

The Genera and Species of Tarsiidae

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Abstract We revise the taxonomy of the primate family Tarsiidae. We classify extant tarsiers in 3 genera—*Tarsius*, *Cephalopachus*, and *Carlito*—each of which originated in the Miocene, or earlier, and each of which is allopatrically distributed within a distinct biogeographic region: Sulawesi, Sundaland, and Greater Mindanao, respectively. Within the genus *Tarsius*, formerly regarded as a single species, *Tarsius spectrum*, we recognize 8 allopatric and parapatric species, 9 if the inclusion of *pumilus* is warranted, and note that more are likely to be described in the near future. We restrict *Tarsius tarsier*, the senior taxon of the genus, to the island of Selayar, off the tip of the southwestern peninsula of Sulawesi. In doing so, it is required that we resurrect *Tarsius fuscus* Fischer 1804, for the population of tarsiers from the southwestern peninsula near the city of Makassar. We note that neither *Cephalopachus* nor *Carlito* has been the subject of anywhere near as much field research as has *Tarsius*; thus we question if the currently accepted α taxonomy for these genera is based on knowledge or ignorance.

Keywords Bantimurung form · Bioacoustics · Biodiversity · Cryptic species · Duet call · Selayar form · Taxonomy

Introduction

For more than half a century, Hill (1955) has stood as the basis for tarsier taxonomy, and all subsequent studies refer to this volume. He recognized 3 allopatric species:

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Tarsius spectrum, *T. bancanus*, and *T. syrichta*. *Tarsius spectrum* was restricted to Sulawesi and surrounding island chains. Five subspecies were recognized: *Tarsius spectrum spectrum*, presumed to originate from an area near the city of Makassar on the southwestern peninsula; *T. s. sangirensis*, from the island of Sangihe, which lies ca. 200 km north of the northern tip of Sulawesi; *T. s. dentatus*, from lowland area of central Sulawesi near the type locality of Labuan Sore; *T. s. pumilus*, from highland areas of central Sulawesi near its type locality of Rano Rano; and *T. s. pelengensis*, from the island of Peleng, which lies southeast of the tip of the eastern peninsula. *Tarsius bancanus* was restricted to a scattering of islands, principally Sumatra and Borneo, now recognized as a subset of the Ice Age landmass known as Sundaland. Four subspecies were recognized: *Tarsius bancanus bancanus*, from the type locality of Bangka Island and also parts of southern Sumatra southwest of the Musi River, *T. b. borneanus* from the island of Borneo, *T. b. saltator*, from the island of Belitung, and *T. b. natunensis*, from the island of Serasan. *Tarsius syrichta* was restricted to islands of the southern Philippines now recognized to have composed the Ice Age landmass known as Greater Mindanao. Three subspecies were recognized: *Tarsius syrichta syrichta* from the type locality of Leyte and also from Samar, *T. s. carbonarius*, from the island of Mindanao, *T. s. fraterculus*, from the island of Bohol.

Following Hill came the work of Niemitz (reviewed by Niemitz 2010) and that of Musser and Dagosto (1987). Although the purpose of the latter revision was to define and delimit the previously misunderstood *Tarsius pumilus*, they also provided a detailed survey and comparison of extant tarsiers. Both studies, that of Niemitz and that of Musser and Dagosto, were based on surveys of museum specimens, and both found strong support for the basic findings of Hill (1955) that tarsiers are classified in 3 highly distinct species. However, in both cases, support for nearly all of the subspecies recognized by Hill was found to be weak or nonexistent. The exceptions were that Niemitz recognized 2 subspecies of *Tarsius spectrum*, *T. s. spectrum* and *T. s. pumilus*, and 2 of *Tarsius bancanus*, *T. b. bancanus* and *T. b. borneanus*, while Musser and Dagosto recognized *Tarsius pumilus* as a distinct species, adapted to the mossy montane forests of Sulawesi at elevations >1800 m.

Shekelle (2008a) noted that subsequent fieldwork and taxonomic investigations were highly skewed toward Sulawesi. Thus, whereas Hill's subspecies of *Tarsius bancanus* and *T. syrichta* were based on populations presumably having resulted from a post-Pleistocene rise in ocean levels, data relevant to the α taxonomy of these 2 species are notably sparse. There is evidence in Hall (2001) that Greater Mindanao might have formed from smaller islands, as was the case for Sulawesi, and thus the α taxonomy of Philippine Tarsiers might possibly have been shaped by far more ancient geological events. Shekelle (2008a) argued that the peculiar distribution of tarsiers on a limited subset of Sundaland bore the stamp of a Holocene range expansion out of a refuge in northern Borneo. Both of these hypotheses could be tested in the future via systematic field studies of complementary data sets.

We present an interim taxonomic revision of the family Tarsiidae, based upon our own review of existing evidence, supplemented by examination of additional museum specimens not included in previous studies. From our work we have discovered additional morphological characters that differentiate what for Hill were his 3 species. Likewise, we note that molecular studies (Meireles *et al.* 2003;

Shekelle 2003; Shekelle *et al.* 2008a, 2010) have shown very deep divisions between what have now emerged as 3 species-groups, indicating that they separated from one another in the Middle or Late Miocene; more recently, Matsui *et al.* (2009) provided molecular clock estimates for the split of Philippine and Western Tarsiers that include dates as far back as the Oligocene and even the Eocene. Under these circumstances, we propose 3 distinct genera of extant Tarsiidae. Further, based on the increasingly convincing evidence that Buffon's tarsier did not come from Makassar, and most likely did come from Selayar Island, *Tarsius tarsier* is restricted to the island of Selayar, and we resurrect Fisher's *Tarsius fuscus* for the population of tarsiers around Makassar on the southwestern peninsula of Sulawesi.

Nomenclature

Though both Erxleben (1777) and Pallas (1778) referred the tarsier to the Linnaean genus *Lemur*, Storr (1780) was the earliest author to separate it as a new genus, *Tarsius*. Dr. Doug Brandon-Jones has kindly examined Storr's publication on our behalf, and reports that the word in fact occurs only in the plural, *Tarsii*, although the singular form of the name was accepted by the International Commission on Zoological Nomenclature in 1936. Storr's name was based on Erxleben's *Lemur tarsier* and on Pallas's *Lemur spectrum*, and the Commission accepted the selection of *Lemur tarsier* Erxleben 1777 as type species by Palmer (1904), correcting an earlier opinion that the type was *Lemur spectrum* Pallas. In any event, it makes little difference; both *tarsier* and *spectrum* were Sulawesi tarsiers (Groves *et al.* 2008; Callou *et al.* 2010).

The next name, *Macrotarsus* Link 1795, was likewise based on Buffon's tarsier.

Gray (1821) included tarsiers in his order Heteronychia of the class Quadrumana; other members of the order were the lemurs and lorises. The tarsiers, in his system, belonged to the family Loridae, and were placed in 2 genera:

Tarsier, *Tarsius*. Geoff. *Lemur tarsium* Pallas.

Rabienus. Gray. *Lemur spectrum* Pallas.

The first of these 2 genera is Storr's, but incorrectly ascribed to E. Geoffroy St. Hilaire and awarded, as type species, a nonexistent name of Pallas's. As Erxleben's *Lemur tarsier*, the type species of Storr's *Tarsius*, was a Sulawesi tarsier, then *Rabienus*, based on Pallas's (genuine!) name, is a junior subjective synonym of *Tarsius*. Groves (1998), assuming the correctness of the common assumption that *Lemur tarsier* Erxleben was either a Philippine Tarsier or was indeterminable, concluded that *Tarsius* Storr is therefore available for a genus containing Philippine Tarsiers, and that this would leave *Rabienus* Gray for Sulawesi tarsiers. This conclusion now appears to be in error: *Tarsius* Storr 1780 is the earliest available name for the Eastern (Sulawesi) Tarsiers.

Swainson (1835) described a genus *Cephalopachus*, and Lesson (1840) described *Hypsicebus*, both erected for Horsfield's *Tarsius bancanus*. Both made reference to the large head, relative to the body, described by Horsfield (1824). These names are available if, as we argue below, the Western Tarsier is regarded as generically distinct from Sulawesi (Eastern) Tarsiers.

No generic name is available for Philippine Tarsiers. We here provide one.

Revision

Extant Tarsiidae are classified within 3 genera, as follows (Fig. 1):

Tarsius Storr 1780

Type species: *Lemur tarsier* Erxleben 1777.

Dentition as a whole: Dentition relatively small.

Maxillary dentition: *Anterior*: Cingulum on upper incisors and canine forms barely more than a slight rim, which does not continue lingually. Upper central incisor high-crowned, contrasting strongly with very reduced lateral incisor. I^2 upright. Upper canine small. *Posterior*: P^2 reduced, tiny compared to adjacent canine; P^3 high-crowned but very slender; P^4 only slightly higher than other premolars, and has only a narrow lingual cusp. Upper molars with hardly any hypocone development. Cingulum on upper molars almost entirely suppressed, and does not form a postero-lingual corner on M^3 , and this is at most slightly indicated on M^1 and M^2 . M^3 is a simple triangle.

Mandibular dentition: *Anterior*: Lower incisors close together, apposed along most of their length. *Posterior*: P_2 relatively small, P_3 slender. On lower molars,

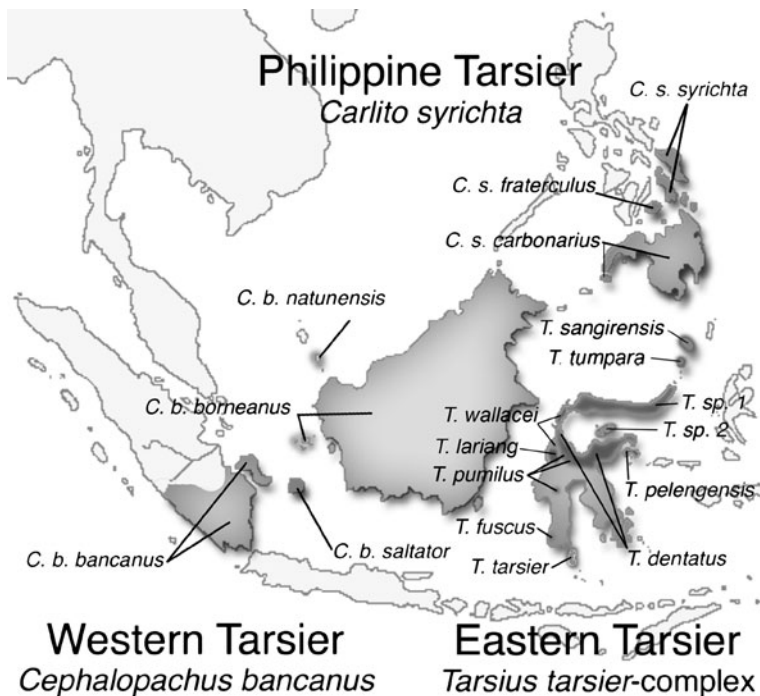


Fig. 1 Distribution map of the genera and species of Tarsiidae. Subspecies of *Cephalopachus* and *Carlito* are illustrated for reference, but the validity of these is questioned.

talonids much wider than trigonids. Paraconids less forwardly produced. Hypoconulid of M_3 short.

Basicranium: Occipital condyle prominent, well defined. Foramen magnum elongated, lozenge-shaped. Auditory bullae narrowed anterior to carotid foramen, which is large and centrally placed. Tympanic tube strongly elongated.

Cranial vault: Cranial vault flatter than other tarsiers. Posterior margin of occiput inflated, seen from above, with no separate median prominence; in side view, inion hardly distinguishable. Temporal lines diverge from orbital margins as they turn backward. Metopic suture remains as visible in adult as other vault sutures.

Facial skeleton: Masseter scar on underside of zygomatic arch broad, extending well forward along lower rim of orbit. Palate narrow; rostrum pinched in behind premolars. Coronoid process low, slopes backward; sigmoid notch rather shallow. Gonial angle not produced backward. Orbits less dorsally extended and less laterally flaring (so that biorbital breadth is 8–10 mm less than greatest skull length), their inferolateral margins entire or only slightly notched. Malar foramen either discrete or, if open to orbit, then forms a very clear cavity in orbital margin. Nasals long (not restricted by median orbital margins), their sides sloping, and project forward over anterior nares, which are wide.

External characters: Eyes less enlarged than other tarsiers. A light postauricular spot in most cases; a bare patch at ear-base; a black paranasal spot nearly always present. Ears markedly elongated, >30 mm long. Facial hair markedly shorter than hair surrounding it, giving the impression of a dark somewhat heart-shaped ring round face.

Tail: Tail dark on dorsal surface, with long, thick dark tuft, usually occupying >100 mm of the tail, and grading into the short hair of rest of upper side of tail. Underside of tail scaly; each scale gives off 3 short hairs, giving it a raspy texture.

Limbs: Tarsus noticeably haired, though often somewhat sparsely; particularly the ventral surface of the tarsus becomes less haired as the tarsier ages, while the dorsal surface remains fully haired at all life stages. Hind limb less elongated than other tarsiers; shank in particular is relatively short; tarsus long compared to rest of foot. Fingers less elongated than other tarsiers. Fingernails not so strongly reduced as other tarsiers, pointed, and with noticeable median keel.

Mammæ: 3 pairs (1 pectoral, 2 abdominal).

Chromosomes: $2n=46$ in *Tarsius dentatus* (Niemitz *et al.* 1991), and we provisionally assume the same for other species in this genus.

Behavior: Sleep in social groups, typically 1 adult male–female pair plus immature offspring, but can be up to 8 individuals; the social organization of these larger groups is not yet understood; male–female pairs perform a sexually dimorphic duet; in larger groups all adults and some subadults join in, creating a family chorus.

Included species: *Tarsius tarsier* (Erxleben 1777); *Tarsius fuscus* Fischer 1804; *Tarsius sangirensis* Meyer 1897; *Tarsius dentatus* Miller and Hollister 1921; *Tarsius pelengensis* Sody 1949; *Tarsius lariang* Merker and Groves 2006; *Tarsius tumpara* Shekelle *et al.* 2008b; *Tarsius wallacei* Merker *et al.* 2010; *Tarsius pumilus* Miller and Hollister 1921 is provisionally placed here (Shekelle 2008b). Sulawesi tarsiers are a taxonomically cryptic cluster of

related species known as the *Tarsius tarsier* (=spectrum)-complex, or, Eastern Tarsiers, i.e., tarsiers from Sulawesi and surrounding islands. As with many other taxonomically cryptic nocturnal taxa, these species are most easily diagnosable via bioacoustics, with subtle morphological variation noticeable subsequent to the identification of acoustic forms, i.e., geographically distinct acoustic variants. Acoustic evidence suggests that there may be ≥ 16 distinct species within the *Tarsius tarsier*-complex, implying that ≥ 8 more remain undescribed (Shekelle *et al.* 2008b; Shekelle 2008c). We are in the process of naming 2 of these, 1 from the Togian Islands, and a second from the northern arm, north and east of the range of *Tarsius wallacei* to the furthest northern tip (a taxon that we suspect will ultimately be subdivided into a total of 3 taxa).

Cephalopachus Swainson 1835

Dentition as a whole. Dentition very large.

Maxillary dentition. *Anterior*: Upper incisors low-crowned, especially the central ones. I^2 slants inward. Upper canine large. There is no, or only a very slight, diastema between upper canine and lateral incisor. *Posterior*: P^2 large; P^4 much higher than other premolars, and with prominent, cuspidate lingual cingulum. Upper molars with strong hypocones. Cingulum of upper molars much better developed than in *Tarsius*; on the posterolingual aspect, the cingulum gives the tooth a projecting corner, making M^3 noticeably widened lingually. On upper incisors and canines, cingulum forms a curving and downwardly concave ridge that surrounds each tooth and on I^2 forms a talon.

Mandibular dentition. *Anterior*: Lower incisors well spaced, slant medially. *Posterior*: P_2 relatively large, P_3 wide. On lower molars, talonids and trigonids of approximately equal width. Paraconids project forward. Talonid of M_3 much longer, more pointed than in *Tarsius*. Hypoconulid on M_3 very elongated.

Basicranium. Occipital condyle less prominent, more a simple thickened rim to foramen magnum. Foramen magnum more rounded. Auditory bulla enlarged and dilated anteriorly; carotid foramen small, shifted laterally. Tympanic tube much less elongated.

Cranial vault. Occiput flat, when seen from above, except for a narrow median ridge running from inion (which is very prominent) up occipital scale to lambda. Cranial vault arched. Temporal lines follow orbital rims medially before turning backward. Metopic suture obliterated in adult.

Facial skeleton. Masseter scar on underside of zygomatic arch narrower and more restricted. Palate wide. Rostrum evenly wide. Coronid process high, vertical, but sigmoid notch relatively shallow. Gonial angle strongly produced backward. Orbits greatly flaring (making biorbital breadth only *ca.* 2–3 mm less than greatest skull length), dorsally projecting, their inferolateral margins strongly emarginated by the malar foramen, which is open to the orbit and is little more than a notch in the orbital margin; orbital rims nearly meet in midline, making interorbital space exceptionally narrow, and greatly reducing the length of the nasals. Nasals higher, with vertical, parallel sides, and not, or hardly, projecting forward over anterior nares, which are narrow.

External characters. Eyes and head enormously enlarged. Head buffy, lighter than body; a dark mark on knee. No postauricular light spot, and no or only a slight bare

patch at ear-base. Ears relatively short, <30 mm long. There is no difference in length of hair on face and on crown or cheeks, though when the eyes are fully open there may be a double-arched furrow above them, somewhat mimicking the circumfacial dark ring of *Tarsius*.

Tail. Tail dark red brown, with brown brush, extending *ca.* 50 mm along tail-tip, and sharply marked off from very short hair on rest of upper surface of tail. Underside of tail naked, with V-shaped sulci separated by longitudinal ridges.

Limbs. Tarsus well-haired. Lower limb enormously elongated, particularly thigh; foot relatively less elongated than rest of limb. Fingers greatly elongated, the third (middle) finger differentially more so than the others. Fingernails very reduced. Fourth toe differentially elongated; tarsus relatively long compared to rest of foot.

Mammae. 3 pairs (1 pectoral, 2 abdominal).

Chromosomes. $2n=80$ (Klinger 1963).

Behavior. Individuals do not sleep in social groups larger than an adult female with 1 immature offspring. *Cephalopachus* does not duet.

Included species: At present, only the type species *Cephalopachus bancanus* (Horsfield 1824) is recognized in this genus, but this is for want of a detailed revision. The characters of the high-altitude tarsier from Borneo recorded by Gorog and Sinaga (2008) suggest initial directions for future taxonomic research in this genus.

Carlito New Genus

Etymology: *Carlito*, “diminutive man of the countryside,” from the German Karl or Carl (country man), and the diminutive suffix from Spanish, *-ito*. We propose this name as an apt description of tarsiers as small primates of the countryside, but more particularly in recognition of Carlito Pizarra, the “Tarsier Man” of the Philippines, featured in nature films such as *The Littlest Alien*, a man of the Visayan countryside who dedicated his life to the pursuit of knowledge about and the conservation of the Philippine Tarsiers.

Dentition as a whole. Dentition large.

Maxillary dentition. *Anterior*: I^1 and I^2 high-crowned. Upper canine large. A noticeable diastema between I^2 and upper canine. *Posterior*: P^2 reduced, tiny compared to adjacent canine; P^4 much higher than other premolars, and with prominent, cuspidate lingual cingulum. Upper molars with strong hypocones, and well-developed cingulum.

Mandibular dentition. *Anterior*: Lower incisors well spaced, slant medially. *Posterior*: P_2 relatively large, P_3 wide. On lower molars, talonids and trigonids of approximately equal width. Paraconids project well forward.

Basicranium. Occipital condyle rim-like. Foramen magnum rounded. Auditory bulla anteriorly dilated; carotid foramen small, shifted laterally. Tympanic tube very elongated.

Cranial vault. Cranial vault arched. Occipital shape like *Cephalopachus*, but with less marked median ridge. Temporal lines follow orbital rims medially before turning backward. Metopic suture obliterated in adult.

Facial skeleton. Masseter scar on underside of zygomatic arch narrower and more restricted. Palate wide; rostrum evenly wide. Coronoid process high, vertical; sigmoid notch deep. Gonial angle extends backward very prominently.

Orbits flaring, though less than in *Cephalopachus* (so that biorbital breadth is some 7–8 mm less than greatest skull length), their inferolateral margins slightly notched by malar foramen; rims somewhat project dorsally. Interorbital space relatively wide. Nasals medium in length; anterior nares narrow.

External characters. Eyes enlarged. No postauricular light spot, and no bare patch at ear base. Ears relatively short, <30 mm long. Facial and circumfacial hair not differentiated.

Tail. Tail poorly pigmented, smooth, virtually naked on upper and under sides except at base, with no tuft; underside of tail smooth, with no scales or ridges, unpigmented (sharply set off from slightly pigmented upper side).

Limbs. Tarsus naked. Hind limb hardly more elongated than in *Tarsius*, the shank and foot being progressively more elongated; metatarsus less elongated vs. foot than in other tarsiers. Fingers somewhat more elongated than in *Tarsius*, but not as greatly as in *Cephalopachus*, and the third (middle) finger not differentially elongated. Fingernails very reduced, but larger than in *Cephalopachus*.

Mammæ. 2 pairs (1 pectoral, 1 abdominal).

Chromosomes. $2n=80$ (de Boer and de Boer-van der Vlist 1973).

Behavior. Individuals do not sleep in social groups larger than an adult female with one immature offspring. *Carlito* does not duet.

Included species. Thus far, only the type species *Carlito syrichta* is recognized in this genus, but this is for want of a modern revision.

Notes. There are good reasons to believe that this new genus is closer to *Cephalopachus* than to *Tarsius*. The sister-genera within Tarsiidae are nonetheless quite distinct and according to molecular chronometric studies, they separated 5.6 Ma (Meireles *et al.* 2003), or 11.1 (4.4–18.5) Ma (Shekelle *et al.* 2010), or 30.8 ± 3.9 (23.4–38.6) Ma based upon protein coding mtDNA, or 20.2 ± 3.3 (14.5–27.4) Ma based upon rRNA coding mtDNA (Matsui *et al.* 2009). Thus, in all likelihood, the *Cephalopachus-Carlito* split occurred by the late Miocene, and possibly as early as the Eocene. We have no hesitation in separating Philippine Tarsiers from Western Tarsiers at the generic level.

Notes on Species Within *Tarsius*: *Tarsius tarsier* and *T. fuscus*

Tarsius tarsier (Erxleben 1777)

1749 “Tarsier or Woolly Jerboa” Buffon, *Histoire Naturelle*, 13, N°MCCXXXV. Locality, in all probability, Selayar Island.

1777 *Lemur tarsier* Erxleben, *Systema Regni Animalis per Classes, Ordines, Genera, Species, Varietates, cum Synonymia et Historia Animalium*: Classis I. Mammalia, 71. Based on Buffon’s tarsier.

1778 *Lemur spectrum* Pallas, *Novae Species Quadrupedum e Glirium Ordine cum Illustrationibus Variis Complurium ex Hoc Ordine Animalium*, 275. “Extremas insulas Oceani indici, praesertim Amboynam” (The furthest islands of the Indian Ocean, probably Amboyna); fixed as Makassar by Hill (1953), but inspection of the text reveals that, although Pallas did have access to original material, the name is actually based on Buffon’s tarsier.

1778 *Didelphys? macrotarsos* Schreber, Die Säugethiere in Abbildungen nach der Natur, 555. Based on Buffon's tarsier.

1781 "Tarsier" Pennant, History of Quadrupeds, 216. "Remotest islands of India, especially Amboina."

1792 *Lemur podje* Kerr, The Animal Kingdom, or Zoological System, of the Celebrated Sir Charles Linnaeus. Class I. Mammalia, 88. Based on Pennant's tarsier.

1795 *Macrotarsus buffonii* Link, Beytrage zur Naturgeschichte, 1, pt.2. Based on Buffon's tarsier.

1796 *Tarsius pallassii* E.Geoffroy St.Hilaire, Magasin encyclopédique (2) 1. Renaming of *Lemur spectrum* Pallas.

1804 *Tarsius daubentonii* Fischer, Anatomie der Maki, 37. Based on Buffon's and Pennant's tarsiers.

1998 "Selayar tarsier": Erroneously thought to be a new species by Groves (1998) based upon his assumption that Buffon's tarsier came from Makassar.

Type: (Paris Natural Museum) PNM CG 1994–2465, A. 3948

Diagnosis: Size similar to or just slightly larger than *Tarsius fuscus*, but hind foot shorter; posterior part of auditory bulla (behind carotid foramen) very short; nasal tip not strongly convex; a small, not very marked, diastema between I² and C'. Pelage more silky; tail pencil short, rather sparse, not black; color tends to be more yellow or brown-toned than mainland Sulawesi taxa; thigh colored as body; black paranasal spot conspicuous, especially over nose itself; conspicuous zone of white or buffy hair on sides of upper lip. Previously referred to as the Selayar Form on bioacoustic evidence.

Description: Tooththrows short; tail pencil tends to be short, but variable (95–124 mm); tail relatively long, 221% of head and body in 2 specimens. Manual pads almost fused in examined specimens. Duet call is described by Nietsch and Burton (2010).

Material: (British Museum of Natural History) BMNH 1939.1320 (Selayar), skin and skull. (Naturalis Leiden) NRL 28690 = cat.c or h = cat.no.5 of Schlegel, 1876 (Selayar), skin and skull; cat.d or i, cat.no.6 of Schlegel, 1876 (Selayar), skin only, juvenile. (Museum Zoologicum Bogoriense) MZB 24301 (Selayar), skin and skull, formerly living specimens: White 45, Pink 24.

Comments: In the discriminant analyses based on cranial and dental variables, the 3 available skulls of this new species fall outside the range of all other samples of *Tarsius* (Groves 1998 unpubl. data).

Tarsius fuscus (Fischer 1804)

1804 *Tarsius fuscus*, s. *fuscomanus* Fischer, Anatomie der Maki, 37.

1804 *Tarsius fischerii* Desmarest, Nouveau Dictionnaire d'Histoire Naturelle, 1st ed., 24:32. Renaming of *Tarsius fuscomanus* Fischer.

Locality: Said to come from Madagascar, but probably an error for Makassar (as recognized by Fischer, himself). Thus, in all probability, Makassar.

Diagnosis: Skull comparatively short, below the range of *Tarsius dentatus*; tooththrows short, the mandibular tooththrow being below, or only just overlapping, the ranges of most other species; nasal tip not strongly convex; a well-marked diastema between I² and upper canine (C'). Hind foot much shorter than that of other species;

fingers long, with long, wide pads. Pelage more reddish brown than that of other mainland species, only somewhat brown on thigh; tail pencil strikingly long, black; black paranasal marks thinner, more Y-shaped over nose; patch of light lateral lip hair small, creamy; bare spot at base of ear small; postauricular spot conspicuous, white; no black along eye-rims; tarsus hair dense, pale.

Description: Tail comparatively short, 143–166% of head and body (Musser and Dagosto 1988). The excellent description by Fischer (1804) tallies exactly with the 2 living specimens on which our description of external features is based (we have not been able yet to study in detail the small American Museum of Natural History series); from this, we infer that the paranasal spot is not marked nor is the white haired zone on the upper lip conspicuous. Thenar and interdigital pads usually fused.

Material: (American Museum of Natural History) AMNH 153553-8 (Lombasang) (skulls; not seen, skull measurements courtesy of Dr. Marian Dagosto). MZB, formerly living specimens: White 26, Pink 26 (both from Pattanuang, near Maros); also two infants, MZB 24305 and -6 (offspring of the living pair, died in infancy).

Comments: The description of this species is necessarily incomplete, because we have been able to examine too few skulls in person.

Table 1 Summary of many of the most conspicuous recognition features for the genera of Tarsiidae

	<i>Tarsius</i>	<i>Carlito</i>	<i>Cephalopachus</i>
Dentition	Smallest	Intermediate	Largest
Eyes	Smallest	Intermediate	Largest
Hind limbs and hands	Shortest	Intermediate	Longest
Tail tuft	Most hirsute: Resembles a test tube brush	Least hirsute: Nearly naked	Intermediate: Resembles a feathered arrow shaft
Tail sitting pad	Friction surface	Dermal skin	Dermal skin with papillary ridges
Mammae	3 pairs	2 pairs	3 pairs
Chromosomes (2n)	46	80	80
Socioecology	Most social: Social groups	Intermediate: No social groups in wild; tolerates social groups in captivity	Least social: No social groups in wild; does not tolerate social groups in captivity
Vocalizations	Most vocal: Duets	Intermediate: No duets	Least vocal: No duets
Distribution	Indonesia: Ice Age Sulawesi, plus disjunct islands including the Sangihe Islands, Togian Islands, Peleng Island, and Selayar Island	Philippines: Ice Age Mindanao	Brunei, Indonesia, Malaysia: A restricted subset of Ice Age Sundaland including Borneo, Sumatra, Bangka, Belitung, Karimata Islands, South Natuna Islands, and others

Conclusion

Extant tarsiers are classified in 3 genera, allopatrically distributed in distinct biogeographic regions: *Tarsius* is found on Sulawesi and surrounding islands; *Cephalopachus* is found on a restricted subset of Sundaland, principally southern parts of Sumatra and the island of Borneo; *Carlito* is found on islands of the southern Philippines that were a single Ice Age landmass, sometimes called Greater Mindanao (Table 1). *Tarsius* currently contains 8 species, 9 if future studies show that the inclusion of *pumilus* is warranted; 2 more are in the process of description, and we suspect ≥ 6 additional species. The speciose α taxonomy of *Tarsius* stands in contrast with the unspeciose α taxonomy for *Cephalopachus* and *Carlito*. We question if this contrast is based upon knowledge, or ignorance, of the α taxonomy of the latter 2 species. Experience has shown that studies of museum specimens were of limited value for the α taxonomy of *Tarsius* until they were supported by field studies; even genetic data, by themselves, have been less valuable than when they have been combined with complementary data sets, such as bioacoustics, morphology, and biogeography. We encourage more fieldwork, especially holistic studies of complementary data sets, to address questions of tarsier α taxonomy.

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