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Tarsius lariang: A New Primate Species from Western Central Sulawesi

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On the basis of morphological, anatomical, and acoustic analyses, the tarsiers of the Gimpu region on Sulawesi belong to a previously undescribed species of the genus Tarsius *Storr, 1780. We describe the new taxon as* Tarsius lariang *new species. In November 2001, S. Merker collected 8 specimens of* Tarsius lariang *near Gimpu, Central Sulawesi, Indonesia. Four of them were transferred to the Indonesian Institute of Sciences at Cibinong to be held in an enclosure, and after their deaths become part of the collection of the Museum Zoologicum Bogoriense, Bogor. The new species is distinctive in pelage, skull, and body proportions, and in vocalization. We describe the unique territorial duet song characteristic for them and place the taxon into a biogeographic framework developed in previous studies.*

KEY WORDS: Gimpu; Palu form; morphology; taxonomy; vocalization.

TARSIUS LARIANG NEW SPECIES

Holotype

MZB 24302, adult male, skin and skull, from Gimpu (01°38′S, 120°02′E, 500 m asl), west of Lore-Lindu National Park, *ca.* 5 km north

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of the river Lariang, Central Sulawesi, Indonesia. Captured alive on November, 12, 2001, died on November, 14, 2001, when transferred to Cibinong, Java.

Paratypes

MZB 24303, adult female; MZB 24304, subadult female (skins and skulls); MZB 24307, adult male (skull only); captured on November 12 and 13, 2001, died in captivity. MZB 24302, -03, -07 collected in collaboration with Dr. Myron Shekelle (University of Indonesia, Jakarta). Shekelle also transferred the type and paratypes to Cibinong to be held in an enclosure at LIPI, the Indonesian Institute of Sciences. After their deaths, the 4 specimens became part of the collection of the Museum Zoologicum Bogoriense (MZB). At the time of their deaths, 3 individuals were fully grown adults and 1 (MZB 24304) was still subadult. We did not discover the cadaver of MZB 24307 before decay had set in, so we could not save the skin, but we could measure the cadaver.

Hypodigm

Apart from the type series, the hypodigm also includes USNM 219452 (female) and 219453 (male), juveniles, which Raven collected in 1917 at Gimpu. Miller and Hollister (1921) included them in their new species *Tarsius pumilus*; but, as Musser and Dagosto (1987) showed, of the 3 specimens that formed the hypodigm of the species only the type actually belongs there, and the 2 juveniles are here identified as specimens of the new species *Tarsius lariang*. S. Merker also captured, measured, and released 4 other individuals, and recorded the duet songs of *ca.* 30 individuals in the wild.

Diagnosis

The new species of the genus *Tarsius* is differentiated from other tarsier species from the mainland of Sulawesi by unique features of pelage, body proportions, skull, and vocalizations.

Pelage

Tarsius lariang is characterized by its very dark gray-buff pelage, lacking brown tones on the thighs; its very dark (often blackish) tail with a thick black terminal pencil; well marked thick, black paranasal stripes; barely expressed, off-white paralabial hair; a small bare spot at the base of the ear;

Fig. 1. *Tarsius lariang*, subadult male (photo: S. Merker). Adults lack the brown tones on the thighs as apparent in this young individual.

well marked black eye rims, especially below eyes; and dark tarsal fur (Fig. 1). The dark colors and lack of brown tones on the thighs distinguish it from all other Sulawesi tarsiers; the blackness and density of the tail pencil, the thickness and linearity of the paranasal black mark, and the form of the black eye rims (better developed along lower rims) distinguish it from its neighbors to the east (*Tarsius dianae*) and north (Tolitoli form); in the poor expression of the paralabial pale zone it resembles *T. dianae* and the Tolitoli form but is distinguished from the Manado form and from *T. tarsier* of the Makassar region; the reduced size of the bare spot at the base of the ear distinguishes it from all but the Tolitoli form. These features are based on an examination of 5 living individuals, as well as the 3 skins in the MZB and the 2 in the USNM. The expression of the paralabial hair is not absolutely diagnostic; but no other Sulawesi population is as dark-toned overall, and the blackness of the eye rims and tail pencil are completely diagnostic.

Body Proportions

The third (middle) finger of the hand is absolutely longer than in any other Sulawesi mainland tarsier (Fig. 9).

Skull and Dentition

The bulla is relatively narrow compared to its length (Fig. 5).

Vocalizations

Tarsius lariang is characterized by a unique duet song; distinguished from congenerics in that entire individual notes of the female song are upwardly frequency modulated (Fig. 10).

Description

The new species, judging by skull length (Fig. 6) and length of first lower molar (Fig. 7), is the largest of the mainland Sulawesi tarsiers; in the genus *Tarsius* it is second in size only to *T. sangirensis* from the Sangihe Islands. In general, the 3 small-island species need no special comparison with *Tarsius lariang*: *T. sangirensis* and *T. pelengensis* differ more from the Sulawesi mainland tarsiers than these latter do from each other, while the Salayar tarsier is at once distinguished by its very poorly developed tail pencil.

Etymology

The name *Tarsius lariang* means Lariang tarsier. The specific name lariang is here used as a noun in apposition, as in Bahasa Indonesia. The river Lariang is a major landmark of the study region. With a total length of 225 km, it is the longest river on Sulawesi (Whitten *et al.*, 2002). The new species probably occurs mainly in an area drained by the Lariang and its tributaries.

Distribution

We found *Tarsius lariang* in the vicinity of the villages Gimpu (01°38′S, 120°02′E, datum: WGS-84), Lempelero (01°39′S, 120°02′E), Tomua (01°36′S, 120°02′E), and Marena (01°34′S, 120°02′E) and recorded its characteristic duet calls on both sides of the Lariang river as well as its

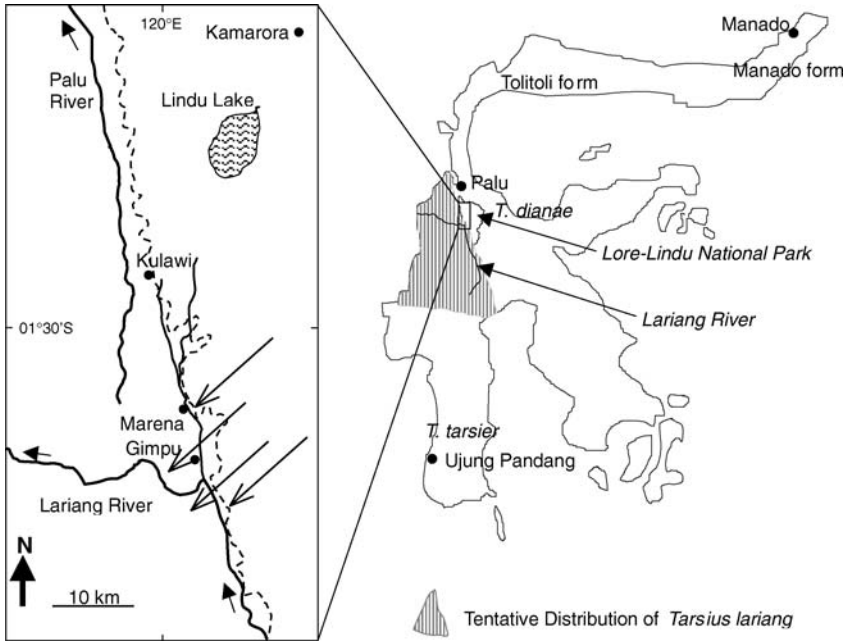


Fig. 2. Sulawesi and the study region. Large arrows in the regional map show locations where we recorded *Tarsius lariang*. The dashed line marks the western border of Lore-Lindu National Park.

northern tributary (Meweh River, with a confluence near Gimpu, Fig. 2). We assume the species to occur within the following boundaries: Palu Bay to the north, the Makassar Strait to the west, Lore-Lindu National Park to the east, and possibly the Karama River, the Toraja Highlands or the Tempe depression to the south. Confirmation of these distributional limits is pending. There is no report on sympatric tarsier species or on possible hybrid forms yet.

TARSIER BIODIVERSITY ON SULAWESI

Most likely, researchers have vastly underestimated the number of species of tarsier on Sulawesi and its offshore islands in the past (Groves, 1998; MacKinnon and MacKinnon, 1980; Nietsch, 1999; Nietsch and Kopp, 1998; Shekelle, 2003; Shekelle *et al.*, 1997). Thus far, aside from the only distantly related montane species *Tarsius pumilus* Miller and Hollister, 1921 (see also Musser and Dagosto, 1987), only the following 4 species have been

scientifically described:

T. tarsier Erxleben, 1777 (synonym *T. spectrum* Pallas, 1778, and many others): Makassar.
T. sangirensis Meyer, 1897: Sangihe Is.
T. pelengensis Sody, 1949: Peleng Is.
T. dianae Niemitz *et al.*, 1991: Central Sulawesi, facing Gulf of Tomini. The correct name for this species may be *Tarsius dentatus* Miller and Hollister, 1921 (Brandon-Jones *et al.*, 2004; Shekelle *et al.*, 1997), but for the moment we retain the better known name.

Ironically, of the 4 spacies, scientists described 1 (the Makassar species) over and over again in the late 18th and early 19th centuries, and another (the Central species) twice. The Manado form *sensu* MacKinnon and MacKinnon (1980) and Shekelle (2003), perhaps the best known of the Sulawesi species because of field observations and the availability of good museum samples, lacks a name, as do ≥ 2 others (1 from the Tolitoli district of the northern peninsula, and 1 from Salayar Is.) whose separateness seems clear. The specimens from Tolitoli may represent the Sejoli form of Shekelle (2003). Tolitoli is on the northern coast of the peninsula, opposite Sejoli on the south coast.

Our description of *Tarsius lariang* new species is also attended by some irony in that researchers described 2 specimens from Gimpu long ago, and recognized them as distinct from other Sulawesi lowland tarsiers (Miller and Hollister, 1921), but mistook them for examples of the strongly distinct pygmy species of the nearby highlands, *Tarsius pumilus* (Musser and Dagosto, 1987).

PREVIOUS FIELD RESEARCH

Subsequent to the 2 specimens Raven collected in 1917, no fieldwork on tarsiers took place in the Lariang region until MacKinnon and MacKinnon (1980), who recorded duet songs of tarsiers in the Palu valley. The description of these songs and the depicted sonagram suggest that their Palu form is *Tarsius lariang*. Niemitz (1984b) also recorded tarsier duet songs at Marena and published sonagrams of them. He believed they to belong to *Tarsius pumilus*, presumably on the basis of Miller and Hollister's (1921) erroneous identification of the species from nearby Gimpu, but the sonagrams, like those of MacKinnon and MacKinnon (1980), show the typical patterns of a duet song of *T. lariang*. A photograph by Niemitz (1984a) at Marena, which is just 8 km north of Gimpu (Fig. 2), shows what is most probably a subadult *Tarsius lariang*.

COMPARISON OF *TARSIUS LARIANG* WITH OTHER SULAWESI TAXA

Sample

Our sample of Sulawesi mainland tarsiers to compare with that of *Tarsius lariang* new species comprises:

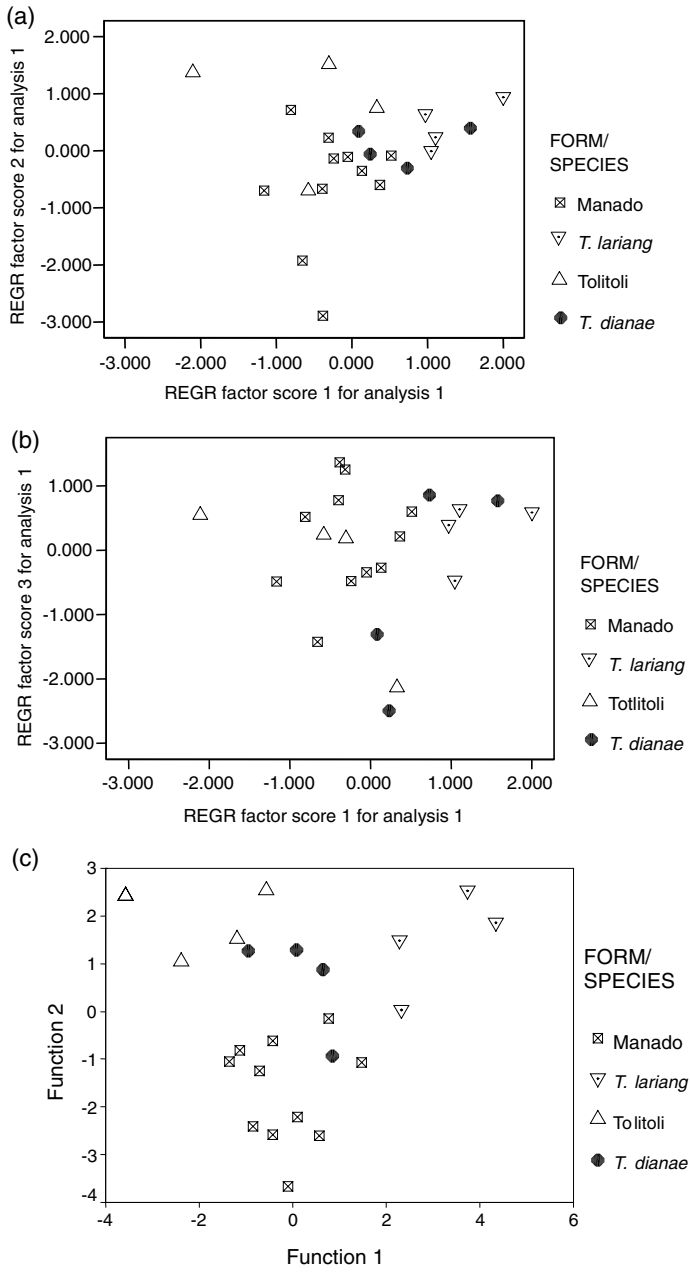
T. dianae: MZB 1 (the type), USNM 4.
T. tarsier: AMNH 4, skulls only, measurements courtesy Dr. M. Dagosto; these are from Lombasang (5°16′S, 119°50′E), about 50 km ESE of Makassar, and in the absence of material from Makassar itself, we treat these as most nearly representing *Tarsius tarsier*. We also treat 2 living specimens kept at Cibinong, near Bogor, Indonesia, courtesy of Dr. M. Shekelle, from the vicinity of Maros, 30 km NNE of Makassar, as *Tarsius tarsier* under the same constraints as the AMNH specimens.
Manado form: Minahasa and Gorontalo regions (Manado to Bumbulan), North Sulawesi: BM 1, MZB 6, USNM 2, ZMB 1, NRL 1, skins and skulls; AMNH 18, skulls only, measurements courtesy of Dr. M. Dagosto.
Tolitoli form: Tolitoli district: USNM 5, skins and skulls.

We studied additional specimens from other parts of Sulawesi, but do not include them here because we cannot combine any of them to form comparative samples. Not every specimen in the preceding list was available for all of the metrical comparisons.

Anatomical and Morphological Distinctiveness

Multivariate analyses (Figs. 3, 4, and 8) show that, on the limited sample of fully grown specimens, *Tarsius lariang* is diagnosably distinct from other Sulawesi taxa. Figures 3 and 4 and Tables I and II show both principal component and discriminant function analyses; the *Tarsius lariang* specimens were largely but not absolutely distinct via principal component analysis, but proved totally distinct when we grouped the material into samples under discriminant function analysis.

In the first discriminant function analysis (Fig. 3), we used 10 variables: skull length, biorbital breadth, breadth of left orbit, basion-bregma height, basion-vertex height, length of anterior bulla (anterior to carotid foramen), length of posterior bulla (posterior to carotid foramen), total bulla length, bulla breadth, and palate breadth at widest point (Table III). Skulls of the following adult specimens were available for the comparison: *Tarsius lariang*, 4 (MZB 24302, -3, -4, -7); Tolitoli, 4 (USNM


(a)
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REGR factor score 1 for analysis 1
FORM/
SPECIES
Manado
T. lariang
Tolitoli
T. dianae
(b)
REGR factor score 3 for analysis 1
1.000
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SPECIES
Manado
T. lariang
Tolitoli
T. dianae

Fig. 3.

200280, -2, -3, -4); *T. dianae*, 4 (MZB 22755, USNM 218070, -1, -2); Manado, 11 (BM 97.1.2.1; NRL 28642; USNM 200282, 217559; MZB 3264, -9; 5017; 6593, -4, -5, -6). The sample of *Tarsius dianae* includes the type series of *T. fuscus dentatus* Miller and Hollister, 1921; the relative status of this name and *T. dianae* Niemitz *et al.*, 1991 will be discussed in a future article. In our first analysis (Fig. 3), the distinctiveness of *Tarsius lariang* relies mainly on its relatively long, narrow bullae.

We reduced the number of variables in Fig. 4 to allow more specimens to be sampled, to permit Makassan *Tarsius tarsier* to be included in the analysis, and to equalize sample sizes and numbers of variables (using more variables than specimens in the average sample skews the analysis in favor of obtaining a positive result, known as a type I error). The separation of *Tarsius lariang* depends again partly on bulla shape, but also on its long but narrow skull.

In both discriminant function analyses, we did not refer to the classification table or use a cross-validated (leave-one-out) analysis, because an individual specimen may be closer to the mean of another sample even if the 2 samples are discrete.

Figure 5 extracts the variables that are most heavily weighted in both analyses: *Tarsius lariang* has a long bulla compared to width—the sample overlaps only slightly with other tarsiers.

Tarsius lariang is the largest species of tarsier of mainland Sulawesi. In total skull length (ANOVA, $F_{4,36} = 7.632$, $p < 0.001$, Fig. 6), it averages significantly larger than those species from the northern peninsula (Tolitoli and Manado form, ANOVA, Tukey-HSD *post hoc* test, $p < 0.001$) or the southern (*T. tarsier*, $p < 0.01$).

In dental size, represented by M_1 mesiodistal length (ANOVA, $F_{3,21} = 4.284$, $p < 0.05$, Fig. 7), it is again the largest Sulawesi tarsier, but note that measurements for *Tarsius tarsier* are not available.

In Fig. 8, based on external measurements, *Tarsius lariang* is differentiated in the same direction as *T. tarsier*; the 2 both have relatively long fingers, short tails, and large terminal finger pads, but *T. lariang* differs from

←

Fig. 3. Principal component and discriminant function analyses based on 10 cranial measurements. **(a)** Principal component analysis: components 1 and 2. **(b)** Principal components analysis: components 1 and 3. **(c)** Discriminant function analysis: DF1 and 2. The principal components are as given in Table I. PC1 accounts for 38.17% of the total variance, PC2 for 16.91%, PC3 for 15.08%. The weightings of the original variables on the first discriminant function, which accounts for 79% of the total variation, are as follows. Skull length = −0.074, Biorbital breadth 0.037, Breadth of single orbit = 0.253, Basion to bregma = 0.431, Basion to vertex = 0.124, Anterior bulla length = −0.587, Posterior bulla length = 0.229, Total bulla length = 1.107, Bulla breadth = −0.856, Palate breadth = 0.399.

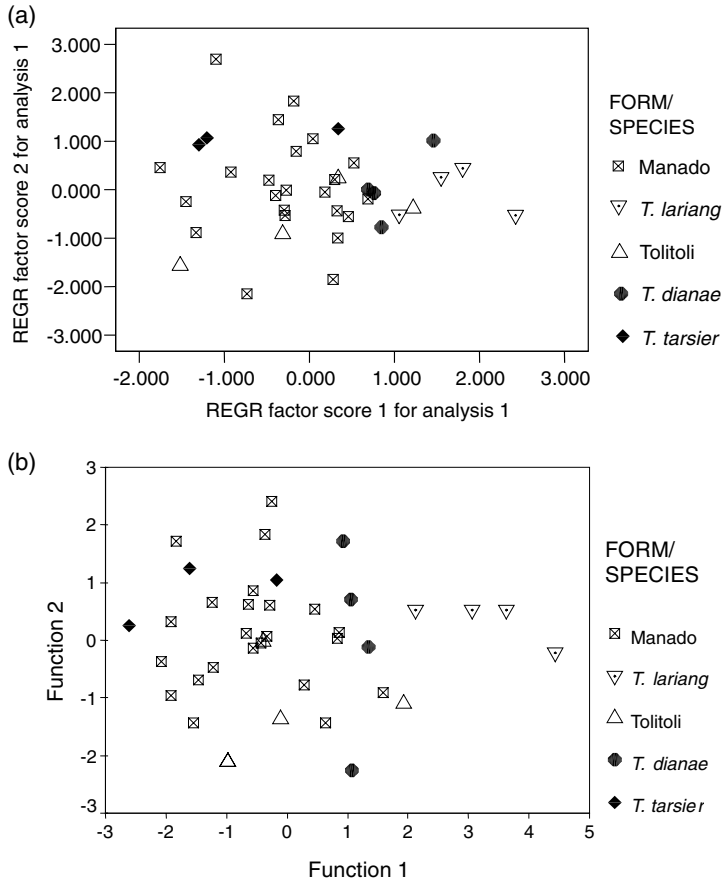

Fig. 4. **(**a**)** Principal component and **(**b**)** discriminant function analyses of Sulawesi tarsiers based on 5 cranial measurements. The first 2 principal components, which account for 50.87% and 24.76% of the total variance respectively, are given in Table II. The weightings of the original variables on the first discriminant function, which accounts for 48% of the total variation, are as follows. Skull length = 0.695, Biorbital breadth = −0.436, Breadth of single orbit = 0.699, Total bulla length = 0.425, Bulla breadth = −0.630.

other samples less markedly than *T. tarsier* does. Figure 9 extracts the variable most heavily weighted in the Fig. 8 analysis, the length of the third finger. *Tarsius lariang* is well outside the range of all other Sulawesi tarsiers (ANOVA, $F_{4,20} = 20.56$, $p < 0.001$, see Fig. 9).

Table I. Principal components for discriminant function analysis of Sulawesi tarsiers based on 10 cranial measurements

	Component		
	1	2	3
sk	0.918	0.206	– 0.036
bi	0.645	0.333	– 0.275
orb	0.627	0.345	– 0.475
bb	0.372	0.502	0.653
bv	0.504	0.599	0.385
ab	– 0.224	– 0.189	0.732
pob	0.703	– 0.490	0.165
bl	0.682	– 0.453	0.237
bu	0.537	– 0.378	– 0.108
pal	0.688	– 0.429	0.022

Note. Extraction method: principal component analysis;
3 components extracted.

Special Comparison Between *Tarsius lariang* and *T. dianae*

Ear measurement data of *Tarsius lariang* obtained on the day of capture as well as a comparison with a large sample of *T. dianae* are in Table IV. *Tarsius dianae* and *T. lariang* are parapatric species with a contact zone in or around Lore-Lindu National Park to the south. Table IV contains ear measurements of 8 live specimens of *Tarsius lariang* (including the type series) as well as mean values for *T. lariang* and *T. dianae*. Merker (2003) collected data for the latter species using the same methodology as in this study. In the analyses of data from live specimens under field conditions, we considered individuals with a body mass ≥ 100 g to be adults. At capture, one type (MZB 24307, no. 6 in Table IV) was still subadult. At its death 14 mo later, it was a fully grown adult, and as such became part of the type series. We considered another individual (MZB 24304, no. 4 in Table IV) as adult according to its body mass, yet after examining its skull and teeth, we

Table II. Principal components for discriminant function analysis of Sulawesi tarsiers based on 5 cranial measurements

	Component	
	1	2
sk	0.894	0.055
bi	0.816	– 0.399
orb	0.816	– 0.200
bl	0.629	0.522
bu	0.127	0.874

Table III. Selected Craniodental Measurements of Population Samples of Sulawesi Tarsius

Form/Species	sk	bl	bu	pal	lo	areui	areut
T. dianae							
Mean	37.550	11.300	6.225	14.740	13.600	9.7760	10.1480
N	4	4	4	5	5	5	5
Std. deviation	0.5082	0.2944	0.2630	0.4159	0.4472	0.54491	0.70857
Minimum	36.8	10.9	6.0	14.1	13.1	9.00	8.97
Maximum	38.2	11.6	6.6	15.2	14.3	10.36	10.80
T. lariang							
Mean	38.350	11.750	5.925	14.925	13.450	9.5025	9.1250
N	4	4	4	4	4	4	4
Std. deviation	0.6952	0.3317	0.0957	0.4573	0.2380	0.63174	0.84244
Minimum	37.4	11.4	5.8	14.3	13.3	8.84	8.14
Maximum	39.0	12.2	6.0	15.4	13.8	10.36	10.00
T. tarsier							
Mean	36.450	110.60	6.550	14.100	12.900	7.1420	7.2620
N	4	5	4	3	5	5	5
Std. deviation	0.7681	0.3209	0.2887	0.4583	0.3536	0.41306	0.25144
Minimum	35.6	10.6	6.2	13.7	12.4	6.60	7.00
Maximum	37.1	11.4	6.9	14.6	13.3	7.48	7.56
Manado							
Mean	36.512	11.118	6.121	14.458	13.385	8.2644	8.5719
N	24	28	28	26	27	27	27
Std. deviation	0.6655	0.2803	0.3966	0.3613	0.4512	1.04020	1.14986
Minimum	35.2	10.7	5.2	13.7	12.0	6.72	7.00
Maximum	37.6	12.0	6.9	15.2	14.2	10.44	11.31
Tolitoli							
Mean	36.260	10.900	5.820	13.720	12.800	7.9580	8.6400
N	5	5	5	5	5	5	5
Std. deviation	1.0139	0.3937	0.4025	0.3899	0.2828	0.71226	0.51633
Minimum	35.4	10.6	5.4	13.3	12.3	7.36	8.28
Maximum	37.8	11.5	6.2	14.1	13.0	9.10	9.50

Note. areaui, Area (length × breadth) of maxillary first molar; areut, area (length × breadth) of maxillary second molar; bl, bulla length; bu, bulla width; lo, length of mandibular toothrow, canine to third molar (7 teeth); pal, pale width across 3rd molars; Sk, total skull length.

revised the status to subadult, and as such, considered it in the type series. Individuals 3 (MZB 24303), 4 (MZB 24304), 5 (MZB 24302), and 6 (MZB 24307) were transferred to Cibinong/Bogor and became the type series. Ear dimensions differ significantly between *Tarsius lariang* and *T. dianae,* with clearly wider ears in the new species (see Table IV). Differences between the 2 taxa are absolutely diagnostic (see previous sections).

Special Comparison Between *Tarsius lariang* and *T. tarsier*

If, as seems likely, specimens from Lombasang and Maros represent *Tarsius tarsier* or a closely similar form, *T. lariang* differs diagnosably from it, by the pelage features in the diagnosis; by the long

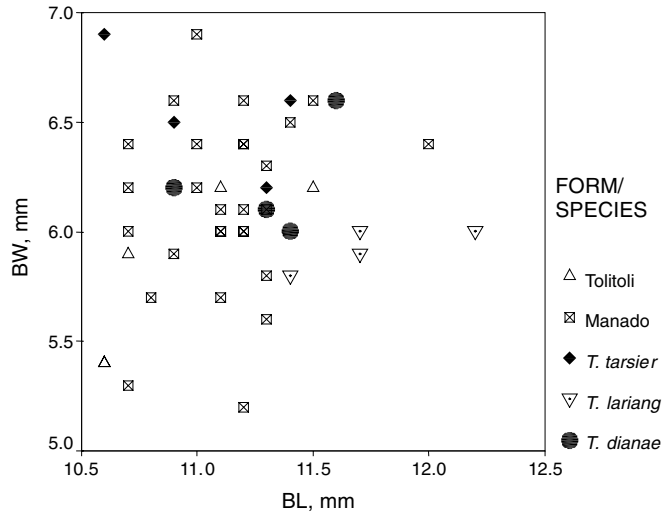

Fig. 5. Bulla width (ordinate) compared to bulla length (abscissa) in Sulawesi tarsiers.

bullae compared to their width (Fig. 5); by the absolutely larger skull (only 4 skulls are available of each species, but $p < 0.01$, Fig. 6); and by the absolutely longer 3rd finger (Fig. 9), though only 2 specimens of *T. tarsier* and 5 of *T. lariang* are available, and even though *T. tarsier* has the second longest fingers of the Sulawesi mainland group.

Dr. Myron Shekelle (in litt., December 4, 2004) informed us that discriminant analysis of the hair patterns of the tail tuft also differentiates the 2 species.

Vocalizations

Researchers have long suspected that duet calls of Sulawesi tarsiers indicate taxonomic diversity (MacKinnon and MacKinnon, 1980; Niemitz *et al.*, 1991; Nietsch, 1999; Nietsch and Kopp, 1998; Shekelle, 2003; Shekelle *et al.*, 1997), following the trend for numerous other nocturnal primates (Bearder *et al.*, 1995; Zimmermann *et al.*, 1988).

Figure 10a shows the typical pattern of a female contribution to a duet song of *Tarsius lariang*. The frequency of the ascending notes ranges from 6 to 7 kHz at the beginning of the song, to 7–9 kHz in the middle, and reaches a peak of 9–14 kHz at the end of the duet (Fig. 10b). The female initiates her song with a long-drawn note *ca.* 1.5 s in length. Subsequent notes are

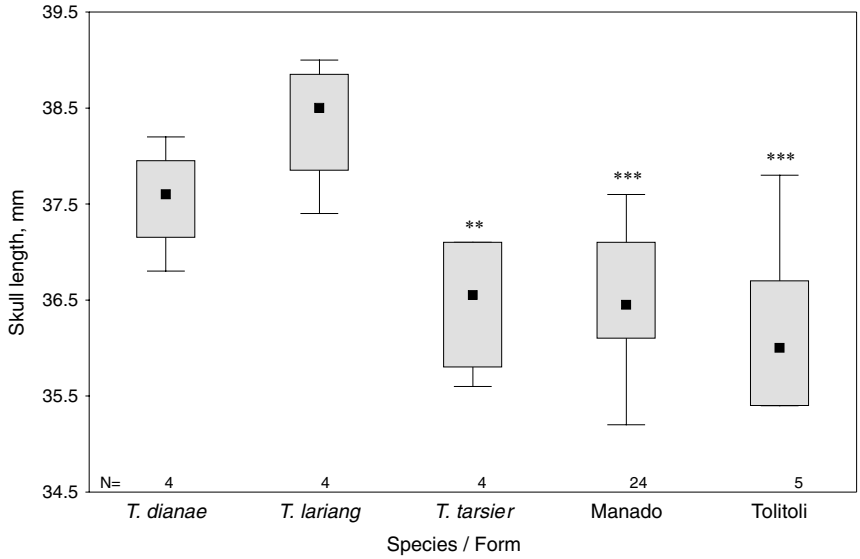

Fig. 6. Skull length (medians, quartiles, and ranges) in Sulawesi tarsiers. Asterisks mark significant difference from *T. lariang* (ANOVA, Tukey-HSD *post hoc* test, $^{**}p < 0.01$, $^{***}p < 0.001$).

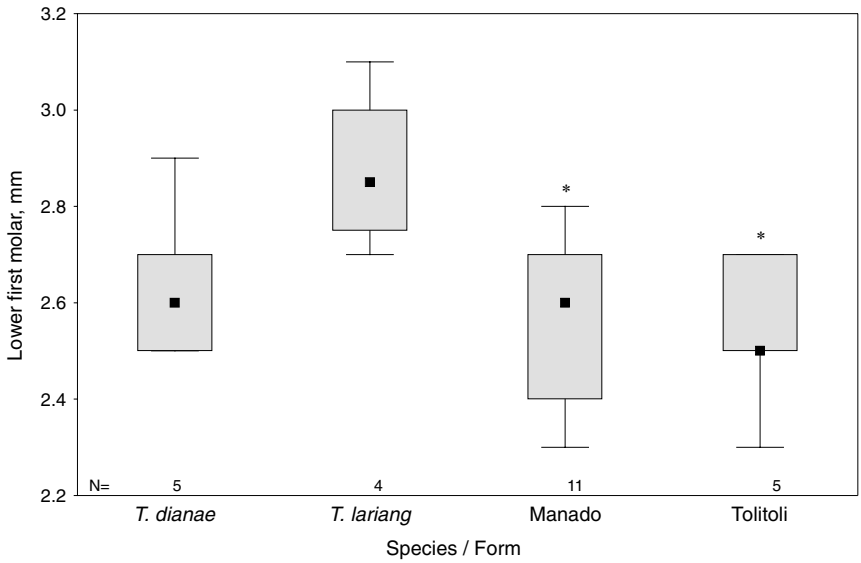

Fig. 7. Mesiodistal length of lower first molar in Sulawesi tarsiers. Asterisks mark significant difference from *T. lariang* (ANOVA, Tukey-HSD *post hoc* test, $^{*}p < 0.05$).

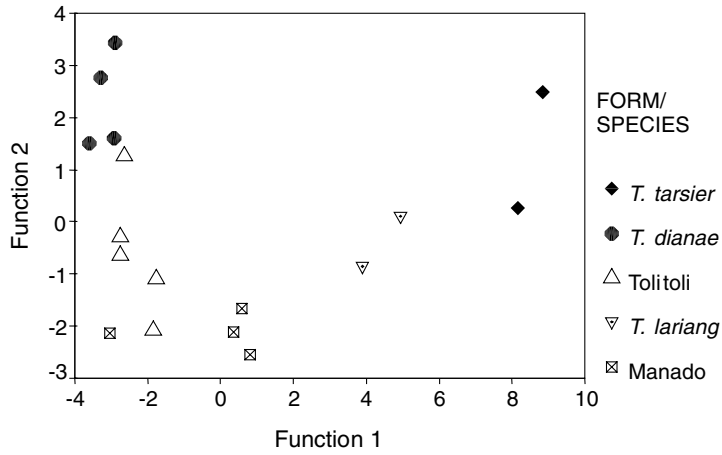

Fig. 8. Discriminant analysis of Sulawesi tarsiers based on 6 external measurements. The weightings of the original variables on the first discriminant function, which accounts for 76% of the total variation, are as follows: Head + body length = −0.193, Tail length = −0.880, Hindfoot length = −0.509, 3rd finger length = 0.915, 3rd finger pad length = 0.857, 3rd finger pad breadth = 0.881, 3rd finger nail length = 0.538, 3rd finger nail breadth = −0.432.

ca. 1 s long and at the end of her part, the duration of the notes decreases to 0.5 s. The whole female song is usually 30–45 s long.

Because of the poor quality of recordings, only a fragment of the male song is in Fig. 10. The male notes range from 4 to 7 kHz at the beginning of the male song and during most of the female's song as well. When the female notes reach peak frequency during the last third of the female part—the male calls also rise in pitch and range from 5 to a maximum of 10 kHz. At that time, the male emits up to 5 squeaks/s—or 5–10 notes per female note (Fig. 10b). When the female is not calling, the intervals between male notes increase slightly. The duration of a male note is < 0.1 s. It consists of only a downwardly modulated part (as in *Tarsius dianae*). The length of the entire male song is very variable and usually reaches >1 min. Males often call without eliciting a female response.

MacKinnon and MacKinnon (1980) and Niemitz (1984b) described the duet songs of tarsiers they recorded in the Palu valley (Fig. 10c) and at Marena (Fig. 10d), respectively. The general structure of the duets is that of *Tarsius lariang*, but in the latter the maximum pitch of the female notes was higher (see earlier) than the 12 kHz MacKinnon and MacKinnon reported (1980). The male notes the authors illustrated (Fig. 10c) consist of an ascending as well as a descending part. Despite analyzing numerous songs,

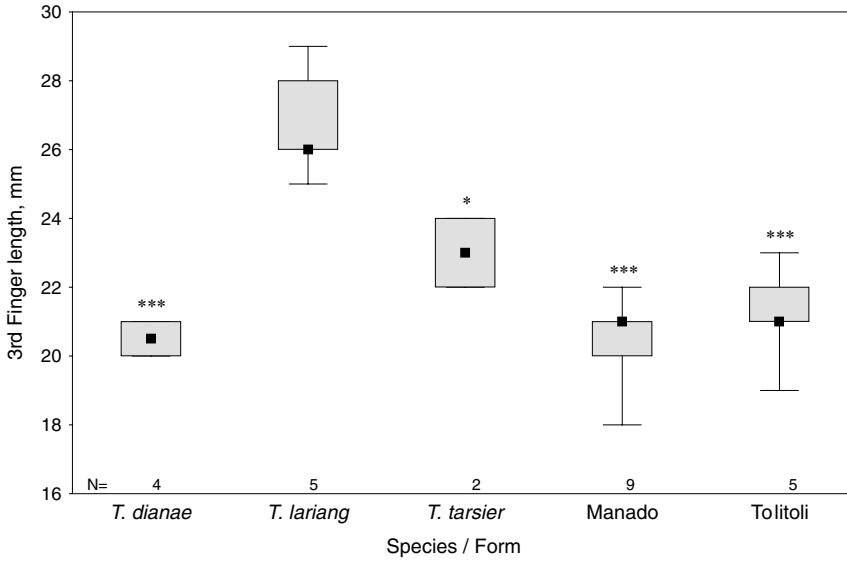

Fig. 9. Length of 3rd finger in Sulawesi tarsiers. Asterisks mark significant difference from *Tarsius lariang* (ANOVA, Tukey-HSD *post hoc* test, $^{*}p < 0.05$, $^{***}p < 0.001$).

we were able to document only male notes that were entirely downwardly modulated. As all authors mentioned in the preceding recorded duet songs in the same region as in this study, the reason for this inconsistency remains in doubt for now and requires further investigation.

Biogeographic Evidence

Shekelle (2003) and Shekelle and Leksono (2004) outlined 2 categories of hypotheses regarding the mammalian speciation and biogeography of Sulawesi:

1. Speciation occurred as a result of isolation on islands of the proto-Sulawesi archipelago before their coalescence into the modern island of Sulawesi during a period of tectonic activity, i.e., *ca.* 20 million yr ago to *ca.* 2 million yr bp, corresponding roughly to the Miocene and Pliocene epochs (Hall, 2001).
2. Putative geographic barriers, explained principally by raising and lowering of ocean levels during the Pleistocene, after the coalescence of microplates, reshaped the diversity and distribution of

Table IV. Ear measurements of 8 live specimens of *Tarsius lariang* (taken at the time of capture) and means for adult ($m \geq 100$ g) *T. lariang* from Gimpu and *T. dianae* from Kamarora

No./species Sex (F = female, M = male)	1 F	2 F	3 F	4 F	5 M	6 M	7 M	8 M	*T. lariang* mean	*n*	*T. dianae* mean	*n*	*t*-test *p* value
Body mass (in g)	72	117[a]	109	100	110	85	112	67	110	5	113	47	n.a
Measurements (in mm)													
Ear breadth (max. width of pinna)	21.3	22.1	23.4	22.9	21.4	23.6	22.0	21.4	22.4	5	19.8	47	**0.004**
Ear height (max. length from tip to base)	35.4	37.4	38.7	35.6	36.2	37.5	36.4	34.8	36.9	5	37.1	20	0.787
Ear length (tip to depth of incis. intertr.)	33.5	33.7	35.4	32.8	33.3	32.7	33.5	31.7	33.7	5	33.0	33	0.202
Ear length superior (from tip to skull)	33.6	31.4	35.6	34.2	31.6	33.2	30.5	29.7	32.7	5	29.8	47	**0.001**
Length of incisura intertragica	3.7	4.2	3.1	2.8	3.8	3.4	3.0	3.5	3.4	5	4.1	20	**0.015**
Width of incisura intertragica	1.7	1.7	1.4	1.6	2.2	1.7	1.7	1.7	1.7	5	—	—	n.a
Length of naked area	7.2	6.3	7.3	7.3	7.6	7.1	6.0	7.2	6.9	5	7.6	20	**0.024**

Note. A bold *p* value of Student's *t*-test indicates significant differences (at the .05 level) between the 2 parapatric species.
Source: Merker, unpublished data.
[a]Female was gravid at time of capture.

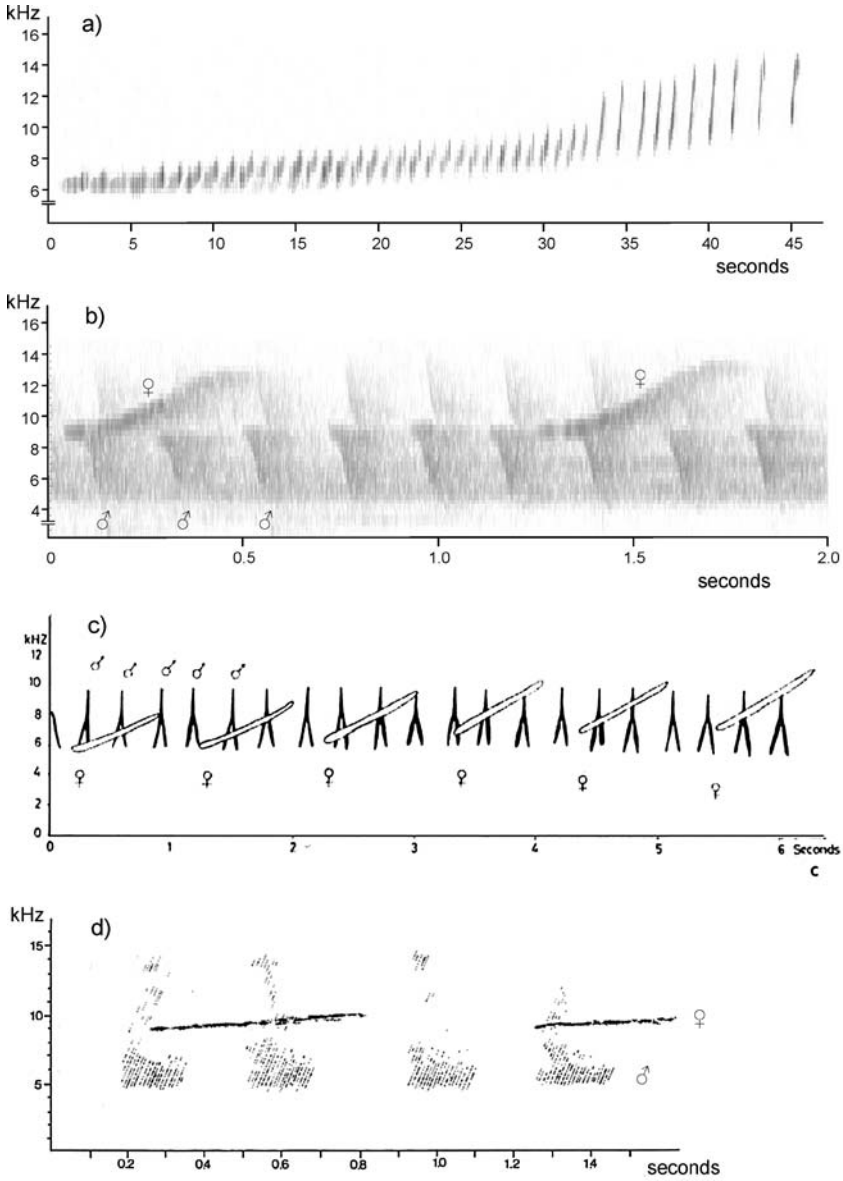

Fig. 10. Spectrograms of vocal duets of *Tarsius lariang*. **(**a**)** Complete female part of a duet song. **(**b) Male and female notes at the end of a duet. **(c)** Fragment of a duet song (redrawn from MacKinnon and MacKinnon, 1980). **(**d**)** Fragment of a duet song (redrawn from Niemitz 1984b).

tarsiers on Sulawesi, similar to what is seen in macaques (Evans *et al.*, 2003; MacKinnon and MacKinnon, 1980; Niemitz *et al.*, 1991).

In contrast to Sulawesi macaques, whose ancestors rafted to the island only 1–3.5 million yr BP (Bynum, 1999; Groves, 1980; Roos *et al.*, 2003), the tarsier radiation on Sulawesi almost certainly dates to the Miocene and was estimated to start *ca.* 10 million yr bp (Shekelle 2003). This date is roughly equivalent to the 11.5 million yr BP date arrived at for Sulawesi's squirrels by Mercer and Roth (2003). Hence tarsiers are more likely to have been influenced by microplate tectonics than younger taxa have been.

Tarsius lariang inhabits parts of a microplate making up the southwestern arm of Sulawesi. According to preliminary observations, the range boundary between the species and *Tarsius dianae*, its neighbor to the east (also known under its possible senior synonym *T. dentatus*), corresponds amazingly well with the Palu-Koro fault dividing 2 microplates that coalesced <5 million yr bp (Hall, 2001). A study by S. Merker focussing on the contact zone between the 2 species is in progress. Regarding the extent of the new species' range to the south, it might be hypothesized that its limit coincides with the boundary between *Macaca tonkeana* and *M. maura* at the Tempe depression (Evans *et al.*, 2003; Fooden, 1969), which implies that *Tarsius lariang* and *T. tarsier* are sister taxa that diverged with the putative Pleistocene barrier at the Tempe depression. The outlined distribution of *Tarsius lariang* would fit the hybrid biogeographic hypothesis (Shekelle and Leksono, 2004) synthesizing biological and geological data, and thus explaining the distribution of tarsier acoustic forms. As the new species is definitely known only from the Gimpu region, the issue requires further investigation.

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