Pteropus Erxleben, 1777
Flying Foxes

Pteropus Erxleben, 1777:130. Type species Vesperillo vampyrus Linnaeus, in part, by subsequent designation (see Hopwood, 1947).

Spectrum Lacépède, 1799:15. Type species Spectrum vampyrus (= Vesperillo vampyrus Linnaeus), by monotypy. Preoccupied by Spectrum Scopoli, a lepidopteran.

Eurycteris Gray, 1866:64. Type species Pteropus phaios Temminck (= Pteropus melanopus), by monotypy.

Pselaphon Gray, 1871:110. Type species Pteropus urinus Temminck (= Pteropus pselaphon Layard), by monotypy.

Sericocterys Matschie, 1899:30. Type species Pteropus rubricollis E. Geoffroy (= Pteropus subunguis Kerri), by original designation.

Desmalopex Miller, 1907:60. Type species Pteropus leucopterus Temminck, by original designation.


Pteropus tonganus (Quoy and Gaimard, 1830)
Pacific Flying Fox

Pteropus tonganus Quoy and Gaimard, 1830:74. Type locality Tonga Islands, Tongatapu Island.

Pteropus geddiie MacGillivray, 1860:1734. Type locality Aneitum Island, Vanuatu.

Pteropus flavicollis Gray, 1871:107. Type locality fixed as Manua Island, Fiji, by Andersen (1912).

Pteropus basiliscus Thomas, 1915:357. Type locality Karkar Island, off the northeast coast of New Guinea.

Pteropus heffernani Troughton, 1930:3. Type locality Tikopia, Santa Cruz Islands.

CONTEXT AND CONTENT. See above. Three subspecies are currently recognized:

P. t. basiliscus Thomas 1915, see above.

P. t. geddiie MacGillivray, 1860, see above (P. t. heffernani Troughton, 1930:3 is a synonym).

P. t. tonganus Quoy and Gaimard 1830, see above.

DIAGNOSIS. The color pattern of P. tonganus, black back with contrasting orange or yellow mantle, is common to several sympatric species of Pteropus. Pteropus tonganus (length of forearm, 120–160 mm) is larger than P. admirabilis (length of forearm, <120 mm) and smaller than P. alecto and P. conspicillatus (length of forearm, >160 mm). P. tonganus lacks a uropatagium, which is found in P. giganteus, P. iylei, P. seychellensis, and P. vampyrus. P. tonganus has a darker ventrum than P. hypomelanus. P. tonganus has shorter ears (<31 mm) than P. macrotis (≥34 mm). P. tonganus is most likely to be confused with P. mariannus. Externally, they are quite similar in appearance, but the skulls can be distinguished by the diameter of the orbit, which is >12 mm in P. tonganus and <12 mm in P. mariannus. P. tonganus lacks the conspicuous paler-colored rings around the eyes of P. ocellaris and the pale crown patch of P. polocephalus (Pierson and Rainey, 1995).

GENERAL CHARACTERS. The pelage of P. tonganus is predominantly seal brown with a sharply contrasting mantle of cream buff to tawny ochraceous (Fig. 1: Wilson and Engrin, 1992:83, fig. 7) in both young and adult bats (Cox, 1983). Russet hairs are intermixed with the seal-brown hairs between the eyes and around the base of the ears. Cream-buff hairs are interspersed with the seal-brown coat on both the dorsal and ventral sides. The forearm and tibia are bare. The chin is covered by very short seal-brown hairs. The throat has one or two patches of tawny ochraceous or russet, which gradually give way to the mantle. Andersen (1912) noted differences between males and females in texture and color of the hairs of the mantle and neck. The stiff, short, oily hairs of the males can vary near the base from uniform buffy to blackish. The long, soft, spreading hairs of the females have concealed seal-brown bases.

Averages and ranges (in parentheses) of external measurements (in mm) for both sexes are: total length, 231 (151–262); length of hind foot, 47.2 (40.5–61); length of ear, 29.1 (20–31); length of forearm, 151.4 (114–175.4); length of tibia, 68.1 (54–76); length of calcar, 19.8 (16–23); longest hairs of back, 12.3 (10–17). Body mass averages 565 g (range, 191–1,099 g—Andersen, 1912; Baker and Baker, 1936; Sanborn and Nicholson, 1950; Wilson and Engrin, 1992; Wodzicki and Felten, 1975). Averages and ranges (in parentheses) of skull measurements (in mm) for both sexes are (Fig. 2): greatest length of skull, 66.4 (56.4–74.6); condylobasal length, 65.9 (55.7–72.2); postorbital width, 7.1 (5.3–9.2); interorbital width, 8.6 (6.6–9.9); zygomatic width, 35.4 (29.3–39.4); mastoid width, 21.6 (19.5–23.6); width of braincase, 22.6 (20.5–24.7); braincase length, 37.3 (33.3–46.9); C–M2 (alv.), 25 (21.7–30.9); rostrum length, 32.4 (29.4–36.7); orbital diameter, 12.4 (11.5–13.0—Andersen, 1912; Sanborn and Nicholson, 1950; Wodzicki and Felten, 1975, 1980).

Baker and Baker (1936) suggested that adult males (≥600 g)

FIG. 1. Pteropus tonganus from Samoa. Photograph by Merin D. Tuttle.
trenchant differences between the subspecies that warrant further examination.

**DISTRIBUTION.** Similar to 80% of other species of *Pteropus*, *P. tonganus* is found only on islands (Rainey and Pierson, 1992). *P. tonganus* is found south of the equator (Fig. 3; Andersen, 1912) from the Schouten Islands (off NE New Guinea), south to New Caledonia, and east to the Cook Islands (Koopman, 1993; Kula, 1992; Marshall, 1983). The westernmost subspecies, *P. t. basiliscus*, is restricted to Karkar and the Schouten Islands, including Koi (Koopman, 1979; Laurie and Hill, 1954; Pierson et al., 1992; Rainey and Pierson, 1992).

The range of *P. t. geddiei* encompasses the Solomon Islands, New Caledonia (including the Loyalty Islands), and Vanuatu. The distribution of *P. t. geddiei* in the Solomon Islands has traditionally been restricted to Rennell and the Santa Cruz Group (Hill, 1958; Phillips, 1969); however, it was recently discovered on Malaita (Flannery, 1989), and Pierson et al. (1992) suggest that it may be widespread, but not common throughout the Solomon Islands. In Vanuatu and New Caledonia *P. t. geddiei* is common, although on New Caledonia *P. ornatiss* is more common (Rainey and Pierson, 1992). In Vanuatu *P. tonganus* has been documented from Malekula, Elephant, Espiritu Santo, Efate, and Pentecost Island (Sanborn, 1931). *P. tonganus* has been reported from the Santa Cruz Islands (Vanikoro, Tapooua, and Santa Cruz), Matena (Swallow) Islands (Napuan), Duff Group (Murasers Island), and Solomon Islands (Tupicia and Rennel—Sanborn, 1931).

The easternmost subspecies, *P. t. tonganus*, occurs from Fiji, Tonga, Wallis, Futuna, and Western and American Samoa to Niue and the southern Cook Islands of Ranotonga and Mangaia (Andersen, 1912; Cox, 1903; Hill, 1979; Pernetta and Wadding, 1978; Pierson et al., 1992; Rainey and Pierson, 1992; Sanborn, 1931; Wilson and Engbring, 1978, 1970). In Samoa it has been found on Tutuila, Aunu'u, Ofu, Olosega, Ta'u, Savai'i, Apolima, Upolu, and Manono Island (Wilson and Engbring, 1972). *P. tonganus* frequently occupies small offshore islands (Wilson and Engbring, 1992). In Fiji *P. t. tonganus* has been recorded from Viti Levu, Vanua Levu, Taveuni, Ovalau, Moala, Totoya, and Naruka, and it is likely to occur on others (Degener, 1949; Pierson et al., 1992; Sanborn, 1931; Wilson and Engbring, 1992). There is no known fossil record of this species.

**ONTOGENY AND REPRODUCTION.** Like most *Pteropus*, *P. tonganus* has only one young per year (Baker and Baker, 1936; Pierson and Rainey, 1992). The time of year varies, depending on subspecies or location. In Samoa births have been observed in January, June, July, August, and October (Banack, 1996; Pierson and Rainey, 1992), and Banack (1996) suggested that in American Samoa, *P. tonganus* reproduces year-round. There is a synchronous breeding season for *P. t. geddiei* on Vanuatu (Baker and Baker, 1936) and New Caledonia, and for *P. t. tonganus* on the Cook Islands (Wodzicki and Felten, 1980); however, young may develop slightly later in New Caledonia (Sanborn and Nicholson, 1950). Conception does occur as late as June or July according to Baker and Baker, 1936, implying a more extended breeding season. After about a six-month gestation period, bats are born in August or early September on Vanuatu (Baker and Baker, 1936) and the Cook Islands (Wodzicki and Felten, 1980). The breeding season of *P. tonganus* in Niue was between March and June, which coincides with the appearance of a favored food, *Syzygium* fruits (Wodzicki and Felten, 1975). Pierson and Rainey (1992) and Pierson et al. (1992) implied a more extended breeding season in Niue, and Grant (1994) suggested that the bats there may give birth year-round as they do in Samoa.

**ECOLOGY.** *Pteropus tonganus* is fairly adaptable, and is found in a variety of habitats and on widely dispersed islands throughout the south Pacific (Pierson et al., 1992). Koopman (1979) characterized it as a supertramp species, because it occurs on smaller, isolated, islands with few other species of bats, and is
absent from large, species-rich islands in the same region (Rainey and Pierson, 1992).

This species is primarily nocturnal and roosts colonially in montane and lowland native forests, along cliffs, islets, in intermediate zone vegetation, fresh water and inland swamps, i.e., in relatively inaccessible sites (Cox, 1983; Pernetta and Walling, 1978; Pierson and Rainey, 1992; White et al., 1988; Wilson and Enghrinding, 1992; Wodzicki and Felten, 1980). P. tonganus is occasionally found in coastal and mangrove swamps. The bats disperse from colonies to forage primarily in natural forest, although agricultural forests and residential areas are also used as foraging sites (Cox, 1983; Pernetta and Walling, 1978; Wilson and Enghrinding, 1992). In American Samoa P. tonganus used four major roosting areas, with some movement between sites (Banack, 1996). The roosts are generally found in undisturbed native forest (Wilson and Enghrinding, 1992) but have been reported from the Kolovai Sanctuary in Tonga and other aggregates of trees in populated areas (Pierson and Rainey, 1992).

Roosting height for P. tonganus ranges from 10 to 35 m (Wodzicki and Felten, 1975). Several tree species preferred for roosting on Rarotonga are Cananga odorata (Annonaceae), Cerbera manghas (Apocynaceae), Guettarda speciosa (Rubiaceae) and Homalium acuminatum, (Flacourtiacae). These four species share the morphological features of sparse leaves and a widely spaced branching pattern (Wodzicki and Felten, 1980). Colonies are generally found on emergent trees (Pierson and Rainey, 1992) allowing for a “free-fall take off,” which may accommodate the large size of P. tonganus (Kingdon, 1974). In Samoa and Vanuatu, Ficus plicata and Gavasusia sp. have been cited as roosting trees (Pierson and Rainey, 1992). The bats tend to roost toward the outside of the tree, and the foliage of a roosting tree may become sparse due to the use of branches by the animals. The gregarious bats are detected most easily by audible squeaking but also by a distinct odor that emanates from inhabited roost sites (Allen, 1939; Cox 1983; Grant, 1994; Wodzicki and Felten, 1975).


As an eclectic forager P. tonganus is able to find food seasonally and has the ability to respond to changes in forest structure and biomass caused by catastrophic events (Marshall, 1983; Wodzicki and Felten, 1975). The presence of a foraging generalist such as P. tonganus may aid plants in the colonization of an island by acting as a pollinator and seed disperser (Elmqvist et al., 1992). In contrast to its continental range where Ceiba pentandra flowers have a varied group of pollinators, the flower is pollinated by a single species on Samoa—P. tonganus (Elmqvist et al., 1992; Pier-
son and Rainey, 1992). *P. tonganus* helps to maintain forest diversity as seed dispersers and are important pollinators within Pacific forest systems (Rainey, 1990; Cox et al., 1991, 1992; Wiles and Fujita, 1992; Wodzicki and Felten, 1980).

Causes of mortality are not well known for any species in the genus. Mortality among *P. tonganus* includes predation, epidemics, hurricanes, hunting, and most importantly, habitat loss (Craig et al., 1994; Pierson and Rainey, 1992). Raptors and snakes are among the few natural predators of insular flying foxes. Due to their low reproductive rate, these animals are sensitive to hunting, introduced predators, and catastrophic events (Cox et al., 1991). Pteropodids make up a large portion of the diet of peregrine falcons (*Falco peregrius*). The range of *P. tonganus* overlaps with that of peregrine falcons in New Caledonia, the Loyalty Islands, the Solomon Islands, and Vanuatu (Pierson et al., 1992; White et al., 1988). Sometime before 1949 there was an epidemic on Savu Savu, Fiji that decimated the *P. tonganus* population, leaving hundreds of bleached bones under every roost tree in the woods (Degener, 1949).

Grant and Banack (in press) documented predation by barn owls on *P. tonganus* in American Samoa. One individual was attacked in a tree while Grant and Banack were radio-tracking it, and an owl was observed attacking a second individual on the wing. Interestingly, the bats weigh about the same as the owls.

Hurricanes can cause dramatic declines in *P. tonganus* populations. In American Samoa, *P. tonganus* populations declined 80–90% following two hurricanes in 1990 and 1991 (Craig et al., 1994; Pierson et al., 1992). Degener (1949) and Cox et al. (1991) state hurricanes are due to loss of habitat, scarcity of food, and subsequent overhunting. When roosts were destroyed and food were unavailable in the forest, the bats ventured into towns, sometimes even during the day, to forage on fallen fruits. They are vulnerable to attack by domestic animals (dogs, cats, pigs) because they are unable to make flight from the ground. Estimates of mortality due to pigs and cats was probably low because these animals forage in the woods and some kills may go unnoticed (Pierson and Rainey, 1992). The exposed bats were also taken by humans for food, but only often for target practice (Daeschbach, 1990; Pierson and Rainey, 1992; Cox et al., 1991).

*Pteropus tonganus* carries both ecto- and endoparasites (Wodzicki and Felten, 1975). Three different, and otherwise unidentified, ectoparasites were found on bats in Fiji (Degener, 1949). Sanborn and Nicholson (1950) speculated that *P. t. geddie* was parasitized by *Cyclopodida oxycephala* Bigot, a bat tick. In American Samoa this species is heavily parasitized by wingless haelines of the family Nycteribiidae (Banack, 1996). Banack (1996) suggested that *P. tonganus* may occasionally shift its roost tree in response to ectoparasite load.

**BEHAVIOR.** The habits of *Pteropus* in general were described by Peale (1848:17–18). His observations remain apt for *P. tonganus*: “The Pteropi are all more or less gregarious; most active in twilight: and when at rest, hang from the branches of trees with their heads downward, using their wings as cloaks to shelter their bodies from the wind, rain, and sun; when they fly, as they have no intermembral membranes, they hold the two hind feet together, which makes them appear to have a tail: they climb with great facility along the under side of the branches and are very destructive to both wild and cultivated plants, as they taste and reject until the ripest and best is found; but we never heard them accused of destroying animal life.”

*Pteropus tonganus* is strongly colonial (Cox, 1983; Craig and Syro, 1992; Permetta and Watling, 1973) and nocturnal (Craig and Syro, 1992; Wilson and Engrbing, 1992; Wodzicki and Felten, 1975). Feeding activity commences at different times depending on location, with bats in some areas foraging well before dark. Wodzicki and Felten (1975) speculated that this diurnal behavior might indicate a larger population size, and Wilson and Engrbing (1992) suggested the difference was due to hunting pressure and other human disturbance. There was little disturbance on Humarikau, Olosega, and Olosanga islands, and the animals began foraging during daylight with little risk (Wilson and Engrbing, 1992). Anderson (1912) suggested that those bats on Tonga that emerged before dusk were driven out by hunger or accidentally disturbed. Disturbances such as hurricanes may disrupt daily activity patterns, and resulting shortages in food supply may cause the bats forage for longer periods and during the day (Craig, et al., 1994; Pierson, et al., in press).

Pteropodidae generally have distinct roosting and foraging areas. Sites may be separated in elevation by distance or by distance across land or ocean (Marshall, 1983; Pierson and Rainey, 1992). Cox (1983) observed hundreds of *P. t. tonganus* coming in from sea at dusk, presumably to feed. *P. tonganus* is known to forage on trees with abundant fruits and flowers such as *Ficus* or *Ceibus*, and individually around trees like *Cocos nucifera* which produce only a few flowers. *P. tonganus* forages at night, often in noisy groups (Elmqvist et al., 1992; Wilson and Engrbing, 1992).

Bats frequently carry their food away from the site of origin, and observations of *P. tonganus* carrying pieces of breadfruit indicate that the bats do not always remain at the foraging site to eat (Wilson and Engrbing, 1992). Pacific flying foxes are known to roost on offshore islands and islands in large numbers and to fly across open water to forage (White et al., 1988; Wilson and Engrbing, 1992). Cox’s (1983) observation of over 300 individuals coming in from sea may suggest group foraging. Group searching may be an effective way to capitalize on a rewarding, but temporary and scattered, resource, because the group would have experience with a more extensive region, greater perception, and additional awareness of possible threats (Marshall, 1983).

Megachirottera use their hind feet to manipulate fruit and peel it or bite off pieces. By moving their tongue against their palate the bats are able to break up the fruit and ingest only the pulp and juice, releasing seeds (Marshall, 1985). In one study in Samoa (Elmqqvist et al., 1992) *P. tonganus* actively defended resources within flowering trees of *Ceiba pentandra*. Early in the season, before the availability of fruits and prior to anthesis, flying foxes defended areas of 1.5–2.0 m from surrounding *P. tonganus* feeding areas. When roosts were destroyed, confrontations normally finished with one animal taking flight or moving to another part of the tree (Elmqvist et al., 1992). There were two bursts of activity, the first during the initial period of nectar production early in the evening, and another just before dawn. The second was made up of smaller individuals presumed to be immature. After anthesis the animals spent considerable time crawling from one flower to another. Visits to a tree lasted from 3 to 19 minutes. During the process of foraging, 50% of *C. pentandra* flowers and developing fruits may be destroyed (Elmqvist et al., 1992).

In Vanuatu, *P. tonganus* forms large colonies from September to January, containing both sexes in large casuarina trees near the shore (Baker and Baker, 1936). The females leave in February when they become pregnant, and appear in June, when they unite in inland maternity camps to give birth to their young. Males remain in the coastal camps from January to June, but apparently disperse from June to September (Baker and Baker, 1936; MacGillivray, 1860; Pierson and Rainey, 1992).

*Pteropus tonganus* is an insectivorous primate. This colony has roosted intermittently for 50 years in a small tree in the village where it may not be reoccupied for 5–10 years (Wodzicki and Felten, 1975). Roosting habits for some populations may be altered by human disturbance. On the island of Niue, *P. tonganus* has been observed roosting singly, in pairs, and in small groups from 20 to 30 animals (Pierson and Rainey, 1992; Wodzicki and Felten, 1980). This deviation from the regularly observed pattern has been attributed to overhunting and deforestation (Wodzicki and Felten, 1975).

In many Pacific nations P. tonganus has traditionally been considered a delicacy, or consumption was limited to certain groups within society (Bani, 1992; Graham, 1992; Rainey, 1990; Sinaraja and Ernig, 1992). Recently there has been an increased demand for P. tonganus as a food source within the nations where it occurs, as well as on other islands such as Guam, where commercial exploitation is driven by the demands of a luxury food market (Cox, 1983; Falanruw, 1988; Graham, 1992; Wiles, 1992; Wiles and Fujita, 1992). Consequently, P. tonganus has suffered as a result of overhunting (Wodzicki and Felten, 1975, 1980). Another problem contributing to population declines in P. tonganus is habitat loss and deforestation (Robertson, 1992; Wilson and Engrhing, 1992). Timber is listed as the natural resource in Fiji and Western Samoa (Wilson and Engrhing, 1992). Much of the interior of 'Upolu (Western Samoa) has been commercially logged and converted to pasture and other agricultural land (Wilson and Engrhing, 1992). On Savai'i (Western Samoa), logging is an even more important industry, although many of the logged areas are replanted or otherwise allowed to return to forest (Wilson and Engrhing, 1992).

REMARKS. The name Pteropus is from a Greek root meaning wing-footed, an allusion to the wing membrane, which arises from the side of the back and the back of the second toe. The specific epithet, tonganus, refers to the type locality of the species, the Tonga Islands.

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Editors of this account were Cynthia E. Rebar, Elaine Anderson, and Karl F. Koopman. Managing editor was Barbara H. Blake.

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