

# A New Tarsier Species from the Togean Islands of Central Sulawesi, Indonesia, with References to Wallacea and Conservation on Sulawesi

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**Abstract:** We describe and name a new species of tarsier from the Togean Islands, in Tomini Bay, bounded by the northern and eastern peninsulas of Sulawesi. In doing so, we highlight how 25 years of sustained research on the alpha taxonomy of Sulawesian tarsiers, *Tarsius*, have helped to identify key conservation priorities in the Sulawesian region of the Wallacea Biodiversity Hotspot.

**Key words:** Biodiversity, bioacoustics, cryptic species, duet call, Togean form, taxonomy, hotspots

## Introduction

The impending global environmental catastrophe of biodiversity loss has been termed the “sixth mass extinction” (for example, Leakey and Lewin 1996), and led Myers *et al.* (2000) to propose that global conservation priorities should focus especially on the “hotspots” method for identifying global conservation priorities; with only so much time and resources, conservation efforts should be spent “where exceptional concentrations of endemic species are undergoing exceptional loss of habitat” (p.853; see also Mittermeier and Rylands 2017). Wallacea is one of the top 25 global hotspots for biodiversity conservation, and Sulawesi is by far the largest landmass within it, and by some measures the highest regional priority for conservation (Wilson *et al.* 2006).

In the time since Niemitz (1984) revised tarsier taxonomy and MacKinnon and MacKinnon (1980) published the first report of wild tarsiers from Sulawesi—wherein they noted the presence of a duet call with geographically-structured variation and the likelihood of much unrecognized taxonomic variation—the number of recognized tarsiers on Sulawesi has

grown from one to twelve (including the species described here). Based on variation in their calls, Shekelle and Leksono (2004) predicted that 16 or more cryptic species would eventually be described from Sulawesi and its surrounding islands. Nietsch and Niemitz (1993) reported tarsiers from the Togean Island chain, and believed that they might be taxonomically distinct. The suggestion to taxonomically separate Togean Island tarsiers was supported by further work on the role of vocalizations in species differentiation among the Sulawesi tarsiers by Nietsch and Kopp (1998) and Nietsch (1999). Shekelle *et al.* (1997) conducted playback tests in the wild that concurred with the findings of Nietsch, i.e. Togean Island tarsiers appeared to be taxonomically separable on the basis of vocalizations. Shekelle (2003) reported that genetic data were consistent with the hypothesis that tarsier acoustic forms, including the Togean form, were distinct species, a finding also supported by Shekelle (2008) and Shekelle *et al.* (2010). The hypothesis that tarsier acoustic groups are distinct species was robustly supported in a fine-grained phylogeographic study of *T. dentatus* and *T. lariang* by Merker *et al.* (2009), who tested sequence data from mtDNA, y-chromosome, and microsatellites against bioacoustics and morphology along a transect that passed through the species boundary.

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**Figure 1.** Skulls of three type specimens (left to right), *Tarsius supriatnai*, *T. spectrumgurskyae* and *T. niemitzi*. Photos by Myron Shekelle.

We present a new molecular phylogeny for Tarsiidae based on 12S mtDNA sequences that offers further support that Togean Island tarsiers are taxonomically separable from other known tarsier taxa.

### *Tarsius niemitzi* sp. nov.

**Holotype:** MZB 32654 (Fig. 1, Table 1), adult male. Museum Zoologicum, Bogoriense, Cibinong, West Java, Indonesia. Collector: Simson Katiandagho, 1 October 2009.

**Type locality:** Desa Benteng, Kecamatan Togean, Kabupaten Tojo Una-Una, Central Sulawesi, Indonesia. Geographical coordinates for Desa Benteng, Togean Island are 0°23'36.7"S, 122°01'37.8"E.

**Hypodigm:** Only the type specimen available.

**Description:** MORPHOLOGY: Surveys of wild populations have indicated that body weight and tail length fall within the range of a number of other *Tarsius* species, including *T. tarsier*, *T. fuscus*, *T. dentatus*, *T. spectrumgurskyae*, and *T. supriatnai*. Body weights and tail lengths may well overlap with all species of *Tarsius*, except *T. pumilus* and possibly some offshore taxa, such as *T. sangirensis*. Body weight: female 104–110 g (n = 2); male 125–138 g (n = 3). Tail length: female = 245–261 mm (n = 2); male 246–258 mm (n = 3) (data from Shekelle 2003). *Tarsius niemitzi* is similar to *T. dentatus* in having darkly pigmented skin, particularly the tail,

**Table 1.** Measurements of type specimens compared with two recently described species *T. spectrumgurskyae* and *T. supriatnai*.

Type specimens	<i>T. spectrumgurskyae</i>	<i>T. supriatnai</i>	<i>T. niemitzi</i>
Acoustic group	Manado form	Gorontalo form	Togean form
Specimen number	MZB3269	MZB6595	MZB 32654
Age	adult	adult	adult
Sex	m	m	m
<b>Measurements following Musser &amp; Dagosto (1987)</b>			
Greatest length of skull	37.1	37.4	38.2
Zygomatic breadth	26.8	26.2	25.8
Breadth across orbits	29.9	29.4	30.1
Breadth of a single orbit	17.2	17.3	17.7
Height of a single orbit	17.9	18.3	17.8
Length of nasals	7.0	6.8	7.4
Breadth of bony palate at M <sup>3</sup>	14.1	14.1	15.1
Length of auditory bulla	11.2	11.8	11.9
Breadth of auditory bulla	6.6	5.6	5.9
Length of anterior part of bulla	5.6	5.9	6.4
Length of posterior part of bulla	6.3	6.4	6.4
Length of upper toothrow, C-M <sup>3</sup>	12.8	12.1	13.0
Length of lower toothrow, C-M <sub>3</sub>	13.3	12.9	14.0
Length of M <sup>1</sup>	2.4	2.0	2.5
Breadth of M <sup>1</sup>	3.5	3.3	3.9
Length of M <sub>1</sub>	2.3	2.0	2.0
Breadth of M <sub>1</sub>	2.2	2.3	2.0
<b>Groves (1998)</b>			
Ear length	23.7	26.1	30.1
Ear width			17.6
Tibia	62.2	63.0	60.6
Tarsus	34.2	34.6	29.2
Length of third finger	25.2	24.1	
Inter orbital	2.2	1.8	2.9
Post orbital width	22.4	21.3	20.9
Nasal breadth	3.6	3.3	3.7
Palatal length	13.6	13.7	14.1
Mesopterygoid fossa width	3.4	3.4	2.7
Ramus angular process	10.3	10.2	10.4
Dentary length	24.2	24.8	24.4
Tail length	230	236	262

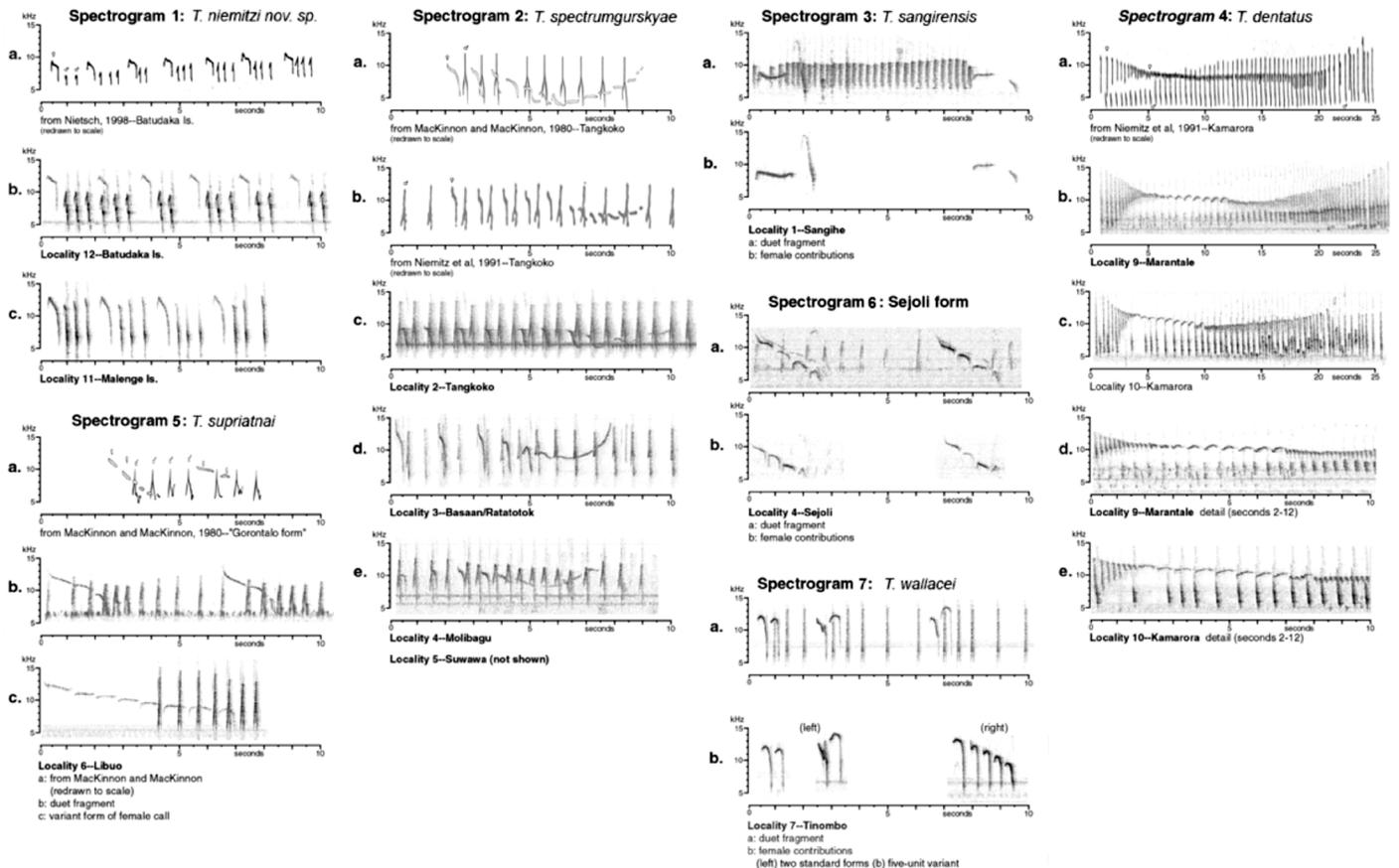
and relatively dark pelage with dark gray facial fur, particularly in adults (Fig. 3). Atypical for tarsier species endemic to small islands, *T. niemitzi* does not have a reduced tail tuft (see Shekelle *et al.* 2008b). VOCALIZATIONS: Spectrograms of the Togean form were published by Nietsch and Kopp (1998) (Fig. 4). Its duet is structurally simple, possibly the simplest of all known tarsier duets (Nietsch and Niemitz 1993). One female call is followed by two or three male calls. The female note is a downward modulated whistle, with a maximum frequency of 12–13 kHz, and a minimum frequency around 6 kHz. Each female note has a duration of about 0.5 seconds and notes are repeated at the rate of about 1 call per 1.5 seconds. The male note resembles a temporally compressed version of the female call: maximum frequency is around 10–11 kHz, and the minimum frequency is 5 kHz or lower. The duration of the male note is only about 0.15 seconds. Male calls occur in a phrase of 2 or 3 notes that gradually ascend in maximum frequency. Togean tarsiers are unique among known tarsier acoustic forms in that they respond in playback experiments to all other tarsier duet calls by duetting themselves (Fig. 5). GENETICS: Shekelle *et al.* (2008a) reported genetic evidence showing Togean Island tarsiers to be a monophyletic clade with an apomorphic 2 base pair deletion in the 12S gene that is diagnostic of the clade. Shekelle *et al.* (2010) used a subset of their previous alignment, which eliminated the region with the 2 bp deletion from the analysis.



**Figure 2.** Top right: Southeast Asia and Australia, with red box indicating contents of Top Left. Top left: Sulawesi, with red box indicating contents of bottom. Bottom: The Togeian Islands in the U-shaped bay of Tomini, bordered in the north and west by the northern peninsula, and the south by the eastern peninsula of Sulawesi, Indonesia. Expected species distribution circled in red, approximate location of type locality marked with red X.



**Figure 3.** Niemitz's tarsier *Tarsius niemitzi* sp. n. from Malenge Island, Sulawesi. Photo by Myron Shekelle, illustration by Stephen D. Nash.



**Figure 4.** Spectrograms for six species of Eastern tarsiers (adapted from Shekelle 2008). The Sejoli form might be conspecific with *T. supriatnai*.

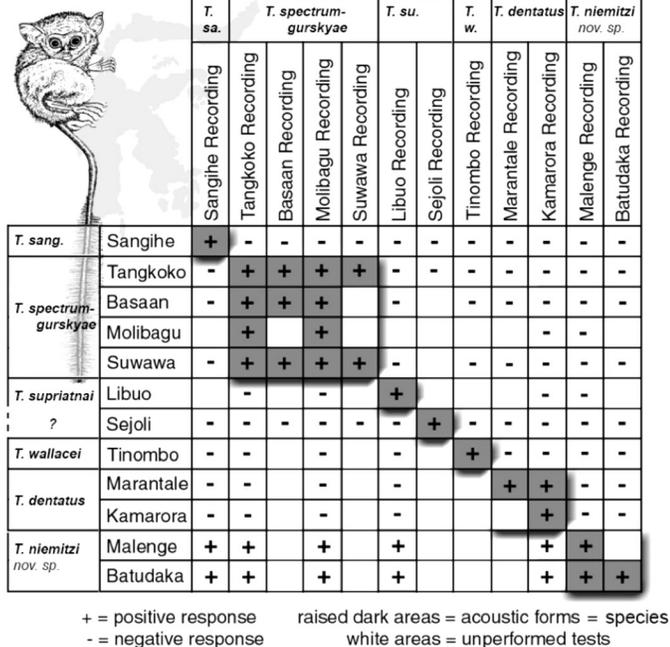


Figure 5. Results of playback tests (adapted from Shekelle 2008).

Nevertheless, Togeian Island tarsiers were still recovered as a monophyletic clade. We performed a new alignment after downloading the sequences from GenBank, and again find a robustly supported monophyletic clade (Fig. 6).

**Diagnosis:** The duet call, and the species provenance and genetics are diagnostic.

**Distribution:** Togeian Islands, except for Una Una (Fig. 2).

**Etymology:** Niemitz’s tarsier. This species is named in honor of Dr. Carsten Niemitz, universally regarded as the father of tarsier field biology. Although his field work was preceded by that of Fogden (1974), it was Niemitz who first dedicated a substantial part of his career to the systematic study of wild tarsiers. Niemitz and his student, Alexandra Nietsch, surveyed tarsiers in Central Sulawesi. Subsequently, reportedly acting on a tip from an Indonesian government official, Rolex Lameanda, Nietsch traveled to the Togeian Islands to survey tarsiers there and, with Niemitz, was the first to report their presence and the likelihood of their taxonomic distinctiveness (Nietsch and Niemitz 1993). We have found no evidence that *Tarsius togeanus* (as per Surjadi and Supriatna 1998, p.281; Ito *et al.* 2008, p.234) and *T. togianensis* (as per Gursky 2007, p.5) are names arising from formal descriptions, and they are as such *nomina nuda*.

**Local Name:** Busing, tangkasi, podi

**Field work:** Nietsch and Niemitz (1993), Shekelle *et al.* (1997), Nietsch and Kopp (1998), Nietsch (1999), Shekelle (2003, 2008).

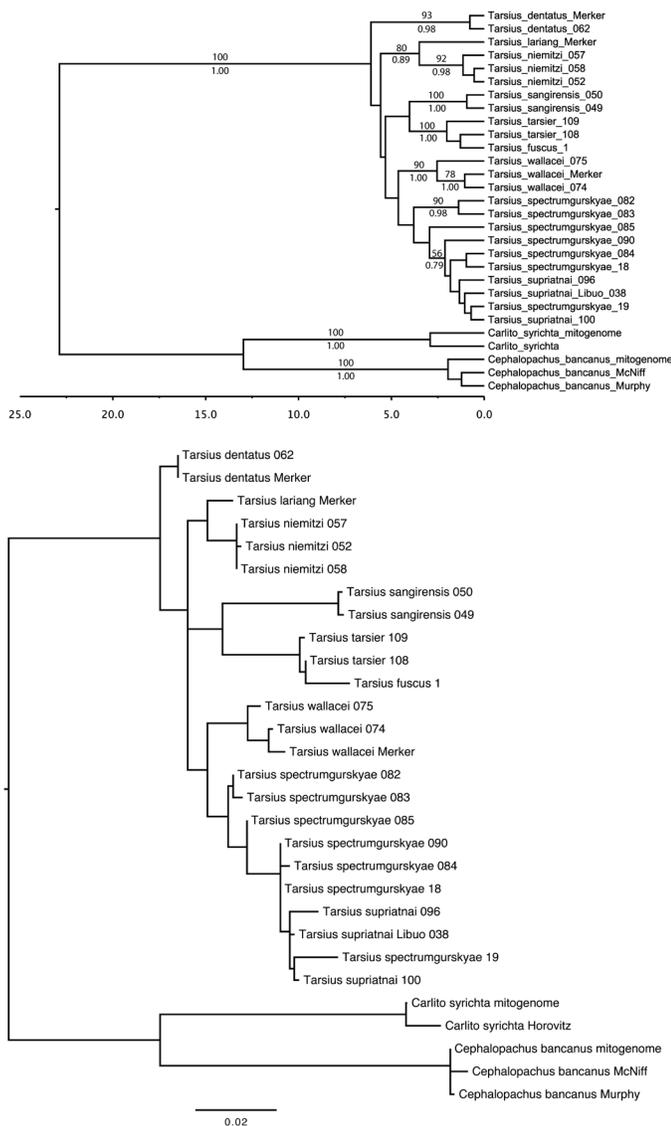
**Material examined:** There is no material that we know of other than the type specimen. Shekelle (2003) observed and photographed several individuals that were captured and released.

## Methods

DNA sequences for the 12S rRNA gene in *Tarsius*, *Carlito*, and *Cephalopachus* were downloaded from GenBank and imported into Geneious Prime 2019.1.1 (Kearse *et al.* 2012). Partial sequences <750 bp in length were discarded. The remaining 29 sequences were aligned in Geneious with MAFFT (Katoh *et al.* 2002; Katoh and Standley 2013). The resulting alignment encompassed 968 bp for 11 tarsiid species. We used PhyML 3.3.20180214 (Guindon *et al.* 2010) to construct a maximum likelihood phylogram and to perform a bootstrap analysis with 500 pseudoreplicates. We employed a GTR +  $\Gamma$  model of sequence evolution with SPR branch swapping. We also analyzed the 12S alignment with MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001) and a GTR +  $\Gamma$  model of sequence evolution. The Bayesian analysis was run for 1,000,000 generations after a burnin of 100,000 generations with four heated chains. A molecular dating analysis was performed with the mcmctree program (Yang and Rannala, 2006) in PAML (Yang 2007). Given the absence of appropriate tarsiid fossils for calibrating the tree, we employed secondary calibrations for three different nodes. First, crown Tarsiidae was calibrated with a minimum age of 20.4 Ma and a maximum age of 25.2 Ma based on five recent timetree studies that are available on timetree.org (Fabre *et al.* 2009; Shekelle *et al.* 2010; Springer *et al.* 2012; dos Reis *et al.* 2012; Pozzi *et al.* 2014). We also employed minimum and maximum age constraints for *Carlito* to *Cephalopachus* (min = 4.8 Ma, max = 18.6 Ma) and crown *Tarsius* (min = 3.4 Ma, max = 11.1 Ma) based on Shekelle *et al.* (2010). The mcmctree analysis was run for 100,000 generations after 10,000 generations of burnin. We performed the analysis with autocorrelated rates and soft-bounded constraints that allowed for 2.5% tail probabilities.

## Results

Figure 6A shows the timetree that resulted from the mcmctree analysis. The maximum-likelihood phylogram (log-likelihood = -2835.37431) from the PhyML analysis of 12S rRNA mtDNA is shown in Figure 6B. The phylogram and timetree are both rooted between *Tarsius* and *Carlito* + *Cephalopachus* following Groves and Shekelle (2010) and Springer *et al.* (2012). Bootstrap support percentages (PhyML) and posterior probabilities (MrBayes) are also shown on the timetree for clades that are supported above the 50% bootstrap and 0.50 posterior probability levels. Relationships among different species of *Tarsius* are not well resolved, but the Togeian Island tarsiers form a well-supported monophyletic clade (bootstrap support = 92%, posterior probability = 0.98). This support level is comparable to that for *T. dentatus* (92.8%) and *T. wallacei* (90.0%).



**Figure 6.** A (above). Time-calibrated phylogeny based on mcmctree (Yang and Rannala 2006) with bootstrap support percentages (PhyML) above branches, and Bayesian posterior probabilities below branches for clades with support values >50% (bootstrap percentages) and 0.50 (posterior probabilities). The timescale is in millions of years. See Table 2 for specimen ID and GenBank accession numbers. B (below). Maximum likelihood phylogram based on PhyML 3.3.20180214 (Guindon *et al.* 2010) analysis of 12S rRNA sequences with a GTR +  $\Gamma$  model of sequence evolution.

## Discussion

We describe a new species of tarsier from the Togean Islands of Central Sulawesi, Indonesia. It was long suspected on the basis of bioacoustic (Nietsch and Niemitz 1993) and biogeographic (Shekelle and Leksono 2004) evidence, and later mtDNA sequence (Shekelle *et al.* 2008). Merker *et al.* (2014) have argued for a cautious interpretation of mtDNA trees, particularly in tarsiers. Indeed, Merker *et al.* (2009) made a far stronger case for the taxonomic separability for the species that Merker and Groves described in 2006, on the basis of morphological, anatomical, and acoustic analyses, than we make here. But as with their experience, we are cautiously optimistic that subsequent analyses, using more

**Table 2.** Specimens in the phylogenetic analysis.

Species	Taxon name on trees	GenBank Accession
<i>Carlito syrichta</i>	Carlito syrichta Horovitz	AF069976
<i>Carlito syrichta</i>	Carlito syrichta mitogenome	AB371090
<i>Cephalopachus bancanus</i>	Cephalopachus bancanus Murphy	AY012131
<i>Cephalopachus bancanus</i>	Cephalopachus bancanus McNiff	AF153001
<i>Cephalopachus bancanus</i>	Cephalopachus bancanus mitogenome	AF348159
<i>Tarsius dentatus</i>	Tarsius dentatus 062	HM470229
<i>Tarsius dentatus</i>	Tarsius dentatus Merker	KC977310
<i>Tarsius lariang</i>	Tarsius lariang Merker	KC977309
<i>Tarsius niemitzi</i> sp. nov.	Tarsius niemitzi 052	HM470219
<i>Tarsius niemitzi</i> sp. nov.	Tarsius niemitzi 057	HM470220
<i>Tarsius niemitzi</i> sp. nov.	Tarsius niemitzi 058	HM470221
<i>Tarsius sangirensis</i>	Tarsius sangirensis 049	HM470205
<i>Tarsius sangirensis</i>	Tarsius sangirensis 050	HM470206
<i>Tarsius tarsier</i>	Tarsius tarsier 108	HM470222
<i>Tarsius tarsier</i>	Tarsius tarsier 109	HM470223
<i>Tarsius fuscus</i>	Tarsius fuscus 1	HM470224
<i>Tarsius wallacei</i>	Tarsius wallacei 074	HM470215
<i>Tarsius wallacei</i>	Tarsius wallacei 075	HM470216
<i>Tarsius wallacei</i>	Tarsius wallacei Merker	KC977311
<i>Tarsius spectrumgurskyae</i>	Tarsius spectrumgurskyae 18	HM470211
<i>Tarsius spectrumgurskyae</i>	Tarsius spectrumgurskyae 19	HM470212
<i>Tarsius spectrumgurskyae</i>	Tarsius spectrumgurskyae 82	HM470207
<i>Tarsius spectrumgurskyae</i>	Tarsius spectrumgurskyae 83	HM470208
<i>Tarsius spectrumgurskyae</i>	Tarsius spectrumgurskyae 84	HM470209
<i>Tarsius spectrumgurskyae</i>	Tarsius spectrumgurskyae 85	HM470210
<i>Tarsius spectrumgurskyae</i>	Tarsius spectrumgurskyae 90	HM470213
<i>Tarsius supriatnai</i>	Tarsius supriatnai 096	HM470217
<i>Tarsius supriatnai</i>	Tarsius supriatnai 100	HM470218
<i>Tarsius supriatnai</i>	Tarsius tarsier Libuo 038	HM470214

genetic markers, will find strong support for the taxonomic separability of *T. niemitzi*, as Merker and others did for *T. lariang*. We strongly encourage further work on tarsier taxonomy using holistic approaches with complementary data sets.

Extant tarsiers are classified in three genera, following Groves and Shekelle (2010), that are allopatrically distributed in distinct biogeographic regions: *Tarsius* is found on Sulawesi and surrounding islands; *Cephalopachus* is found on a restricted subset of Sundaland, principally southern Sumatra and the island of Borneo; *Carlito* is found on islands of the southern Philippines that were a single Ice Age landmass, sometimes called Greater Mindanao. *Tarsius* contains twelve species (in order of seniority): *T. tarsier* (= *spectrum*), *T. fuscus*, *T. sangirensis*, *T. dentatus* (= *dianae*), *T. pumilus*, *T. pelengensis*, *T. lariang*, *T. tumpara*, *T. wallacei*, *T. spectrumgurskyae*, *T. supriatnai*, and now *T. niemitzi*. Burton and Nietsch (2010) reported three more unnamed taxa from the

Southeastern peninsula of Sulawesi. Shekelle and Leksono (2004) predicted Sulawesi would ultimately be shown to be home to at least 16 distinct tarsier taxa. The speciose alpha taxonomy of *Tarsius* stands in contrast with that of *Cephalopachus* and *Carlito*. We question if this contrast is based upon knowledge or ignorance of the alpha taxonomy of the latter two genera, and we encourage more fieldwork in order to answer this question (see Brandon-Jones *et al.* 2004).

## Conservation

One of the most significant outcomes of 25 years of sustained research on the alpha taxonomy by one of us (MS) and subsequently by colleagues (for example, Merker and Groves 2006; Merker *et al.* 2009, 2010; Driller *et al.* 2015) has been to identify the critical conservation hotspots in the Sulawesi region (i.e. Sulawesi plus nearby islands), of the Biodiversity Hotspot of Wallacea (Fig. 7). Reclassifying a single widespread species into numerous allopatric and parapatric cryptic sibling species has the secondary effect of clarifying conservation priorities (Bickford *et al.* 2007).

Specifically, the *T. tarsier* species complex (i.e. all of the species of *Tarsius* except for *T. pumilus*), listed as Lower Risk / Near Threatened (LR/nt) in 2000, would likely be listed as Vulnerable (VU), were it classified as a single species (Fig. 7, Table 3). With reclassification, taxa in this species complex range from VU to Critically Endangered (CR) (Fig. 7, Table 3). Four of the sixteen taxa hypothesized by Shekelle and Leksono (2004) are VU, seven are EN, one is CR, and four are DD (Fig. 7, Table 3).

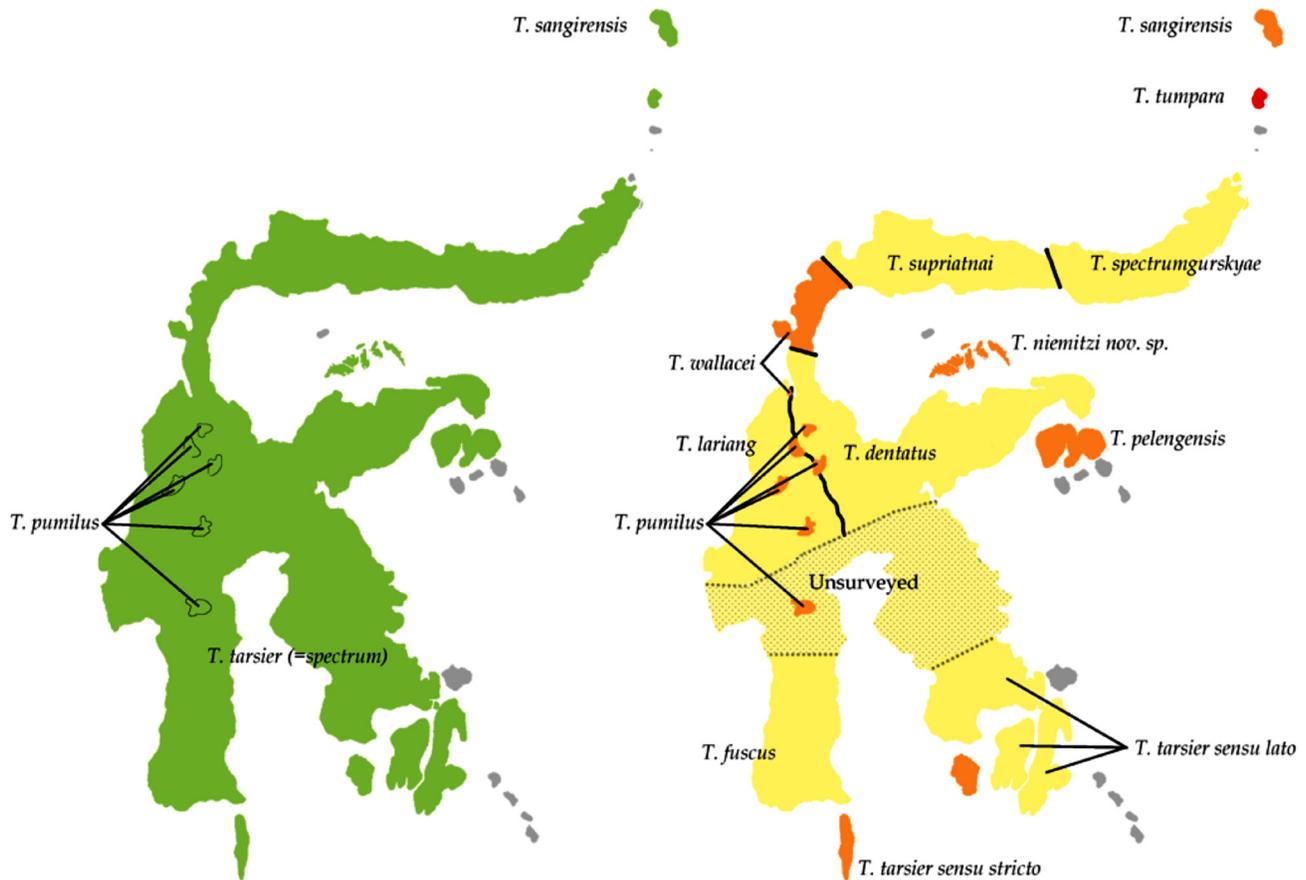
Gursky *et al.* (2008), following previous work by Supriatna *et al.* (2001) and Shekelle and Leksono (2004) estimated that the Togeian Island tarsier would be Endangered [EN], and that the Togeian Islands were a unique area of endemism in Sulawesi, in that they possess native tarsiers, lack native monkeys, and appear to be geologically separated from the Sulawesi mainland by an ocean barrier that exceeds 120 m in depth—believed to be deeper than the lowest ocean levels during Pleistocene glacial maxima. Each of these assertions are hypotheses for further testing. The broader implication is that the Togeian Islands possess a largely endemic biota of taxa that do not disperse easily across water barriers.

**Table 3.** Conservation status for 16 Indonesian tarsier taxa and populations (listed in Brandon-Jones *et al.*, 2004) show the impact of 25 years of sustained research on the alpha taxonomy of Sulawesian tarsiers of the genus *Tarsius* toward priority areas in the Wallacea Biodiversity Hotspot.

Taxon/Population		Location	Conservation Status		
			IUCN 2000	Indonesian Primate CAMP (Supriatna <i>et al.</i> 2001)	Gursky <i>et al.</i> (2008)
1.	<i>Tarsius tarsier</i> Selayar form	Selayar Is.	LR/nt	EN (B1ab)	EN (B12bc)
2.	Kendari Form	Sulawesi: near Kendari	LR/nt**	EN (B1ab)	DD
3.	Buton Form*	Buton Island	LR/nt**	VU (B1ab)	VU (B12bc)
4.	Kabaena Form*	Kabaena Is.	Not Evaluated (NE)	Not Evaluated (NE)	EN (B12bc)
5.	<i>Tarsius fuscus</i> Makassar form	Sulawesi: near Makassar	LR/nt**	VU (B1ab)	DD
6.	<i>Tarsius sangirensis</i> Sangihe form	Sangihe & Siau Is. (Sangihe only)	LR/nt**	EN (B1abc)	EN (B12bc)
7.	<i>Tarsius dentatus</i> (=dianae) Kamarora form	Sulawesi: E. central	LR/cd	LR/nt	VU (B12ac)
8.	<i>Tarsius pumilus</i>	Sulawesi: central montane 1800-2200m	DD	DD	EN (B12c)
9.	<i>Tarsius pelengensis</i> Peleng form	Peleng Is.	DD	EN (B1ab)	EN (B12ab)
10.	<i>Tarsius lariang</i> Palu Form	Sulawesi: W. central	LR/nt**	LR/nt	DD
11.	<i>Tarsius tumpara</i> Siau population	Siau Is.	LR/nt**	EN (B1abc)	CR (B12bc)
12.	<i>Tarsius wallacei</i> Tinombo Form	Sulawesi: N. peninsula, Tinombo to Ampibabo, and Uwemanje	LR/nt**	LR/nt	EN (B12bc)
13.	<i>Tarsius spectrumgurskyae</i> Manado Form	Sulawesi: N. peninsula, Gorontalo to northeast tip	LR/nt**	LR/nt	VU (B12bc)
14.	<i>Tarsius supriatnai</i> Gorontalo form	Sulawesi: N. peninsula, Gorontalo to Tanjung Pangajene, possibly to Sejoli	LR/nt**	LR/nt	VU (B12bc)
15.	Sejoli form	Surveyed only at Sejoli	LR/nt**	LR/nt	DD
16.	<i>Tarsius niemitzii</i> sp. nov. Togeian form	Togeian Islands	LR/nt**	EN (B1ab)	EN (B12bc)

\*These populations still remain classified with *T. tarsier*, but are implausibly disjunct, and are hypothesized to be three separate taxa.

\*\*These populations were classified with *T. tarsier* (=spectrum) in 2000.



**Figure 7.** Mapping the priority areas hotspots in the Wallacea Biodiversity Hotspot: a 25-year effort. (L) 2000 and prior, (R) present based upon combined sources (Supriatna *et al.* 2001; Gursky *et al.* 2008; IUCN Red List). Green = LR/NT, Yellow = VU, Orange = EN, Red = CR. Note: distribution of *T. pumilus* is a conjectural representation of regions between 1800–2200 m above sea level in the species' polygon.

## Acknowledgments

We are deeply saddened by the passing of our colleague and coauthor, Colin Groves, on November 30, 2017. Colin was described by Jane Goodall as the world's greatest primate taxonomist, and while we concur, that description only scratches the surface of his expertise. A recent bibliography of his work indicates that from his very first taxonomic description, *Didermocerus sumatrensis harrissoni* Groves, 1965 (Perissodactyla: Rhinocerotidae) [= *Dicerorhinus sumatrensis harrissoni*], up to and including this tarsier, Colin Groves authored the description of two new families, five new genera, and 56 species or subspecies (Rookmaaker and Robovsky 2018).

The fieldwork for this study was conducted long ago, and was supported by the National Science Foundation under Grant No. INT 0107277 to MS, and grants from the Primate Action Fund (now managed by the Global Wildlife Conservation), and Primate Conservation, Inc. to MS. Sponsorship for MS in Indonesia during that period was provided by Noviar Andayani of the Center for Biodiversity and Conservation Studies, University of Indonesia, and by the Indonesian Institute for Science. Permits for conducting research in conservation areas and for trapping tarsiers were provided by the Indonesian Department of Forestry. Participation by MS was

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### Appendix: A Dedication

In another sad twist to this work, on 12 April 2019, as we were in the final editing of this manuscript, Eslie Arteban Tamalagi, known as Ecil, passed away suddenly at the age of 47. Ecil was a field assistant for virtually every tarsier field project in this report, including those by Shekelle, Stefan Merker, and Christine Driller, and, we believe, Alexandra Nietsch on her trip to the Togean Islands. Ecil was highly esteemed as a scout leader, outdoorsman, naturalist, and conservationist, besides being one of the most dependable and well-liked tarsier field biologists in Sulawesi. We dedicate this work to his memory. Photo from Ecil's Facebook page.

