

DISTRIBUTION AND BIOGEOGRAPHY OF TARSIERS

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ABSTRACT

Three clearly distinct taxa of tarsiers each inhabit a distinct biogeographic region: Western tarsiers, from island areas of Sundaland; Philippine tarsiers from Greater Mindanao; and Eastern tarsiers from Sulawesi and nearby islands. Multiple species and / or subspecies have been described from each region, and continued investigations into the alpha taxonomy of each group are warranted. Within each region tarsiers currently have discontinuous distributions, at least partly the result of anthropogenic habitat alterations. Their presence in a variety of primary and secondary habitats indicates that the historical distribution of tarsiers may have once been much more continuous, perhaps limited more by elevation and ocean barriers than by variation among lowland habitats. The distributions of Philippine and Eastern tarsiers conform well to Ice Age landmasses. The distribution of Western tarsiers does not, and is hypothesized to indicate a Holocene range expansion. A model of historical biogeography is here presented, wherein events in the Miocene led to the isolation of the three species groups. Tarsiers' last appearance in the fossil record of mainland Asia also occurs during the Miocene.

Keywords: *Tarsius*, Taxonomy

INTRODUCTION

All known tarsier taxa are distributed either allopatrically or parapatrically; there is not a single known case of sympatric tarsiers. Understanding their geographic distributions, therefore, is crucial for understanding tarsier taxonomy. Extant tarsiers have a curious distribution on a scattering of southeast Asian islands. They are found on both sides of Wallace's Line, which approximates the separation between the Asian and Australian biotic communities, and although fossil tarsiers are found on mainland Asia, none exist there today (Hill 1955, Niemitz 1984, Musser & Dagosto 1987). Hill (1953, 1955) classified tarsiers into three species, all in the genus *Tarsius* and each endemic to a distinct biogeographic region: *Tarsius syrichta* Linnaeus, 1758, from islands of the southern Philippines; *Tarsius spectrum* Pallas, 1778 from Sulawesi and surrounding islands; and *Tarsius bancanus* Horsfield, 1824, from various islands of the Sunda Shelf including Borneo, southern Sumatra, Bangka, Belitung, the Karimata Islands, the South Natuna Islands, and several smaller islands. Brandon-Jones *et al.* (2004) provided an argument, which was greatly elaborated on by Groves *et al.* (this volume), that *T. tarsier* Erxleben, 1777 is a senior subjective synonym of *T. spectrum* (Fig. 1).

There are several conspicuous anatomical features that are diagnostic of each species group. Relative eye size is largest in Western tarsiers, smallest in Eastern tarsiers, and intermediate in Philippine Tarsiers, while relative ear length is largest in Eastern tarsiers, smallest in Western tarsiers, and intermediate in Philippine tarsiers (Niemitz 1984). The mid-tarsal segment appears naked or nearly naked in Philippine tarsiers, but is well-furred in both Eastern and Western tarsiers. The tails of all tarsiers are long and superficially rat-like, but the amount of fur varies among the species groups. Eastern tarsiers have the most fur on the tail, its appearance being almost like a bottlebrush. Philippine tarsiers have the least fur on the tail, with very short, sparse hairs that are almost invisible unless viewed at close range (although the tail tufts in a large collection of *T. syrichta carbonarius* from Mindanao, in Chicago's Field Museum, approach the condition seen in *T. bancanus*, unpublished data). Western tarsiers are intermediate, having a noticeable tuft of fur on the tail, but not nearly so much as do Eastern tarsiers (Fig. 2).

Hill (1955) accepted subspecies within each of the three species he recognized, but remarked that some of these were of dubious distinctiveness. Niemitz (1984) also used the three species taxonomy, but he synonymized the bulk of Hill's subspecies,

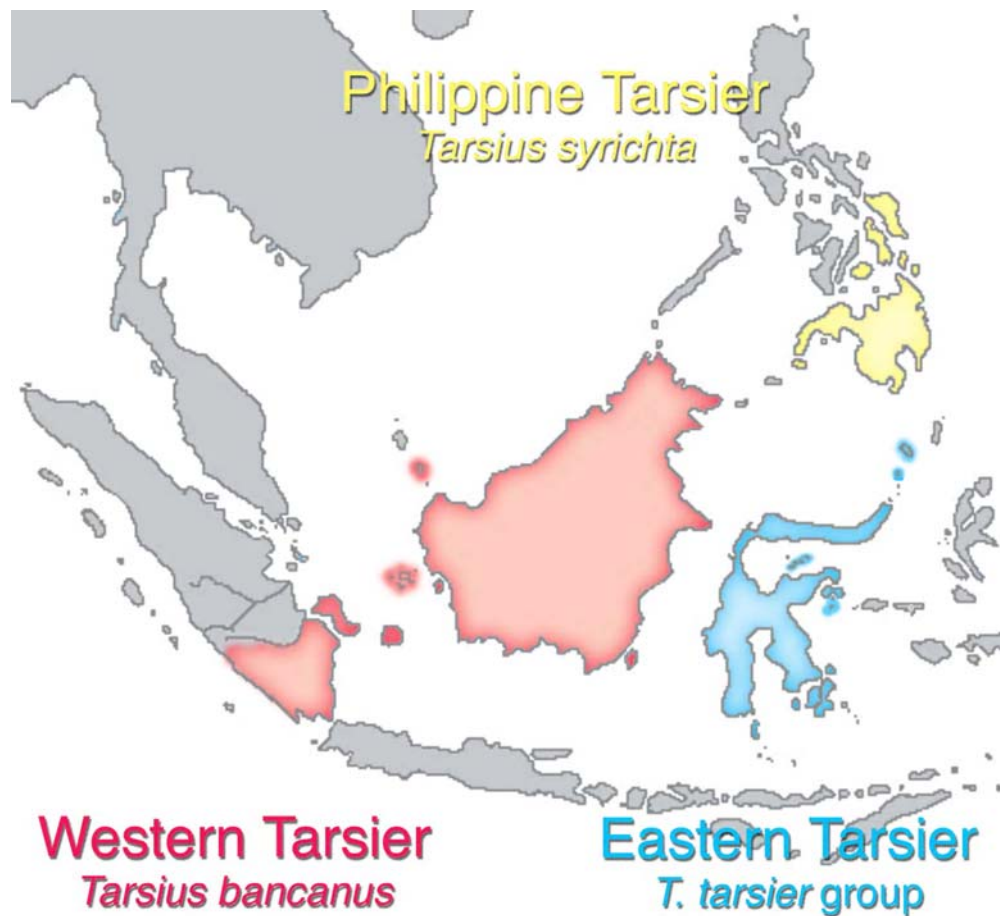


Figure 1: Distribution of Extant Tarsiers. The northwestern boundary of tarsiers in Sumatra is figured here as the Musi River, but this is speculative. The actual distribution is less continuous than figured here, tarsiers being rare or nonexistent in high elevations and tarsiers having gone locally extinct in many areas of intense human usage.

accepting only two subspecies of *T. bancanus* and two subspecies of *T. tarsier* (= *T. spectrum*). Several authors have noted that, based upon acoustic and biogeographic evidence, numerous other unrecognized taxa of tarsiers are likely to exist within *T. tarsier* (MacKinnon & MacKinnon 1980; Niemitz *et al.* 1991; Nietsch & Niemitz 1993; Nietsch & Kopp 1998; Nietsch 1999; Shekelle 2003). The trend after Niemitz has been to recognize each of Hill's subspecies of *T. tarsier* as a distinct species, including: *T. pumilus* Miller & Hollister, 1921, (Niemitz 1985; Musser & Dagosto 1987; Groves 1998, 2001), *T. sangirensis* (Feiler 1990; Shekelle *et al.* 1997; Groves 1998, 2001), and *T. pelengensis* (Groves 2001). Additionally,

Niemitz *et al.* (1991) described a new taxon, *T. diana*, from central Sulawesi. However, Shekelle *et al.* (1997) surveyed tarsiers at the type localities of both *T. diana* and *T. dentatus*, Miller & Hollister, 1921 and found the same acoustic form at both locations, indicating that *T. diana* is quite likely a junior subjective synonym of *T. dentatus*. Other forms, not included in Hill's list of *T. tarsier* subspecies have since been described, including *T. larian* (Merker and Groves 2006) from central Sulawesi and *T. sp.* (Shekelle *et al.* in press), an insular population from Siau Island, North Sulawesi (Table 1).

Tarsiers from Sulawesi are now recognized as a species complex with at least seven species and



Figure 2: Anatomical variation among tarsier species groups. Western tarsiers have the largest eyes, shortest ears, and longest legs and hands. Eastern tarsiers have the smallest eyes, longest ears, and shortest legs and hands. Philippine tarsiers are intermediate in all of these. Eastern tarsiers have the furriest tail, Philippine the least furry, and Western tarsiers are intermediate. The mid-tarsal segment of the hind foot is nearly naked in Philippine tarsiers, but is well-furred in both Western and Eastern tarsiers (adapted from Shekelle 2003). Photos Myron Shekelle (c) 2008, except where noted.

Table 1: Review of Tarsier Taxonomy.

Hill 1955	Niemitz 1984	Musser & Dagoso 1987	Groves 2001	Brandon-Jones 2004	This Paper
<i>T. syrichta syrichta</i>	<i>T. syrichta</i>	<i>T. syrichta</i>	<i>T. syrichta</i>	<i>T. syrichta</i>	<i>T. syrichta</i>
<i>T. s. carbonarius</i>	*	**		<i>T. s. carbonarius</i>	<i>T. s. carbonarius</i>
<i>T. s. fraterculus</i>	*	**		<i>T. s. fraterculus</i>	<i>T. s. fraterculus</i>
<i>T. bancanus bancanus</i>	<i>T. b. bancanus</i>	<i>T. bancanus</i>	<i>T. b. bancanus</i>	<i>T. b. bancanus</i>	<i>T. b. bancanus</i>
<i>T. b. borneanus</i>	<i>T. b. borneanus</i>	**	<i>T. b. borneanus</i>	<i>T. b. borneanus</i>	<i>T. b. borneanus</i>
<i>T. b. saltator</i>	*	**	<i>T. b. saltator</i>	<i>T. b. saltator</i>	<i>T. b. saltator</i>
<i>T. b. natunensis</i>	*	**	<i>T. b. natunensis</i>	<i>T. b. natunensis</i>	<i>T. b. natunensis</i>
<i>T. spectrum</i>	<i>T. spectrum</i>	<i>T. spectrum</i>	<i>T. spectrum</i>	<i>T. spectrum</i>	<i>T. spectrum</i>
<i>T. s. sangirnesis</i>	*	**	<i>T. sangirnesis</i>	<i>T. sangirnesis</i>	<i>T. sangirnesis</i>
<i>T. s. pumilus</i>	<i>T. s. pumilus</i>	<i>T. pumilus</i>	<i>T. pumilus</i>	<i>T. pumilus</i>	<i>T. pumilus</i>
<i>T. s. dentatus</i>	*	**	***	<i>T. dentatus</i>	<i>T. dentatus</i>
<i>T. s. pelengensis</i>	*	**	<i>T. pelengensis</i>	<i>T. pelengensis</i>	<i>T. pelengensis</i>
			<i>T. diana</i> ***		<i>T. lariang</i>
					<i>T. sp.</i> (Siau)

* Niemitz found museum specimen variation to be insignificant among several taxa accepted by Hill

** Musser and Dagosto found museum specimen variation to be an insufficient basis for determining the validity of several taxa accepted by Hill

*** cited Shekelle et al. 1997 for noting a likely conflict between *T. diana* and *T. dentatus*.

**** according to Brandon-Jones et al., a taxon “whose recognition is doubtful and requires further investigation”

probably more, and it now seems plausible that each of Hill’s three tarsier species may be a cluster of closely related taxa. To sidestep the current debates on the numbers of taxa and their formal names, I refer to Hill’s three species—*T. syrichta*, *T. tarsier* (i.e. *T. spectrum*), and *T. bancanus*—by the common names, Philippine, Eastern, and Western tarsiers, respectively, with the assumption that each of these is monophyletic and that each might be a constellation of related taxa, that is, species groups. The assumption of monophyly within species groups has not been exhaustively examined, but is consistent with the results of Musser & Dagosto (1987) and Groves (1998).

Musser & Dagosto (1987) indicated that their morphologic analysis of museum specimens supported two distinct clades of tarsiers, a *T. bancanus* / *T. syrichta* clade, and a *T. tarsier* / *T. pumilus* clade. Groves (1998) went further and

suggested generic separation of the Eastern tarsiers from a Philippine-Western tarsier clade based upon his own analyses of morphological variation. Genetic data (Shekelle *et al.* 2001; Meireles *et al.* 2003) indicate that generic separation of Philippine and Western tarsiers might also be warranted if one were to accept a time-based classification scheme, such as proposed by Goodman *et al.* (1998) and Groves (2001). The value of designating new tarsier genera is that each species group could be addressed by a formal name (as opposed to the common names, Eastern, Western, and Philippine tarsiers, for example); and, if taxonomy is to be an information retrieval system, it might symbolically emphasize the underappreciated variation among tarsier species groups in taxonomy, behavior, and ecology (see Shekelle 2003). Nevertheless, for the time being I prefer to retain a single genus for extant tarsiers for the reasons that:

(1) *Tarsius* as used by Hill is a clearly defined monophyletic clade with only three species; (2) taxonomic variation in addition to that accepted by Hill, and the question of whether or not Hill's subspecies should be elevated to full species level is the focus of much ongoing research and debate; and (3) the monophyly of each of Hill's three species groups, although seemingly sensible, has not been rigorously tested. Thus, the dangers of classifying tarsiers in one or two new genera at this point are that ongoing research might show either or both of them to be either monotypic or not monophyletic.

Previous Estimates

Before estimating the historical distribution of tarsiers, I review previous work to examine how current knowledge helps resolve discrepancies, errors, and omissions.

Regarding erroneous reports there are claims of tarsiers having originated from outside the range listed by Hill (1955), Niemitz (1984), and Musser & Dagosto (1987), including the islands of Luzon, Ambon, Savu, Java, and even Madagascar. Cabrera (1923) questioned the accuracy of Camel's (1705) report of tarsiers from Luzon, and there are no longer serious discussions of Luzon being within the historical range of tarsiers. Fischer (1804) reported that tarsiers in his study were allegedly from Madagascar, but he went on to infer that Madagascar had been confused with Makassar, a port city on Sulawesi. Hill (1955) discounted Pallas's (1778) report of tarsiers from Ambon.

Reports of tarsiers from Java and nearby Savu are still sometimes treated seriously by researchers (e.g., Niemitz 1984). Savu (= Sabu) is south of Flores in the Lesser Sunda Island chain. The nearest known tarsier populations are those in South and Southeast Sulawesi, from which Savu is separated not only by hundreds of kilometers of open ocean in the Flores Sea, but also by the island of Flores itself. It is separated from Sumatran tarsiers and hypothetical Javan tarsiers by the islands of Bali, Lombok, Sumbawa, and Sumba. Thus any dispersal for tarsiers to Savu would not only have to cross expanses of open ocean, but would also have to skip over one or

more intervening islands along the route. It would give tarsiers a strikingly discontinuous distribution – much more so than they already have. Given the lack of any additional reports of tarsiers from Savu, it seems prudent to assume that Savu is outside the range of tarsiers.

Jentink (1892) provides two Javan locales for tarsiers, Surabaya and Preanger (near Bandung). The possibility of tarsiers on Java is more plausible than Savu and warrants careful consideration. Tarsiers are present on Sumatra. Sumatra and Java were a single landmass as recently as the last ice age. So, it is conceivable that tarsiers had a historical distribution on Java. Contrary to this, however, there is no evidence of tarsiers on Java today. This leaves three possibilities:

1. Tarsiers are present on Java today but their presence has gone unnoticed.

2. Tarsiers are locally extinct on Java today, but were present in Jentink's time.

3. The historical distribution of tarsiers does not include Java and Jentink's records are erroneous, possibly owing to specimens transported from elsewhere and purchased at the localities provided by Jentink.

I argue that the weight of the evidence argues for the third possibility.

Regarding the first possibility listed above, tarsiers are small, nocturnal, and cryptic by nature, such that the possibility that their presence has gone unnoticed in one or more areas should not be discounted— at least until an experienced tarsier field biologist has conducted surveys. Tarsiers are recorded in the wet lowlands of Way Kambas National Park, just across the Sunda Straits from Java in the province of Lampung on the island of Sumatra (Yanuar and Sugardjito 1993). The most extensive pristine lowland habitat on Java today is Ujung Kulon National Park, at the extreme western end of Java, surrounded on three sides by the Sunda Straits and less than 200 km from Way Kambas. If the historical distribution of tarsiers were to include Java, it is highly probable that their distribution would include the Ujung Kulon area. Ujung Kulon National Park has been the subject of several field surveys, including some that have used

nocturnal camera trapping, without any evidence of tarsiers (Whitten et al. 2002). Indeed, one experienced tarsier field biologist has been surveying Ujung Kulon National Park for more than 20 years with no evidence whatsoever of tarsiers, while he was able to easily locate them in Bukit Barisan Selatan National Park, less than 200 km from Ujung Kulon on the southern end of Sumatra; his opinion is that the evidence is overwhelming that tarsiers are not present in Ujung Kulon (Haerudin R. Sadjudin of Yayasan Cipta Citra Lestari, personal communication).

The possibility that tarsiers have gone locally extinct on Java might seem plausible, even likely, if one adopted a misconception that tarsiers are relictual taxa clinging to survival in their isolated island homes. Several lines of evidence counter this assumption, however. First, nearly 40 years of field research contradict the misconception that tarsiers, being a relictual taxon, are therefore teetering on the precipice of extinction. On the contrary, tarsiers have been found to be a weedy animal that exists in high densities in a remarkable array of habitats and varying human use (Niemitz 1984, Merker 2003, Shekelle 2003). Indeed, Island Biogeography Theory predicts that it is unlikely for tarsiers to have gone locally extinct on an island as large as Java, while they persist on tiny islands such as Sangihe, Siau, Serasan, and Subi. Nevertheless, the human population density of Java is among the highest in the world, and several Holocene extinctions are known to have occurred there, such as the Javan tiger. The wet lowland habitat of Ujung Kulon is suitably pristine to support the only remaining population of the Javan rhinoceros on Java. It seems unlikely that tarsiers, with a home range of a few hectares at most, could have gone locally extinct from Ujung Kulon, and indeed all of Java, while rhinoceroses remain.

Thus, strong evidence exists that tarsiers are currently absent from Ujung Kulon National Park. By comparison with a much more vulnerable taxon, the Javan rhino, we can extrapolate that it is unlikely that tarsiers exist on Java today, or did so in the past. The most reasonable assumption is that the historical distribution in Sundaland stops at the Sunda Straits, and the two records of tarsiers on Java in Jentink—

the only evidence of tarsiers on Java— are erroneous, and direct examination of the specimens might shed further light.

Hill's (1955) distribution map of the genus *Tarsius* (upon which most subsequent research has been based) includes a few discrepancies from what is known today. For instance, he shows *T. bancanus natunensis* as being from the North Natuna Islands, and absent from the South Natuna Islands, when in fact, the actual distribution is the reverse (Chasen 1940). Hill omits Basilan, off the southwestern tip of Mindanao, from the range of the Philippine Tarsier, but Musser & Dagosto (1987) list specimen 35256 from the Museum of Comparative Zoology, Harvard University (MCZ) as being from Basilan. Likewise, Biliran Island, off the northern tip of Leyte is excluded from the range of Philippine Tarsiers, but Neri-Arboleda *et al.* (2002) list Biliran as having tarsiers. Hill's map shows a spotty, discontinuous distribution of Eastern tarsiers that entirely omits the southwestern peninsula of Sulawesi, even though Hill himself identified the type locality of *T. spectrum* as Makassar (= Ujung Pandang). Indeed, evidence from museum specimens indicates that the distribution of Eastern tarsiers is far more continuous than appears in Hill's map (Musser & Dagosto 1987), and subsequent field surveys have found tarsiers almost everywhere they have been looked for (e.g. MacKinnon & MacKinnon 1980; Nietsch 1999; Nietsch & Kopp 1998; Nietsch & Babo 2001, Nietsch & Burton 2002; Shekelle 2003, Shekelle & Leksono 2004). Likewise, *Tarsius bancanus borneanus* is marked by Hill (1955) as present in coastal regions of Borneo, but not the central regions (generally of higher elevation), perhaps because this species was thought to be present only in extreme lowlands (e.g. Clark 1924). Gorog and Sinaga's (this volume) capture of a tarsier from the montane interior of Borneo contradicts both Clark and Hill.

Distribution maps in Hill (1955), Niemitz (1984), and Musser and Dagosto (1987) all show the distribution of tarsiers on the west coast of Sumatra as extending northward about to the city of Bengkulu. On the east coast, however, Niemitz (1984) and Musser and Dagosto (1987) show the distribution stopping at what appears to be the Musi River, while Hill's map

shows it extending further to what is possibly the Hari River. All three depict a predominantly coastal distribution. Hard evidence to resolve this discrepancy is lacking, but anecdotal reports from locals indicate that tarsiers are not present in the vicinity of the Hari River.

Musser & Dagosto (1987) omit the Buton Island chain from the distribution of Eastern Tarsiers, but subsequent field surveys by Nietsch & Burton (2002) reported tarsiers from Kabaena and Buton. They are presumably on Muna, as well, but owing to deforestation, Burton was unable to locate any (Nietsch, personal communication). Musser & Dagosto (1987) omit Subi Island, although it is biogeographically linked to Serasan (see Banks 1949). Suroso Leksono reported that during surveys in 2003, inhabitants of Subi claimed tarsiers existed there, although he did not see them himself (personal communication).

An Hypothesis of The Historical Extent of Occurrence

In the following sections, I hypothesize the historical extent of occurrence for tarsiers. These hypotheses are meant to be refutable statements that can be corrected by future field surveys and more careful examination of available museum specimens. The hypotheses are based on the assumption that historical distributions on landmasses known to contain tarsiers are limited more by elevation than by habitat type, but regions of high elevation are not specifically excluded from the distribution maps for reasons of practicality. Tarsier densities vary by habitat type (see Merker 2003) and the hypothesis that the presence of tarsiers in various sub-optimal habitats, such as agroforestry and *alang-alang*, could represent sink populations has not been examined (Wright 2003).

In many cases, evidence is lacking (e.g. the precise limit of the distributions of Western and Philippine tarsiers in the Jolo archipelago, the precise eastward limit of Eastern tarsiers in the Banggai Islands, etc.). In other cases, the data (or distribution maps, rather) are conflicting (e.g. the northwestern boundary of Western tarsiers on Sumatra being the Musi River or the Hari River, etc.).

Eastern Tarsiers

To the east of Wallace's Line, I hypothesize a historical distribution of Eastern tarsiers that is nearly continuous on Sulawesi and surrounding islands, including all land areas that were exposed during the Ice Ages (Fig. 3). *Tarsius pumilus*, a montane endemic, is known from three specimens collected between 1800-2200 m in elevation (Miller & Hollister 1921, Musser & Dagosto 1987, Maryanto & Yani 2004). Records of other Eastern tarsiers, of the *T. tarsier*-complex, exist from sea level to 1500 m (MacKinnon & MacKinnon 1980; Musser & Dagosto 1987; Shekelle 2003). Eastern tarsiers have been recorded in almost all habitats except areas with dense human populations, areas of intensive agriculture where all potential sleeping sites have been cleared, and areas where pesticides and / or herbicides are used intensively (MacKinnon & MacKinnon 1980; Shekelle *et al.* 1997; Leksono *et al.* 1997). Any current gaps in the distribution of Eastern tarsiers are hypothesized to be recent events owing to human activity, such as habitat destruction.

The range of these tarsiers extends to the offshore island groups of Togian (Nietsch & Niemitz 1993; Shekelle *et al.* 1997), Banggai (Sody 1949), Selayar (Musser & Dagosto 1987; Nietsch & Babo 2001), and Buton (Nietsch & Burton 2002). A chain of volcanic islands leads north from the northernmost tip of Sulawesi, and of these, at least Siau and Greater Sangihe are known to have tarsiers (Meyer 1897). The neighboring limestone islands of the Talaud chain do not, however (Yunus Masala, Forest Ranger, North Sulawesi, personal communication). Nor does it seem that tarsiers have crossed the narrow Salue Timpaus Strait to the Sula Islands—Taliabu, Mangole, and Sanana—as there are no records of tarsiers from there, although Whitten *et al.* (2002) indicate that these are geologically part of Sulawesi. Similarly, there is a chain of islands, the Bonerate Islands, which run southeast from Selayar into the Flores Sea toward the Lesser Sunda Islands, from which there are no reports of tarsiers. The same is true for the Tukang Besi Archipelago, southeast of Buton Island.

Several species of Eastern tarsiers have been described. Reviews are found in Hill (1955), Niemitz

(1984), Musser & Dagosto (1987), Groves (1998, 2001), Shekelle (2003) and Brandon-Jones *et al.* (2004). Excluding known synonyms, these include *Tarsius tarsier* Erxleben, 1777 (type locality most probably Makassar, South Sulawesi); *T. sangirensis* Meyer, 1897 (type locality, Greater Sangihe Island*, North Sulawesi); *T. pumilus* Miller & Hollister, 1921 (type locality, Rano Rano, Central Sulawesi); *T. dentatus* Miller & Hollister, 1921 (type locality, Labua Sore, Central Sulawesi); *T. pelengensis* Sody, 1949 (type locality, Peleng Island, Central Sulawesi), *T. lariang* Merker and Groves, 2006 (type locality, Gimpu, Central Sulawesi), and *T. sp.* (Shekelle *et al.* in press) (type locality, Siau Island, North Sulawesi) (Fig. 4). Several other populations probably warrant taxonomic separation (MacKinnon & MacKinnon 1980; Nietsch & Niemitz 1993; Shekelle *et al.* 1997; Nietsch & Kopp

1998; Groves 1998; Shekelle 2003; Brandon-Jones *et al.* 2004). Notably, Sulawesi is the only place with parapatrically distributed tarsiers (e.g. *T. dentatus* and *T. lariang*).

*Sangi and Sangir are alternate spellings of Sangihe.

**Laboea Sore, Labuan Sore, and Laboean Sore are all alternate spellings of Labua Sore.

Philippine tarsiers

The current distribution of Philippine tarsiers is thought to be spotty, but I hypothesize a historical distribution that was nearly continuous on islands that made up the ice age landmass of Greater Mindanao (Heaney 1985) (see also Neri-Arboleda 2002) (Fig. 5). This includes Mindanao, Samar, Leyte, and Bohol, as well as the smaller islands of Siargo, Dinagat, Basilan,

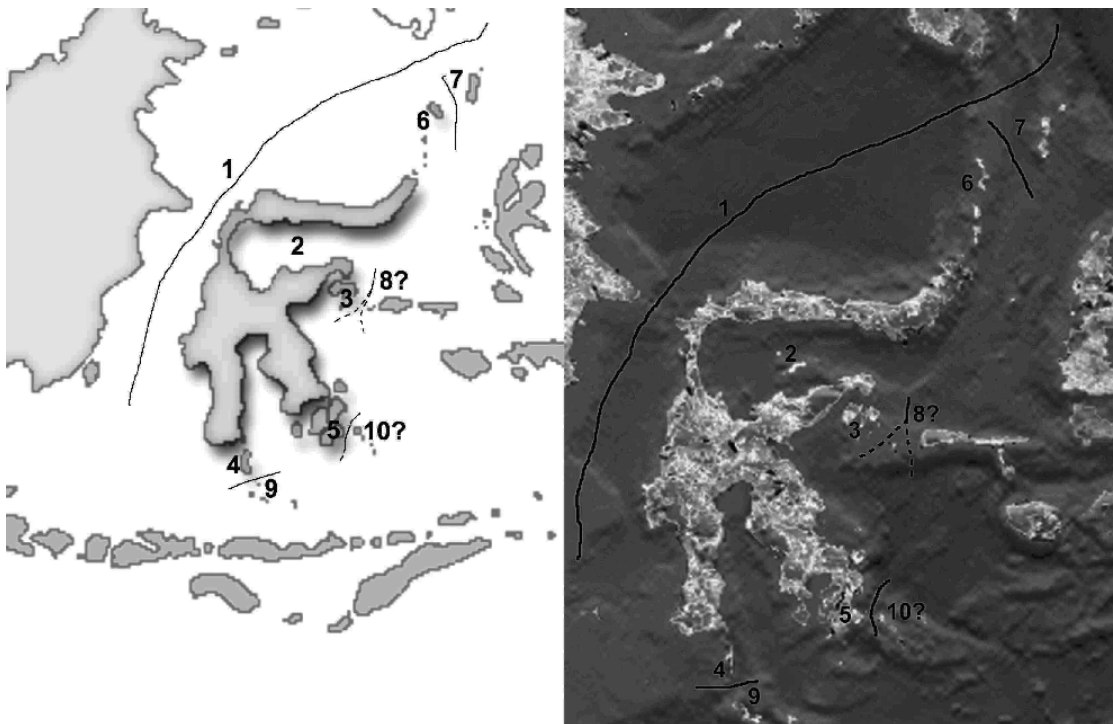


Figure 3: Distribution of Eastern Tarsiers—schematic (left) and satellite (right) views. The hypothesized historical range of these tarsiers extends as far west and north as Wallace’s Line (1), and includes the island of Sulawesi and the offshore island groups of Togian (2), Banggai (3), Selayar (4), Buton (5), and Sangihe (6). The northwestern limit of the range of Eastern Tarsiers lies between Sangihe Island and the Talaud Island chain to the northeast (7). Eastwards, it appears that the range is bounded by the Salue Timpau Strait (8). From the southwestern peninsula, the distribution stops between Selayar Island and the Bonerate Islands (9), and from the southeastern peninsula, the boundary lies between the Buton Islands and the Tukang Besi Islands (10).

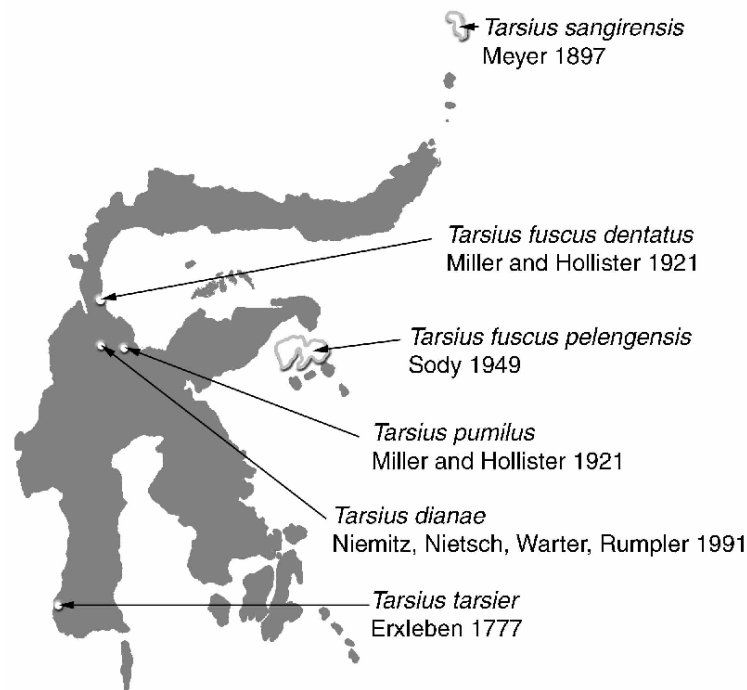


Figure 4: Map of Eastern Tarsier type localities, with the names as they appeared in the original descriptions. The type localities of both *T. dentatus* and *T. diana* are illustrated for reference, although they are now treated as synonyms.

Biliran, and many others. Although commonly thought of as an exclusively lowland taxon (e.g. Fulton 1939; Wharton 1950; Dagosto & Gebo 1997; Neri-Arboleda *et al.* 2002), Gorog & Sinaga (this volume) review evidence for Philippine tarsiers above 800 m. They have been recorded from a variety of primary and secondary habitats (Rickart *et al.* 1993; Dagosto & Gebo 1997; Neri-Arboleda *et al.* 2002).

I find no records of tarsiers from Palawan, or other islands that extend from the northwest corner of Borneo, and neither Hill (1955), nor Niemitz (1984), nor Musser & Dagosto (1987) indicate that these regions have (or have ever had) tarsiers. Tarsiers have not crossed the narrow straits that separate Samar from Luzon, Leyte from Masbate, nor Bohol from Cebu. The Jolo Archipelago makes a logical dispersal corridor between Borneo and Mindanao, but I can find no records of tarsiers there, other than from Basilan near the southwestern tip of Mindanao (Musser & Dagosto 1987). Dagosto *et al.* (2003) state that tarsiers are absent from this archipelago, except for Basilan.

Three subspecies of Philippine tarsiers have been described, but their taxonomic distinctiveness has been questioned (Hill 1955; Niemitz 1984; Musser

& Dagosto 1987; Groves 2001; Brandon-Jones *et al.* 2004). These include: *Tarsius syrichta syrichta* Linnaeus, 1758, (type locality, Samar); *Tarsius syrichta fraterculus* Miller, 1910, (type locality, Bohol), and *T. s. carbonarius* Heude, 1899 (type locality, Mindanao). Tarsiers from other islands are classified as *T. s. syrichta*, but this gives that taxon an illogically disjunct distribution, and other classifications are more probable. For instance, should *T. s. carbonarius* warrant taxonomic separation, then tarsiers from Basilan Island are more likely referable to *T. s. carbonarius*.

Western tarsiers

The Western tarsier has, perhaps, the most curious distribution of all in that it has an incomplete distribution on the ice age landmass, Sundaland (Fig. 6). Western tarsiers are recorded from several parts of Borneo, where I hypothesize a historical distribution that is nearly continuous. They have also been found in southern areas of Sumatra and a few smaller islands including Bangka, Belitung, the Karimata Islands, and the South Natuna Islands (Chasen 1940, Hill 1955, Musser and Dagosto 1987). Like other tarsiers,



Figure 5: Distribution of Philippine Tarsiers—schematic (left) and satellite (right) views. Philippine Tarsiers have been found on islands that composed the ice age landmass, Greater Mindanao. These include Mindanao (1), Samar (2), Leyte (3), Bohol (4), and many smaller islands. Tarsiers have not been reported from Palawan (5) nor other islands that extend from the northwestern tip of Borneo. The northern extent of the range of these tarsiers is the narrow strait that separates Samar from Luzon (6). Philippine Tarsiers have not crossed the narrow expanse of ocean that separates Leyte from Masbate (7) to the north and Cebu (8) to the west. Similarly, tarsiers from Bohol have not crossed the narrow straits that separate Bohol from Cebu (9). Tarsiers are recorded from Basilan, off the southwestern tip of Mindanao, but their presence in the Jolo archipelago (between 10 and 11) is uncertain, although this is a logical dispersal corridor between Borneo and Mindanao. Wallace’s Line (12) demarcates the southern and eastern limits of the Philippine Tarsiers.

Western tarsiers have been recorded from a variety of primary and secondary habitats (Clark 1924, Fogden 1974, Niemitz 1979, Crompton and Andau 1986). As with Philippine tarsiers, Western tarsiers are most often recorded as a lowland species from sea level to 100-200 m (e.g. Clark 1924), but Grog and Sinaga (this volume) report a tarsier capture from 1200 m on Borneo.

The entire extent of occurrence of Western tarsiers is on the Ice Age landmass Sundaland, but not all of Sundaland has tarsiers. For instance, tarsiers are absent from the Asian mainland, all areas of Sumatra except the southernmost tip, and the North Natuna Islands. Also, there are no credible accounts of tarsiers on Java or Bali. I hypothesize the northwestern boundary of tarsiers in Sumatra to be the Musi River, as did Musser and Dagosto (1987), but this has not been confirmed with surveys and other possibilities exist, such as the Hari River (Hill 1955).

Four subspecies of Western tarsiers have been described, but again, their taxonomic

distinctiveness has been questioned (Hill 1953, 1955, Niemitz 1984, Musser and Dagosto 1987, Groves 1998, 2001, Brandon Jones et al. 2004). These include: *Tarsius bancanus bancanus* Horsfield, 1821, (type locality, Jebus (=Jeboos), on the northwest tip of the island of Bangka); *Tarsius bancanus borneanus* Elliot, 1910, (type locality, Borneo), *T. b. saltator* Elliot, 1910, (type locality, Belitung (=Beliton), and *T. b. natunensis* Chasen, 1940, (type locality, Serasan Island).

Biogeographic Inferences

Several authors have inferred that extant tarsiers are closely related taxa (e.g. MacKinnon and MacKinnon 1980, Musser and Dagosto 1987, Simons 2003), but that otherwise reasonable inference appears to be contradicted by genetic data that indicates that the origin of all three clades dates to the Miocene. Meireles et al. (2003) used nDNA for a molecular clock estimate of 5.6 mya for the split between Western and Philippine tarsiers. Preliminary results of mtDNA sequence data reported by Shekelle et al. (2001) that

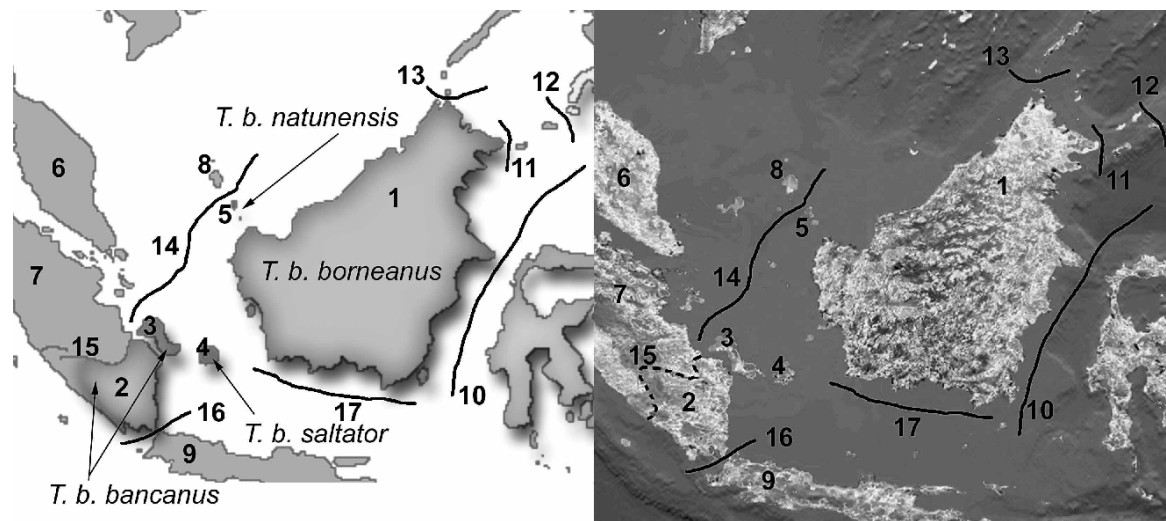


Figure 6: Distribution of Western Tarsiers—schematic (left) and satellite (right) views. Western Tarsiers presumably have a nearly ubiquitous historical distribution on Borneo (1). They have also been found on southern parts of Sumatra (2), Bangka (3), Belitung (4), and the South Natuna Islands (5). They have not been recorded from the Asian mainland (6), most of Sumatra (7), the North Natuna Islands (8), nor are there reliable reports from Java (9). The eastern extent of their distribution is Wallace's Line (10). To the north, their distribution is limited somewhere in the Jolo Archipelago (11, 12), and somewhere before the Philippine island of Palawan (13). Their westward distribution corresponds with the drowned riverbed of the ice age Sunda River (14), and one of its modern day tributaries, shown here as the Musi River (15). Western Tarsiers did not cross the Sunda Straits (16), nor did they disperse south of Borneo (17).

found Philippine, Eastern, and Western tarsiers to be an unresolved trichotomy that most likely dates to the middle Miocene. In the preliminary analysis, genetic distances among Philippine, Eastern, and Western tarsiers were nearly as great as the average genetic distances among hominoids. The average genetic distance among the three tarsier species groups was 0.1157, while the average genetic distance for *Hylobates* vs. *Homo* and *Pan* was 0.1272. Even allowing for unequal rates of evolution, it is most likely that Philippine, Eastern, and Western tarsiers are not particularly closely related taxa.

Morley (1998) found evidence of biotic exchange across the Makassar Straits in palynological data at 17 mya, 14 mya, 9.5 mya, 3.5 mya, and 1 mya. The genetic data reported by Shekelle et al. (2001) are most consistent with tarsiers crossing the Makassar Straits at any of the three older dates identified by Morley, and least consistent with the two younger dates. Hall (2001) identified the most likely time for faunal exchange across the Makassar Straits as being about 10 mya, based upon reconstructions of tectonic activity. Mercer and Roth (2003) used a molecular

clock date to estimate the arrival of squirrels to Sulawesi as approximately 11.5 mya, indicating that at least some of the small terrestrial mammals from Sulawesi are as ancient as I hypothesize for tarsiers. The last known record of tarsiers from mainland Asia is a Miocene fossil from Thailand (Ginsburg and Mein 1986). There is an intriguing synchronicity, therefore, between the fossil record, the estimated divergence of extant tarsiers based on mtDNA, the molecular clock date for squirrels, and two independent predictions for biotic exchange across the Makassar Straits, all during the middle Miocene. It is worth noting that both Musser and Dagosto (1987) and Groves (1998) argued that Philippine and Western tarsiers form a clade relative to Eastern tarsiers based on morphological data. Such a tree topology is consistent with this hypothesis. Results of the preliminary mtDNA analysis found an unresolved trichotomy, but this does not imply a trifurcation.

Some inferences about tarsier biogeography within species groups can be drawn from the estimated historical distributions. Notably, the incomplete distribution of Western tarsiers on Sundaland

contrasts sharply with the distributions of Philippine and Eastern tarsiers that cover all of Greater Mindanao and Sulawesi, respectively. At first glance, one might invoke the paradigm that tarsiers are a relictual taxon and are experiencing a gradual range reduction in Sundaland. An alternative hypothesis, however, is that Western tarsiers experienced a marked range expansion at the end of the last ice age. Banks (1949) hypothesized that the ice age Sunda River, which flowed northward from Sumatra and between the North and South Natuna Islands, formed an east-west faunal boundary in Sundaland. Brandon-Jones (1996) further hypothesized that large tracts of Sundaland were too dry to support habitat suitable for tropical primates in much of the Pleistocene. His hypothesis includes the prediction that many tropical primates experienced marked Holocene range expansions throughout Sundaland as Holocene climatic patterns permitted the spread of wetter, more suitable habitats (see also Meijaard 2003). The Western tarsiers appear to fit the predictions of both Banks and Brandon-Jones.

The historical distribution of Philippine tarsiers is, essentially, a perfect fit with the ice age landmass, Greater Mindanao. They are typically regarded as a lowland species, but have been recorded above 800 m. Other than elevation, there are no known ecological constraints that would restrict their historical distribution throughout much of Greater Mindanao. It is not known when tarsiers dispersed to the Philippines, nor from where, but it is probable that they have been genetically isolated from other tarsiers since the Miocene, as mentioned previously. The subspecies of Philippine tarsiers recognized by Hill (1955) are allopatric populations on islands that separated after the end of the last ice age, implying a relatively short time frame for differentiation of Philippine tarsier populations. Thus, the current best guess for diversification within Philippine tarsiers is that a panmictic population on Greater Mindanao became fragmented as ocean levels rose at the end of the last ice age. Other possibilities should not be overlooked, however, given the several million years that Philippine tarsiers were isolated from Western and Eastern tarsiers, including the possibility of deeper

biogeographic patterns on Greater Mindanao, such as are present on Sulawesi.

Dagosto et al. (2003) cited evidence that the Zamboanga peninsula is geologically part of Sundaland, and accreted onto the main body of Mindanao about 5 mya, with the first evidence of emergent land in the late Miocene. These events seem to be conspicuously coincidental to the 5.6 mya molecular estimate for the origins of the Philippine tarsier clade. Additionally, they point out that changing ocean levels have subsequently rearranged the configuration of emergent land in Greater Mindanao several times, creating possibilities for vicariance events that could promote taxonomic diversity, such as is seen in Sulawesi. Unfortunately, the museum specimens of Philippine tarsiers are heavily concentrated from the Davao region of Mindanao (51 out of 60 specimens examined by Dagosto et al. 2003), and field studies are hampered the Philippine tarsiers' lack of a duet call with which to survey them and provide an initial estimate of population subdivision.

The historical distribution of Eastern tarsiers includes all areas of Sulawesi that were exposed during the ice ages, as well as several landmasses that probably were not contiguous with Sulawesi during those times, including the Sangihe Islands, Banggai Islands, Togian Islands, and Selayar. There is a montane form recorded from three localities between 1800-2200 m. Lowland forms are common up to 1100 m (Merker 2003), and have been recorded up to 1500 m (MacKinnon and MacKinnon 1980). It is not known when tarsiers migrated to Sulawesi, nor from where, but it is probable that they have been genetically isolated from other tarsiers since the Miocene, and almost certainly predate the coalescence of Sulawesi into a single landmass from a diverse archipelago (Hall 2001). The parapatric tarsiers on Sulawesi are hypothesized to be evidence of this ancient archipelago (Shekelle and Leksono 2004). Eastern tarsiers, therefore, are like the reverse of Philippine tarsiers; several allopatric populations were isolated on different islands, and then brought together by tectonic activity in the last 1-2 million years to form parapatric populations.

Several generalizations can be drawn from the historical distributions of tarsiers hypothesized above. First, tarsiers are found in almost all lowland habitats that have not been severely degraded. Second, tarsier distributions are limited by elevation, the maximum reported elevation for Eastern tarsiers is 2200 m, for Western tarsiers is 1200 m, and for Philippine tarsiers is in excess of 800 m. Some of these differences could be sampling error, but an endemic montane species is recorded from Sulawesi, as opposed to Sundaland and the Philippines for which there is no known endemic montane tarsier. Mountain ranges limit dispersal to higher elevations, but are not known to form barriers to dispersal around the flanks. Third, other landforms, such as rivers are not effective barriers to tarsier dispersal over geologic time. In only a single instance is a river hypothesized to be a species boundary, i.e. the northern boundary of *T. bancanus* on Sumatra. Fourth, the chief barrier to dispersal in almost all instances is open ocean. Only on Sulawesi are parapatric tarsier populations known, and many of the contact zones are interpreted as evidence of an ancient archipelago, one that is predicted by geologic data. Finally, the presence of tarsiers on both sides of Wallace's Line might suggest a certain aptitude for rafting across open ocean over geologic time intervals. The fact that tarsiers have not crossed numerous narrow ocean straits in the Philippines and Sulawesi, however, conflicts with this assessment, and successful dispersal by rafting is probably very rare for tarsiers.

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REFERENCES

- Banks, E. 1949. *Bornean Mammals*. Kuching, Malaysia: The Kuching Press.
- Brandon-Jones, D. 1996. The Asian Colobinae (Mammalia: Cercopithecidae) as indicators of Quaternary climatic change. *Bio. J. Linn. Soc.* 59:327-350.
- Brandon-Jones, D, AA. Eudey, T. Geissmann, CP. Groves, DJ. Melnick, JC. Morales, M. Shekelle, & CB. Stewart. 2004. Results from the Workshop 'Primate Taxonomy for the New Millennium': Asian Primate Classification. *Inter. Journal of Primatology* 25(1):97-164.
- Camel, G.J. 1705. *Philos. Trans.* xxv. 2197-2204.
- Cabrera, A. 1923. On the identification of *Simia syrichta* Linnaeus. *Journal of Mammalogy* 4:89-91.
- Chasen, FN. 1940. A handlist of Malaysian mammals. *Bulletin of the Raffles Museum* 15:1-209.
- Clark, WEL. 1924. Notes on the living tarsier (*Tarsius spectrum*). *Proc. Zool. Soc. London* (1924): 217-223.
- Crompton, RH & PM. Andau. 1986. Locomotion and habitat utilization in free-ranging *Tarsius bancanus*: a preliminary report. *Primates* 27(3): 337-355.
- Dagosto, M & D. Gebo. 1997. A preliminary study of the Philippine tarsier in Leyte. *Asian Primates* 6:4-8.
- Dagosto, MDL, DL. Gebo & CN. Dolino. 2003. The natural history of the Philippine tarsier (*Tarsius syrichta*). In *Tarsiers: Past, Present, and Future*. Wright PC, Simons EL, Gursky S (eds) pp:237-259. New Brunswick, New Jersey: Rutgers University Press.
- Feiler, A. 1990. Über die Säugetiere der Sangehe- und Talaud-Inseln – der Beitrag A. B. Meyers für ihre Erforschung (Mammalia). *Zoologische Abhandlungen des Staatlichen Museums für Tierkunde Dresden*, 46: 75–94.
- Fischer, G. 1804. *Anatomie der Maki und der ihnen verwandten Thiere*. Frankfurt am Main.
- Fulton, JF. 1939. A trip to Bohol in quest of *Tarsius*. *Yale J. Biol. Med.* 11:561-573.

- Ginsburg, L & P. Mein. 1986. *Tarsius thailandica* nov. sp., Tarsiidae (Primates, Mammalia) fossile d'Asie. *C. R. Academie of Science (Paris)* t.304, ser. II, (19):1213-1215.
- Goodman, M, CA. Porter, J. Czelusniak, SL. Page, H. Schneider, J. Shoshani, G. Gunnell & C. Groves. 1998. Toward a phylogenetic classification of Primates based on DNA evidence complemented by fossil evidence. *Mol. Phyl. Evol.* 9:585-598.
- Gorog, AJ, & MH. Sinaga. 2008. A tarsier capture in montane forest on Borneo. In *Primates of the Oriental Night* edited by Shekelle M, I. Maryanto, C. Groves, H. Schulze, H. Fitch-Snyder. (eds) (this volume).
- Groves, CP. 1998. Systematics of tarsiers and lorises. *Primates* 39:13-27.
- Groves, C. 2001. *Primate Taxonomy*. Washington D.C.: Smithsonian Institution Press. 350 p.
- 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*, Metcalf I, Smith J, Morwood M, Davidson I. (eds) pp:35-56. Lisse: Swets and Zeitlinger Publishers.
- Heaney, LR. 1985. Zoogeographic evidence for Middle and Late Pleistocene land bridges to the Philippine islands. *Mod. Quaternary Res. SE Asia* 9:127-143, figs. 1-3.
- 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.
- Jentink, FA. 1892. Catalogue systématique des mammifères. Muséum d'Histoire Naturelle des Pays-Bas. Tome XI. E.J. Brill, Leide.
- Leksono, SM, Y. Masala & M. Shekelle. 1997. Tarsiers and agriculture: thoughts on an integrated management plan. *Sulawesi Primate Newsletter* 4(2):11-13.
- 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.
- Meijaard, E. 2003. Mammals of south-east Asian islands and their Late Pleistocene environments. *Journal of Biogeography* 30(8):1245-1257.
- Meireles, CM, J. Czelusniak, SL. Page, DE. Wildman, & M. Goodman. 2003. Phylogenetic position of tarsiers within the order Primates: evidence from γ -globin DNA sequences. In *Tarsiers: Past, Present, and Future*. Wright PC, Simons EL, Gursky S. (eds) pp:145-160. New Brunswick: Rutgers UP.
- Mercer, JM, & VL. Roth (2003). The effects of Cenozoic global change on squirrel phylogeny. *Science* 299:1568-1572.
- Merker, S. 2003. Vom Aussterben bedroht oder anpassungsfähig? - Der Koboldmaki *Tarsius diana* in den Regenwäldern Sulawesi. PhD-Dissertation, University of Goettingen, Germany.
- Merker, S. & CP. Groves. 2006. *Tarsius larian*: A new primate species from western central Sulawesi. *Int. J. Primatol.* 27: 465-485.
- Meyer, AB. 1897. Säugethiere vom Celebes- und Philippinen-Archipel, I. *Abhandlungen und Berichte des Kaiserlich Zoologischen und Anthropologischen-Ethnologischen Museums zu Dresden*, 6: I-VIII, 1-36.
- Miller, Jr. GS, & N. Hollister. 1921. Twenty new mammals collected by H. C. Raven in Celebes. *Proceedings of the Biological Society of Washington* 34:93-104.
- Morley, RJ. 1998. Palynological evidence for tertiary plant dispersals in the SE Asian region in relation to plate tectonics and climate. In *Biogeography and Geological Evolution of SE Asia*. Hall R, Holloway JD (eds) pp:211-234. Leiden: Backhuys.

- 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.
- Neri-Arboleda I, P. Stott & NP. Arboleda. 2002. Home ranges, spatial movements, and habitat associations of the Philippine tarsier (*Tarsius syrichta*) in Corella, Bohol. *J. Zool. Lond.* 257:387-402.
- Niemitz, C. 1979. Results of a field study on the Western tarsier (*Tarsius bancanus borneanus* Horsfeld, 1821) in Sarawak." *Sarawak Museum Journal* 27 (1979a): 171-228.
- Niemitz, C. 1984. Taxonomy and distribution of the genus *Tarsius* Storr, 1780. In *Biology of Tarsiers*. Niemitz C. (ed) pp:1-16. New York: Gustav Fischer Verlag.
- Niemitz, C. 1985. Der Koboldmaki - Evolutionsforschung an einem Primaten. *Naturwiss Runch* 38:43-49.
- Niemitz, C, A. Nietsch, S. Warter, & Y. Rumpler. 1991 *Tarsius diana*: A new primate species from Central Sulawesi (Indonesia). *Folia Primatologica* 56:105-116.
- Nietsch, A. 1999. Duet vocalizations among different populations of Sulawesi tarsiers. *Int. J. Primatol.* 20(4):567-583.
- Nietsch, A & C. Niemitz. 1993. Diversity of Sulawesi tarsiers. *Deutsche Gesellschaft fur Säugetierkunde* 67:45-46.
- Nietsch, A & ML. Kopp. 1998. Role of vocalization in species differentiation of Sulawesi Tarsiers. *Folia primatologica* 68(suppl.1):371-378.
- Nietsch, A & N. Babo. 2001. The tarsiers of South Sulawesi. In *Konservasi Satwa Primata*. pp:114-119. Yogyakarta: Fakultas Kedokteran Hewan dan Fakultas Kehutanan Universitas Gajah Mada University - Yogyakarta.
- 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.
- Rickart, EA, LR. Heaney, PD. Heideman, & RCB. Utzurum. 1993. The distribution and ecology of mammals on Leyte, Biliran and Maripipi Islands, Philippines. *Fieldiana Zoology* 72:1-62.
- Shekelle, M. 2003. Taxonomy and biogeography of Eastern Tarsiers. Doctoral thesis. Washington University, St. Louis.
- Shekelle, M, SM. Leksono, Ichwan LLS, & Y. Masala. 1997. The natural history of the tarsiers of North and Central Sulawesi. *Sulawesi Primate Newsletter*, 4 (92):4-11.
- Shekelle, M, JC. Morales & DM. Melnick. 2001. Genetic and acoustic evolution among Eastern Tarsiers of northern and central Sulawesi. Presented at the International Society of Primatologists, 14th Congress, Adelaide, Australia. January 7-12, 2001.
- Shekelle, M, & SM. Leksono (2004) "Rencana Konservasi i Pulau Sulawesi: Dengan Menggunakan Tarsius Sebagai 'Flagship Taxon'". *Biota* 9 (1):1-10.
- Shekelle, M, C. Groves, S. Merker & J. Supriatna. In Press. *Tarsius tumpara*: A New Tarsier Species from Siau Island, North Sulawesi. *Primate Conservation* 2008 (23).
- Simons, EL. 2003. The fossil record of tarsier evolution. In *Tarsiers: Past, Present, and Future*. Wright PC, Simons EL, Gursky S (eds) pp:9-34. New Brunswick, New Jersey: Rutgers University Press.
- Sody, HJV. 1949. Notes on some Primates, Carnivora, and the babirusa from the Indo-Malayan and indo-Australian regions. *Treubia* 20:121-185.
- Wharton, CH. 1950. The tarsier in captivity. *Journal of Mammalogy* 31(3):260-268.
- Whitten, A, M. Mustafa, & G. Henderson. 2002. *The Ecology of Sulawesi*. 2nd ed. Singapore: Periplus.
- Yanuar, A & J. Sugardjito. 1993. Population survey of primates in Way Kambas National Park, Sumatra, Indonesia. *Tiger Paper*. 30-36