DISTRIBUTION OF TARSIER ACOUSTIC FORMS, NORTH AND CENTRAL SULAWESI: WITH NOTES ON THE PRIMARY TAXONOMY OF SULAWESI'S TARSIERS

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ABSTRACT

This study uses field surveys of wild tarsier populations to assess the relationship between described tarsier taxa and acoustic forms. Surveyed regions of North and Central Sulawesi contain eight acoustic forms and five described taxa. There is synonymy between acoustic form and taxonomic form in two instances, minimally, and two of the taxonomic forms appear to be synonymous with each other. Thus, if tarsier acoustic forms are distinct taxa, as has been hypothesized (MacKinnon and MacKinnon 1980, Niemitz *et al.* 1991, Nietsch and Kopp 1998), then as many as ten tarsier taxa may be present in the region that has been surveyed thus far. Acoustic forms were identified with playback tests using populations of wild tarsiers and corroborated with heuristic spectrographic analyses. Spectrograms of three previously undescribed acoustic forms of tarsiers are presented, along with spectrograms from four acoustic forms that were already known. The distributions of tarsier taxa and acoustic forms are presented. Comments are made regarding the nature and validity of each taxon. *Tarsius sangirensis* is recognized as a distinct species. *Tarsius dianae* is likely a junior synonym of *T. dentatus*. The whereabouts and location of the type locality of *T. pumilus* are discussed.

Keywords: Distribution*, Tarsius* spp*,* vocalization

INTRODUCTION

The primary taxonomy of Sulawesi's tarsier has been in question for the past twenty years. Results of collecting expeditions from the eighteenth century up to 1949 led to the description of five distinct tarsier taxa from Sulawesi and its surrounding islands. By 1984, however, Niemitz had simplified the taxonomy, classifying Sulawesi's tarsiers into a single species, *Tarsius spectrum*, with two subspecies, *T. spectrum*, and *T. pumilus* (Table 1). *Tarsius spectrum* is now accepted as a junior synonym of *T. tarsier* (see Groves *et al.* this volume). Just prior to this, MacKinnon and MacKinnon (1980) reported the first observations of wild *Tarsius tarsier*, wherein they commented that there were clearly several distinct taxa of tarsiers on Sulawesi. At the same time, the classification and taxonomy of nocturnal primates was undergoing substantial revision. Prompted in part by the Recognition Concept of Species (Paterson, 1985), numerous cryptic sibling species were ultimately identified where once taxonomists had recognized only a single species. Th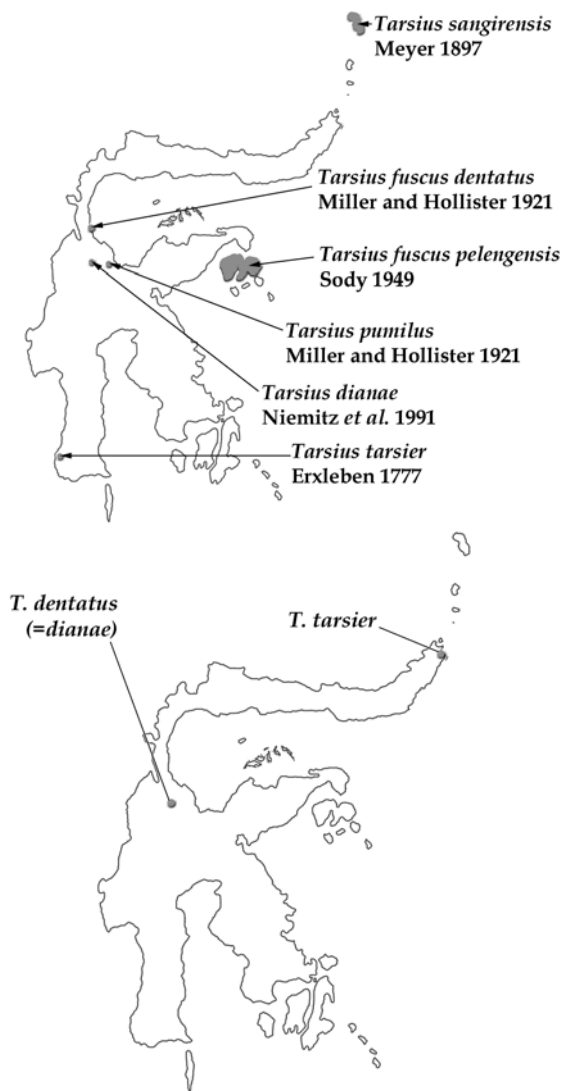is led to the argument that the number of species in nocturnal taxa, in particular, had been underestimated (e.g. Bearder *et al*, 1995; Masters, 1998). In addition to this taxonomic revision of Sulawesi's other primate, the macaque, showed as many as seven species where once there was thought to be just two (e.g. Fooden, 1980; Groves, 1980). This created awareness of Sulawesi's interesting biogeographic phenomenon of colonization and radiation (Whitten *et al.* 1987), thereby lending further credence to the hypothesis that several cryptic sibling species exist among Sulawesi's tarsiers.

Prior to 1984, five distinct tarsier taxa had been described from the region of Sulawesi and its surrounding islands (Figure 1). These are: *Tarsius tarsier* Erxleben, 1777, type locality Makasar (see discussion); *T. sangirensis* Meyer, 1897, from Greater Sangihe Island, North Sulawesi; *T. pumilus* Miller and Hollister, 1921, from Rano Rano, Central Sulawesi; *T. dentatus* Miller and Hollister, 1921, from Labuan Sore, Central Sulawesi; and, *T. pelengensis* Sody, 1949, from Peleng Island. The taxonomic history of tarsiers, and specifically Sulawesian tarsiers, is confusing and riddled with nomenclatural arguments and instability.

**Table 1.** Taxonomic Revisions of Sulawesi's Tarsiers 1949-1984

Taxon	Sody 1949	Hill 1955	Niemitz 1984a
T. tarsier (=*spectrum*)	species	species	species
T. sangirensis	subspecies	subspecies	jr. synonym
T. pumilus	(not mentioned)	subspecies	subspecies
T. dentatus	subspecies	subspecies	jr. synonym
T. pelengensis	subspecies	subspecies	jr. synonym

Eastern Tarsier Taxa (prior to this study)   MacKinnon & MacKinnon 1980
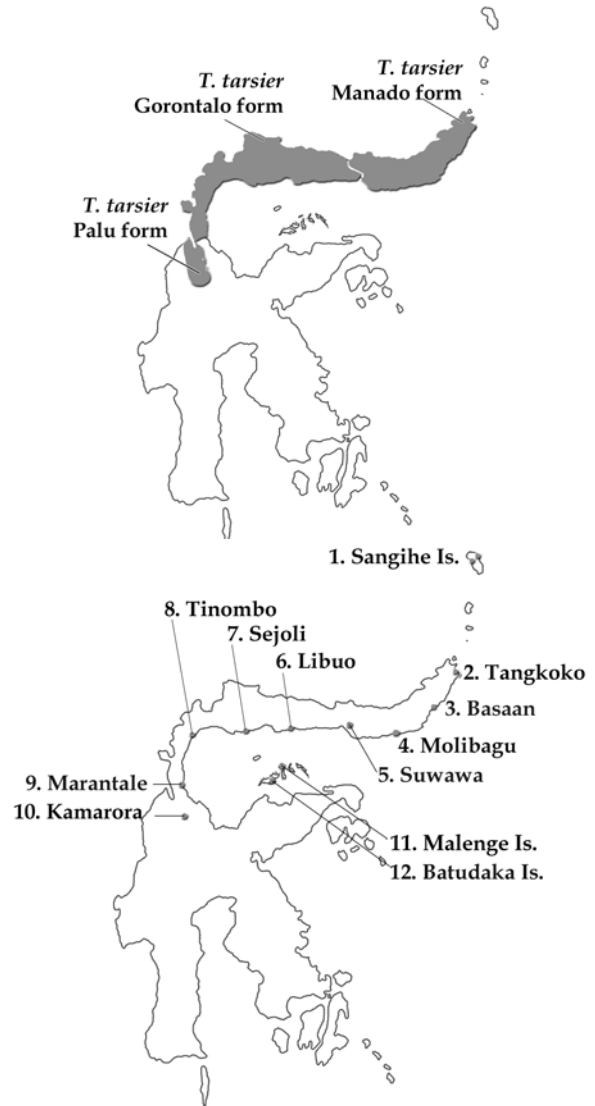
Niemitz *et al.* 1991   Sampling Localities

Figure 1: Location of taxa, acoustic forms, and sampling localities. MacKinnon and MacKinnon (upper right) recognized three acoustic forms. Niemitz *et al.* (lower left) named *T. dianae* based upon comparisons with tarsiers from the northern tip of Sulawesi. Neither of these works addressed in detail the other described taxa of Eastern tarsiers (upper right).   This study sampled a transect at approximately 100 km intervals.
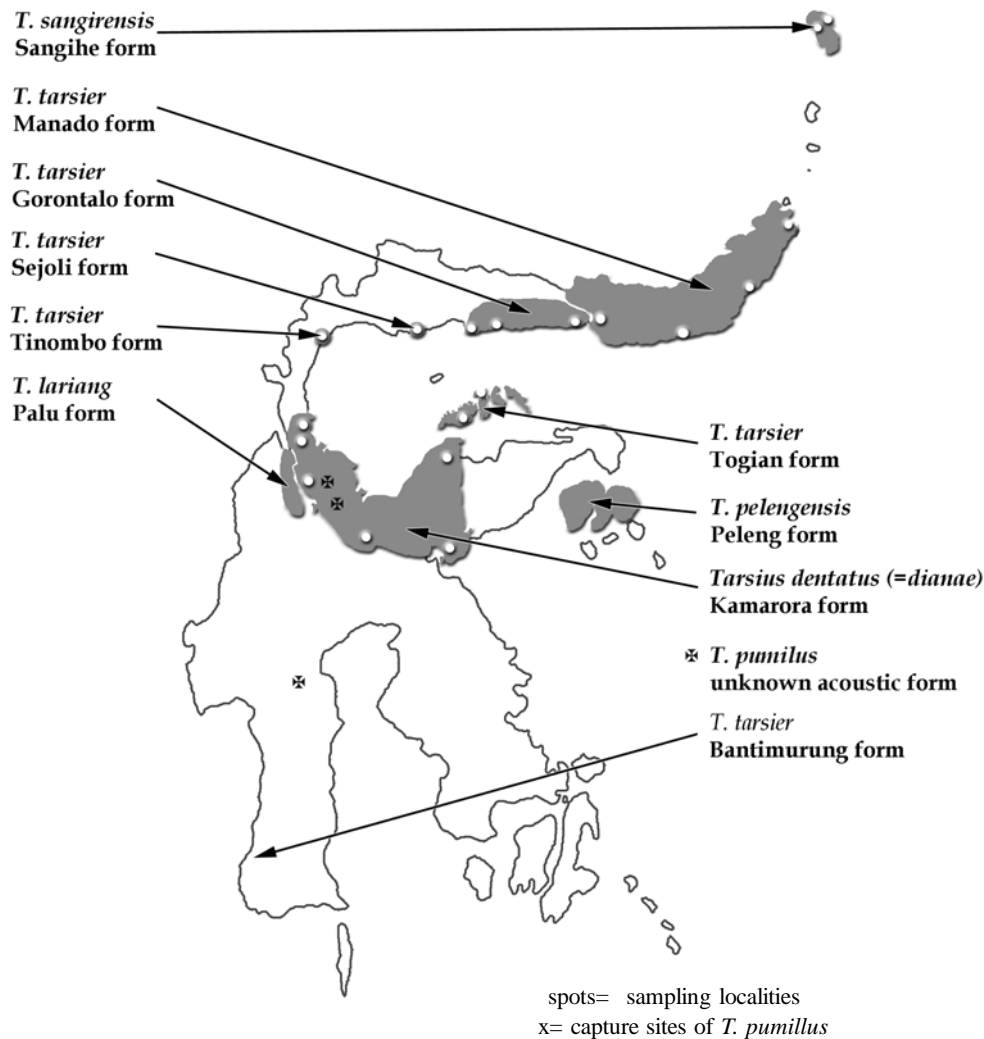
spots= sampling localities
x= capture sites of *T. pumillus*

Figure 2. Distributions of Eastern tarsier taxa and acoustic forms.

functions, and which co-inhabit biogeographic faunal zones with Sulawesi's macaques. Included with this hypothesis was the possibility of an altitudinal variant, the small-bodied montane tarsier of central Sulawesi, *T. pumilus*. They concluded by stating "there is clearly much more taxonomic work to be done to sort out the Sulawesi tarsiers, but we would predict that there are more forms to be found in southern Sulawesi, and on the offshore island groups of Selayar, Peleng, and Sangihe-Talaud."

Following the suggestion of MacKinnon and MacKinnon, several research teams began investigations into the primary taxonomy of Sulawesian tarsiers. On one front, field primatologists began to collect data from wild Sulawesian tarsiers. Niemitz (1984b) surveyed tarsiers in Central Sulawesi and published preliminary spectrograms of tarsiers from Marena. Niemitz *et al.* (1991) conducted more surveys in North and Central Sulawesi that led to the description of a new species from the highlands of Central Sulawesi, *Tarsius dianae* (Niemitz *et al.* 1991). They made similar observations to those of MacKinnon and MacKinnon, stating "there may be a constellation of nocturnal tarsier species paralleling the set of closely related diurnal macaque species in Sulawesi" (Figure 1).

Nietsch (1993, 1994) and Nietsch and Kopp (1998) continued investigations into the primary taxonomy of Sulawesian tarsiers, concentrating on the role of tarsier vocalizations. Nietsch documented the *T. dianae* acoustic form at Kebun Kopi (north of Palu along the Tawaeli-Toboli Road) and at Lake Poso, in addition to the type locality at Kamarora. She also reported hearing duets that sounded like the *T. dianae* acoustic form at Ampana and Morowali, but these were unconfirmed by playback or spectral analysis (Nietsch, 1994). Nietsch and Kopp (1998) also provided experimental evidence that "differences in duet structure are reliable indicators of taxonomic differentiation", in that duets of heterospecifics were less effective in prompting responses from caged animals than were the calls of conspecifics. Based on analogies with song function in gibbons, she concluded that tarsiers from Tangkoko, Kamarora, and the Togian Islands were each likely to be a separate species.

While fieldwork in Sulawesi was progressing, analyses of museum specimens were also being undertaken. Musser and Dagosto (1987) recommended the re-elevation of *T. pumilus* to full specific status as a small-bodied tarsier endemic to the montane forests of the central highlands. Feiler (1990) argued for the re-elevation of tarsiers from the Sangihe Islands to full specific status, *T. sangirensis*, based on cranial measurements. Groves (1998) concluded that the distinctive characters of Feiler were insignificant when compared with a larger sample, but he also argued for reviving *T. sangirensis* based upon morphometric variation in dental and cranial characteristics. Groves further mentioned the possible justification for separating the Sulawesian tarsiers from *T. syrichta* and *T. bancanus* at the generic level.

In spite of the advances made by field surveys and analyses of museum specimens, some nagging issues remained, and new ones had been created. First, populations of, *T. pumilus* and *T. pelengensis* were not included in the recent field surveys. Second, the surveys of MacKinnon and MacKinnon (1980) and Niemitz *et al.* (1991) did not make thorough comparisons between acoustic forms and pre-existing taxa, nor did either study employ systematic surveys. While it is understandable that preliminary work be *ad hoc,* two issues of confusion were generated by the advances that these two studies made: (1) what were the relationships between acoustic forms and the five described taxa from Sulawesi? and, (2) what variation existed between the widely separated sample points of the field surveys?

This project began with reconnaissance surveys in 1994, and collecting expeditions followed in 1995 and 1996. The goal was to use a transect to "connect-the-dots", as it were. A transect that encircles Tomini Bay, with a few minor auxiliary transects, would pass through all of the type localities of all described tarsier taxa from Sulawesi, with the notable exception of *T. tarsier*, as well as all of the previously identified acoustic forms (Figure 2). Based on evidence available at the time, 200 km sampling intervals were initially indicated. The results of initial surveys, however, indicated greater diversity than predicted by the previous studies, and sampling intervals were reduced to 100 km. Even this proved insufficient in the region from Gorontalo to Palu. Preliminary findings included: (1) identification of seven acoustic forms in the areas of North and Central Sulawesi that were partially surveyed by MacKinnon and MacKinnon (1980) and by Niemitz *et al.* (1991); (2) additional evidence for the re-elevation *T. sangirensis* to full-specific status; and, (3) the possibility of a nomenclatural conflict between *T. dianae* and *T. s. dentatus* (Shekelle *et al.* 1997).

METHODS

Data were collected on wild tarsiers from 12 localities in North and Central Sulawesi (Figure 1). Nine of the localities lie at approximately 100 km intervals along a transect that connects Tangkoko (the reference population for *T. tarsier*), and Kamarora, the type locality of *T. dianae*. The other three localities lie along two auxiliary transects that connect island populations with the main transect: (1) Great Sangihe Island, about 200 km north of Sulawesi; and (2) two locations in the Togian Islands of Tomini Bay, Batudaka Island and Malenge Island.

Recordings of wild tarsier vocalizations were made using either a Sony WMD 6C with a Sennheiser MKE 300 microphone, or a Sony TR-600 Hi8 camcorder with either the internal microphone or with a Sennheiser MKE 300. Many recordings were made of naturally occurring vocal duets at dusk or dawn. Other recordings were made of tarsiers that were baited to sing by playing the recording of a conspecific. The current study does not discriminate natural from baited vocalizations, although this difference may be important for understanding variation within an acoustic form.

For spectral analysis, recordings were replayed on the same machine that made the original field recording, and these were converted to digital "*.wav" files using an analog to digital converter. This was facilitated by the computer program "Cool 96" (copyright 1992-1996, Syntrillium Software). The following options were employed: sample rate (44100 Hz); resolution (1024 bands); windowing function option (Blackmann); spectral plot style (logarithmic energy plot with 120 dB range); dither transform results (on). Spectrogram files were pasted into Photoshop 5.0 (copyright 1989-1998 Adobe Systems Inc.) and were transformed to standardize the x- and y-axes, as well as to improve legibility.

For playback experiments, a test tape was made in the field of unaltered wild tarsier recordings, one call per locality, each call being separated by a gap of silence. The duration of each duet call and the duration of each period of silence were standardized. Positioning of the speakers (Sony SRS 77G) and volume were standardized as well as could be done (speakers were positioned at a distance of 10-20 meters from the sleeping site, volume was set to full). An unhabituated group of tarsiers was exposed to the tape between 8 a.m. and 3 p.m. A positive response was recorded if the tarsiers in question began vocalizations that led to a duet call while a recorded duet was being played, or during the period of silence that followed.

The time of day (8 a.m. to 3 p.m.) was chosen because tarsiers are normally sleeping and are not normally vocalizing. Thus any positive response should be the result of the experiment, not some other

factor. Also, a recording of the local duet call was played approximately one hour before and after the playback test. The playback test is, therefore, bracketed by positive responses, and this helps to ensure that any negative responses were not caused by other factors (e.g. the tarsiers did not hear the recording, the tarsiers had moved off to another site, the tarsiers were frightened into silence by the presence of researchers, etc.). If, during the course of the playback test, a positive result was recorded (i.e. the tarsiers began to sing), the test was paused for a minimum of 1/2 hour in order to let the tarsiers settle down. Thus, subsequent positive responses are likely to be the result of subsequent recordings, not because of continued excitability as a result of the previous positive response.
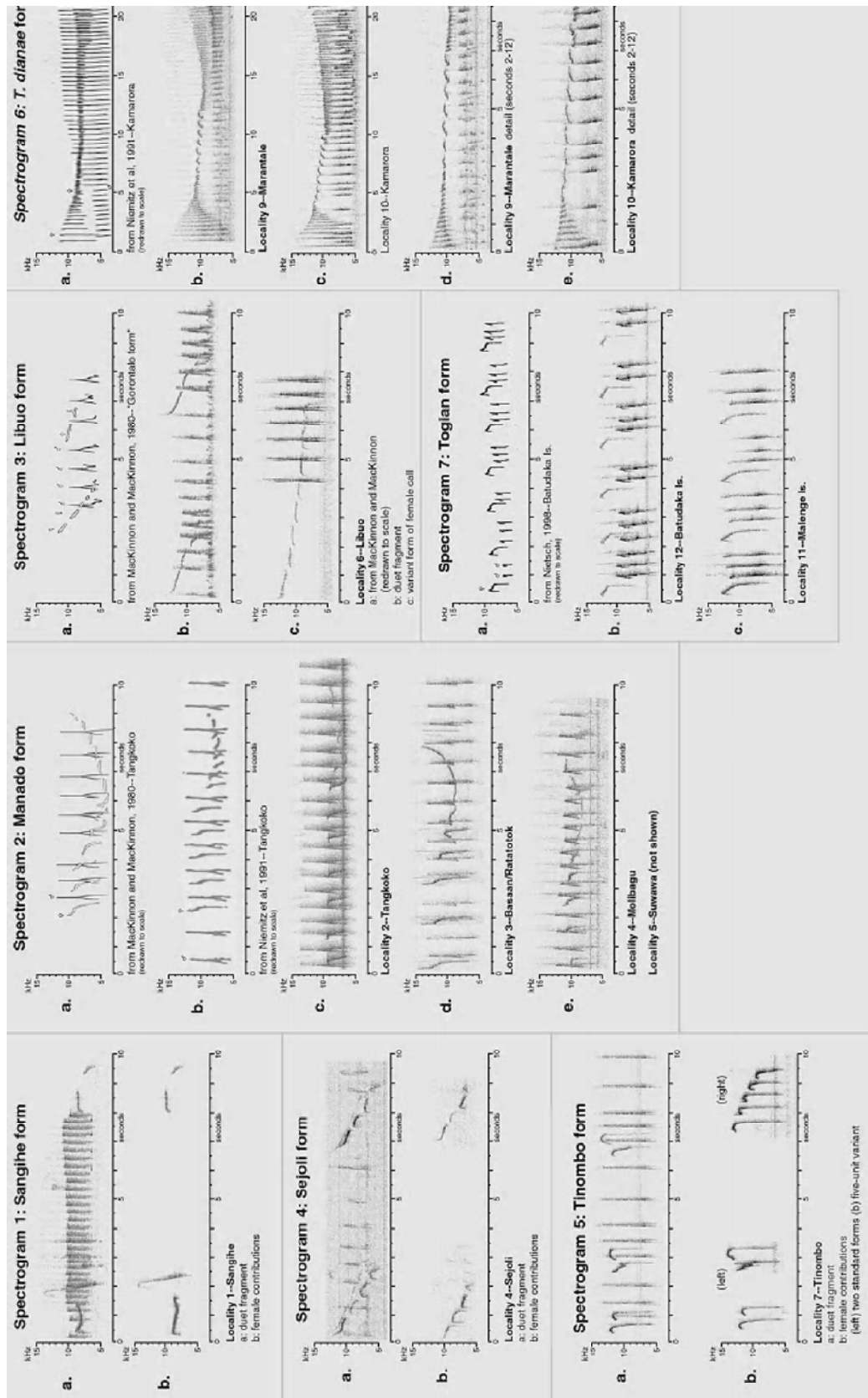
Playback tests are time consuming. Typically, only one formal test was performed per locality. Results of the formal tests were often corroborated, however, through numerous informal tests. Informal tests occurred during survey and trapping, when trial-and-error of playback was used to locate tarsier nests and to bait the tarsiers into the nets.

Since the playback tape was made in the field from recordings collected during survey, not all reciprocal tests could be conducted. Tarsiers from localities that were visited early in the study, such as Molibagu, were not exposed to recordings of tarsiers from localities that were visited subsequent to fieldwork at Molibagu. In other words, if tarsier recordings from locality x were played for tarsiers at locality y, it is not necessarily true that recordings from locality y were played for tarsiers at locality x. When conducted, however, the results of reciprocal tests were typically equal, i.e., the graph is symmetrical along the axis $x = y$.

RESULTS

Playback experiments reveal the presence of seven acoustic forms in the study area with geographically-structured variation (Figure 3).

From north to south along the transect, the first acoustic form (site 1), the Sangihe form, is unique

Spectrogram 1: Sangihe form

Locality 1—Sangihe
a: duet fragment
b: female contributions

Spectrogram 2: Manado form

from MacKinnon and MacKinnon, 1980—Tangkoko
(redrawn to scale)

from Niemitz et al, 1991—Tangkoko
(redrawn to scale)

Locality 2—Tangkoko

Locality 3—Bassan/Ratatotok

Locality 4—Molibagu

Locality 5—Suwawa (not shown)

Spectrogram 3: Libuo form

from MacKinnon and MacKinnon, 1980—"Gorontalo form"

Locality 6—Libuo
a: from MacKinnon and MacKinnon
(redrawn to scale)
b: duet fragment
c: variant form of female call

Spectrogram 4: Sejoli form

Locality 4—Sejoli
a: duet fragment
b: female contributions

Spectrogram 5: Tinombo form

Locality 7—Tinombo
a: duet fragment
b: female contributions
(left) two standard forms (b) five-unit variant

(left)   (right)

Spectrogram 7: Toglian form

from Nietsch, 1998—Batudaka Is.
(redrawn to scale)

Locality 12—Batudaka Is.

Locality 11—Malenge Is.

Spectrogram 6: T. dianae form

from Niemitz et al, 1991—Kamarora
(redrawn to scale)

Locality 9—Marantale

Locality 10—Kamarora

Locality 9—Marantale detail (seconds 2-12)

Locality 10—Kamarora detail (seconds 2-12)

Spectrograms

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	Sangihe Recording	Tangkoko Recording	Basaan Recording	Molibagu Recording	Suwawa Recording	Libuo Recording	Sejoli Recording	Tinombo Recording	Marantale Recording	Kamarora Recording	Malenge Recording	Batudaka Recording
Sangihe	+	-	-	-	-	-	-	-	-	-	-	-
Tangkoko	-	+	+	+	+	-	-	-	-	-	-	-
Basaan	-	+	+	+		-		-	-	-	-	-
Molibagu		+		+						-	-	
Suwawa	-	+	+	+	+	-		-	-	-	-	-
Libuo		-		-		+				-	-	
Sejoli	-	-	-	-	-	-	+	-	-	-	-	-
Tinombo	-	-		-		-		+	-	-	-	-
Marantale	-	-		-		-			+	+	-	-
Kamarora	-	-		-		-				+	-	-
Malenge	+	+		+		+				+	+	
Batudaka	+	+		+		+				+	+	+

+ = positive response   raised dark areas = acoustic forms
- = negative response   white areas = unperformed tests

Figure 3. Results of Playback Tests Spectrograms for Seven Acoustic Forms of Sulawesian Tarsiers

and found only on Greater Sangihe Island. The second acoustic form (sites 2-5), the Manado form, is found at Tangkoko, Ratatotok/Basaan, Molibagu, and Suwawa. The third acoustic form (site 6), the Libuo form, is unique to Libuo. The fourth acoustic form (site 7), the Sejoli form, is unique. The fifth acoustic group (site 8), the Tinombo form, is unique. The sixth acoustic form (sites 9-10), the *T. dianae* form, is found at Marantale and Kamarora. The seventh acoustic group (sites 11-12), the Togian form, is found at Malenge Island and Batudaka Island, in the Togian Islands.

The seventh acoustic group is interesting. Results of reciprocal tests were unequal. Recordings of the duet call from all sites successfully baited these tarsiers to respond, i.e. a positive response. When recordings of the Togian Island form were played at other sites, however, the recordings did not bait the tarsiers to sing, i.e. a negative response. These results were tested and re-tested, always to the same effect.

Togian Island tarsiers seem not to discriminate among acoustic forms as do other tarsiers in the study group.

The playback test from site 5, Suwawa, had an anomaly. During the course of the formal playback test, the target group responded to all calls. During informal tests, prior to the formal test, however, tarsiers from this locality did not respond to the duet calls of other acoustic forms. The formal test was conducted on the last day of fieldwork under sub-optimal conditions. Various conditions of the test were not met (e.g. the minimum pause of ½ hour between positive results was not observed). Time constraints did not allow for the formal test to be repeated. This study tentatively rejects the results of the formal test for those of the informal tests. Further testing is warranted.

Recordings of wild tarsiers in this study were made under field conditions and are generally of poor quality. They are not well suited for spectral analysis. The following are very general descriptions of the vocal duets. These descriptions are presented with the principal goal of facilitating fuller understanding of what is illustrated in the spectrograms. They are not meant to be definitive statements of the characteristics of the given acoustic forms. The descriptions use the following terms: unit = one part of a multi-part call; call = one coordinated, repeated vocalization. The difference between a unit and a call is somewhat arbitrary, but it is nevertheless a useful distinction for describing tarsier vocal duets.

The Sangihe form is a previously undescribed acoustic form. It is characterized by a two-unit female call and a rapid series of male calls (spectrogram 1a). The female contributions include the standard call, and at least one variant that occurred at the end of a duet (spectrogram 1b), both of which have two units. The first unit of the standard female call is a long whistle, over one second long with energy concentrated around 8 kHz (spectrogram 1b, far left). The second unit rapidly descends from over 14 kHz to below 6 kHz. The variant is shorter, and does not ascend above 10 kHz (spectrogram 1b, far right). Spacing between the female calls varies, but is typically 8-10 seconds from the start of one call to the start of the next (not pictured). The male calls are wide-band chirps that rapidly rise and descend (7 kHz, to over 10 kHz, to less than 7 kHz) in a span of only 0.15 seconds. The male produces these calls at the rate of about 4-6 calls per second.

The Manado form was originally described by MacKinnon and MacKinnon (1980), and was further examined by Niemitz *et al.* (1991), each of whom used recordings made at Tangkoko (spectrograms 2a and 2b) (Table 2). The duet is a series of synchronized male and female calls that precede a crescendo of ascending whistles by the female. Initially, the female call is a descending whistle that drops from around 10 kHz to below 6 kHz over the span of approximately 0.3 seconds. The female makes these calls about once per second. The female calls decrease the degree to which they descend in pitch, gradually flattening out, and finally, they begin to ascend. During this portion, the call can become highly synchronized (e.g., spectrogram 2d, seconds 6-8). In between, and on top of the female calls, are male calls. These are wide-band chirps that rise and descend rapidly (6 kHz, to 13 kHz, to less than 6 kHz), all in a span of only 0.2 seconds. The male produces these at a rate of about 2 per second. The overall length of one such vocal phrase varies greatly but they do not usually repeat any faster than about once per 10 seconds.

MacKinnon and MacKinnon (1980) originally described the Libuo form as the Gorontalo form (spectrogram 3a). This acoustic form is characterized by a two- or three-unit female call accompanied by male calls (spectrogram 3). The female call has a standard form (spectrogram 3b) and at least one variant (spectrogram 3c). The standard female call is a long whistle that descends from around 13 kHz to about 7 kHz in two or three units. A variant, in spectrogram 3c is similar to the standard call, but with 5-8 units that may take up to 7 seconds total, each unit being about 0.6-1.0 seconds and separated by a momentary pause. The female calls repeat with a minimum periodicity of around 6 seconds from the start of one call to the start of the next. The male calls, wide-band chirps that rise and descend (6 kHz, to 10-12 kHz, and back to 6 kHz) in about 0.15 seconds, punctuate the spaces in the female call (e.g.

Table 2: Provisional Assessment of Primary Taxonomy of Sulawesian Tarsiers

	Taxon name	Acoustic form	Reference	Distribution (type locality = bold face)	Issue
1.	*T. tarsier* Erxleben 1777	Bantimurung form	Unpublished data	**Makassar**	Ongoing investigations of the recently rediscovered type specimen may allow for a more accurate localization of the type locality
2.	*T. sangirensis* Meyer 1897	Sangihe form	Feiler, 1990; Shekelle et al, 1997; Groves, 1998	**Gr. Sangihe Is.**	The insular population will likely be shown to be taxonomically distinct.
3.	*T. dentatus* Miller and Hollister 1921	*T. dianae* form	Niemitz et al, 1991; Shekelle et al, 1997	**Labuan Sore**, Kamarora, Marantale, Kebun Kopi, Lake Poso, Ampana(?), Morowali(?)	apparent nomenclatural conflict with *T. dianae*
4.	*T. pumilus* Miller and Hollister, 1921	?	Niemitz, 1985; Musser and Dagosto, 1987	**Rano Rano**, Latimojong Mts., Mt. Rorekatimbu	Living specimens remain unobserved to science.
5.	*T. pelengensis* Sody, 1949	Peleng form		**Peleng Is.**	Notable similarities between the duet form of this species and that of *T. dentatus* may indicate a close relationship, possibly at the subspecific level.
6.	*T. lariang* Merker & Groves 2006	Palu form	MacKinnon and MacKinnon, 1980; Niemitz, 1984; Merker and Groves, 2006	**Gimpu**, Palu Valley, including Marena	Niemitz's (1984) *T. pumilus* from Marena is not *T. pumilus*, but more likely, the Palu form of MacKinnon and MacKinnon (1980)
7.	*T. tarsier* population	Manado form	this paper; MacKinnon and MacKinnon, 1980	Tangkoko, Ratatotok, Molibagu, Suwawa	Most field studies of *T. spectrum* refer to this population
8.	*T. tarsier* population	Gorontalo form = Libuo form	this paper; MacKinnon and MacKinnon, 1980; Shekelle et al 1997	Libuo	Distribution reported here much smaller than that reported by MacKinnon and MacKinnon (1980)
9.	*T. tarsier* population	Sejoli form	this paper; Shekelle et al, 1997	Sejoli	replaces MacKinnon and MacKinnon's (1980) Gorontalo form in the area of Sejoli
10.	*T. tarsier* population	Tinombo form	this paper; Shekelle et al, 1997	Tinombo	replaces MacKinnon and MacKinnon's (1980) Gorontalo form in the area of Tinombo
11.	*T. tarsier* population	Togian form	this paper; Nietsch, 1994; 1998; Shekelle et al 1997	Malenge Is., Batudaka Is.	has been argued to be a distinct taxon based on experimental playback evidence (Nietsch, 1998), strongly supported by genetic data (Shekelle et al, this volume)

spectrogram 3b, seconds 0-2), and then continue at the rate of about one per second between female calls.

The Sejoli form is a previously undescribed acoustic form. The recordings from this locality are of particularly low quality, but even so, some resemblances to the Libuo form are apparent. This acoustic form has a four-unit female call accompanied by male calls (spectrogram 4a). The female call begins at about 12 kHz and descends in a series of four whistles to about 5 kHz. The first two units are rather smooth in their descent, but the final two have fine oscillations in pitch (spectrogram 4b, seconds 1.5-2.5). The entire call lasts about 2.5 seconds. The male calls, very faint in this spectrogram, are wide-band chirps that rise and fall from about 7 kHz to 11-12 kHz in about 0.15 seconds. The male repeats his calls with a periodicity of about 0.6 to 1.1 seconds. The period seems to gradually increase when the female is not calling. Relative to other tarsier duets, the duet in this spectrogram does not seem to be particularly well synchronized between the male and female calls. Few recordings were made from this locality, and it cannot be concluded whether this is characteristic of the Sejoli form.

The Tinombo form is a previously undescribed acoustic form. It is remarkable for the vocal diversity of the female. In its simplest form, it bears similarities to the Togian form (see below), but the female repertoire is far greater than in Togian Island tarsier. Structurally, it is a simple duet with one female call followed by two to four male calls (spectrogram 5a). The female call is typically in two units, but is sometimes a single unit (not figured here), particularly in the early part of a duet. The basic female unit is a hook-shaped whistle that descends from around 12 kHz to about 5 kHz in about 0.4 seconds. Two of these units are sometimes given in rapid succession, the intervening gap being only 0.1 seconds (spectrogram 5b, far left). More often, the hook-shaped unit is preceded by a peculiarly modulated whistle that begins at around 13 kHz, descends to below 10 kHz, rises again to a point higher than the initial frequency, and finally, descends to nearly 5 kHz, all in the span of only 0.3-0.4 seconds (spectrogram 5b, middle). Another female variant, much rarer than

the first two described forms, is a series of five hook-shaped units that occur in rapid succession (spectrogram 5b, far right). Each of the units has a terminal frequency of about 5 kHz, but the maximum frequency of each unit gradually descends, the first having a maximum frequency of about 14 kHz and the last having a maximum frequency of just 10 kHz. The male calls are also quite interesting. They are wide-band chirps, like other male tarsier calls, but they modulate from 5 kHz to over 13 kHz, and back again to 5 kHz, in about 0.10 seconds. The male produces these calls at a rate that varies from about 0.5-1.0 seconds, the interval lengthening when the female is not calling.

The *T. dianae* form was originally described by Niemitz *et al.* (1991) based on recordings made from Kamarora. They published renderings of a spectrogram that has been re-scaled here for comparative purposes (spectrogram 6a). This acoustic form features a longer duet that is characterized by many repeated calls. It is a challenge to make accurate, legible spectrograms of these duets due to their length. The re-scaled version of the figure from Niemitz *et al* (1991) offers a glimpse at the overall character of the duet. In the early portion of the duet, the female gives fast, repetitive wide-band chirps that descend from around 15 kHz to around 5 kHz in only 0.3 seconds or less, at the rate of 2-3 calls per second. The rate of repetition gradually increases to about 7 calls per second, as the range of frequency modulation gradually narrows to a band centered at about 10-11 kHz (spectrograms 6b, seconds 6-12; 6c, seconds 4-9). The female gives about 7 relatively narrow-band calls that are between 10-11 kHz, and last about 0.7 seconds each. Following this, she begins again to give rapid chirps, first in a narrow band centered around 10 kHz, then gradually increasing the frequency range of the calls until they descend from about 12 kHz to 8 kHz. The male call is also a wide-band chirp that descends from around 8 kHz to around 5 kHz. These are repeated at the rate of about two per second. The frequency range of these calls widens slightly as the female's calls flatten out. It is during this portion (spectrograms 6b, seconds 6-12; 6c, seconds 4-9) that the duet becomes more highly

synchronized, with the male and female calls beginning in almost perfect unison (spectrograms 6d, seconds 4.0-6.5; 6e, seconds 4-7). Following this, synchronization of male and female calls remains tight with the female giving either two or three calls per male call (spectrograms 6d, seconds 7-10; 6e, seconds 7-10).

Spectrograms of the Togian form were originally published by Nietsch and Kopp (1998) (spectrogram 7a). Structurally, this is a simple duet with one female call being followed by two or three male calls. Like the Tinombo form, the female call is a hook-shaped whistle, although the top of the hook is less smooth in the Togian tarsier. The maximum pitch is about 12-13 kHz (although the figure by Nietsch shows this to be only about 10 kHz), and there is a sharp descent to around 6 kHz. The call lasts about 0.5 seconds and is repeated at the rate of about 1 call per 1.5 seconds. The male call is shaped like a temporally compressed version of the female call. Maximum pitch is around 10-11 kHz, and the call descends precipitously to 5 kHz or lower. The male call lasts only about 0.15 seconds. Male calls are performed as a series of 2 or 3 calls that gradually ascend in maximum pitch.

DISCUSSION

Acoustic Data:

Results from this study reveal seven acoustic forms of tarsiers in the study area. Within a form, there are self-evident similarities in duet structure. There is also excellent interobserver reliability between MacKinnon and MacKinnon (1980), Niemitz *et al.* (1991), Nietsch and Kopp (1998), and myself, evidenced in the spectrograms. Spectrograms recorded from tarsiers at Tangkoko in the late 1970's, late 1980's, and late 1990's show stability of form that is reassuring that form of tarsier call persists over time.

Mate Recognition theory predicts that tarsier vocalizations are a species-specific system that evolves in such a way as to advertise the fitness of mating partners. It follows, then, that so too must the tarsier auditory system evolve in such a way as to receive and process those vocalizations, filtering signal from noise. Thus, for the purposes of this study, an acoustic form of tarsiers is the most inclusive group of animals that have a similar and appropriate behavioral response to a given vocalization (e.g. groups of tarsiers that respond to a recorded vocal duet with the performance of a vocal duet). Hypothetically, each acoustic form is a distinct taxon, but this remains to be verified.

It is easy to see from the spectrograms, that there is quantitative variation in the vocal duets within an acoustic form, and qualitative variation among acoustic forms. Some of the most obvious quantitative variation is the frequency (in kHz) of the female calls seen in spectrogram 2. For example, the final note of the female's crescendo varies from around 9 kHz in spectrograms 2b and 2c, to 11 kHz in spectrogram 2a and 2e, to fully 15 kHz in spectrogram 2c. Since 2a, 2b, and 2c are all from one locality, Tangkoko, it is probable that this is variation that normally occurs within an acoustic form.

In contrast, however, it is more difficult to make meaningful quantitative comparisons among the acoustic forms. What are the homologies, for example, between the crescendos of the Manado form and the hook-shaped female calls from the Togian Islands? The nature of quantitative comparisons of differences is that they are, in fact, comparisons of similarities. Things that are different are, simply, different. Thus it is with tarsier acoustic forms that some characters suitable for quantitative comparisons within a form are unsuitable for comparisons among forms. Homologies for quantitative comparison likely do exist among acoustic forms, but finding them will require further study.

Notes on Tarsier Taxonomy:

Several issues trouble the taxonomy and classification of Sulawesian tarsiers. Primary among these was, until recently, the lack of a type specimens for *Tarsius tarsier* (see Groves *et al.* this volume). Second to this is the likelihood of unrecognized cryptic taxa. Investigations into acoustic variation have uncovered eight distinct acoustic forms: the seven described in this study plus MacKinnon and MacKinnon's (1980) Palu form. Third, there is a large

problem between two independent lines of investigation: surveys of museum specimens are based primarily on analyses of skeletons and pelts, while field surveys rely heavily on acoustic data and data from wild tarsiers that are trapped and released. While complementary studies often lead to dynamic advances in understanding, the unfortunate situation at hand is that many diagnostic characters used in the museum studies are impractical to score on a living tarsier (e.g. relative inflation of the auditory bulla anterior to the carotid foramen), and museum specimens cannot be scored for acoustic forms. Thus, the kernel of the problem is complementary taxonomic investigations have produced data sets that cannot be compared with each other.

A clear taxonomic statement that identifies *T. tarsier*, clarifies the relationship between known acoustic forms and described taxa, and which states the distribution of these forms, where known, is needed.

Tarsius tarsier: This taxon is based on Buffon's tarsier and is believed to come from Makassar (Groves *et al.* this volume). Makassar was not sampled in this study, but subsequent surveys show a highly distinctive duet from near to Makassar (unpublished data). Thus, each of the acoustic forms discussed here are likely to be distinct taxa.

Tarsius sangirensis: Although this taxon was treated as a subspecies by both Sody (1949) and Hill (1955) and synonymized with *T. spectrum* by Niemitz (1984a), there is general agreement between Feiler (1990), Shekelle *et al.* (1997), and Groves (1998) that this is a valid species. The type locality is Greater Sangihe Island and the type specimen, according to Hill (1955) is in the Dresden Museum. This taxon is distributed sparsely throughout Greater Sangihe Island. There are reports that tarsiers exist on other islands in the Sangihe Island group (e.g. Siau Island). Subsequent surveys indicate tarsiers are still present on Siau, although they are quite rare, and the acoustic form is distinct from that of *T. sangirensis*. The local name is *sengkasi* (bahasa Sangihe). One family referred to tarsiers as *higo*.

Sangihe Island tarsiers can be easily and confidently diagnosed from *T. tarsier* by the tail and

the tarsi, both of which are more sparsely haired with hairs that are shorter than in *T. tarsier*—the characters on which this taxon was based (Meyer, 1897). These distinctive characteristics of *T. sangirensis* are intermediate between *T. tarsier* and *T. syrichta*, which is curious because Greater Sangihe Island is about midway between Sulawesi and the Philippine island of Mindanao. *Tarsius sangirensis*, nevertheless, is clearl related to the *T. tarsier*-complex.

Regarding Sangihe Island tarsiers, Musser and Dagosto (1987) state that "the tail, although less densely haired than in typical *T. spectrum*, is not at all similar to the sparsely haired tail of *T. syrichta*." While this is true, it does not argue against the uniqueness of *T. sangirensis*. They also state that, "the tarsus is sparsely haired, but some individuals of *T. spectrum* do resemble *T. syrichta* in this regard". I disagree. None of the mainland Sulawesian tarsiers in this study approximated the condition in *T. syrichta*, nor did they resemble *T. sangirensis*. Furriness of the tarsus changes with age: infants have densely haired tarsi with hair that extends onto the hands and feet. Adults gradually lose some of that hair, particularly on the hands, feet and ventral/superior aspect of the tarsi, which may appear nearly nude in adults (unpublished data). The dorsal/inferior aspect of the tarsi of *T. tarsier* are always haired. The same is true of *T. sangirensis*, but the hair is shorter and less dense.

Groves (1998) found that *T. sangirensis* is distinctive from all other Sulawesian tarsiers in having large and broad skulls, long toothrows, and short lateral incisors. Shekelle *et al.* (1997) found them to be distinguished from other Sulawesian taxa in having a higher average body weight, a unique acoustic form, and several unusual behavioral characteristics including a tendency toward less sociality while sleeping, and a preference for more exposed sleeping sites—which may be due, in part, to habitat degradation.

Some authors including Groves (1998) have indicated that *T. sangirensis* may have a less distinctive postauricular white spot (a synapomorphy that links all Sulawesian taxa), and finer, less wooly fur. To the former, I disagree. The fur of *T. sangirensis* is perhaps finer and less wooly than that of *T. tarsier*,

but it is also most certainly lighter. The dorsal aspect of the body and limbs is a light, milk chocolate-like brown. It has less of the distinctive brown and black mottled appearance of *T. spectrum*. The underside is almost pure white as is the postauricular white spot (see photo of *T. sangirensis* in Rowe, 1996, p.55—the postauricular white spot is visible at the base of the ear, and, faintly, at the top of the ear). It may be that the museum specimens bear some artifacts of preservation or aging that have turned the pelts dark.

Tarsius dentatus: This taxon was treated as a questionably valid subspecies by both Sody (1949) and Hill (1955), and was synonymized with *T. spectrum* by Niemitz (1984). The infant tarsier in Rowe (1996) that is labeled as *T. dentatus* is misidentified. It is a tarsier from Libuo.

The type locality of *T. dentatus* is Labua Sore. Dr. Lenora Bynum studied macaques in that region for several years in the early 1990's and her surveys indicate that the site, which is also important for macaque taxonomy, goes by the name Labuan Sore (pers. comm.). When I visited there in April and May of 1996 local people agreed that there is a coastal site called Labuan Sore. [This is, perhaps, a corruption of *labuhan sore*, or, "evening anchorage"]. It is coastal and treeless, so I surveyed the nearby agricultural lands around the village of Marantale and used these as my reference sample for *T. dentatus*.

Tarsiers at Marantale exhibited the vocal duets of *T. dianae*. Thus, it raises the strong possibility of nomenclatural conflict.

Tarsius pumilus: There is agreement that *T. pumilus* is a valid taxon (Niemitz 1985, Musser and Dagosto 1987, Groves 1998, and Maryanto and Yani 2004). It is known from only three localities: the type locality, Rano Rano, at 1800 m in Central Sulawesi, the Latimojong Mountains at 2200 m in South Sulawesi, and from 2200 m on Mt. Rorekatimbu, but it is thought to be distributed throughout the mossy montane forests of the central region of Sulawesi at elevations over 1800 m. It is distinctive in its very small body size, head and body length being about 75% that of *T. tarsier* (Musser and Dagosto, 1987).

The controversy with this taxon is not its validity, but its whereabouts. Tremble *et al.* (1993)

surveyed the locality listed in Musser and Dagosto (1987) as being the type locality for over one month without finding any sign of tarsiers (Yakob Muskita, pers. comm.). An experienced six-member team spent a chilly night at 1800 m on the flank of Mt. Nokilalaki for this study without finding evidence of tarsiers. Musser spent considerable time in the montane forests of Central Sulawesi in the 1970s without encountering tarsiers (Musser and Dagosto, 1987). The question remains where is *T. pumilus*?

Tarsius pelengensis: This taxon was described by Sody (1949) but considered weak by Hill (1955) and synonymized with *T. spectrum* by Niemitz (1984a). Musser and Dagosto (1987) noted that museum samples from Peleng were distinctively large, but they refrained from confirming its status as a valid subspecies, conclusions that were also reached by Groves (1998). Acoustic surveys were conducted by James Burton (Nietsch and Burton 2002), and the resulting spectromgrams show clear similarities with those of *T. dentatus*.

Tarsius dianae: Described as a distinct species by Niemitz *et al* (1991) based upon a unique vocal duet, several minor characters of appearance, some behavioral differences, and possibly a unique karyotype. As mentioned previously, there is a likely nomenclatural conflict between this taxon and *T. dentatus*.

Manado form: This form exists as an acoustic variant and not yet a recognized taxon. It is synonymous with the Manado form of MacKinnon and MacKinnon (1980) and Shekelle *et al* (1997). Based on acoustic data, the distribution is from the northeastern tip of Sulawesi to the faunal break at Gorontalo. It includes Tangkoko Nature Reserve, from where most research on wild *Tarsius spectrum* originates. The most common local names are *tangkasi* (*Bahasa Minahasa*) in the northern part of the range, and *mimito* (*Bahasa Gorontalo*) in the southern part.

Libuo form: This form exists as an acoustic variant and not yet a recognized taxon. It is synonymous with the Gorontalo form of MacKinnon and MacKinnon (1980) and the Libuo form of Shekelle *et al* (1997). Acoustic surveys presented here suggest

that it has a much more restricted range than that presented by MacKinnon and MacKinnon, who report the range as being the same as that of *M. hecki*, i.e. the entire northern peninsula from Gorontalo to just north of Palu. My acoustic surveys indicate that the distribution of this acoustic form is limited to an area no greater than that bounded by Gorontalo in the east, and Moutong/Molosipat in the west. The local name of tarsiers in this region is *mimito* (*Bahasa Gorontalo*).

Sejoli form: This form is an acoustic variant and not yet a recognized taxon. It is synonymous with the Sejoli form of Shekelle *et al.* (1997), and replaces the Gorontalo form of MacKinnon and MacKinnon (1980) in the area around the North Sulawesi-Central Sulawesi provincial boundary. Sejoli is a small village in the vicinity of Moutong and Molosipat. Acoustic surveys indicate that the distribution of this acoustic form is limited to an area no greater than that bounded by Tanjung Panjang in the east, and Tinombo in the west.

Tinombo form: This form is an acoustic variant and not yet a recognized taxon. It is synonymous with the Tinombo form of Shekelle *et al.* (1997), and replaces the Gorontalo form of MacKinnon and MacKinnon (1980) in the vicinity of Tinombo. Acoustic surveys indicate that the distribution of this acoustic form is limited to an area no greater than that bounded by Sejoli in the east, and Marantale in the south.

Togian form: This form is an acoustic variant and not a recognized taxon. It is synonymous with the Togian form of Shekelle *et al.* (1997), and the Togian tarsiers of Nietsch and Kopp (1998). The confirmed distribution of this acoustic form is limited to the islands of Malenge and Batudaka, but it is reasonable to assume that its distribution extends to all of the Togian Islands (except perhaps Una Una), as the Togian Islands were a single land mass and were possibly connected to Sulawesi as recently as the last Ice Age (Whitten *et al.* 1987). Nietsch and Kopp (1998) has argued for the taxonomic separation of this acoustic form on the strength of experimental evidence from playback tests where captive *T. tarsier* were exposed to recordings of the vocalizations of the Togian tarsiers, as well as those of *T. dentatus*, and conspecific *T. tarsier*. Several language groups exist in the Togian Islands and there are likely to be many local names. I recorded a few including: *bunsing*, *tangkasi*, and *podi*.

Palu form: MacKinnon and MacKinnon (1980) originally described this acoustic form. They list the distribution as being the valley of the Palu River. This form has recently been described as *T. lariang* by Merker and Groves (2006).

Other acoustic forms: MacKinnon and MacKinnon (1980) reported that a colleague, Dr. Dick Watling, recorded three additional tarsier acoustic forms, all from Central Sulawesi, but they did not state where in Central Sulawesi he made these recordings. It is not necessary to assume that Watling's forms are all new and unpublished. For example, it could be that his forms are, say, *T. dianae*, the Tinombo form, and the Togian form, all of which come from Central Sulawesi. Nevertheless, additional acoustic forms almost certainly exist, undiscovered, on Sulawesi.

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REFERENCENS

Banks, E. 1949 Bornean Mammals. Kuching, Malaysia: The Kuching Press.

Bearder, SK, PE. Honess & L. Ambrose. Species diversity among galagos with special reference to mate recognition. In: Alterman L *et al.*, editors. Creatures of the Dark: The Nocturnal Prosimians. New York, Plenum press. p 331-352.

Feiler, A. 1990. Ueber die Saugetiere der Sangihe- und talaud-Inslen- der Beitrag AB Meyers Fur ihre Erforschung (Mammalia). *Zoologische Abhandlungen Staatliche Museum fur Tierkunde in Dresden* 46:75-94.

Fooden, J. 1980. Classification and distribution of living macaques (*Macaca* Lacepede, 1799). In Lindburg DG, editor. The Macaques: Studies in Ecology, Behavior, and Evolution. New York: Van Nostrand Reinhold Company. p1-9.

Groves, CP. 1980. Speciation in *Macaca*: The view from Sulawesi. In Lindburg DG, editor. The Macaques: Studies in Ecology, Behavior, and Evolution. New York: Van Nostrand Reinhold Company.

Groves, C. 1998. Systematics of tarsiers and lorises. *Primates* 39(1):13-27.

Gursky, S. 1994. Infant care in the spectral tarsier. *International Journal of Primatology* 15(6):843-855.

Gursky, S. 1995. Group size and composition in the spectral tarsier, *Tarsius spectrum*: implications for social organization. *Tropical Biodiversity* 3(1):57-62.

Gursky, S. 1997. Modeling maternal time budgets: the impact of lactation and infant transport on the time budget of the spectral tarsier, *Tarsius spectrum*. Dissertation Thesis. SUNY Stony Brook.

Gursky, S. 1998. Conservation status of the spectral tarsier *Tarsius spectrum*: population density and home range size. *Folia Primatoligica* 1998:69(suppl 1):191-203.

Hill, WCO. 1953. Notes on the taxonomy of the genus *Tarsius*. *Proceedings of the Zoological Society of London* 123:13-16.

Hill, WCO. 1955. Primates: Comparative Anatomy and Taxonomy. II. Haplorhini: Tarsioidea. Edinburgh: Edinburgh University Press.

Horsfield, T. 1821. Zoological Researches in Java. London: Black, Kingsbury, Parbury, Allen.

Clark, WEL. 1924. Notes on the living tarsier (*Tarsius spectrum*). *Proceedings of the Zoological Society of London* p217-223.

MacKinnon, J & K. MacKinnon. 1980. The behavior of wild spectral tarsiers. *International Journal of Primatology* 1(4):361-379.

Maryanto, I & M. Yani. 2004. The third record of pygmy tarsier (*Tarsius pumilus*) from Lore Lindu National Park, Central Sulawesi, Indonesia. *Tropical Biodiversity* 8(2): 79-85.

Masters JC. 1998. Speciation in the lesser galagos. *Folia Primatologica* 69(suppl 1):357-370

Miller Jr., GS, & Hollister N. 1921. Twenty new mammals collected by H. C. Raven in Celebes. *Proceedings of the Biological Society of Washington* 34:93-104.

Musser, GG, & M. Dagosto. 1987 The identity of *Tarsius pumilus*, a pygmy species endemic to the montane mossy forests of Central Sulawesi. *American Museum Novitates* (2867):1-53.

Niemitz, C. 1984a. Taxonomy and distribution of the genus *Tarsius* Storr, 1780. In Niemitz C, editor. The Biology of Tarsiers. New York: Gustav Fischer Verlag. p1-16.

Niemitz, C. 1984b. Vocal communication of two tarsier species (*Tarsius bancanus* and *Tarsius spectrum*). In Niemitz C, editor. The Biology of Tarsiers. New York: Gustav Fischer Verlag. p129-142.

Niemitz, C. 1985 Der Koboldmaki-Evolutions-forschung an einem Primaten. *Naturwiss Runsch* 38:43-49.

Niemitz, C, A. Nietsch, S. Warter, & Y. Rumpler. 1991. *Tarsius dianae*: A new primate species from Central Sulawesi(Indonesia)." *Folia Primatologica* 56:105-116.

Nietsch A. 1993. Vocal acoustics and social behavior in tarsiers. In Creatures of the Dark: The Nocturnal Prosimians Conference in Durham, North Carolina.

Nietsch A. 1994. A comparative study of vocal communication in Sulawesi tarsiers. ICongress of the International Primatological Society in Denpasar, Bali, Indonesia. p310 1994.

Nietsch, A & C. Niemitz. 1993. Diversity of Sulawesi tarsiers. *Deutsche Gesellschaft fur Saugetierkunde* 67:45-46.

Nietsch, A & M. Kopp. 1998. Role of vocalizations in species differentiation of Sulawesi tarsiers. Folia Primatologica 69(suppl 1)371-378.

Nietsch, A & J. Burton. 2002. Tarsier Species in Southwest and Southeast Sulawesi. *Abstracts*, The XIXth Congress of the International Primatological Society (IPS), 4-9 Aug. 2002, Beijing, China: 20-21.

Pallas, PS. 1778. *Novae species quad e glirium ordine cum illustrationibus variis complurium ex hoc ordine animalium.* Erlangen: W. Walther.

Paterson, HEH. 1985. The recognition concept of species. In Vrba ES. editor. Species and Speciation. Pretoria: Transvaal Museum. p21-29

Patton JL, MNF. da Silva, & JR. Malcolm. 1994. Gene genealogy and differentiation among arboreal spiny rats (rodentia: echimydae) of the Amazon basin: a test of the riverine barrier hypothesis.

Peres, CA, JL. Patton, & MNF. da Silva. 1996. Riverine boundaries and gene flow in Amazonian saddle-back tamarins. *Folia Primatologica* 67:113-124.

Rowe, N. 1996. Pictorial Guide to the Primates. New York: Pogonia Press.

Shekelle, M, S. Mukti, LLS. Ichwan & Y. Masala Y. 1997. The natural history of the tarsiers of North and Central Sulawesi. Sulawesi Primate Project Newsletter.

Sody, HJV. 1949. Notes on some Primates, Carnivora, and the babirusa from the Indo-Malayan and indo-Australian regions. Treubia 20:121-185.

Tremble, M, Y. Muskita & J. Supriatna. 1993. Field observations of *Tarsius dianae* at Lore Lindu Nation Park, Central Sulawesi, Indonesia. *Tropical Biodiversity* I(2):67-76.

Wallace, AR. 1876. The Geographical Distribution of Animals, Vol. 1. London: MacMillan.

Whitten, A, M. Mustafa & G. Henderson. 1987. The Ecology of Sulawesi. Yogyakarta, Indonesia: University of Gajah Mada Press.

Woollard, HH. 1925. The anatomy of *Tarsius spectrum. Proceedings of the Zoological Society of London* 70:1071-1184.