

TAXONOMIC HISTORY OF THE TARSIERS, EVIDENCE FOR THE ORIGINS OF BUFFON'S TARSIER, AND THE FATE OF *Tarsius spectrum* Pallas, 1778

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ABSTRACT

A survey of the history of tarsier taxonomy indicates that *Tarsius tarsier* Erxleben, 1777 is a senior subjective synonym of *T. spectrum* Pallas, 1778. Buffon's tarsier, long thought lost or possibly destroyed, has been recently rediscovered and is identified as being eastern in origin (i.e. from within what has previously been classified as *T. spectrum* or the *T. spectrum* complex). The identification of Buffon's tarsier as an Eastern tarsier alters Hill's taxonomy by making *T. spectrum* a junior subjective synonym of *T. tarsier*. Eastern tarsiers become the type species of the genus. Our work, conducted, before the rediscovery of Buffon's specimen, is based on illustrations of the skin and cranium by Daubenton. Investigations of Buffon's specimen are ongoing, but do not alter our fundamental conclusions. Daubenton's illustration of the cranium shows a nasal profile that is not consistent with published illustrations of Philippine and Western tarsiers. Several other characteristics are argued to be consistent with Buffon's tarsier being eastern in origin.

Keywords: *T. tarsier*, *T. bancanus*, *T. syrichta*, Taxonomy

A BRIEF HISTORY OF TARSIER TAXONOMY

- Linnaeus's tarsier

Standing last in the list of Linnaeus's (1758) 21 species of the genus *Simia* is *Simia syrichta*, reading as follows:

S. caudata imberbis, ore ciliisque vibrissatis.
*Syst.nat.*3.

Cercopithecus luzonicus minimus. *Pet.gaz.*
21.t.13.t.11.

Habitat in Luzonum insulis.

Cabrera (1923) showed that Petiver ("Pet.") took his 1705 description in turn from the papers of a Jesuit missionary, G.J. Camel, who was clearly referring to a tarsier, and that the locality, Luzon is probably to be explained as being a place to which tarsiers were traded from nearby Samar. Cabrera (1923) used the form *Tarsius syrichtus*, but, as Linnaeus (1758) spelt the name *Syrichta* with a capital initial letter, it is probable that he was using it as a noun in apposition (he began adjectives with a small letter), so it does not change gender: see Musser & Dagosto, 1987.

Consequently, the earliest available name for a Philippine tarsier is *syrichta* Linnaeus, 1758. Cabrera's (1923) mention of Samar may be taken as a restriction of the type locality.

Cabrera's (1923) opinion that *Simia syrichta* is a Philippine tarsier has been supported by numerous authors since that date. Hill (1953a,b), in his influential revision, accepted Cabrera's (1923) assessment of Linnaeus's *Simia syrichta* as the Philippine tarsier; so did Musser & Dagosto (1987). Remarking on its essential accuracy, Niemitz (1984) translated Camel's description, including the comment, "it is said to live on charcoal, but this is wrong"!

Meyer (1895), not knowing all this, described the Philippine tarsier as *Tarsius philippinensis*, with type locality Samar, while Heude (1898:164) clearly thought that he was the first to name a Philippine tarsier when he described *T. carbonarius* from two specimens from Mindanao: from the Gulf of Davao and the valley of the River Poulangui. He distinguished this from the only other species he knew, "*Tarsius spectrum* de Java" (sic), by dental characters and by the narrowness and greater length

of the skull, adding, in a curious but quite independent echo of Camel, “On m’a dit qu’il mangeait du charbon!”

Buffon’s tarsier

Buffon (1749:87, and pl. 219) gave the vernacular name Tarsier or Woolly Jerboa to an animal he received from an unknown locality. Remarking on its long hind legs and other characters, he described

“the inferior part of the hind legs” as being hairless and its tail as being, like that of the jerboa, garnished with long hairs towards the tip.

It is not clear exactly what is meant by “the inferior part of the hind legs” – evidently, not necessarily the whole of the tarsus, because in the plate the proximal part of the tarsus is haired (Figure 1). This, and the conspicuously tufted tail, eliminates



Figure 1: Buffon’s tarsier. This illustration has the gestalt of an Eastern tarsier in having a tail that is more hirsute than is common in Western and Philippine tarsiers, relatively small eyes, long and pointed ears, woolly appearance of the fur, and similarities of the relative leg length (from Buffon 1765).

the almost naked-tailed Philippine tarsier (Figure 2). The head is not excessively broad, and the very long, dark, conspicuous tail tuft suggests it is not a Western tarsier. Buffon's colleague Daubenton published, as an addendum (p.114 [N°MCCXXXV]), a description of the skull and skeleton of the tarsier (always assumed, perhaps not correctly, to be of the same specimen). A plate of the skull and skeleton was published by Fischer (1804), who called it "Daubenton's tarsier". Poor as they are, the figures show the relatively small orbits and long braincase of the Sulawesi tarsier (Figure 3).

Other than a few specimens mounted for public display, I. Geoffroy St. Hilaire (1851:ii, fn.2) found Buffon's collection neglected, and "ne tardait pas à être attaqué par les insectes". Nonetheless, the mounted tarsier specimen does still exist; it is the subject of a paper in preparation by CPG, in collaboration with C. Callou and J. Cuisin. Suffice it to say that it is indeed a Sulawesi tarsier, and we cannot understand why Elliot (1910) baldly claimed that its "bare tarsi and nearly naked tail" (sic!) shows it came from the Philippines. Elliot refused to fix a type locality and considered it indeterminable, adding that as Pallas's *spectrum* was based upon it, "*Tarsius spectrum* must be dropped from the list of recognized species".

Buffon was the main source for Erxleben's (1777:72) name *Lemur tarsier*, which consequently is not a Philippine tarsier as listed by Hill (1953a), but is the earliest available name for a Sulawesi tarsier.

Schreber (1778:554) cited Buffon and Erxleben for the description of his *Didelphys? macrotarsos*, which he inclined to think was actually a marsupial. Gmelin (1788) cited Buffon first, and Pennant second, for his *Didelphis macrotarsus*. Link (1795) likewise based the name *Macrotarsus buffonii* on Buffon's tarsier, as did Audebert (1797) for *Tarsius daubentonii*.

Pallas's tarsier

Pallas (1778) also based *Lemur spectrum* in Buffon's tarsier, but referred to it a specimen in the museum of his late friend Schlosser, which in effect formed the bulk of his description. He stated that it came from "the furthest islands of the Indian Ocean,

probably Ambon", and is called *podje* by the Macassans. Pallas described its teeth and its general external appearance, ending with "*Cauda nudiuscula*", meaning "Tail virtually naked". According to Smit et al. (1986), Schlosser's cabinet may have been purchased by Boddaert, but thereafter nothing is known about it. Hill (1953a) argued that the description was that of a Sulawesi tarsier, and fixed the type locality as Macassar (=Makassar, until recently known as Ujung Pandang, but the name recently reverted to its original, Makassar), because of Pallas's mention of its Macassan name, *podje*. Possibly influenced by Sody (1949), Niemitz (1984:13) influentially gave the type locality as Minahasa (far northern Sulawesi). In the absence of any evidence to the contrary, Hill's fixation is better substantiated.

As Cabrera (1923) recognized, *Lemur tarsier* Erxleben, 1777, based on Buffon's description (see above), predates *Lemur spectrum* Pallas, 1778 and *Didelphys? macrotarsos* Schreber, 1778. Unfortunately, therefore, the well-known name *Tarsius spectrum*, commonly used for Sulawesi lowland tarsiers, must be superseded by *Tarsius tarsier* (Erxleben, 1777).

Geoffroy (1796) later redescribed Pallas' specimen as *Tarsius pallassii*.

-Pennant's tarsier

Pennant (1771) redescribed Buffon's tarsier, and ten years later (Pennant, 1781) he described "two fine specimens from the cabinet of Doctor *Hunter*" as having

A pointed visage... hairs on the legs and feet short, white, and thin; tail almost naked: the greater part round and scaly, like that of a rat; but grows hairy towards the end, which is tufted.

Citing Pallas (1778), Pennant (1781) gave Amboina (=Ambon) as the locality, and *podje* as the Macassan name. Later Kerr (1792) paraphrased Pennant's (1781) description, naming it *Lemur podje*.

"Doctor Hunter" is almost certainly the famous surgeon John Hunter (1728-1793), whose

Eastern tarsiers



Philippine tarsier

Western tarsier

T. b. bancanus
 Tarsier photos © Myron Shekelle, 2002, except *T. syrichta*, Sheena Hynd
T. s. fraterculus
T. s. sangirensis
T. tarsier (unknown prov.)
T. tarsier Togian Islands
T. dentatus

Figure 2: Diagnostic value of tarsier tails. The Philippine tarsier in this figure has a very slight, almost invisible tuft of fur on the distal few centimeters of the tail. The tuft fur is sparse, very short, and light in coloration. Western tarsiers have a clearly apparent tuft of fur on the distal end of the tail, in appearance like that of a feathered arrow shaft. The fur on the tail of Eastern tarsiers is altogether different than the other two and gives the tail of an Eastern tarsier an appearance similar to that of a bottle brush. The tail fur of Eastern tarsiers is generally longer, darker, and the tuft typically covers as much as 1/3 to 1/2 of the length of the tail, but it develops gradually along the length of the tail such that its actual length is difficult to measure accurately. In *T. sangirensis*, the tail tuft is in the same position as it is in other Eastern tarsiers, but the fur is shorter, sparser, and lighter in color. (adapted from Shekelle 2003)

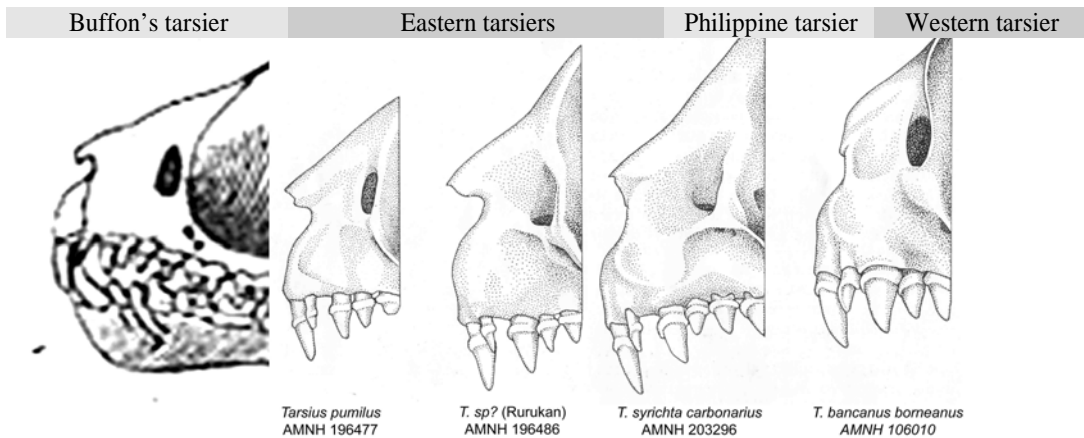


Figure 3a: Buffon's tarsier is most similar to Eastern tarsiers in the shape of the nasal profile (adapted from Musser and Dagosto 1987, Fischer 1804, and Shekelle 2003).

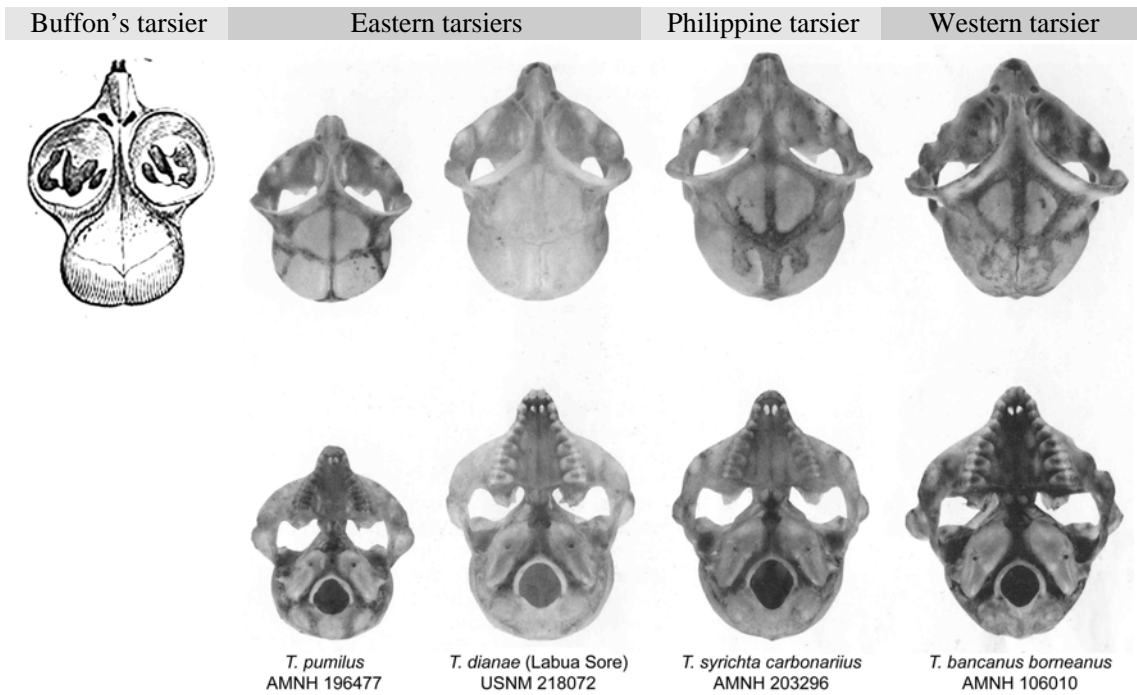


Figure 3b: Buffon's tarsier is most similar to Eastern tarsiers in that the shape of the cranium is oblong and has a slight postorbital constriction (adapted from Musser and Dagosto 1987 and Fischer 1804). Note: *Tarsius diana*e is a junior synonym of *T. dentatus*

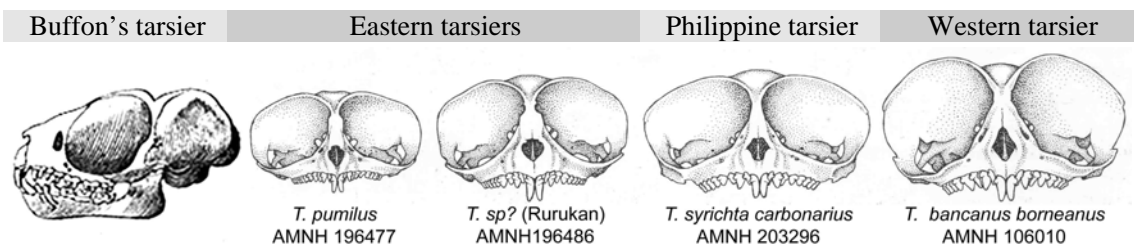


Figure 3c: Buffon's tarsier is most similar to Eastern Tarsiers in the relative height of the orbits and the braincase (adapted from Musser and Dagosto 1987 and Fischer 1804).

anatomical preparations and manuscripts were bequeathed to the nation under the trusteeship of the Royal College of Surgeons collection upon his death, forming the basis for what became the Hunterian Museum. The Royal College of Surgeons took a direct hit during the Second World War, and many valuable specimens were destroyed, presumably including the tarsiers.

Although the description is not absolutely clear-cut, the “pointed visage” and the description of the tail strongly suggest a Sulawesi tarsier, so *Lemur podje* Kerr, 1792 is best regarded as a junior synonym of *Lemur tarsier* although it is of course available to anyone who might consider Hunter’s specimens as distinct.

Fischer’s revision of tarsiers

Fischer (1804) considered that he had evidence for not one but three species of tarsier: *Tarsius pallassii* (adopting Geoffroy’s renaming of *Lemur spectrum* Pallas, 1778), *T. daubentonii* (an explicit renaming of *Lemur tarsier* Erxleben, 1777 and *Didelphis macrotarsus* [sic] Gmelin, 1788, apparently unaware of Audebert’s similar action), and a new species *T. fuscus* or *fuscomanus*. This new species was said to have come from Madagascar, probably (as he remarked) an error for Macassar. His description of the tail could only be that of a Sulawesi tarsier. Differences between his three species, which in effect, therefore, are all Sulawesi tarsiers, are based on stages of wear on the incisors and other features.

Hill (1953a) presumed that the type of Fischer’s *T. fuscus* was lost, and there seems no contrary evidence. *Tarsius pallassii* and *T. daubentonii* are objective junior synonyms of *Lemur spectrum* and *Lemur tarsier*, respectively. Given the type locality, Macassar, for all three of Fischer’s taxa, *T. fuscus* (which he also called *T. fuscomanus*) must rank as a subjective junior synonym of *Lemur tarsier*, despite the fact that Miller and Hollister (1921), obscurely, referred to “*Tarsius fuscus fuscus* from northeastern Celebes”.

Desmarest (1804) combined Fischer’s first two species into one, which he called “Tarsier aux mains rousses, *Tarsius spectrum* Geoffroy” [sic],

including Buffon’s, Pallas’s and Pennant’s tarsiers; and renamed the third “Tarsier aux mains brunes, *Tarsius fischerii* = *T. fuscomanus* Fischer”.

Other 19th century revisions of tarsiers

Horsfield (1824) described the first well-localised tarsier, *Tarsius bancanus* from Jeboos (=Jebus), Bangka. It was described as being dark, lacking upper central incisors (but the type was evidently an infant, and having rounded, horizontal ears, shorter than the head, and a flatter facial profile (Figure 4). Horsfield (1824) compared it to Fischer’s (1804) three species, citing *T. fuscus* as *T. fischeri*.

Fitzinger’s (1870) revision differed little from Horsfield’s (1824) arrangement, recognising four species: *Tarsius spectrum* (based on Pallas’s tarsier, and from Ambon), *T. fuscomanus* (Fischer’s tarsier, but said to be from Mindanao and Bohol), *T. daubentonii* (including Buffon’s, Pennant’s, Schreber’s and Erxleben’s tarsiers, from Celebes, Selayar and Borneo), and *Tarsius bancanus* (from Sumatra and Bangka). His nomenclature aside, his revision is noteworthy for being the first to compare Philippine and Sulawesi tarsiers, and to widen the known distribution by the inclusion of some new localities.

Meyer (1897) had a different view of the nomenclature. He used *Tarsius fuscus* Fischer for the Sulawesi tarsier, *T. philippensis* Meyer (1895) for the Philippine species, and *T. spectrum* (Pallas) for the one from Borneo (which he also knew from the Karimata and Natuna Is., Belitung and Sumatra). He described a new species, *T. sangirensis* from the Sangihe Is. This represents a further step towards a modern understanding of the species of tarsiers.

20th century revisions

Elliot (1910) described two new species, *Tarsius saltator* from Belitung and *Tarsius borneanus* from the Landak River, West Kalimantan. Chasen (1940) regarded these as subspecies of the only species he recognized, *Tarsius tarsier* Erxleben, and described a further subspecies, *T. t. natunensis* from Sirhassen, in the South Natuna Is.

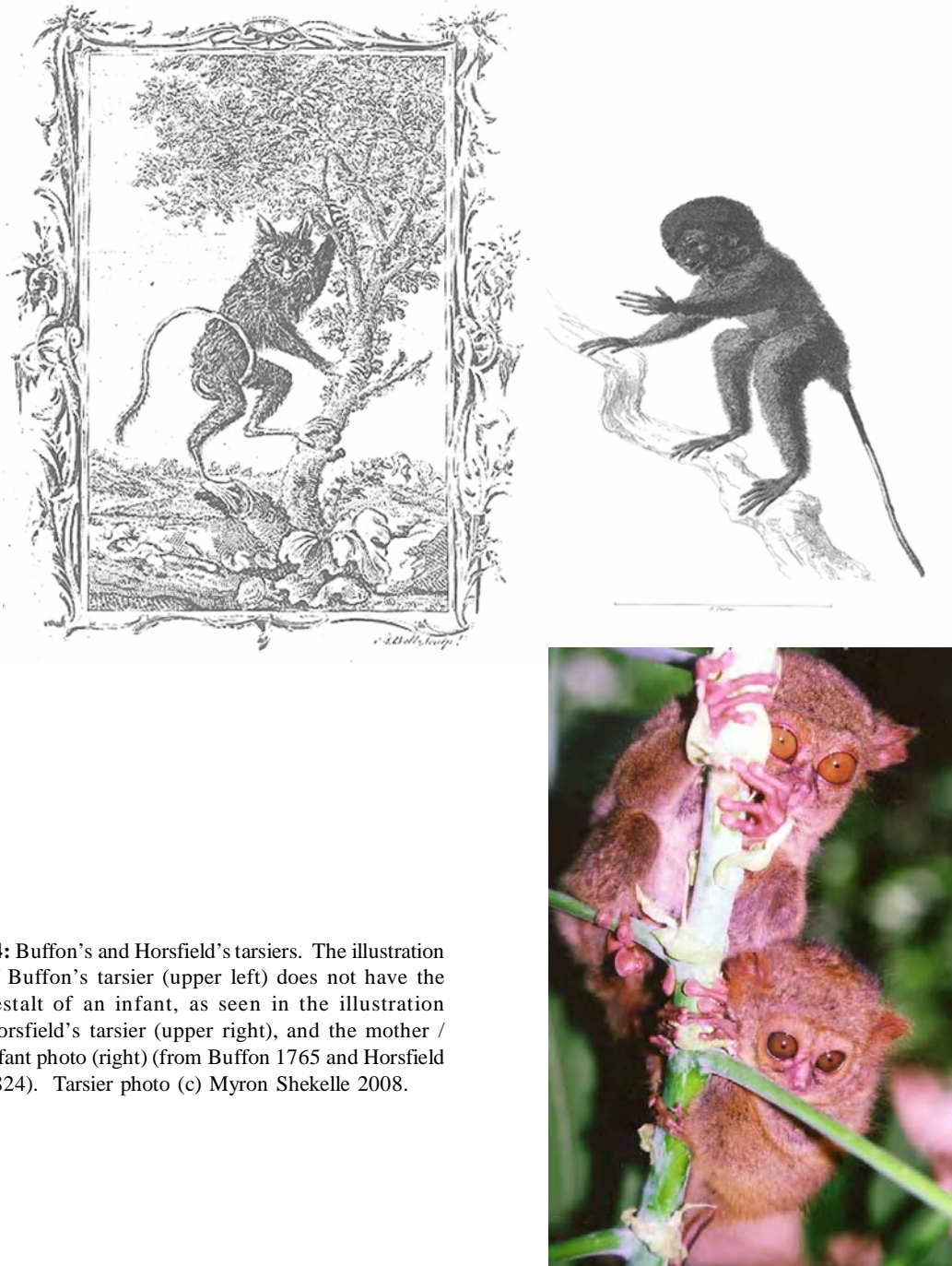


Figure 4: Buffon’s and Horsfield’s tarsiers. The illustration of Buffon’s tarsier (upper left) does not have the gestalt of an infant, as seen in the illustration Horsfield’s tarsier (upper right), and the mother / infant photo (right) (from Buffon 1765 and Horsfield 1824). Tarsier photo (c) Myron Shekelle 2008.

Miller (1910:404) described a new species, *Tarsius fraterculus*, from Bohol in the Philippines, said to resemble *T. philippensis* but smaller in size.

Miller & Hollister (1921) described two new tarsiers from Sulawesi: *Tarsius fuscus dentatus*, from Labuan Sore in the lowlands near Parigi, and *Tarsius pumilus*, from Rano Rano, in the central highlands.

To *T. pumilus* they referred two specimens from Gimpu, in the nearby lowlands, in addition to the type. *Tarsius pumilus* is a valid species, but the Gimpu specimens do not belong to it (Musser & Dagosto, 1987); more recently, Merker & Groves (2006) have included them in their new species, *Tarsius lariang*.

Sody (1949:138-143) adamantly assigned Sulawesi and Western tarsiers to separate species, but could not decide whether those from the Philippines were identical to either or neither of them. He used *T. fuscus* for the Sulawesi tarsier, and *T. bancanus* for the Western. In *T. bancanus* he recognised *T. b. bancanus* (synonym *saltator*) and *T. b. borneanus*, without mentioning Chasen's *naturensis*. In *T. fuscus* he recognized *T. f. fuscus* from Minahassa, *T. f. dentatus* from central Sulawesi ("very weak"), a new subspecies *T. f. pelengensis* from Peleng ("we must acknowledge that we are describing a very poor race"), and *T. f. sangirensis* from Great Sangir ("a very good race").

It was Hill (1953a,b) who first definitively split *Tarsius* into three species, revising their nomenclature (Hill, 1953a) and describing in detail the striking differences in their tails (1953b). His revision was followed for over 30 years, and has been the basis for all subsequent treatments.

Niemitz (1984a) reviewed the differences between the three species, commenting on the synonymy and refusing to recognize any subspecies except for *T. s. spectrum* and *T. s. pumilus*, and *T. b. bancanus* and *T. b. borneanus*. Contrary to Hill (1953a), however, Niemitz indicated Minahassa as the type locality of *T. spectrum* (1984:13).

Musser & Dagosto (1987) further reviewed some of the nomenclatorial history of tarsiers. They accepted that Linnaeus's *Simia syricta* was a Philippine tarsier, but were skeptical of the association of Pallas's *Lemur spectrum* with Sulawesi tarsiers although provisionally prepared to accept Hill's (1953a) opinion. They revised the differences between *T. bancanus*, *T. syricta* and *T. spectrum*, indicating that the first two are somewhat more closely related than either is to the third. Most importantly, Musser & Dagosto (1987) pointed out that the type specimen of *Tarsius pumilus* represents a valid species, and that Miller & Hollister (1921) had muddied the waters by inexplicably assigning to it the two Gimpu specimens (which are juveniles of what Musser and Dagosto regarded as the one and only lowland species, *T. spectrum*). Their demonstration that *T.*

pumilus is a valid species raised the number recognized since Hill (1953a) from three to four.

Feiler (1990) proposed raising *T. sangirensis* Meyer, 1897 to specific rank.

Niemitz et al. (1991) described a new species, *Tarsius diana*, from central Sulawesi without, however, comparing their new taxon to *T. fuscus dentatus*, even though the type localities of these two taxa are separated by only about 80 km.

Groves (1998) produced a preliminary revision of tarsiers, corroborating the provisional findings of Musser & Dagosto (1987) that the Philippine species, *T. syricta*, is closer to *T. bancanus*, but nonetheless very distinct, while *T. pumilus* is closer to *T. spectrum*. Discriminant analysis of admittedly small samples confirms that, within *T. spectrum* (understood broadly), samples from the mainland, Selayar (a single specimen), Peleng and Sangihe are all distinct, and the latter at least is probably a distinct species. On the mainland, northern and central Sulawesi samples separate, if less clearly.

Finally Merker and Groves (2006) described another new species from Sulawesi: *Tarsius lariang* from Gimpu, Central Sulawesi. This finally resolved the true identity of the two juveniles from Gimpu which had been spuriously associated by Miller and Hollister with *Tarsius pumilus*, and unceremoniously expelled from that species by Musser and Dagosto.

Generic names for tarsiers

The earliest generic name for tarsiers is *Tarsius* Storr, 1780, based on *Lemur tarsier* Erxleben, 1777, hence on Buffon's tarsier, a Sulawesi tarsier (see above). The next name, *Macrotarsus* Link, 1795, was likewise based on Buffon's tarsier.

E. Geoffroy St. Hilaire (1812) also listed *Tarsius*, in his *Strepsirrhini*, citing no sources for the generic name but listing two species, *T. spectrum* (referring to Buffon and to Pallas) and *T. fuscomanus* (referring to Fischer).

Gray (1821) included tarsiers in his order Heteronychia of the class Quadrumana; other members of the order were the lemurs and lorises. His tarsiers belonged to the family Loridae, and were placed in two genera:

Tarsier, *Tarsius*. Geoff. *Lemur tarsium* Pallas.
Rabienus. Gray. *Lemur spectrum* Pallas.

The first of these two genera is incorrectly ascribed to E. Geoffroy and awarded, as type species, a non-existent name of Pallas's. *Rabienus*, based on Pallas's genuine name, is a junior subjective synonym of *Tarsius*.

Swainson (1835) described a genus *Cephalopachus*, and Lesson (1840) described *Hypsicebus*, both erected for *T. bancanus* Horsfield, 1824. These names are available if the Western tarsier is regarded as generically distinct from Sulawesi tarsiers. Presuming *Lemur tarsier* Erxleben, 1777 was correctly identified as a Philippine tarsier, Groves (1998) concluded *Tarsius* Storr is available for a genus containing Philippine tarsiers, leaving *Rabienus* Gray for Sulawesi tarsiers; but as *L. tarsier* Erxleben actually refers to a Sulawesi tarsier (see above), Groves's (1998) conclusion is error. No generic name is available for Philippine tarsiers.

DISCUSSION

Given this history, *Tarsius spectrum* is a junior objective synonym of *T. tarsier*. At first glance, the loss of this name, that has been used for tarsiers for over two centuries, seems regrettable. There is a silver lining, however, since the name *T. spectrum* is also associated with more taxonomic ambiguity than any other tarsier nomen. At one time or another, virtually all species of tarsier were referred to as *Tarsius spectrum*, though not always at the same time. Consequently, Clark's (1924) "Notes on the living tarsier (*Tarsius spectrum*)" is an account of *T. bancanus borneanus*. Likewise, Woollard's (1925) monograph "Anatomy of *Tarsius spectrum*" is not an Eastern tarsier, but a Western tarsier. Adding further to the confusion, Eastern Tarsiers were not generally referred to as *T. spectrum* until Hill (1955). Prior to that time, Eastern tarsiers were referred to by a plethora of names, but most often as *T. fuscus*. Thus, it is no overstatement to say that, prior to Hill, the majority of references to *T. spectrum* referred to something other

than an Eastern tarsier, while nearly all references to Eastern tarsiers used a name other than *T. spectrum*.

A further consolation is that it turns out that not one, but a number of different species inhabit Sulawesi, each restricted to a particular part of the island. It will possibly cause less confusion if the name *Tarsius spectrum* applies to none of them than if it is applied to different species, by different authors.

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