

Two New Tarsier Species (Tarsiidae, Primates) and the Biogeography of Sulawesi, Indonesia

Myron Shekelle¹, Colin P. Groves^{2†}, Ibnu Maryanto³, and Russell A. Mittermeier⁴

¹*Department of Anthropology, Western Washington University, Bellingham, WA, USA*

²*School of Archaeology and Anthropology, Australian National University
Canberra, ACT, Australia*

³*Museum Zoologicum Bogoriense, LIPI, Cibinong, Indonesia*

⁴*IUCN SSC Primate Specialist Group, and Conservation International, Arlington, VA, USA*

Abstract: We name two new tarsier species from the northern peninsula of Sulawesi. In doing so, we examine the biogeography of Sulawesi and remove the implausibly disjunct distribution of *Tarsius tarsier*. This brings tarsier taxonomy into better accordance with the known geological history of Sulawesi and with the known regions of biological endemism on Sulawesi and the surrounding island chains that harbor portions of the Sulawesi biota. The union of these two data sets, geological and biological, became a predictive model of biogeography, and was dubbed the Hybrid Biogeographic Hypothesis for Sulawesi. By naming these species, which were already believed to be taxonomically distinct, tarsier taxonomy better concurs with that hypothesis and recent genetic studies. Our findings bring greater clarity to the conservation crisis facing the region.

Keywords: Biodiversity, bioacoustics, cryptic species, duet call, Manado form, Gorontalo form, Libuo form, taxonomy

Introduction

Groves and Shekelle (2010) reviewed and revised tarsier taxonomy. In place of Hill's (1955) familiar taxonomy with three species, *Tarsius tarsier* (= *spectrum*), *T. bancanus*, and *T. syrichta*, they recognized three genera: *Tarsius*, *Cephalopachus*, and *Carlito*, respectively. They argued this change was warranted for several reasons: (1) genetic evidence indicated that each of Hill's species was likely to have originated by the middle Miocene or earlier; (2) variation among Hill's species was both under-appreciated and unrecognized; and (3) the increasing number of recognized taxa of extant tarsiers, particularly numerous cryptic sibling taxa from Sulawesi, was creating an unwieldy classification. In this revision, they also restricted the senior taxon of the genus *Tarsius*, *T. tarsier*, to the island of Selayar, and resurrected *T. fuscus* for the Makassar form of the southwest peninsula. This taxonomy left *T. tarsier* with an implausibly disjunct distribution, including Selayar Island off the southwest peninsula, the northern peninsula beyond Tinombo, and the southeast peninsula. Our current work addresses two populations of tarsiers (Tarsiidae, Primates) north of the range of *Tarsius wallacei*.

Tarsius spectrumgurskyae sp. nov.

Holotype: Museum Zoologicum Bogoriense (MZB), Cibinong, Indonesia, 3269, adult male, collected by Mohari in August 1908.

Type locality: Manado, North Sulawesi

Hypodigms: (1) MZB: 3264, 3266, 3269, 6596 (Manado), skins and skulls; 6593 (Mapanget, Minahasa), skin and skull; 6594 (Tondano, Tonsea Lama, Manado), skin and skull. (2) BMNH 1897.1.2.1-2 (Rurukan), skins and skulls; 1897.1.2.1 (Manado), skin; 1939.1322-3 (Minahasa), skins. (3) MZB 5017 (Manado), skull only. (4) USNM 217559 (Manembo Nembo), skin and skull; 83967 (Rurukan), skin and skull; 219454 (Rano Rano), skin and skull. (5) AMNH 196479, 196480, 196481, 196482, 196483, 196484, 196485, 196486 (Rurukan) and 196487, 196488 (Klabat).

Etymology: Gursky's spectral tarsier. This species is named in honor of Dr. Sharon Gursky, who has dedicated most of her professional life to studying the behavioral ecology of this species. Most of her work on this species was published using a taxonomy that is now superseded, in which

†Colin P. Groves 1942-2017

● **Shekelle 2008:**

1. Tinombo
2. Sejoli
3. Libuo
4. Suwawa
5. Molibagu
6. Ratatotok
7. Tangkoko

● **Driller *et al.* 2015:**

- A. Ogatemuku
- B. Labanu
- C. Duasaudara

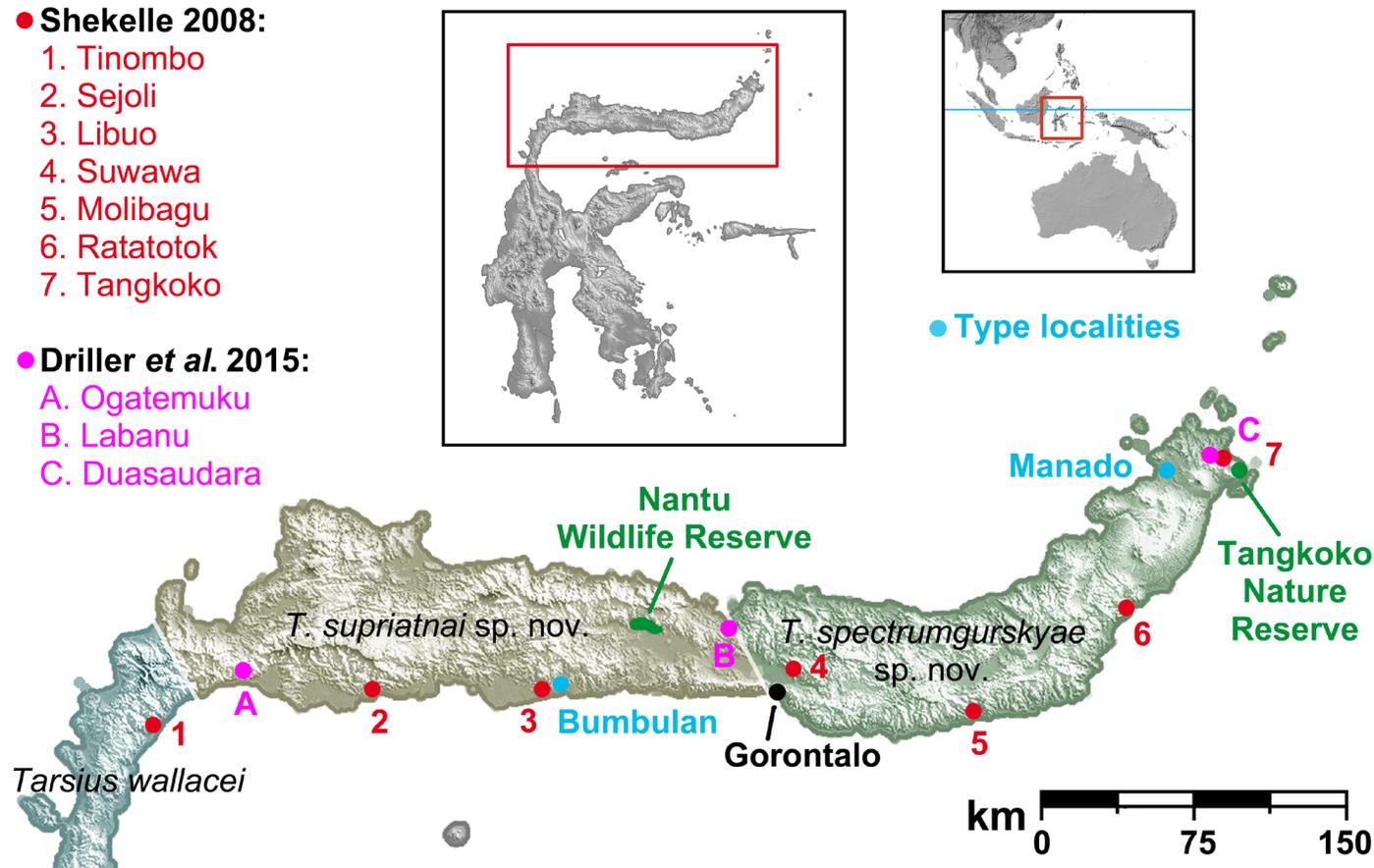


Figure 1. The Northern Peninsula of Sulawesi, Indonesia, showing type localities, species distributions, sampling points of Shekelle (2008) and Driller *et al.* (2015), and two key protected areas.

her population was classified as *Tarsius spectrum*. Ongoing reclassification, therefore, created an unfortunate disconnect between the species name used in her publications, and the most up-to-date taxonomic revision. Thus, by naming this species *Tarsius spectrumgurskyae*, it forever links the names *Tarsius* and *spectrum* with the population of animals that she studied.

Local Name: Tangkasi, Wusing

Distribution: Field surveys have identified the diagnostic call of this species from Tangkoko in the north to Suwawa, on the western edge of Dumoga-Bone National Park (Fig. 1). Field surveys also found this acoustic form at Ratatotok (and nearby Basaan) and Molibagu (Shekelle 2008), as well as at Labanu and Duasaudara (Driller *et al.* 2015). These data imply that this species shares a zone of endemism with two macaque species, *Macaca nigra* and *M. nigrescens* (see Evans *et al.* 2003).

Field work: MacKinnon and MacKinnon (1980), Niemitz *et al.* (1991), Gursky (1994, 1995, 1997, 1998a, 1998b, 1998c, 2000a, 2000b, 2000c, 2002a, 2002b, 2002c, 2003), Shekelle *et al.* (1997), Nietsch and Kopp (1998), Nietsch (1999), Shekelle (2003, 2008), Driller *et al.* (2015).

Diagnosis: As with many species of Eastern Tarsier, the clearest field diagnosis of living specimens is from a spectrogram of its duet call or through playback tests (Figs. 2 and 3). As there is no known case of sympatry among extant tarsiers,

the best diagnosis of museum and other deceased specimens is by provenance, or genetic analysis, although some diagnostic morphological characters are indicated.

Morphology: Resembling *T. supriatnai* n. sp. and *T. pelengensis*, and contrasting with other species of the genus in the prominent brown patches on the thigh (they are lighter, yellower, in *T. wallacei* and *T. dentatus*, and inconspicuous or absent in other species); resembling *T. supriatnai* n. sp. and *T. fuscus*, and contrasting with other species, in the presence of a tail pencil that is both long and black; resembling *T. supriatnai* n. sp. and *T. wallacei* in the prominence of the white postauricular spot, and in the comparative sparseness of the hair on the tarsus (not, however, as sparse as in *T. sangirensis*); resembling *T. supriatnai* n. sp. alone in the prominence and white color of the hair on the sides of the upper lip, the prominent black eye rims, the dark color of the tarsus hair, the general partial fusion of pads on the manus, the long posterior portion of the auditory bulla, broad palate, narrow upper molars, strongly convex nasal tip, and the presence of a noticeable diastema between P^2 and C^1 . Differs from *T. supriatnai* n. sp. and all other species in the genus in the small size of the prominent bare spot at the base of the ear, and the comparatively short hindfoot and, especially, middle finger length relative to the (large) head-and-body length.

Vocalizations: the duet call of this species is fully diagnostic in spectrographic analysis and by playback tests, and is described below (Figs. 2 and 3).

Genetics: Shekelle *et al.* (2008, 2010) found their small genetic data set to be broadly consistent with the hypothesis that acoustic forms are distinct species, but did not find the Manado form to constitute a single monophyletic clade. More recently, Driller *et al.* (2015), using more genetic evidence, found support for the separation of *T. spectrumgurskyae* and dated its divergence at 0.3 mya.

Description

Morphology: Surveys of wild populations indicate that body weight and tail length are within the range of several other species of *Tarsius*: body weight (female 95–119 g, $n = 24$; male 104–126 g, $n = 11$), tail length (female = 213–268 mm, $n = 22$; male = 220–258 mm, $n = 9$) (data from Shekelle 2003). Surveys of museum specimens indicate the posterior portion of the auditory bulla is long; the palate is broad; upper molars are narrow; the nasal tip is strongly convex; there is a noticeable diastema between I^2 and C^1 . The tail pencil is long, thick and black; the thigh is browner than the body; the white patch on the sides of the upper lip is conspicuous; the bare spot at the base of ear is present, tending to be small; the tarsal hair is of medium length, and fairly dark. *Tarsius spectrumgurskyae* is large, but smaller than *T. dentatus* and overlaps the ranges of the small species such as *T. fuscus*, so that size is not

diagnostic; the auditory bulla is comparatively short, despite the length of its posterior portion; tooththrows are fairly long, but variable; pelage is grey-buff like most mainland Sulawesi tarsiers (*T. fuscus* the exception); usually noticeably browner on the thigh; the tail is comparatively short, 121–210% of head and body; the black paranasal spot is well-marked; the eye-rim is usually conspicuously black. Thenar and first interdigital pads usually partly (incompletely) fused. Cranial and external proportions overlap with those of other northern and central species, but dental proportions do not (Groves 2003) (refer to Figs. 4 and 5, Table 1).

Vocalizations: The Manado form was originally described by MacKinnon and MacKinnon (1980), and further examined by Niemitz *et al.* (1991), Shekelle *et al.* (1997), Nietsch and Kopp (1998), Nietsch (1999), and Shekelle (2003, 2008). More recently, Yi *et al.* (2014) found that the Manado and Gorontalo forms are easily separable with quantitative analysis. The duet begins with a series of synchronized female and male notes. The duet often begins with a female note, but pre-duet calling makes this difficult to determine with certainty. Male calls are chevron-shaped chirps that rise from ~6 kHz to ~13 kHz, and then descend to less than 6 kHz. The duration of each note is ~0.2 seconds. The female phrase is a series of ~9–15 notes, which are far more varied in terms of frequency, frequency modulation, and duration, than are those of the male. The duration of the female phrase varies, but

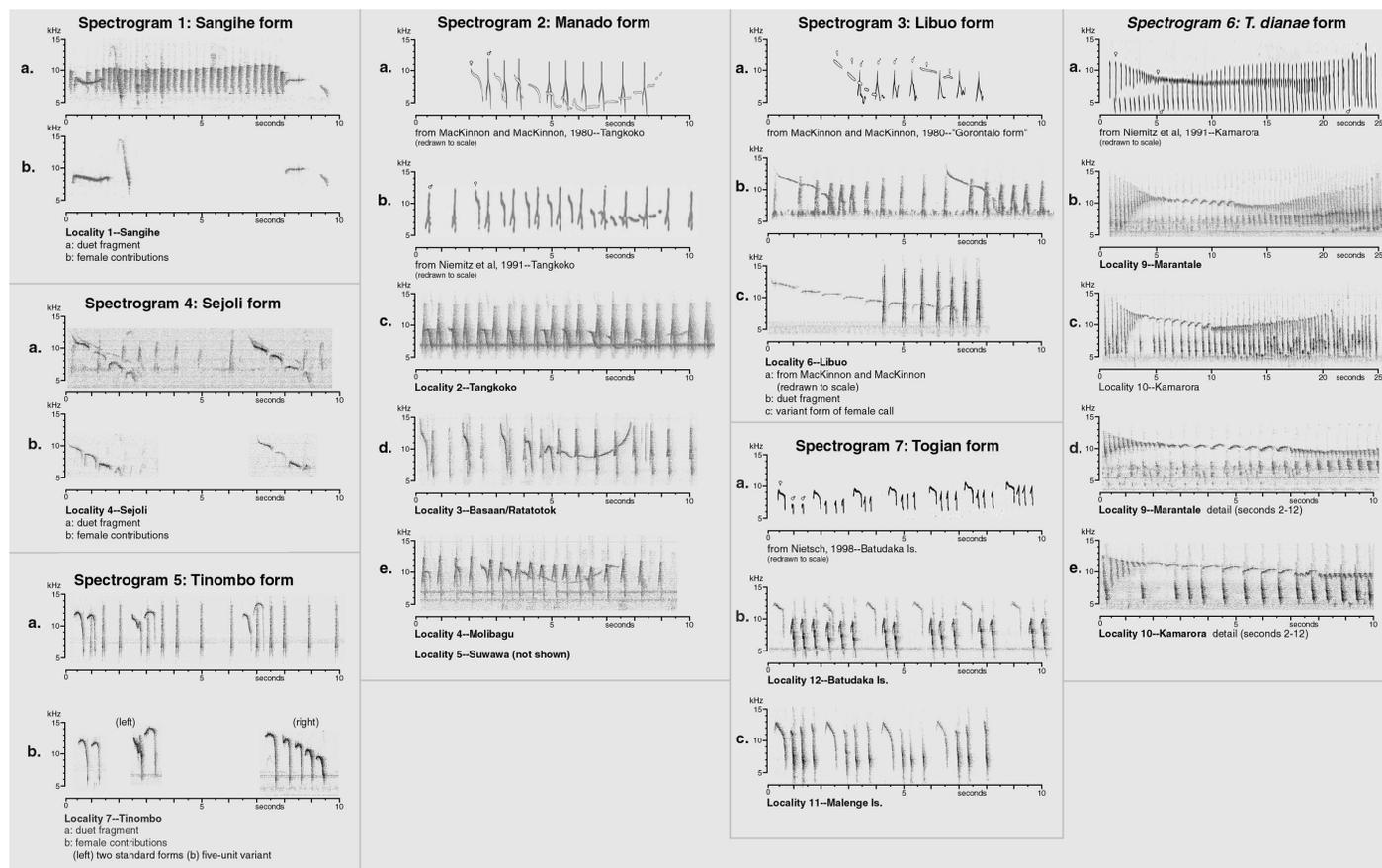


Figure 2. Spectrograms for seven acoustic forms of Eastern tarsiers (from Shekelle 2008). Spectrograms 1a, 1b (*Tarsius sangirensis*); Spectrograms 2a–2e (*T. spectrumgurskyae* n. sp.); Spectrograms 3a–3c (*T. supriatnai* n. sp.); Spectrograms 4a, 4b (*T. supriatnai* n. sp.); Spectrograms 5a, 5b (*T. wallacei*); Spectrograms 6a–6e (*T. dentatus* = *dianae*); Spectrograms 7a–7c (*T. tarsier* “Togian form”, putative unnamed species).

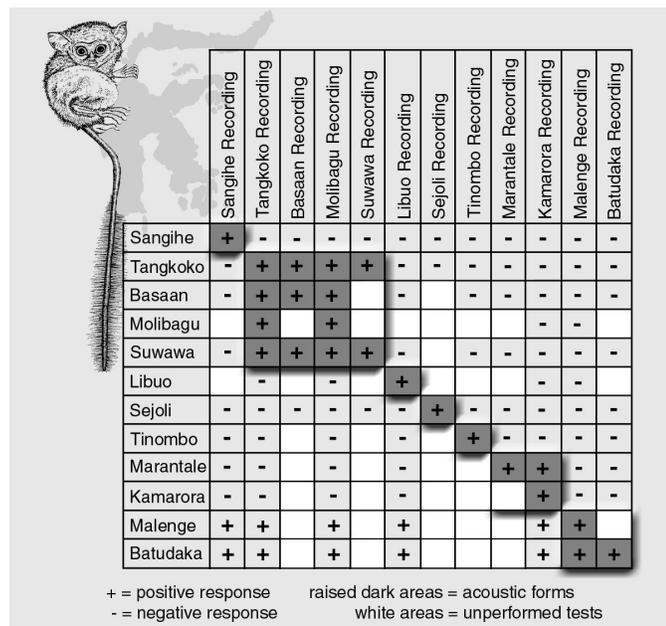


Figure 3. Results of playback tests (from Shekelle 2008).

is often ~7 sec. It can be divided into three sections. At the beginning of the duet, the female calls are descending whistles, which begin high, ~10 kHz or higher, and descend rapidly to a final frequency below 6 kHz. There is much variation among populations in the initial frequency of the female calls, with populations at the northern end of the range of this species (e.g., Tangkoko) tending to use lower initial frequencies (~10 kHz), and those further south (e.g., Ratatotok, Molibagu) using much higher initial frequencies (12–15 kHz). As the duet progresses, the initial frequency descends and terminal frequency ascends gradually until, in the second section of the female phrase, the notes become nearly unmodulated, the frequency of these relatively flat notes being at a midpoint between the initial and terminal frequencies of the first note, therefore ~8–10 kHz. In the final section of the female phrase, the notes begin to ascend in pitch, with the terminal frequency of the final call being approximately the same as the initial frequency of the first call. The duet can be further characterized as follows: (1) the duration of the female notes increase from ~0.3 sec to ~1 sec, or more; (2) the interval between female notes decreases, from >1 sec to ~0.1 sec; and (3) the synchronization between male and female notes increases, with male calls filling the short gap between the female notes (refer to Fig. 2, particularly spectrogram 2d).

Tarsius supriatnai sp. nov.

Holotype: Museum Zoologicum Bogoriense (MZB), Cibinong, Indonesia, 6595, adult male, collected by J. J. Menden, 10 May 1939.

Type locality: Bumbulan, Gorontalo.

Hypodigms: 1) AMNH 153286, 153287, 153288, 153289, 153290, 153291 (Bumbulan), 2) MZB 6595 (Bumbulan), skin and skull; (3) Rijksmuseum voor Natuurlijk Historie NRL cat. a or f (Gorontalo).

Etymology: Jatna’s tarsier. This species is named in honor of Dr. Jatna Supriatna, who has dedicated most of his professional life to the conservation of Indonesian biodiversity, and has sponsored much of the foreign collaborative work done on tarsiers.

Local Name: Mimito

Distribution: On the northern peninsula from the Isthmus of Gorontalo westward at least as far as Sejoli, and probably as far as Oгатemuku (see Driller *et al.* 2015), but not as far as Tinombo (Fig. 1).

Field work: MacKinnon and MacKinnon (1980), Shekelle *et al.* (1997), Shekelle (2003, 2008), and Driller *et al.* (2015).

Diagnosis: See above for *T. spectrumgurskyae*, duet call and provenance are absolutely diagnostic. Genetics diagnose a *T. spectrumgurskyae* – *T. supriatnai* clade from all others and are hypothesized to be themselves distinct. Driller *et al.* (2015) estimated a divergence date of 0.3 mya for the separation of the two.

Morphology: *Tarsius supriatnai* is very similar morphologically to *T. spectrumgurskyae* n. sp. (see under that species), differing in the generally larger bare spot at the base of the ear, the less shortened hindfoot, the very long tail, and longer middle finger.

Description

Morphology: Surveys of wild populations indicate body weight and tail length are probably within the range of several other species of *Tarsius*, but the sample sizes are small: body weight (female = 104–114 g, n = 2; male = 135 g, n = 1); this gives the superficial appearance that body weight dimorphism might be greater for this species, 81%, but with the sample sizes being so low we discourage speculation along these lines until more data have been collected; tail length (female = 232–243 mm, n = 2; male = 246 mm, n = 1) (data from Shekelle 2003). Surveys of museum specimens indicate a species with skull and teeth very similar to *T. spectrumgurskyae* n. sp., but the two specimens, compared to nine of the latter that were measured, have a lower anterior central incisor, and larger first and second molars, but not third molar (refer to Figs. 4 and 5, Table 1).

Vocalizations: MacKinnon and MacKinnon (1980) originally described the Gorontalo form, a form that was referred to as the Libuo form in various papers by Shekelle (Shekelle *et al.* 1997; Shekelle 2003, 2008). The duet of this acoustic form is characterized by a ~2-to-5-note female phrase accompanied by male calls. The frequencies of the female notes are each comparatively flat, in sharp contrast with the frequency modulated notes of the first section of the female phrase in the Manado form. The first of these notes begins at ~13 kHz and the last is ~7 kHz. Each note is about 0.6–1.0 sec in duration, with notes being separated by a brief gap of ~0.1 sec. The female phrase is repeated several times during the duet, with ~6 seconds elapsing from the end of one phrase to the start of the next. The male notes are wide-band, chevron-shaped chirps that ascend in frequency from ~6 kHz to ~10–12 kHz, before descending back again to ~6 kHz. In a well-coordinated

Gorontalo

Manado

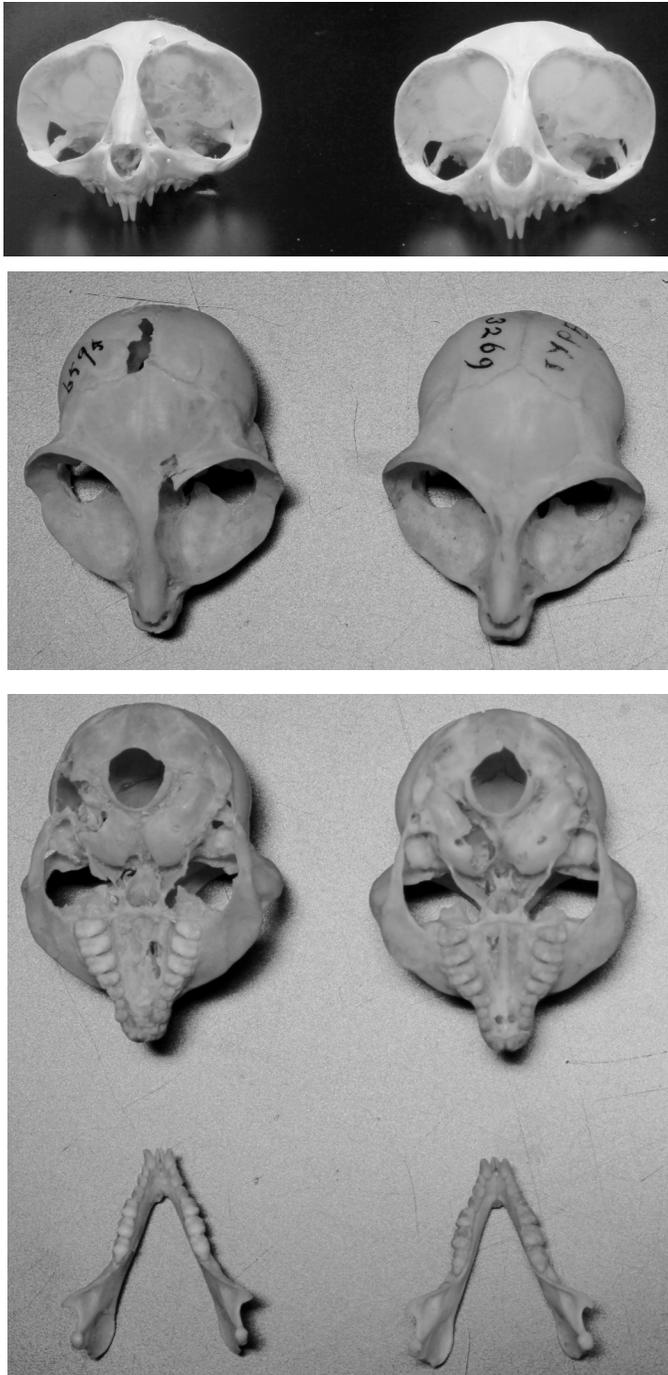


Figure 4. Type specimens. Top: frontal view of crania. Middle: inferior view of crania. Bottom: superior view of crania and mandibles, with occlusal surfaces of upper and lower dentition.

duet, the male notes occur in the gaps between the female notes. Between female phrases, male notes continue at the rate of about one per second. Again, as mentioned above, Yi *et al.* (2014) found that the Manado and Gorontalo forms are easily separable with quantitative analysis. The Sejoli form was described as distinct by Shekelle *et al.* (1997) and Shekelle (2003, 2008) on the basis of field playback tests, but not on the basis of either qualitative or quantitative variation in



Figure 5. Photographs of two new species: A) Gursky's spectral tarsier *Tarsius spectrungruskyae* n. sp. from Tangkoko Nature Reserve (photo by Alfrets Masala). B) Jatna's tarsier *Tarsius supriatnai* n. sp. (photo by Russell Mittermeier).

spectrographic analysis. The recordings were of admittedly low quality, but even so, had obvious resemblances to the Gorontalo form. Given the paucity of the evidence for the distinctiveness of this form, and in the interests of taxonomic conservatism, we do not separate the Gorontalo and Sejoli acoustic forms at this time. Further investigation may warrant their taxonomic separation.

Type specimens	<i>T. spectrumgurskyae</i> Manado form MZB3269	<i>T. supriatnai</i> Gorontalo form MZB6595
	Adult male	Adult male
Musser and Dagosto (1987)		
Greatest length of skull	37.1	37.4
Zygomatic breadth	26.9	26.2
Breadth across orbits	29.9	29.4
Breadth of a single orbit	17.2	17.3
Height of a single orbit	17.9	18.3
Length of nasals	7.0	6.8
Breadth of bony palate at M ³	14.1	14.1
Length of auditory bulla	11.2	11.8
Breadth of auditory bulla	6.6	5.6
Length of anterior part of bulla	5.6	5.9
Length of posterior part of bulla	6.3	6.5
Length of upper toothrow, C-M ³	12.8	12.1
Length of lower toothrow, C-M ₃	13.3	12.9
Length of M ¹	2.4	2.0
Breadth of M ¹	3.5	3.3
Length of M ₁	2.3	2.0
Breadth of M ₁	2.2	2.3
Groves (1998)		
Length of head and body	167	125
Ear length	23.7	26.1
Ear width		
Tibia	62.2	63.0
Tarsus	34.2	34.5
Length of third finger	25.2	24.1
Inter orbital	2.2	1.8
Post orbital width	22.4	21.3
Nasal breadth	3.6	3.3
Palatal length	13.6	13.7
Mesopterygoid fossa width	3.4	3.5
Ramus angular process	10.3	10.2
Dentary length	24.2	24.8
Tail length	230	236

Table 1. Measurements (in mm) of type specimens. The headings in the table, “Musser and Dagosto 1987” and “Groves 1998”, refer to the measurements used in those two studies, not necessarily the measurements reported in those two detailed description of methodology).



Figure 6. Gursky’s spectral tarsier *Tarsius spectrumgurskyae* n. sp. (left) and Jatna’s tarsier *Tarsius supriatnai* n. sp. (right). Illustrations by Stephen D. Nash.

Genetics: As with *T. spectrumgurskyae* sp. n. (above), Shekelle *et al.* (2008, 2010) found genetic data to be broadly consistent with the hypothesis that acoustic forms are distinct species, but did not find the Manado form to be a single monophyletic clade, while Driller *et al.* (2015), with superior genetic evidence in both quantity and quality, supported their separation, with an estimated divergence date of 0.3 mya.

Additional material examined: We provisionally classify the following specimens within *T. supriatnai*, USNM 200281 (Sungai Paleleh), USNM 200280, 200281, 200282, 200283, 200284 (Toli Toli).

Conclusions

The results of this manuscript stem from the workshop, Primate Taxonomy for the New Millennium, held in Orlando, Florida, in January 2000. That workshop not only produced a consensus taxonomy for primates (Brandon-Jones *et al.* 2004), but also offered a research agenda: in the best interests of science and conservation to resolve the alpha taxonomy for the clade of each participant’s expertise, and to do so before it is too late—before extinction wipes out the story of our evolutionary history. Toward those ends, we describe two new tarsier species, which provide a better fit with the biogeography of Sulawesi (see Hall 2001; Evans *et al.* 2003; Shekelle and Leksono 2004), and removes the implausible discontinuity in the distribution of *T. tarsier* that occurred after tarsiers from the central core and southwestern peninsula were studied and named (e.g., Merker and Groves 2006; Merker *et al.* 2010; Groves and Shekelle 2010).

Species distributions on Sulawesi typically conform with (1) the geological history of the island as it coalesced from a proto-Sulawesi archipelago (see Hall 2001), and (2) geographic features associated with range fragmentation during the Pleistocene (Evans *et al.* 2003). During the Miocene and Pliocene, distributions appear to have been shaped by dispersal among islands (see Shekelle and Leksono 2004). Parapatric species boundaries formed when two islands with sibling taxa accreted to one another, forming a single island. These boundaries seem to remain stable for vast stretches of time, >1 mya (Merker *et al.* 2009). The process of island accretion is thought to have been completed by ~1 mya, forming the modern island of Sulawesi. Subsequent to that event, species distributions were reshaped by range fragmentation, owing to the unstable climate during the Pleistocene (see Evans *et al.* 2003).

In concordance with these two processes, ancient dispersal and more recent range fragmentation (see Shekelle and Leksono, 2004), the western boundary of *T. supriatnai* is hypothesized to be the microplate suture that lies between Timombo and Oгатemuku. The boundary between *T. supriatnai* and *T. spectrumgurskyae* is hypothesized to be the Isthmus of Gorontalo. If the broad hypothesis for Sulawesi biogeography, as proposed by Shekelle and Leksono, is generally true, then the phylogenetic tree for tarsiers should show the split between *T. supriatnai* and *T. spectrumgurskyae*, which are

separated by Pleistocene range fragmentation at the Isthmus of Gorontalo, to be younger than the split between *T. wallacei* and a *T. supriatnai* – *T. spectrumgurskyae* clade, which are separated by a more ancient accretion of two islands into a single landmass. These are, indeed, the results found by Driller *et al.* (2015), thereby offering further support for the Hybrid Biogeographic Hypothesis for Sulawesi (Shekelle and Leksono, 2004).

Our results also shed further light on the ongoing conservation crisis within the conservation hotspot of Wallacea (Myers *et al.* 2000). Biodiversity is often clustered in regions of endemism, and this is particularly true in Sulawesi, as demonstrated above by the process of species distribution formation. Primates, most of which are threatened at some level, serve as one vitally important flagship species for habitat conservation (Estrada *et al.* 2018). Thus, one key to stemming the current onslaught on biodiversity is to protect habitat by identifying primate species, naming them, Red-Listing them, and promoting them as flagship species to assist habitat conservation; tarsiers make excellent candidates for this conservation strategy on Sulawesi (refer to Shekelle and Leksono 2004).

It is vital to complete the process of identifying the alpha taxonomy of tarsiers before deforestation erases the evidence of the evolutionary history of the clade. The study by Merker *et al.* (2009), which offered robust support for the hypotheses advanced in this paper, would have been impossible were it not for large stretches of unbroken primary forest. This is because discontinuities in habitat lead to isolation, which then invariably leads to discontinuities among populations. With the passage of time it becomes increasingly difficult, and then even impossible, to infer whether the discontinuities among populations that were once continuous, but which were made allopatric by anthropogenic habitat loss, were caused by speciation, or perhaps by isolation by distance followed by genetic drift. Given tarsiers' role as flagship species for protecting all of the biodiversity on Sulawesi, as well as in other regions, urgent action on tarsier alpha taxonomy holds forth the opportunity to protect habitat that will assist the conservation of other species: babirusa, anoa, Sulawesi macaques, cuscus, and all the other species within this critically important biodiversity whether they have been identified and named by science or not. Therefore, the next step for conservation is to assess the conservation status of the two new species we report, both of which we expect to be threatened at some level, and use these to assist conservation efforts within their ranges, particularly in the critically important habitats of the greater Tangkoko conservation region in North Sulawesi, and the Nantu Wildlife Reserve in the province of Gorontalo (Fig. 1).

The etymology of these species has two functions. First, the name *Tarsius spectrum* is associated with much confusion, such that virtually all extant tarsiers have been classified under that name at one time or another, whereas today none are, though the name is still well-known to primatologists. To remove that confusion, and to correct an unfortunate

disconnect resulting from reclassification, *spectrumgurskyae* connects for all time the name “*spectrum*” with the population of tarsiers that Gursky has spent her life studying. Second, the names honor two scientists who have played outsized roles in the study and conservation of tarsiers

Extant tarsiers are classified in three genera, allopatrically distributed in distinct biogeographic regions: *Tarsius* is found on Sulawesi and surrounding islands; *Cephalopachus* is found on a restricted subset of Sundaland, principally the southern parts of Sumatra, and the islands of Borneo, Bangka, and Belitung; *Carlito* is found on islands of the southern Philippines that were a single Ice Age landmass, sometimes called Greater Mindanao. *Tarsius* contains 11 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*. Burton and Nietsch (2010) reported evidence for three more putative unnamed taxa from the Southeastern peninsula. Shekelle and Leksono (2004) predicted that 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*, but we question if this contrast is not rather based on an absence of evidence, as opposed to the evidence of absence. We encourage more fieldwork in order to answer this question.

We conclude by reminding readers of the words with which Shekelle *et al.* (2008) concluded their description of *Tarsius tumpara*, published nearly ten years ago, and assert that they are more pertinent than ever:

“The bleak situation indicates that some primate species in Sulawesi may go extinct before they have even been identified, leaving scientists with unpleasant and controversial choices for taxonomy and conservation. We foresee increased criticism and controversy down either path: either publishing new species at an increased pace with the heightened chance of error, or not doing so at the risk that primate species are driven to extinction before they have been recognized and named.” (p. 63)

Acknowledgments

The impetus for this study came from Dr. Lynn Clayton. Field research was facilitated by her, and her team as part of the research program “Conservation Biology of the Paguyaman Forest in Northern Sulawesi.” We are, therefore, extremely grateful to the State Ministry for Research, Technology and Higher Education (Ristekdikti), the Research Centre for Biology of the Indonesian Institute of Sciences (LIPI), and Dr. John Tasirin, Sam Ratulangi University, Manado. We also thank the Directorate General for Forest Protection and Nature Conservation, Ministry of Forestry and Environment, Government of Indonesia. Financial support for the field station at Nantu was provided by the “Save Our Species” Program and ADM Capital Foundation. Save Our Species is a joint initiative of the Global Environment Facility,

IUCN and the World Bank; a fundamental goal is to ensure the long-term survival and well-being of threatened species and their critical habitats for biodiversity conservation. The authors sincerely hope their work will help Lynn Clayton in efforts to conserve vital forests in Gorontalo province. Further financial support was provided to MS by Conservation International. MS teaches a field school for Indonesian field biologists in collaboration with Manado State University; the efforts of the students there have been invaluable, including Maryati Abiduna, David Switly Sengkey, and Alen Piri. 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 Margot Marsh Biodiversity Foundation, the Gibbon Foundation, 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. Current funding for MS is from the National Geographic Society. Permits for conducting research in conservation areas and for trapping tarsiers were provided by the Indonesian Department of Forestry. We thank Stefan Merker and an anonymous reviewer for suggestions that improved this manuscript immeasurably.

Literature Cited

- Brandon-Jones, D., A. A. Eudey, T. Geissmann, C. P. Groves, D. J. Melnick, J. C. Morales, M. Shekelle and C.-B. Stewart, 2004. Asian primate classification. *Int. J. Primatol.* 25: 97–164.
- Burton, J. and A. Nietsch. 2010. Geographical variation in duet songs of Sulawesi tarsiers: evidence for new cryptic species in south and southeast Sulawesi. *Int. J. Primatol.* 31: 1123–1146.
- Driller, C., S. Merker, D. Perwitasari-Farajallah, W. Sinaga, N. Anggraeni and H. Zischler. 2015. Stop and go—waves of tarsier dispersal mirror the genesis of Sulawesi Island. *PLoS ONE* 10(11) e0141212. DOI: 10.1371/journal.pone.0141212
- Estrada, A. *et al.* 2017. Impending extinction crisis of the world's primates: why primates matter. *Science Advances* 3 (1): e1600946.
- Evans, B. J., J. Supriatna, N. Andayani, M. I. Setiadi, D. C. Cannatella and D. J. Melnick. 2003. Monkeys and toads define areas of endemism on Sulawesi. *Evolution* 57: 1436–1443.
- Groves, C. P. 1998. Systematics of tarsiers and lorises. *Primates* 39:13–27.
- Groves, C. P. 2003. The tarsiers of Sulawesi. In: *Tarsiers: Past, Present, and Future*, P. C. Wright, E. L. Simons and S. Gursky (eds.), pp.179–195. Rutgers University Press, New Brunswick, NJ.
- Groves, C. P. and M. Shekelle. 2010. The genera and species of Tarsiidae. *Int. J. Primatol.* 31: 1071–1082.
- Gursky, S. L. 1994. Infant care in the spectral tarsier, (*Tarsius spectrum*), Sulawesi, Indonesia. *Int. J. Primatol.* 15: 843–853.
- Gursky, S. L. 1995. Group size and composition in the spectral tarsier: implications for social organization. *Trop. Biodiv.* 3: 57–62.
- Gursky, S. L. 1997. Modeling Maternal Time Budget: The Impact of Lactation and Infant Transport on the Time Budget of the Spectral Tarsier, *Tarsius spectrum*. PhD dissertation, State University of New York, Stony Brook, NY.
- Gursky, S. L. 1998a. The conservation status of the spectral tarsier, *Tarsius spectrum*, in Sulawesi Indonesia. *Folia Primatol.* 69: 191–203.
- Gursky, S. L. 1998b. The effect of radio transmitter weight on a small nocturnal primate: data on activity time budgets, prey capture rates, mobility patterns and weight loss. *Am. J. Primatol.* 46: 145–155.
- Gursky, S. L. 1998c. The conservation status of two Sulawesi tarsier species: *Tarsius spectrum* and *Tarsius dianae*. *Primate Conserv.* (18): 88–91.
- Gursky, S. L. 2000a. The effect of seasonality on the foraging and locomotor behavior of an insectivorous primate. *Int. J. Primatol.* 21: 477–495.
- Gursky, S. L. 2000b. Allo-parental care in spectral tarsiers. *Folia Primatol.* 71: 39–54.
- Gursky, S. L. 2000c. Sociality in the spectral tarsier. *Am. J. Primatol.* 51: 89–101.
- Gursky, S. L. 2002a. The determinants of gregariousness in the spectral tarsier. *J. Zool., Lond.* 256: 1–10.
- Gursky, S. L. 2002b. Predation on a spectral tarsier by a snake. *Folia Primatol.* 73: 60–62.
- Gursky, S. L. 2002c. The behavioral ecology of the spectral tarsier. *Evol. Anthropol.* 11: 226–234.
- Gursky, S. L. 2003. The effect of moonlight on the behavior of a nocturnal prosimian primate. *Int. J. Primatol.* 24: 351–367.
- Hall, R. 2001. Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea. In: *Faunal and Floral Migrations and Evolution in SE Asia-Australia*, I. Metcalf, J. Smith, M. Morwood and I. Davidson (eds.), pp.35–56. Swets and Zeitlinger, Lisse.
- Hill, W. C. O. 1955. *Primates: Comparative Anatomy and Taxonomy. II. Haplorrhini: Tarsioidea*. Edinburgh University Press, Edinburgh.
- MacKinnon, J. and K. MacKinnon. 1980. The behavior of wild spectral tarsiers. *Int. J. Primatol.* 1: 361–379.
- Merker, S. and C. P. Groves. 2006. *Tarsius lariat*: A new primate species from western central Sulawesi. *Int. J. Primatol.* 27: 465–485.
- Merker, S., C. Driller, D. Perwitasari-Farajallah, J. Pamungkas and H. Zischler. 2009. Elucidating geological and biological processes underlying the diversification of Sulawesi tarsiers. *Proc. Natl. Acad. Sci. USA* 106: 8459–8464.

- Merker, S., C. Driller, H. Dahrudin, Wirdateti, W. Sinaga, D. Perwitasari-Farajallah and M. Shekelle. 2010. *Tarsius wallacei*: a new tarsier species from Central Sulawesi occupies a discontinuous range. *Int. J. Primatol.* 31: 1107–1122.
- Musser, G. G. and M. Dagosto. 1987. The identity of *Tarsius pumilus*, a pygmy species endemic to the montane mossy forests of Central Sulawesi. *Am. Mus. Novitat.* 2867: 1–53.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Niemitz, C., A. Nietsch, S. Warter and Y. Rumpler. 1991. *Tarsius diana*: a new primate species from Central Sulawesi (Indonesia). *Folia Primatol.* 56: 105–116.
- Nietsch, A. 1999. Duet vocalizations among different populations of Sulawesi tarsiers. *Int. J. Primatol.* 20: 567–583.
- Nietsch, A. and M.-L. Kopp. 1998. Role of vocalization in species differentiation of Sulawesi tarsiers. *Folia Primatol.* 68(suppl.1): 371–378.
- Nietsch, A. and C. Niemitz. 1993. Diversity of Sulawesi tarsiers. *Z. Saugetierkd.* 67: 45–46.
- Shekelle, M. 2003. Taxonomy and Biogeography of Eastern Tarsiers. Doctoral thesis, Washington University, St. Louis, MO.
- Shekelle, M. 2008. Distribution of tarsier acoustic forms, north and central Sulawesi: with notes on the primary taxonomy of Sulawesi's tarsiers. In: *Primates of the Oriental Night*, M. Shekelle, C. P. Groves, I. Maryanto, H. Schulze and H. Fitch-Snyder (eds.), pp.35–50. Research Center for Biology, Indonesian Institute of Sciences, Bogor, Indonesia.
- Shekelle, M. and S. M. Leksono. 2004. Rencana konservasi di Pulau Sulawesi: dengan menggunakan *Tarsius* sebagai flagship species. *Biota* 9(1): 1–10.
- Shekelle, M., S. Leksono, L. S. I. Ichwan and Y. Masala. 1997. The natural history of the tarsiers of north and central Sulawesi. *Sulawesi Primate Newsl.* 4(2): 4–11.
- Shekelle M., J. C. Morales, C. Niemitz, L. S. I. Ichwan and D. M. Melnick. 2008. The distribution of tarsier mtDNA haplotypes for parts of north and central Sulawesi: a preliminary analysis. In: *Primates of the Oriental Night*, M. Shekelle, C. P. Groves, I. Maryanto, H. Schulze and H. Fitch-Snyder (eds.), pp. 51–69. Research Center for Biology, Indonesian Institute of Sciences, Bogor, Indonesia.
- Shekelle, M., R. Meier, I. Wahyu, Wirdateti and N. Ting. 2010. Molecular phylogenetics and chronometrics of Tarsiidae based on 12s mtDNA haplotypes: evidence for Miocene origins of crown tarsiers and numerous species within the Sulawesi clade. *Int. J. Primatol.* 31: 1083–1106.
- Yi, Y., M. Shekelle, Y. Jang and J. C. Choe. 2015. Discriminating tarsier acoustic forms from Sulawesi's northern peninsula with spectral analysis. Paper presented at the 84th Annual Meeting of the American Association of Physical Anthropologists, 25–29 March 2015, St. Louis, MO.

Authors' addresses:

Myron Shekelle, Department of Anthropology, Western Washington University, Bellingham, WA, USA, **Colin P. Groves**, School of Archaeology and Anthropology, Australian National University, Canberra, ACT 0200, Australia, **Ibnu Maryanto**, Museum Zoologicum Bogoriense, LIPI, Cibinong, Indonesia, and **Russell A. Mittermeier**, Conservation International, 2011 Crystal Drive, Arlington, VA 22202, USA. E-mail of first author: <mshekelle@tarsier.org>.

Received for publication: 30 September 2016

Revised: 11 February 2017

Printed: 28 December 2017

