.5) using a burn-in value of 3000 (trees) and with the median height annotated to each node.

Node support in a ML framework was obtained by constructing 1000 bootstrap replicates with RAxML (“thorough” bootstrap option, 100 replicates) (Stamatakis 2006) using the Python-based GUI developed by Silvestro and Michalak (2012). The concatenated matrix was partitioned and the GTR + I +  $\Gamma$  model was applied across partitions.

## Morphometry

We found a total of 22 specimens in the collections of the AMNH (1 specimen), ANSP (1), BMNH (8), MCZ (3), MHNP (2), BOKU (1), and USNM (6) (acronyms of the collections are defined in the “Acknowledgements”). These specimens are likely to be all of the available specimens of the genus *Jabouilleia* worldwide. Measurements were generally performed by Renner (exceptions are labeled as such in Table 1).

Besides noting species and subspecies, as indicated on the labels, we added information (when available) on country, exact location, elevation, the collectors, and collection date. We measured with a digital caliper to the nearest 0.1 mm for hard parts and 0.5 mm for feathers. In general, we followed the measuring guide of Eck et al. (2011). We measured bill length from the distal end of the operculum to the tip (which mostly resembles the exposed culmen) as well as bill width and bill height at the operculum. The wing was measured from the bend of the wing to the tip of the longest primary, unflattened on the bird’s right side. The tarsus was measured from the distal to the proximal end of the tarsometatarsus on the bird’s right side

(Svensson 1992). The outer and innermost rectrices were measured from insertion to the tip of the innermost/outermost rectrix on the bird’s right side (all bilateral measures were preferably obtained on the right side; they were only measured on the left body side if they could not be measured on the right side or there was a defect on the right side). Tail furcation was calculated as the innermost minus the outermost rectrix. We measured the hallux claw on the ventral side of the claw from the skin to the tip.

We tested the variance in the morphometric measurements with an ANOVA for each parameter based on the statistical hypothesis that we had two groups (Myanmar vs. Vietnam/Laos). We tested whether each parameter was normally distributed with a Shapiro–Wilk test (except for the tarsus, all were normally distributed,  $p > 0.05$ ) and subsequently applied a Kruskal–Wallis ANOVA to the tarsus.

## Results

Unexpectedly, the two *Jabouilleia* taxa did not present as a monophyletic clade in the multilocus tree: *J. danjoui* was a sister to *R. albostratus*, albeit with poor support, and *J. naungmungensis* was a sister to both of them (Fig. 1). This relationship must be treated with care, because it relies on the mitochondrial signal only (a TGFB2 sequence was not available for *R. albostratus*). A sister-group relationship between the *Jabouilleia*/*R. albostratus* clade and the Long-Billed Wren Babbler *Rimator malacoptilus* received strong support. The uncorrected  $p$ -distance value between *J. danjoui* and *R. albostratus* was 5.1% (*cytb* sequence comparison), whereas the genetic divergence between *J. naungmungensis* and the latter two was greater (7.0–7.7%). That distance is comparable to genetic divergences between sister species from the same clade, e.g., *Ptilocichla leucogrammica*/*P. falcata* (7.1%) and *Malacocincla sepiaria*/*M. abotti* (9.4%), and greatly exceeds genetic distances between sister species from other babbler clades, e.g., *Alcippe grotei*/*A. poioicephala* (4.0%). The  $p$ -distance value between the two *Jabouilleia* species corresponded to a divergence time estimate of about 8 Mya, i.e., a Late Miocene lineage split.

Measurements were taken from 22 specimens from the genus *Jabouilleia* (Table 1; Fig. 2). The Myanmar-endemic *J. naungmungensis* is significantly distinctive in some morphometric features: the bill and hallux nail are significantly longer in the Hkakabo Razi population (*naungmungensis*) as compared with specimens from all other localities (ANOVA, bill length:  $df = 1$ , deviance = 7.161,  $p < 0.001$ ; wing:  $df = 1$ , deviance = 0.256,  $p < 0.001$ ; hallux nail:  $df = 1$ , deviance = 14.045,  $p < 0.001$ ). The innermost tail length



and tail furcation also show significant differences (ANOVA, innermost tail length:  $df = 1$ , deviance = 4.198,  $p = 0.040$ , tail furcation  $df = 1$ , deviance = 7.767,  $p = 0.005$ ); however, there is considerable overlap, at least for the innermost tail length (Fig. 2).

## Discussion

Recognition of a new species, particularly one with close allopatric relatives, is a complex procedure; one that includes careful review by recognized experts from within the taxonomic group. Such a process was followed in *The Auk's* editorial review when the paper originally describing *J. naungmungensis* was accepted for publication (Rappole et al. 2005).

Collar and Robson (2007) chose to disregard recognition of the species in their account of the bird's closest known relative, *J. danjoui*, listing it as a subspecies of the Vietnamese bird. Their decision, as subsequently explained in a paper by Collar (2011), was based on a morphometric analysis and a plumage color analysis. The morphometric analysis, as described by Collar (2011), involved comparison of measurements from two *J. naungmungensis* with those from 11 *J. danjoui* for four parameters, and did not include a statistical comparison. Though del Hoyo and Collar (2016) recognized *J. naungmungensis* as a full species based on a previously published sound recording (Rappole et al. 2008: Fig. 2 on p. 625) and differences in plumage coloration, they justified the previous subspecific rank in Collar and Robson (2007) with a “mistaken claim of morphometric differences” in the original description. However, with our new analysis, we provide firm evidence of significant differences between the two taxa in question in five out of ten biometric parameters. Thus, distinctive morphometrics support the recognition of the two as separate species.

However, Collar (2011) evidently leaned most heavily on plumage color analysis in his initial decision, although it should be noted that in his analysis, he applied a scoring method developed by Tobias et al. (2010), which was published after he had already published his original decision not to recognize *J. naungmungensis* as a separate species (Collar and Pilgrim 2007). In any event, for the plumage color comparison, Collar used three plumage color traits when comparing two *J. naungmungensis* with three *J. danjoui*. Based on this comparison of the individual scores for each trait and a total score of four for all traits combined, he concluded that the plumage color differences between *J. naungmungensis* and *J. danjoui* were “insufficient to achieve species status” (Collar 2011). Remarkably, del Hoyo and Collar (2016) came to a different conclusion

by applying the same methodology to the same traits without analyzing any new data (i.e., they used the same data as before). Such inconsistencies in species diagnosis are one reason why the scoring method has been repeatedly criticized—it is prone to subjectivity and other potential pitfalls (Curry 2015; Martens 2014; Peterson and Moyle 2008).

Plumage color is, of course, an important characteristic of birds, given their dependence on vision. However, it is suspect when used as a sole defining character in taxonomic decisions regarding separation of species (Päckert 2015). There are at least four reasons why extreme caution should be taken in this regard: (1) taxa that are known to be members of the same species (based on known interbreeding) can differ significantly in color (e.g., among many possible examples in Rasmussen and Anderton 2005, the northwestern versus southeastern forms of the Red-faced Liocichla *Liocichla phoenicea*); (2) taxa that are known to be members of different species can show very little difference in color (e.g., again among many possible examples, several members of *Empidonax*, *Phylloscopus*, *Thamnophilus*, *Elaenia*, etc.); (3) color can vary significantly based on the methods used for specimen preparation, handling, and storage as well as with age (Armenta et al. 2008; Doucet and Hill 2009); and (4) color assessments performed without applying a quantitative method (such as spectrometry) are subjective, varying among observers (Peterson and Moyle 2008).

In our original description of *J. naungmungensis* as a unique species separate from its allopatric congener, *J. danjoui*, we were careful to present all of the information available in 2005 documenting the differences between the two species: acoustic, ecologic, and morphometric. For the purposes of this paper, we reperformed the morphometric work using a single investigator and included all 22 known specimens (14 *danjoui*, 4 *naungmungensis*, 4 *parvirostris*; all included in tests; Table 1; Fig. 2). In addition, we performed a new genetic analysis to augment the work done by S. Reddy (see citation in Renner and Rappole (2011), page 156), which has not been published to date (see “Results” section above and Fig. 2).

The results of our genetic work show a genetic distance value of >7% (*cytb*) between *J. naungmungensis* and *J. danjoui*. This distance equals or exceeds mean pairwise distances among other sister species in babblers, as we have shown. Thus, despite justified and reasonable criticism of the use of genetic distances as a threshold indicative of species status in birds (Rheindt and Austin 2005; Thomson et al. 2014), we consider *J. naungmungensis* to be genetically distinctive. Mean ages of Holarctic bird species (i.e., divergence time estimates for the split from their sister) have been estimated as corresponding to the Miocene/Pliocene boundary: 5.7–7.1 Ma for Himalayan

species pairs (Price et al. 2014), about 5 Ma for Nearctic species pairs (Klicka and Zink 1997), and 3.9 Ma in a comprehensive comparison of avian genera (Johns and Avise 1998); sister species were not considered in the latter study, only randomly drawn congeners. Regardless of all the uncertainties associated with molecular dating, the deep split between *J. naungmungensis* and *J. danjoui* clearly exceeds intraspecific genetic variation in passerine birds as assessed to date. Moreover, the phylogenetic relationships between *Jabouilleia* and *Rimator* are not completely resolved. Paraphyly of *Jabouilleia* would be a strong argument against uniting *J. danjoui* and *J. naungmungensis* under the same species-level taxon. However, the sister-group relationship between the Indochinese *J. danjoui* and *R. albostratus* from Sumatra has received support only from mitochondrial genes and so further information from multi-locus data sets including *R. pasquieri* from northern Vietnam is needed. In any case, conspecific classification of *R. m. albostratus* and *R. m. malacoptilus* (Dickinson and Christidis 2014; under the genus *Napothera*) is not supported by our phylogeny (for the species status of the latter and *R. albostratus*, see del Hoyo and Collar 2016). Nevertheless, the deep split between *J. naungmungensis* and its eastern sister clade reflects a rather common phylogeographic pattern at the species level, i.e., an east–west disjunction between Central Himalayan endemics and their eastern Himalayan/Indochinese/Indo-Myanmar counterparts (Martens 2015; Päckert et al. 2012, 2015).

We recognize that there can be no completely definitive answer in the recognition of allopatric species. However, not to recognize two species as different as *J. naungmungensis* and *J. danjoui* undermines the entire process because of the very large number of congeners that are recognized as separate species based on far weaker data. In conclusion, based on an integrative concept of taxonomy, *J. naungmungensis* is a full species with significant and clear differentiation in the three independent and commonly used character sets of morphology (own data), genetics (own data), and bioacoustics (Rappole et al. 2008).

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