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Pacific Flying Foxes (Mammalia: Chiroptera): Two New Species of *Pteropus* from Samoa, Probably Extinct

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ABSTRACT

Two new species of flying foxes (genus *Pteropus*) from the Samoan archipelago are described on the basis of modern museum specimens collected in the mid-19th century. A medium-sized species (*P. allenorum*, n. sp.) is introduced from the island of Upolu (Independent Samoa), based on a specimen collected in 1856 and deposited in the Academy of Natural Sciences of Philadelphia. It has not been collected again, and we regard it as almost certainly extinct. This species is smaller bodied and has much smaller teeth than both extant congeners recorded in the contemporary fauna of Samoa (*Pteropus samoensis* and *P. tonganus*). The closest relative of this new species may be *Pteropus fundatus* of northern Vanuatu. The disjunct historical distribution of these two small-toothed flying foxes (in Vanuatu and Samoa) suggests that similar species may have been more extensively distributed in the remote Pacific in the recent past. Another species, a very large flying fox with large teeth (*P. coxi*, n. sp.), is described from two skulls collected in Samoa in 1839–1841 during the U.S. Exploring Expedition; it too has not been collected since. This robust species resembles *Pteropus samoensis* and *Pteropus anetianus* of Vanuatu in craniodental conformation but is larger than other Polynesian *Pteropus*, and in some features it is ecomorphologically convergent on the Pacific monkey-faced bats (the pteropodid genera *Pteralopex* and *Mirimiri*). On the basis of eyewitness reports from the early 1980s, it is possible that this species survived until recent decades, or is still extant. These two new Samoan species join *Pteropus tokudae* of Guam, *P. pilosus* of Palau, *P. subniger* of the Mascarenes, and *P. brunneus* of coastal north-eastern Australia as flying

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foxes with limited insular distributions that survived at least until the 19th century but are now most likely extinct.

INTRODUCTION

Capable of flight, bats are the only mammals to have naturally colonized many of the remote oceanic islands and archipelagos of the Pacific—eastern Melanesia, Polynesia, and Micronesia, including the islands of Vanuatu, Fiji, New Caledonia, Samoa, Tonga, Wallis and Futuna, Niue, the Cook Islands, New Zealand, Lord Howe Island, Guam, the Marianas, Palau, and the Carolines (Flannery, 1995). Some insect-eating bats are found in modern and subfossil insular faunas throughout the region, including representatives of the emballonurid genus *Emballonura* (Micronesia, Vanuatu, Fiji, Samoa, Tonga); the hipposiderid *Hipposideros* (Vanuatu); the vespertilionids *Miniopterus* (Vanuatu, New Caledonia), *Myotis* (Vanuatu, possibly Samoa), *Nyctophilus* (New Caledonia, formerly Lord Howe, possibly Fiji), and *Chalinolobus* (Lord Howe, New Zealand); the molossid *Chaerephon* (Vanuatu, Fiji, formerly Tonga); and the monogeneric family Mystacinidae (*Mystacina*), today endemic to New Zealand (Hill and Daniel, 1985; Flannery, 1995; Hand et al., 1998; Parnaby, 2002a; Helgen and Flannery, 2002; Simmons, 2005). Most remote Pacific bat species, however, are fruit- and nectar-feeding species classified in the family Pteropodidae (see Andersen, 1912). The genus *Pteropus* (the “flying foxes”) is represented by a diverse complement of species in eastern Melanesia, Micronesia, and Polynesia (extending as far east as the Cook Islands). Also occurring in the region are two older generic lineages endemic to the remote Pacific—*Notopterus* (two species of blossom bats, known from the modern faunas of New Caledonia, Vanuatu, and Fiji, as well as the subfossil record of Tonga) and *Mirimiri* (one species of “monkey-faced bat”, recorded only from montane forests on the island of Taveuni in Fiji) (Hill and Beckon, 1978; Flannery, 1995; Parnaby, 2002b; Helgen, 2005; Palmeirim et al., 2007).

In the 18th and 19th centuries, European explorers of Pacific archipelagos encountered a number of endemic vertebrate species—especially birds, but also lizards and bats, which became rapidly extinct soon after their

discovery by science. Setting aside New Zealand and the Hawaiian Islands, both of which are well known as epicenters of historical (as well as prehistoric) avian extinction (Tennyson and Martinson, 2006; Worthy and Holdaway, 2002; Pratt, 1994; Ziegler, 2002), some of the better documented examples of Polynesian extinctions prior to the 20th century include the Tahitian Sandpiper (*Prosobonia leucoptera*) and Raiatea Parakeet (*Cyanoramphus ulietanus*) of the Society Islands, which were last recorded before 1800; the Mysterious Starling (*Aplonis mavornata*) of the Cook Islands, the Tongan Giant Skink (*Tachygia microlepis*), and the Tahiti Parakeet (*Cyanoramphus zealandicus*), all of which were last recorded in the first half of the 19th century; and the Samoan Wood-Rail (*Pareudiastes pacificus*), last recorded in the latter half of the 19th century (Flannery and Schouten, 2001). There are many other avian examples (Steadman, 2006b). The arrival of European impacts in the Pacific during the 1700s and 1800s clearly fostered or accelerated an astonishing extinction pulse in these insular vertebrate faunas—a pulse that has carried on unabated and today threatens the survival of many critically endangered species throughout the region (Flannery, 1995; Stattersfield et al., 1998; Steadman, 2006b).

The purpose of the present paper is to bring to light two additional examples of Polynesian vertebrate species—both previously unnamed flying foxes—that have not been recorded since the 19th century. Both new species originate from the archipelago of Samoa in West Polynesia (figs. 1, 2), where only two species of *Pteropus* (*P. tonganus* and *P. samoensis*) are known in the contemporary fauna (e.g., Andersen, 1912; Cox, 1983; Wilson and Engbring, 1992; Flannery, 1995; Banack, 1996, 1998; Brooke, 2001). One of the new species is recorded by a single museum specimen collected on the island of Upolu in 1856. Deposited in the collections of the Academy of Natural Sciences of Philadelphia, this specimen has been overlooked by systematists since the time of its collection. (Although identified as “*Pteropus pselaphon*?” in the Academy’s accession catalog and as

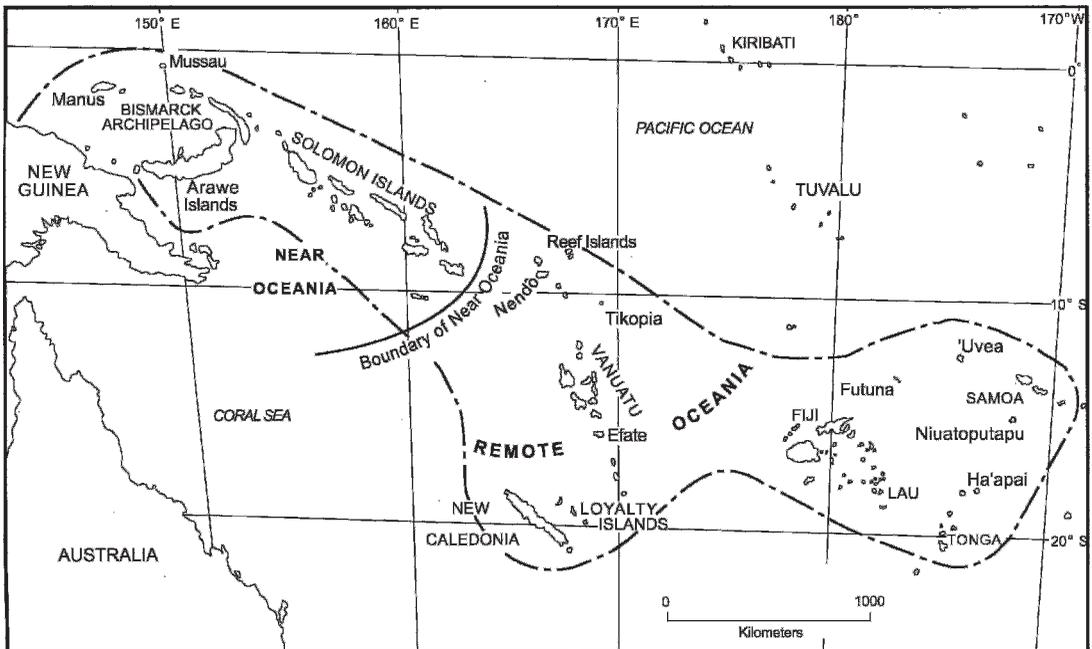


Fig. 1. Map of the southwest Pacific region. Adapted from Steadman (2006b).

“*Pteropus tonganus*” on its skull box, it bears no particular morphological resemblance to either of these species.) The other species is represented by two skulls in the United States National Museum in Washington, D.C., collected in Samoa during the 1838–1842 U.S. Exploring Expedition to the Pacific (see Wilkes, 1844; Peale, 1848; Cassin, 1858; Philbrick, 2003). These have been identified and cataloged as *Pteropus samoensis* since their collection, and they even apparently formed part of the hypodigm for the original taxonomic description of *P. samoensis* by Peale (1848). However, we argue that these two skulls represent a species distinct from (and, presumably, formerly sympatric with) *P. samoensis*, with a considerably more robust skull and teeth than any extant *Pteropus* from Polynesia. We describe both of these overlooked Samoan bat taxa as new species, and designate a lectotype for *Pteropus samoensis* Peale, 1848, to preserve the traditional usage of this epithet (i.e., for the shorter faced and more cranially robust of the two *Pteropus* species known to survive in Samoa today; Andersen, 1912; Wilson and Engbring, 1992).

MATERIALS AND METHODS

Specimens discussed herein are deposited in the collections of the American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AM); Academy of Natural Sciences, Philadelphia (ANSP); Natural History Museum, London (BMNH); Museum of Comparative Zoology at Harvard University, Cambridge, Mass. (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Museum für Naturkunde, Humboldt Universität, Berlin (ZMB); and Zoological Museum of the University of Copenhagen, Copenhagen (ZMUC).

Terminology for cranial and dental features follows Giannini et al. (2006) and Giannini and Simmons (2007). All measurements of length are in millimeters. Standard external measurements for most museum specimens were recorded by the original collectors in the field; in other cases forearm lengths were measured from dry skins or from specimens preserved in alcohol. Craniodental and exter-

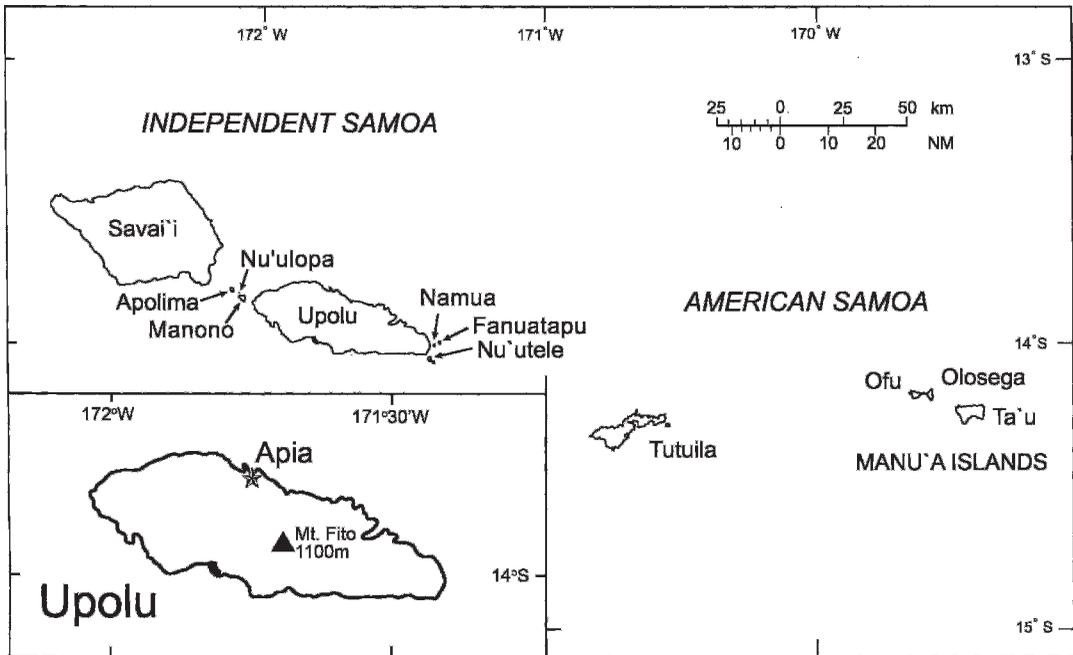


Fig. 2. A map of Samoa, showing political boundaries and principal islands, with inset showing the location of Apia on the island of Upolu, the type locality of *Pteropus allenorum*. Adapted from Steadman (2006b).

nal variables were measured with hand-held callipers to the nearest 0.1 mm. Single-tooth measurements are measured on the crown.

For wing measurements (chord or straight-line lengths in the case of curved phalangeal measurements), digit is abbreviated as “D”, metacarpal as “M”, and phalanx as “P”; thus, D2P2 refers to the second phalanx of the second digit, and so forth.

Cranial measurements are abbreviated (and, where necessary, defined) as follows: CBL, condylobasal length; ONL, orbitonasal length, here defined as the distance from the anterior edge of the orbit to the midpoint of the premaxillae; ZYG, greatest bizygomatic width; MTR, alveolar length of maxillary toothrow, C1–M2; CC, external, alveolar distance across upper canines; M1M1, external, alveolar distance across upper first molars, M1–M1; M2M2, external, alveolar distance across upper second molars, M2–M2; BBC, breadth of braincase at zygomata; ML, greatest length of mandible; CHM, height of mandible to coronoid process; LTR, alveolar length of mandibular toothrow, c1–m3; LM1,

length of first upper molar; WM1, width of first upper molar. Unless otherwise noted, all craniodental measurements are based only on adult skulls, identified as those in which the mature dentition is fully in place and the basioccipital-basisphenoid (basilar) suture is completely fused. Because our measured samples of *Pteropus* species featured in this paper do not exhibit statistically significant intersexual metric differences in these sampled craniodental variables (i.e., *t*-test comparisons, $p > 0.05$), we have pooled adult males, adult females, and unsexed adult skulls in our univariate tabulations and morphometric analyses. We calculated standard descriptive statistics (mean, standard deviation, and observed range) for the samples of populations and species listed in table 1. Our plottings of specimen scores in multivariate analyses provide visual patterns that reflect similarity or contrast in the combination of all cranial and dental dimensions among samples of different species. Principal components analyses and discriminant function analyses were computed using the combination of

TABLE 1
Forearm and Selected Cranial Measurements of the Four Flying Foxes of Samoa

Values for Fijian *P. samoensis* and *P. anetianus* of Vanuatu are shown for comparison (provided for each sample are mean \pm SD, range of measurements, and sample size) Measurements for Samoan and Fijian populations based on adult specimens at AM, AMNH, ANSP, BMNH, USNM, and ZMUC. Cranial measurements for *P. anetianus* are based on specimens at AMNH, BMNH, and USNM; external measurements for *P. anetianus* are compiled from Andersen (1912), Felten and Kock (1972), and Flannery (1995) where explicit measurements were provided by those sources. Asterisked values refer to an estimated measurement from an incomplete skull.

	<i>P. allenorum</i>	<i>P. tonganus</i>	<i>P. coxi</i>	<i>P. samoensis</i>	<i>P. samoensis</i>	<i>P. anetianus</i>
	Samoa subadult	Samoa adults	Samoa adults	Samoa adults	Fiji adults	Vanuatu adults
Forearm	116 — <i>n</i> = 1	138 \pm 5.6 130–146 <i>n</i> = 11	— — —	140 \pm 6.0 128–154 <i>n</i> = 15	128 \pm 4.2 122–134 <i>n</i> = 10	126 \pm 6.3 117–135 <i>n</i> = 17
CBL	50.0 — <i>n</i> = 1	62.0 \pm 1.29 59.7–64.1 <i>n</i> = 16	— — —	58.1 \pm 1.50 55.7–60.3 <i>n</i> = 17	58.7 \pm 0.97 57.1–59.8 <i>n</i> = 7	58.9 \pm 14.5 55.1–60.7 <i>n</i> = 17
ONL	16.5 — <i>n</i> = 1	21.5 \pm 0.89 19.5–22.7 <i>n</i> = 19	19.9 19.6–20.3 <i>n</i> = 2	18.4 \pm 0.77 16.6–20.1 <i>n</i> = 23	18.8 \pm 1.03 17.6–20.7 <i>n</i> = 11	18.0 \pm 0.80 16.4–19.4 <i>n</i> = 21
ZYG	26.0 — <i>n</i> = 1	34.3 \pm 1.58 31.8–37.1 <i>n</i> = 19	37.5* 37*–38 <i>n</i> = 2	33.9 \pm 1.40 31.8–37.4 <i>n</i> = 19	34.3 \pm 1.10 32.0–35.7 <i>n</i> = 10	35.5 \pm 1.28 31.7–37.7 <i>n</i> = 19
BBC	20.6 — <i>n</i> = 1	21.9 \pm 0.62 20.5–23.0 <i>n</i> = 19	23.6 — <i>n</i> = 1	21.7 \pm 0.57 20.6–22.9 <i>n</i> = 23	22.1 \pm 0.51 21.3–23.2 <i>n</i> = 10	22.1 \pm 0.84 20.4–23.4 <i>n</i> = 19
MTR	18.4 — <i>n</i> = 1	23.6 \pm 0.60 22.7–24.9 <i>n</i> = 19	23.5 23.4–23.6 <i>n</i> = 2	21.7 \pm 0.61 20.4–22.6 <i>n</i> = 23	21.7 \pm 0.85 20.0–22.8 <i>n</i> = 11	22.1 \pm 0.57 20.3–22.8 <i>n</i> = 20
CC	9.7 — <i>n</i> = 1	11.7 \pm 0.53 10.8–12.7 <i>n</i> = 19	12.8 12.7–12.9 <i>n</i> = 2	11.8 \pm 0.39 10.8–12.5 <i>n</i> = 23	11.6 \pm 0.61 10.0–12.2 <i>n</i> = 11	11.9 \pm 0.67 9.9–13.0 <i>n</i> = 21
M2M2	13.0 — <i>n</i> = 1	15.0 \pm 0.69 13.9–16.4 <i>n</i> = 19	15.4 15.2–15.7 <i>n</i> = 2	14.1 \pm 0.62 13.1–15.6 <i>n</i> = 19	14.4 \pm 0.55 13.7–15.6 <i>n</i> = 9	14.6 \pm 0.62 13.0–15.4 <i>n</i> = 19
ML	38.7 — <i>n</i> = 1	50.5 \pm 1.37 48.3–51.3 <i>n</i> = 19	50.6 50.6–50.7 <i>n</i> = 2	47.2 \pm 1.18 44.0–48.9 <i>n</i> = 23	46.3 \pm 1.19 43.2–47.6 <i>n</i> = 11	47.7 \pm 1.31 43.3–49.9 <i>n</i> = 21
MH	17.7 — <i>n</i> = 1	24.0 \pm 1.07 21.1–25.3 <i>n</i> = 19	28 27.7–28.3 <i>n</i> = 2	25.8 \pm 1.40 21.5–27.8 <i>n</i> = 23	24.0 \pm 0.91 22.7–25.3 <i>n</i> = 11	27.2 \pm 1.15 24.4–28.5 <i>n</i> = 21
LTR	— <i>n</i> = 1	26.7 \pm 0.77 25.9–28.2 <i>n</i> = 19	27.2 26.6–27.8 <i>n</i> = 2	24.9 \pm 0.70 22.5–25.9 <i>n</i> = 23	24.8 \pm 0.84 22.8–25.4 <i>n</i> = 11	25.5 \pm 0.84 23.2–26.9 <i>n</i> = 20
LM1	4.2 — <i>n</i> = 1	5.05 \pm 0.21 4.84–5.50 <i>n</i> = 17	5.92 5.89–5.94 <i>n</i> = 2	5.41 \pm 0.23 4.98–5.85 <i>n</i> = 22	4.90 \pm 0.19 4.76–5.17 <i>n</i> = 4	5.5 \pm 0.34 4.77–6.06 <i>n</i> = 22
WM1	1.9 — <i>n</i> = 1	2.99 \pm 0.21 2.64–3.43 <i>n</i> = 17	3.15 3.12–3.17 <i>n</i> = 2	2.80 \pm 0.13 2.45–3.08 <i>n</i> = 22	2.59 \pm 0.09 2.47–2.67 <i>n</i> = 4	3.0 \pm 0.23 2.53–3.34 <i>n</i> = 22

cranial and dental measurements indicated in table 1, with the exception of CBL (unavailable for either available skull of *P. coxi*) and BBC (measurable in only one of the two skulls

of *P. coxi*), omitted to allow for the inclusion of these critical samples. All measurement values were transformed to natural logarithms prior to analysis. Principal components were



Fig. 3. The fragmentary holotype skin of *Pteropus allenorum* (ANSP 1234, preserved in alcohol).

extracted from a covariance matrix, and canonical variates were extracted from the discriminant function analyses. The software program Statistica 8.0 (Statsoft, Tulsa, Okla.) was used for all analytical procedures.

SYSTEMATICS

Pteropus allenorum, new species

HOLOTYPE: The holotype of *Pteropus allenorum* is ANSP 1234, a skin in alcohol (fig. 3) with the cranium and mandible removed and cleaned (fig. 7), collected at Apia (13°49'S, 171°44'W), a harbor and settlement on the island of Upolu (and today the capital of Independent, or Western, Samoa; fig. 2), apparently by H.C. Caldwell in April 1856 (see below), and donated to the museum by W.S.W. Ruschenberger. Judging from its craniodental development (fig. 7; see Helgen, 2004a; Giannini et al., 2006), this unsexed specimen is a nearly mature subadult.

A faded tag bearing scripted ink writing accompanies the skin in alcohol, which we take to be the original or at least the oldest tag associated with it. Both this tag and another—affixed to the specimen, less faded, and bearing writing in pencil—give the provenance of the specimen as “Apia, Upolu”. Written in ink on the mandible is the faded annotation “Apia”. The accession catalog, skull box, and a penciled label inside the skull box give the

locality as “Navigator Islands, Apia, Apola”. (The “Navigator Islands” is a 19th-century appellation for the Pacific archipelago today known as Samoa, incorporating the modern-day political boundaries of both Independent Samoa and American Samoa; see Wilkes, 1844; Keesing, 1934.) The relatively large and high island of Upolu (area 1100 km², maximum elevation ca. 1100 m), home to the harbor of Apia, is the second largest island in the Samoan archipelago (after the adjacent island of Savai'i, with area 1820 km² and maximum elevation ca. 1850 m).

The faded tag in the alcohol jar with the holotype also bears the date “April 1856”. We consider this most likely to be the specimen's date of collection, rather than the date of accession at ANSP. (Other specimens listed on the same page of the ANSP mammal accession catalog list a “Date of Presentation” to the museum a decade later, in 1865 or 1866.) Tags associated with the jar of alcohol and the skull bear the name “Dr. W.S.W. Ruschenberger” or “W.S.W.R.”, who is listed in the ANSP accession catalog under the column of “Donor”, rather than “Collector”.

Amongst “Donations to the Museum” received in 1857, the *Proceedings of the Academy of Natural Sciences of Philadelphia* gives the following entries, listed consecutively (Anonymous, 1858: i):

A collection of Echinodermata, Acelephae, and Mollusca in alcohol, from the Navigator

Islands. Presented by Drs. W. S. W. Ruschenberger, and Henry Clay Caldwell, U.S.N[avy].

A specimen of *Pteropus* from the same locality.

Based on its unique and concordant label data (noting its collection in Samoa in 1856 and presentation to the museum by Ruschenberger) we strongly suspect that this latter specimen mentioned amongst the *Proceedings* donations in 1857 is the holotype of *P. allenorum*, and not any other specimen of *Pteropus* currently in the collections (or listed in the catalogs) at ANSP.

Fowler (1901) discussed and described ichthyological collections from Samoa likewise donated to ANSP by Ruschenberger and Caldwell, of which he noted: "The following specimens were collected many years ago by Dr. H.C. Caldwell, by whom they were presented to the Academy." Fowler also described the new taxon *Mugil caldwelli*, noting that he "named this species for Dr. Caldwell, who collected the type." We have been unable to discover if Ruschenberger actually took part in the collecting efforts in Samoa in 1856, or if he was simply a financial sponsor of these exploratory efforts. It is clear, however, that Caldwell was directly responsible for the collection of some zoological specimens during this voyage to Samoa. We suspect based on the evidence at hand that he (or his assistants and colleagues during his visit to Apia) was the collector of the holotype of *Pteropus allenorum*.

The holotype is the only specimen of *Pteropus allenorum* known to us.

DIAGNOSIS: *Pteropus allenorum* is a relatively small to medium-sized (figs. 4–8) member of the genus *Pteropus* (forearm 116 mm in the young holotype), probably with a brown head, tinged with russet; a golden-brown mantle, dusky brown back, and warm brown limbs and wing membranes; very small cheek-teeth (with an upper cheektooth size gradient such that $P3 > P4 < M1$, according to overall bulk), but proportionally large canines and incisors; a moderately elongate rostrum; and a relatively gracile mandible.

DISTRIBUTION: *Pteropus allenorum* is recorded historically only from the Samoan

island of Upolu. We speculate that, like most native elements in the Samoan avifauna (Steadman, 2006b), the actual historic or prehistoric distribution of this species was not limited solely to this single island, but probably extended to Savai'i and to other islands of Samoa, if not to adjacent archipelagos (even if Upolu truly was its last place of occurrence). Further excavations of subfossil material in Samoa and further study of subfossil material from the adjacent archipelagos of Tonga and Fiji may help to clarify the past distribution of this species. It is not yet reported from the subfossil record of Tonga, the only Polynesian archipelago where the chiropteran subfossil record has been studied in some detail (Koopman and Steadman, 1995), although in light of the elucidation of this species in the historical fauna of Samoa, closer study of *Pteropus* osteological material from Tongan excavations is certainly warranted. Although likely extinct, we suggest that *P. allenorum* should be sought after during future biotic inventory efforts in Samoa on the chance that an overlooked extant population survives somewhere in the archipelago (see Discussion, below).

ETYMOLOGY: We have chosen the specific epithet *allenorum* to honor the name of Allen, in the plural. The epithet simultaneously acknowledges Harrison Allen (1841–1897), a zoologist, anthropologist, and physician (Hrdlicka, 1914), who assembled much of the ANSP chiropteran collection in the late 19th century, and Allen Drew, who kindly hosted the Helgens during a visit to Philadelphia in 2006, during which the holotype of *allenorum* was first examined. We suggest "Small Samoan Flying Fox" as an appropriate common name.

DESCRIPTION: As noted above, the only available specimen of *Pteropus allenorum* is represented by a skin stored in alcohol with an accompanying skull that, although broken, preserves most cranial features. The skin is fragmentary and fragile but includes the head skin (separated from the rest of the body), most of the dorsal skin of the body, the limbs and wing membranes (somewhat decayed and partly discolored), and some other small clumps of fur. Because it has been preserved in alcohol for more than 150 years and its overall state of preservation is poor, it is

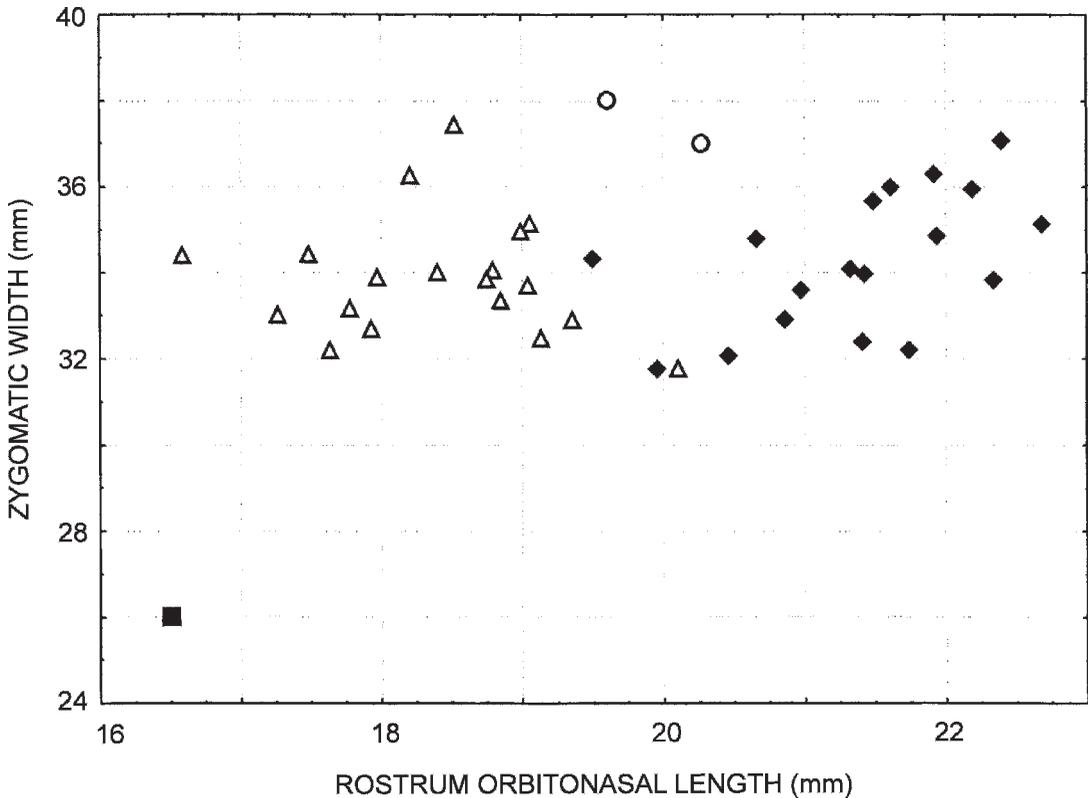


Fig. 4. Bivariate ecomorphological contrasts in Samoan *Pteropus*. A plot of rostral (orbitonasal) length versus zygomatic width discriminates the four *Pteropus* species recorded from Samoa. Sample represents all adult specimens (or nearly adult in the case of the unique holotype of *P. allenorum*) from the Samoan archipelago. Open triangles indicate *P. samoensis*; closed diamonds, *P. tonganus*; closed square, *P. allenorum*; open circles, *P. coxi*.

difficult to characterize the original external appearance of this specimen. Based on the single specimen available, we think that the best that can be stated is that the holotype probably had a brown head tinged with russet, a golden-brown mantle, a dusky brown back, and warm brown limbs and wing membranes. We suggest that the general appearance of *P. allenorum* was probably that of a rather “furry” flying fox, similar in pelage quality to *P. samoensis* (see photograph in Flannery, 1995), in which the fur is longish and not strongly adpressed, as opposed to many flying foxes (such as *P. tonganus*), in which the fur tends to be shorter, sleeker, and often clearly adpressed dorsally. The lengths of the hairs in the fur on the mid-back reach to about 25 mm. The fur is sparser and paler on the front of the face, and there is no darkened eye-ring

encircling the eye. The forearm in the holotype measures 116 mm, and we expect that fully grown adults would have a forearm length of ca. 116–125 mm, smaller than either extant Samoan congener, *Pteropus samoensis* and *P. tonganus* (see table 1).

The holotype cranium is broken behind the orbits, but most of it is preserved in two intact pieces, which we carefully reconstructed to prepare an image of the overall skull (fig. 7). Compared to other *Pteropus*, the rostrum is of “moderate length” sensu Andersen (1912). Despite its youth, the postorbital processes are rather well developed. The back of the palate forms a broad “U” shape. We estimate the condylobasal length of the (nearly mature but broken) holotype skull of *allenorum* to be 50 mm and the zygomatic width to be ca. 26 mm; measurements of full-grown adults would

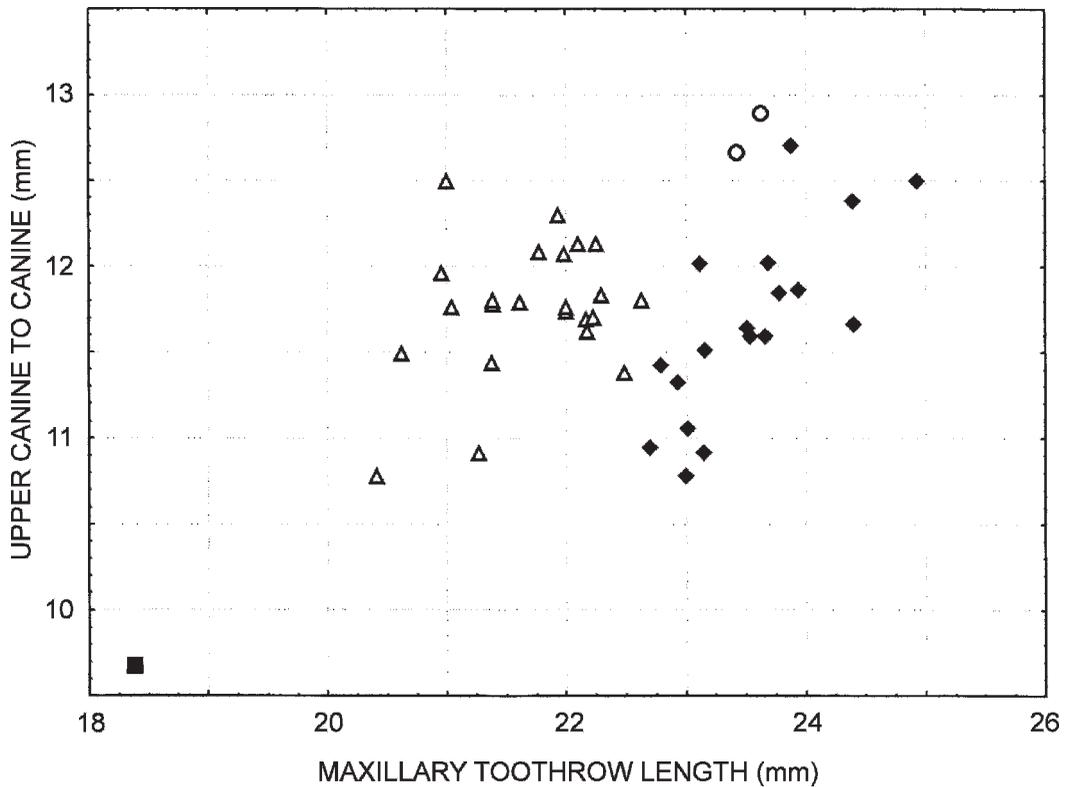


Fig. 5. Bivariate ecomorphological contrasts in Samoan *Pteropus* (continued). A plot of maxillary tooththrow length versus the distance across the upper canines also discriminates the four *Pteropus* species recorded from Samoa. Sample and symbols as for figure 4.

thus somewhat exceed these values, particularly in zygomatic width.

A striking feature of *P. allenorum* is the small size of the teeth relative to the size of the skull, even when perfectly unworn, as in the holotype. As indicated above, the very small skull and teeth of *P. allenorum* allow for its instant discrimination against the sympatric large-toothed forms *P. tonganus* and *P. samoensis* (figs. 4–8; table 1). The upper dentition is largely complete in the holotype (right C1 is loose from the jaw but preserved in the box; right P1 is missing, represented only by an empty alveolus). The upper incisors are proportionally very broad (fig. 7). The canines are long and narrow, with a moderately developed posterior cingulum. P1 is present. The cheekteeth posterior to P1 are relatively very small and narrow. The length of the maxillary tooththrow (C1–M2) measures 18.0 mm, markedly smaller than in Samoan con-

geners (table 1; fig. 5). The soft palate is not preserved.

The holotype mandible is complete and gracile in overall appearance. It has comparatively weak posterior processes (fig. 7), resembling *P. fundatus* of Vanuatu (Felten and Kock, 1972), yet it is more gracile in the reduced size of the coronoid and angular processes despite its slightly larger overall size compared to that species. The incisors and canines and most of the right premolars and molars have been dislodged from the mandible but are preserved separately in the skull box (we reinserted these to provide the dorsal view of the mandible and its dentition, fig. 7). The lower canines and incisors are much larger (both in absolute and relative terms) than the corresponding teeth in *P. fundatus*. The posterior premolars and molars are small and rather narrow, but p1 is especially well developed.

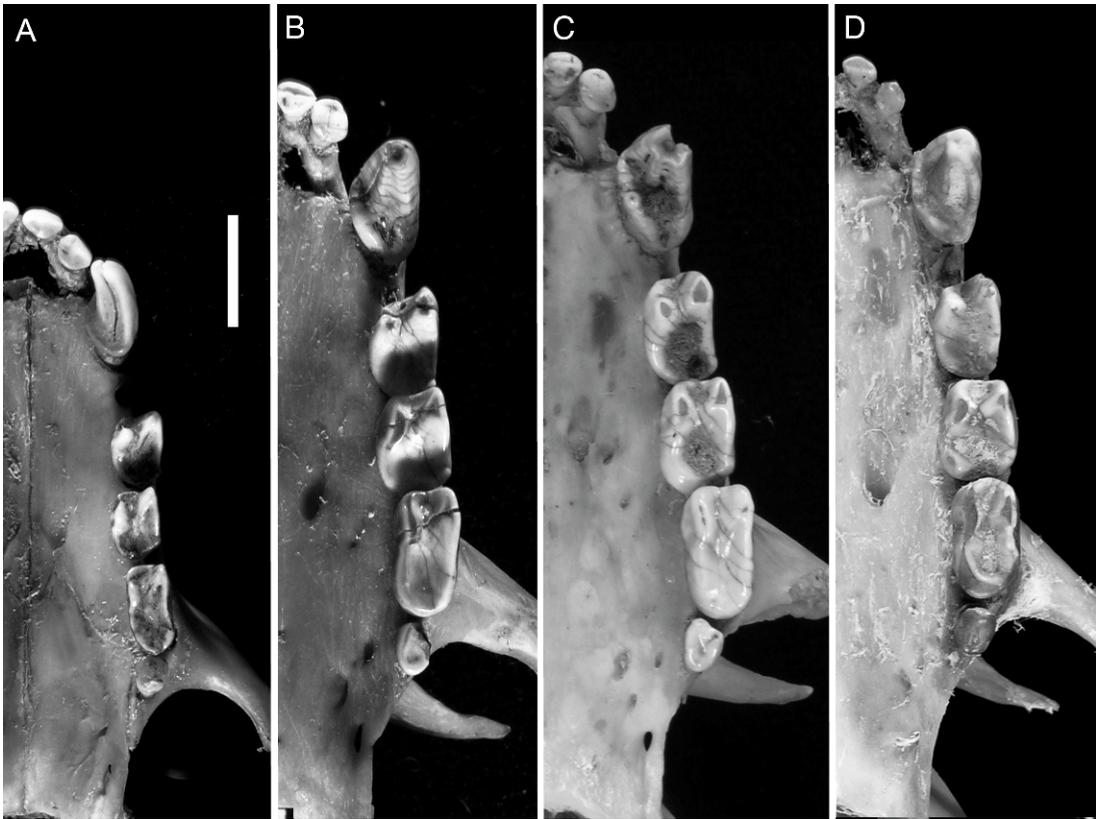


Fig. 6. Maxillary tooththrows of the four *Pteropus* species of Samoa, to scale. **A**, *Pteropus allenorum* (ANSP 1234, unsexed subadult); **B**, *Pteropus samoensis* (ANSP 1867, unsexed adult); **C**, *Pteropus coxi* (USNM 3791, adult, probably male); **D**, *Pteropus tonganus* (AMNH 68738, adult male). Scale bar = 5 mm.

Overall, the skull of *P. allenorum* requires closest comparison with *P. fundatus*, a flying fox of similar cranial and dental size, also endemic to a remote Pacific archipelago (Vanuatu). The premolars and molars of *P. allenorum* match those of *P. fundatus* closely in both shape and absolute dimensions (table 2). More striking dental contrasts between *P. allenorum* and *P. fundatus* lie in the comparative size of the anterior dentition. In *P. allenorum* the incisors are much broadened and the canines vertically and anteroposteriorly relatively more elongate than in *P. fundatus* (fig. 7). We suggest that this juxtaposition of relatively less massive cheekteeth but more massive incisors and canines in *P. allenorum* relative to *P. fundatus* probably reflects salient differences in feeding mode and ecology between these two ecomorphologi-

cally distinctive taxa. *P. allenorum* also can be distinguished immediately from *P. fundatus* by its darker coloration (*P. fundatus* is a pale flying fox; fig. 9) and its larger body and skull size (the forearm measures 95–102 mm [$n = 21$] and condylobasal length measures 44–49 mm [$n = 17$] in adult *P. fundatus*; Felten and Kock, 1972; Flannery, 1995; compare to *P. allenorum* in table 1). Given their morphological similarity and geographic proximity in the remote Pacific, *P. allenorum* and *P. fundatus* may be close relatives within the genus *Pteropus*. However, we stress that similarities between them may not necessarily reflect a close phylogenetic relationship, but perhaps instead a shared pattern of ecomorphological convergence on isolated Pacific archipelagos. A study drawing on molecular sequence data from a wide taxonomic and geographic sample

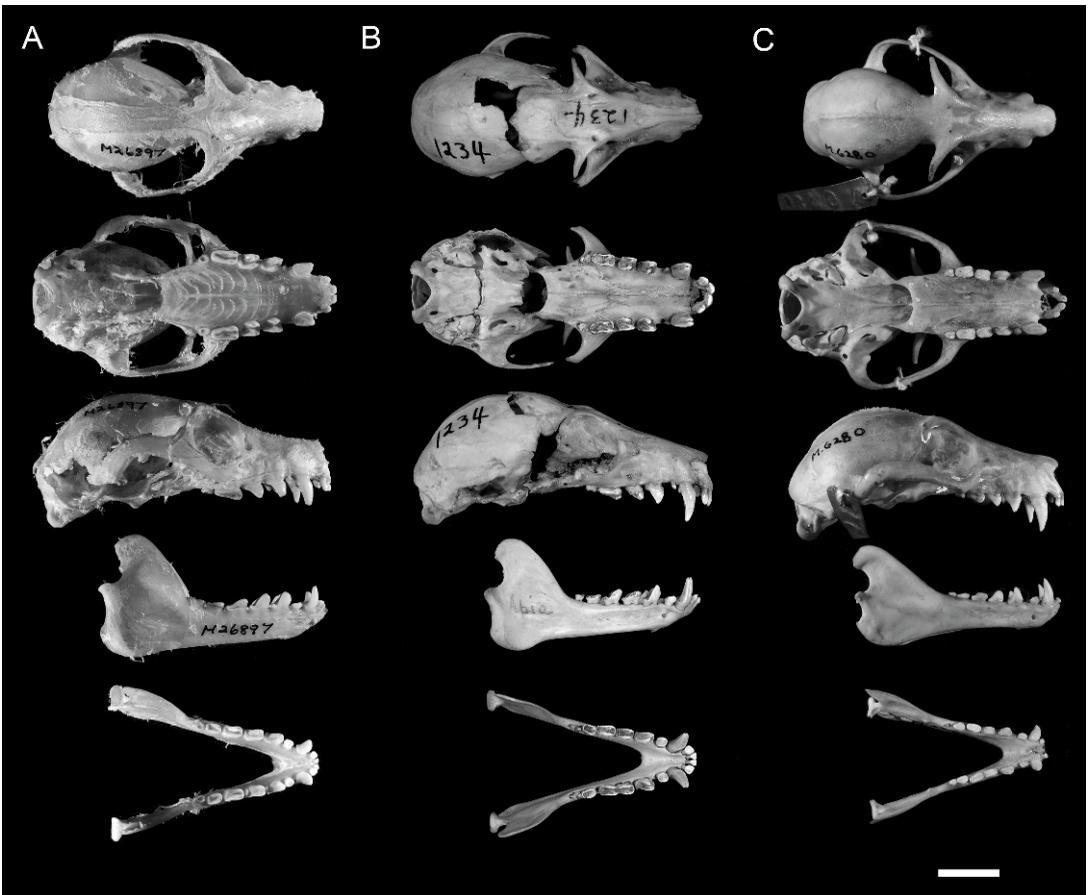


Fig. 7. Skulls of smaller-toothed, medium-sized *Pteropus* species of the southwest Pacific region. **A**, Partially cleaned skull of *Pteropus fundatus*, endemic to Vanuatu (AM M26897, adult male, Mota); **B**, reconstructed skull of *Pteropus allenorum*, endemic Samoa (ANSP 1234, unsexed subadult, Upolu); **C**, skull of *Pteropus mahaganus*, endemic to the Solomon Archipelago (AM M6280, adult male, Bougainville). Scale bar = 10 mm.

of *Pteropus* is needed to distinguish between these possible scenarios (see Giannini et al., 2008).

The dentition of *Pteropus allenorum* is considerably less reduced than that of *Pteropus scapulatus* (of Australia and southern New Guinea) and the presumed phylogenetic allies of that species (*P. woodfordi* and *P. mahaganus* of the Solomon Islands and *P. gilliardorum* of the Bismarck Archipelago), which have relatively small and nearly featureless cheekteeth and together are thought to constitute a distinctive Australian and Pacific group of specialist nectar-feeding flying foxes (Thomas, 1888; Andersen, 1912;

Sanborn, 1931; Van Deusen, 1969; Flannery, 1995; Bonaccorso, 1998; Helgen, 2004a; although see Giannini et al., 2008). However, *Pteropus allenorum* shares with these species a similarly gracile mandible, relatively large canines, small cheekteeth, and similar body size (e.g., fig. 7), attributes suggestive of similarities in lifestyle, although likely convergently derived.

Like *P. allenorum*, *Pteropus vetulus* Jouan, 1863 (a New Caledonian endemic), is a small Pacific *Pteropus* with very small cheekteeth, broad upper and lower incisors, and a conspicuously large p1. Like *P. allenorum*, it is also a rather darkly colored *Pteropus* with

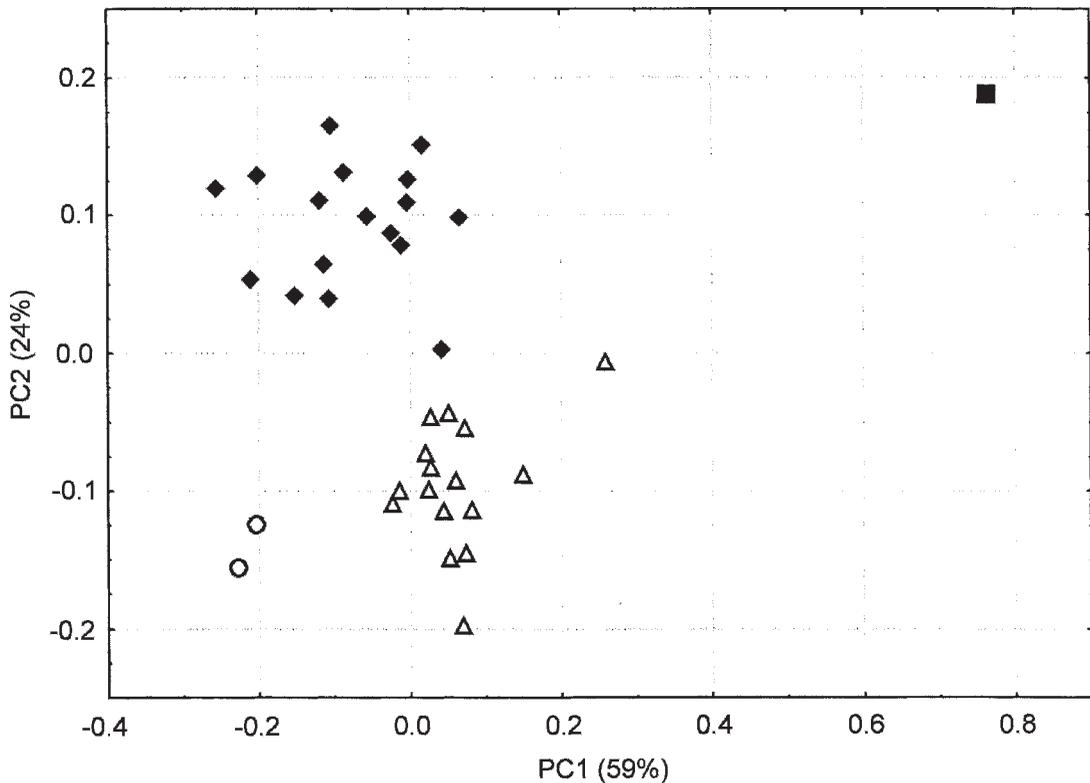


Fig. 8. Multivariate morphometric comparisons in Samoan *Pteropus* (principal components analysis), drawing from 10 log-transformed craniodental measurements, divide the four *Pteropus* species recorded from Samoa into four discrete quadrant clusters. Sample and symbols as for figure 4. In this case, overall size can be visualized on the first component (increasing from right to left), while the loadings on the second component serve as an indication of general “robustness” (increasing from top to bottom). See text and table 3. Parenthetical numbers on the axes indicate the proportion of variance for each principal component (see table 3).

thick and furry rather than adpressed dorsal pelage (see photograph published by Flanery, 1995: 299). *Pteropus allenorumi* is distinguished from *P. vetulus* by its larger skull and body size (the forearm measures 92–112 mm in adult *P. vetulus*); dorsoventrally longer canines (short and deep in *P. vetulus*); simpler upper first molar (labial edge subdivided into two distinct cusps in *P. vetulus*); proportionally more elongate and evenly sloping rostrum (blunter, with more precipitous slope downward from the braincase in lateral profile in *P. vetulus*); upper cheektooth size (bulk) gradient such that $P3 > P4 < M1$ ($P3 < P4 > M1$ in *P. vetulus*); less pronounced occipital cresting (strongly marked, with a subrectangular posterior braincase conformation in *P. vetulus*);

and more gracile mandible with a less developed angular process and lower coronoid process (slightly more robust with broader and higher respective processes in *P. vetulus*). Selected wing and leg measurements in the holotype of *P. allenorumi* are as follows (in mm, measured from wet skin): pollex (with claw) 48.5, (without claw) 42.6; D2M 58.7; D2P1 17.5; D2P2 12.5; D3M 78.4; D3P1 57.3; D3P2 67.1; D4M 77.9; D4P1 50.6; D4P2 45.5; D5M 85.0; D5P1 37.7; D5P2 38; tibia ca. 52; hindfoot (with claws) 30, (without claws) 28.

NATURAL HISTORY: That *Pteropus allenorumi* has such a markedly reduced dentition relative to its extant and extinct Samoan congeners undoubtedly reflects differences in its overall diet relative to those species. It may

TABLE 2
Measurements of Premolars and Molars in *Pteropus allenorum* and *P. fundatus*, Two Relatively Small Pacific *Pteropus*
 L indicates length; W, width

	<i>P. allenorum</i>		<i>P. fundatus</i>	
	ANSP	AM	AM	AM
	1234	M26898	M26897	M26896
	?	male	male	female
P3 L	3.4	3.3	3.5	3.2
P3 W	2.1	2.1	2.1	1.9
P4 L	3.2	3.4	3.3	3.3
P4 W	2.1	2.3	2.5	2.1
M1 L	4.2	4.2	4.3	4.3
M1 W	1.9	2.2	2.2	2.0
M2 L	1.9	1.6	1.9	1.6
M2 W	1.3	1.2	1.4	1.3
p1 L	1.9	1.5	1.8	1.7
p1 W	1.6	1.6	1.7	1.5
p3 L	3.4	3.3	3.5	3.1
p3 W	1.7	1.9	1.8	1.7
p4 L	3.5	3.3	3.4	3.3
p4 W	1.9	2.0	1.9	1.7
m1 L	3.6	3.5	3.4	3.6
m1 W	1.9	2.0	1.8	1.9
m2 L	2.7	2.6	2.9	2.6
m2 W	1.8	1.7	1.8	1.7
m3 L	1.4	1.5	1.7	1.4
m3 W	1.2	1.1	1.3	1.0

TABLE 3
Principal Components Analysis Comparing 36 *Pteropus* Skulls from Samoa

Factor loadings, eigenvalues, and percentage of variance for the first three principal components in a principal components analysis are included. Principal components are extracted from a covariance matrix of 10 log-transformed cranial and dental variables; see figure 8, where the first two components are plotted.

	PC1	PC2	PC3
ONL	-0.7125	0.6602	0.0844
ZYG	-0.8246	-0.2427	0.0664
MTR	-0.9207	0.2991	0.0855
CC	-0.7654	-0.4451	0.1307
M2M2	-0.7184	0.3431	0.1674
ML	-0.9378	0.2100	0.1338
MH	-0.5859	-0.7038	0.3107
LTR	-0.9449	0.1669	0.1222
M1L	-0.4139	-0.8000	-0.2295
M1W	-0.8795	-0.0120	-0.4397
Eigenvalues	0.0298	0.0123	0.0031
% variance	58.9999	24.4082	6.0630



Fig. 9. Skins of the endemic *Pteropus* of Vanuatu. A, *P. fundatus*, AM M26896, adult female, Mota. B, *P. anetianus*, USNM 278062, adult female, Espiritu Santo.

have specialized as a nectar-feeder or by eating inflorescences or smaller fruits and nuts than those typically utilized by these larger bats, as the smaller-toothed species *P. mahaganus* and *P. fundatus* (fig. 7) do in the Solomon archipelago and Vanuatu, respectively (Bonaccorso, 1998; Flannery, 1995). However, no notes about ecological attributes or context of collection are associated with the holotype of *Pteropus allenorum*, such that nothing is firmly recorded of its basic biology.

The morphological resemblance between *P. allenorum* and *P. fundatus* of northern Vanuatu (fig. 7) may indicate that similar small-bodied flying foxes were formerly more widespread throughout the Pacific theatre. If so, their discovery in the modern faunas or subfossil records of Fiji, Tonga, and on other islands of the Vanuatu and Samoan archipelagos might be expected in the future. For example, the current geographic restriction of *P. fundatus* to the small outlying Banks and Torres island groups of Vanuatu (Flannery, 1995) seems likely to be a relictual distribution indicative of “pseudoendemism” in that ar-

chipelago (Steadman, 1997, 2006a). In this vein, we note with interest that Hickey (2007) discussed a small, dark-colored, inflorescence-eating *Pteropus* observed on the large island of Malekula in Vanuatu. Hickey (2007) speculated that if not a juvenile *P. tonganus*, this might be a small flying fox related to *P. fundatus*. The chiropteran faunas of Vanuatu and Fiji undoubtedly remain incompletely inventoried, so future discoveries are certainly to be expected (Helgen and Flannery, 2002; Helgen, 2004c, 2005).

Pteropus coxi, new species

HOLOTYPE: The holotype of *Pteropus coxi* is USNM 3791, skull of an adult, probably male, from the “Samoan Is.,” collected during the U.S. Exploring Expedition of 1838–1842. The skin of this specimen bore the number 3953 but is now apparently lost (L.K. Gordon, in litt.).

PARATYPE: USNM 3790, skull of an adult, probably female, from “Samoan Is.,” also collected during the U.S. Exploring Expedition. The skin of this specimen bore the number

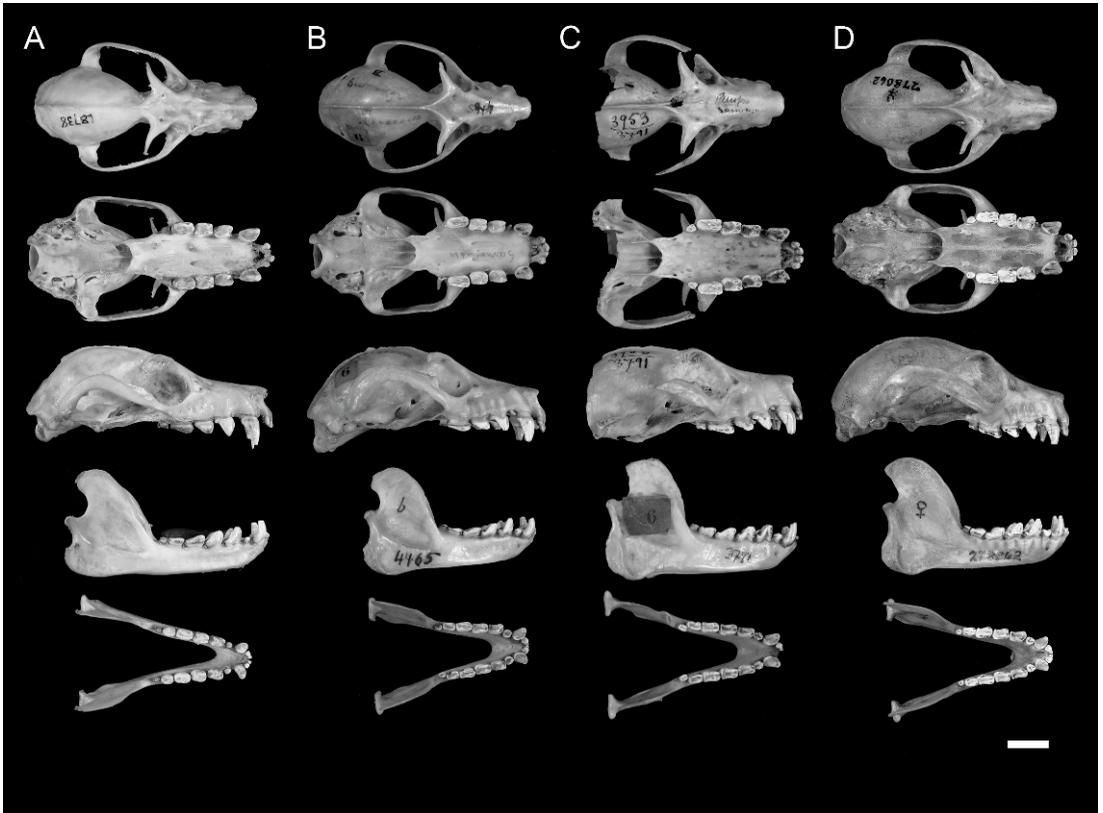


Fig. 10. Skulls of the four larger *Pteropus* species of Vanuatu and Polynesia. **A**, *P. tonganus* (AMNH 68738, adult male, “Samoa”); **B**, *P. samoensis* (USNM 4465, unsexed adult, “Samoa Archipelago”); **C**, *P. coxi* (USNM 3953/3791, probably male, “Samoa Archipelago”); **D**, *P. anetianus* (USNM 278062, adult female, Espiritu Santo, Vanuatu). Scale bar = 10 mm.

3952 but, like the holotype skin, is now apparently lost (L.K. Gordon, in litt.).

DIAGNOSIS: *Pteropus coxi* is a large flying fox similar in cranial conformation to *P. samoensis* and *P. anetianus*—with a robust skull featuring a rostrum of moderate length, a mandible with heavily developed posterior processes, and large molars—but considerably larger than *P. samoensis* and *P. anetianus* in cranial size, with larger canines and cheekteeth (figs. 4–6, 8, 10, 14). Apart from *P. tuberculatus* of the Santa Cruz Islands (an outlying island group between the Solomon archipelago and Vanuatu), *P. coxi* is the only species in the genus in which the very large upper canines sometimes (in the case of *P. coxi*, in one of the two available specimens) bear a secondary, posterior cusp.

DISTRIBUTION: The U.S. Exploring Expedition visited the Samoan archipelago from 7 October to 10 November in 1839, exploring the islands of Tutuila, Upolu, Savai’i, and the Manua group; some members of the expedition also returned to Upolu for visits in following years (one ship, the Porpoise returned 4–8 September 1840 to Upolu; two ships, the Peacock and Flying Fish, returned 6 February to 6 March 1841; M. Grunes, in litt.). *Pteropus coxi* is known only by the holotype and paratype, which were collected at some time during the U.S. Exploring Expedition, but localized only generally to the “Samoa Is.[lands]” or “Samoa Isle” on their accompanying labels. We regard *P. coxi* as a Samoan endemic, although the precise insular extent of its historical distribution

TABLE 4

Specimens of *Pteropus* from Samoa at USNM Collected during the U.S. Exploring Expedition (all of which apparently comprise the original hypodigm or syntype series of *Pteropus samoensis*)

<i>Pteropus samoensis</i> Peale, 1858	
USNM 3788/3949	“Samoan Archipelago”, adult, skin (3949) and skull (3788)
USNM 3789	“Samoan Arch.”, adult female, skull, accompanying skin (USNM 3950) missing
USNM 3947	“Samoan Archip.”, adult, skin
USNM 4465	“Samoan Ids”, adult, skull
USNM 22562	Tutuila Island, adult, skull, accompanying skin (8594) missing
USNM 37860/8597	Tutuila Island, adult, skin (8597) and skull (37860). Lectotype of <i>Pteropus samoensis</i> Peale, 1858, designated herein (see figs. 12, 13)
USNM 37861/8593	Olusinga (Olosega) Island, adult male, skin (8593) and skull (37861)
USNM 37862/8596	Tutuila Island, adult female, skin (8596) and skull (37862)
USNM 37878/8595	Upolu Island, adult, skin (8595) and skull (37878)
<i>Pteropus coxi</i> , n. sp.	
USNM 3790	“Samoan Isle”, skull, accompanying skin (3952) missing
USNM 3791	“Samoan Isle”, skull, accompanying skin (3953) missing
<i>Pteropus tonganus</i> Quoy and Gaimard, 1830	
USNM 3954	“Samoan Island”, adult male, skin with skull in situ
USNM 3955	“Samoan Isle”, adult, skin without skull
USNM 38681/3956	“Samoan Isle”, subadult, skin (38681) and skull (3956)

remains unknown. Future subfossil excavations in Samoa may clarify its prehistoric or historical distribution.

ETYMOLOGY: The specific epithet honors Dr. Paul A. Cox of the Institute for Ethnomedicine in Jackson Hole, Wyoming, in recognition of his research on flying foxes, tropical ecology, and biodiversity conservation in Pacific archipelagos in general and in Samoa in particular. We suggest “Large Samoan Flying Fox” as an appropriate common name for this species.

DESCRIPTION: Nothing is known with certainty about the external appearance of *P. coxi*, because the skins originally associated with both skulls have been lost and cannot be traced (L.K. Gordon, in litt.). However, a few clues are available that may help to envision its appearance. First, the skull of *P. coxi* is larger and more robust than its sympatric congeners on Samoa, an indication that it was probably a heavier bat than *P. samoensis* and *P. tonganus*, with a somewhat longer forearm. Another clue to its appearance may be found in the original description of *Pteropus samoensis* by Peale (1848). The U.S. Exploring Expedition collected *P. samoensis*, *P. tonga-*

nus, and *P. coxi* in Samoa in 1839-1841, but Peale (1848) implicitly referred all of these to *P. samoensis* in his original description of *P. samoensis*, noting:

The species was first discovered on the island of Tutuila, and subsequently in all the islands of the Samoan Group; we obtained numerous specimens, and found the young animals somewhat-lighter coloured than the old ones, but in other respects there is but little variation in colour or size.

In preparing his description of *P. samoensis*, we assume from his comments that Peale had all or most Samoan *Pteropus* specimens from the U.S. Exploring Expedition at hand (of these, those that are specifically localized indicate their collection on Tutuila, Upolu, and Olusinga [= Olosega] Islands; table 4). The skins of both specimens of *P. coxi* (in addition to the still-available skulls) were apparently still extant in 1848 and were apparently referred to *P. samoensis*. As such, we suggest that these specimens can be assumed to have formed part of the original hypodigm of *Pteropus samoensis* (as can

several specimens of *P. tonganus* collected in Samoa during the expedition; see below, where we designate a lectotype for *P. samoensis* to preserve its traditional taxonomic association). Peale's (1848: 20–21) statement about variation (reiterated in the observations of Cassin [1858] a decade later) might allow us to infer that the skins of *P. coxi* were not especially different in overall pelage patterning and form from his series of true *P. samoensis*, which he characterized as “head ... tawny, the front gray; ears small, rounded, black; neck of the old animals rufus [sic], in the younger animals tawny, body and throat reddish-brown; hair erect, and somewhat woolly, most smooth on the back; wing-membranes black; irides brown.” Although *P. coxi* is undoubtedly a larger bat than *P. samoensis*, Peale's (1848) statement about the lack of noticeable size variation in his series also suggests that the skins of *P. coxi* were probably not markedly larger in apparent size as compared to true *P. samoensis* (and *P. tonganus*).

The skull of *P. coxi* is larger and more robustly constructed than that of *P. samoensis*, with a broader rostrum and palate; a longer maxillary tooththrow featuring more massive individual teeth; broader and thicker zygomata and postorbital processes; and a dentary with a deeper ramus, more massive coronoid, condylar, and angular processes, and more heavily sculpted surfaces for muscular attachments. The canines are more massive in general (vertically taller, broader, more anteroposteriorly elongate), and the upper canines bear more prominent internal ridging. In the holotype, the right upper canine bears a groove separating a small secondary cusp from the main body of the canine, and a similar, incipient secondary cusp can be seen on the left upper canine. The paratype, a somewhat younger animal judging from toothwear, also with massive canines, does not have these same secondary cusps. This trait may be individual in its variability, but it could also be a sexual difference. Males and females differ in canine size and robusticity in many species of pteropodids, including many if not most species of *Pteropus* (Andersen, 1912: 75: “canines in males of nearly all species longer and heavier than in females”). Individual premolars and molars

are both wider and longer in *P. coxi* than in *P. samoensis* (e.g., table 1). P1 (upper) is very small but persists in the adult dentition. The first lower premolar (p1) is large. In general cranial robustness, particularly in the conformation of the mandible, *P. coxi* resembles *P. anetianus* of Vanuatu, with which it is most closely allied in our morphometric comparisons (e.g., fig. 14), but the two species differ both in cranial and dental size (greater in *P. coxi*) as well as in the proportional length of the rostrum (longer in *P. coxi*). In its extreme cranial robustness, large teeth, and incipient (if variable) secondary cusps in the upper canines, *P. coxi* might be regarded as ecomorphologically convergent to some extent on the cranially robust and large-toothed Pacific “monkey-faced bats” of the Solomon archipelago (genus *Pteralopex*) and Fiji (genus *Mirimiri*), which occur in the broader region but not in Samoa, and to which flying foxes are not immediately related (Hill and Beckon, 1978; Flannery, 1995; Parnaby, 2002b; Helgen, 2005). (These large bats are thought to feed on nuts, hard, thick-skinned fruits, and perhaps tree exudates; Flannery, 1995; Fisher and Tasker, 1997; Helgen, 2005.)

NATURAL HISTORY: Nothing is known of the habits or biology of *P. coxi*, the largest of Polynesian flying foxes, and we assume that the species is now extinct, perhaps for longer than a century, as the only known specimens were collected in 1839–1841.

However, published observations from the early 1980s by the botanist Paul Cox, discussing a flying fox of unusual size in Samoa, could indicate that *P. coxi* survived until recently. In his paper on the bats of Samoa, Cox (1983) noted an encounter with “*Pteropus samoensis*”:

I will never forget the first time I saw one of these giant bats in the rainforest. One day, while climbing a tree, I saw what appeared to be an eagle flying away from a liana flower. The bat I saw in my field glasses appeared to have a wingspan of five feet or more and lacked the white fur on the back of the neck that characterizes the locally common flying fox, *P. tonganus*. This large bat was black and its behavior was completely unusual. I later thoroughly enjoyed watching them soar,



Fig. 11. Color variation in the extant *Pteropus* spp. of Samoa. **A**, *P. tonganus* (USNM 566603, adult female, "Samoa"), dorsal coloration pattern; **B**, *P. samoensis* (USNM 338624, adult male, Tutuila), dark phase (most common); **C**, *P. samoensis* (USNM 565827, adult female, Tutuila), white phase (very rare); **D**, *P. samoensis* (USNM 3947, unsexed young adult, "Samoa Archipelago"), pale, straw-colored phase (less common in Samoa, more common in Fiji).



Fig. 12. Skull of USNM 8597/37860, lectotype of *Pteropus samoensis* Peale, 1848. Scale bar = 10 mm.

eagle-like, high above the forest in midday sun.

In this paper, Cox (1983) concluded that *P. samoensis* is perhaps the largest species of *Pteropus* anywhere—a strange claim, considering that *P. samoensis* is a medium-sized member of the genus, and even sympatric *Pteropus tonganus* is slightly heavier (despite equivalent forearm lengths in Samoa [table 1], body mass averages 383 g in three adult Samoan *P. samoensis* and 410 g in nine adult Samoan *P. tonganus* at USNM). After an attempt to collect verifying voucher specimens, and further reflection, Cox (1984a) noted:

Two specimens [later] shot by hunters were confirmed as *P[teropus] samoensis* by Dr. Karl Koopman at the American Museum of Natural History. These had wingspans of only 3.5 feet, the size considered typical for the species. The larger bats that I observed appeared to behave like normal *P. samoensis*, however their size raises the possibility that my observations include a second, but undescribed endangered species. These findings emphasize the paucity of available information and the urgency of a thorough investigation.

Understandably, most subsequent authors have attributed Cox's observations of giant black bats to somewhat exaggerated or fantastical descriptions of *Pteropus samoensis* (e.g., Wilson and Engbring, 1992), a conclusion that Cox apparently later accepted (Cox, 1999). However, we raise the possibility (however slight) that Cox instead encountered the species that we describe here as *P. coxi*, a very large species of Samoan flying fox that is probably closely related to *P. samoensis*, with which it must occur (or have occurred) sympatrically. If Cox truly observed *P. coxi* in the forests of Upolu in 1981, then he has provided the only known description of its external features—i.e., that it is “black”, with a wingspan of ca. “5 feet” (= 1.5 m) (Cox, 1983; later revised to “4 feet” [= 1.2 m] by Cox, 1999). Certainly neither *P. samoensis* nor *P. tonganus* achieves such a large body size in Samoa (Wilson and Engbring, 1992). That



Fig. 13. Skin of USNM 8597/37860, lectotype of *Pteropus samoensis* Peale, 1848. A, dorsal view. B, ventral view.

Cox's clearest observations of this large bat took place in upland forests during the day (Cox, 1983, 1984a), when *P. samoensis* also flies (e.g., Andersen, 1912; Wilson and Engbring, 1992; Thomson et al., 1998, 2002), provides the only ecological information that might conceivably refer to *P. coxi*.

Cox's (1984a) prescient call regarding the "urgency of a thorough investigation" into the possibility that more than two extant species of *Pteropus* persist in Samoan forests has gone unheeded. This urgency has increased with the passage of time and with the discoveries reported herein. To us, Cox's account raises the slight possibility that populations of *P. coxi* could persist in Samoa, especially in remote montane habitats on the high forested islands of Upolu and Savai'i. This possibility

should be pursued in further biological explorations in the archipelago and in interviews with local communities throughout Samoa. Should *P. coxi* persist in Samoa as a rare species, some field studies that have attempted to document the biology of "*Pteropus samoensis*" in recent years (e.g., Cox, 1983; Wilson and Engbring, 1992; Banack, 1996, 1998; Brooke, 2001) could conceivably be based on studies of more than one biological species (i.e., *P. samoensis* and *P. coxi*), even after distinctions between *P. samoensis* and *P. tonganus*, sometimes confused in the past, were made clear to Samoan fieldworkers (Wilson and Engbring, 1992). Although it is tempting to associate this newly elucidated taxon with Cox's observations in the early 1980s, we suggest that these are best viewed

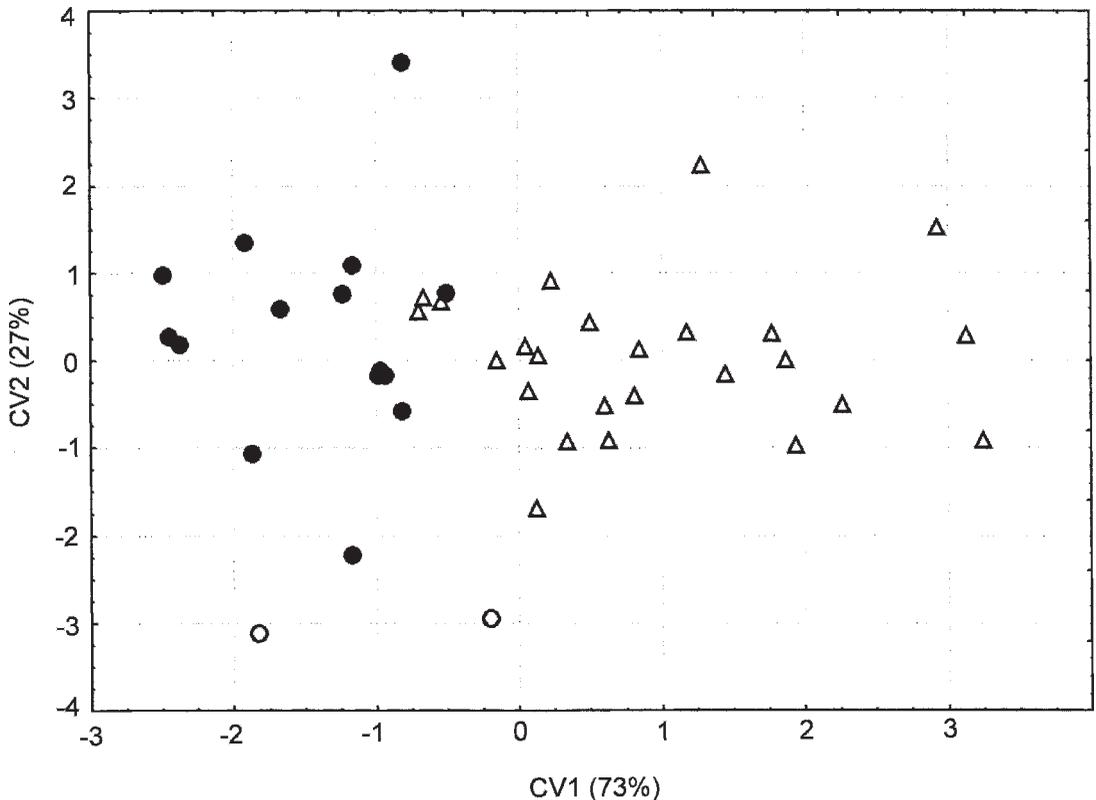


Fig. 14. Bivariate plot of the two canonical variates in a discriminant function analysis contrasting samples identified as *Pteropus samoensis* (Fiji and Samoa, triangles), *Pteropus anetianus* (Vanuatu, closed circles), and *Pteropus coxi* (Samoa, open circles). Parenthetical numbers on the axes indicate the proportion of variance for each variate (see table 5).

with skepticism in the absence of any additional evidence for the recent survival of *P. coxi*. A dark brown color phase is the most common coloration pattern in Samoan populations of *Pteropus samoensis* (fig. 11), and the wingspan of flying foxes is difficult to estimate from any distance. As such, Cox's (1983, 1984) observation of very large, blackish bats in flight during the day could easily be based on sightings of *P. samoensis*. Furthermore, while 20th-century specimens of *P. samoensis* and *P. tonganus* from Samoa are not uncommon in museums (e.g., AM, AMNH, ANSP, USNM, ZMUC), we know of no museum specimens of *P. coxi* collected since the type series was taken more than 160 years ago. Regardless of whether more than two species of *Pteropus* survive today in Samoa, it is clear to us from our own experiences and from our close reading of relevant literature that it is indeed

only *P. samoensis* and *P. tonganus* that have been regularly encountered by field biologists working in Samoa during the past 15 years (e.g., Wilson and Engbring, 1992; Craig and Syron, 1992; Elmquist et al., 1992, 1994; Craig et al., 1994a, 1994b; Morrell and Craig, 1995; Grant and Banack, 1995, 1999; Banack, 1996, 1998; Pierson et al., 1996; Grant et al., 1997; Miller and Wilson, 1997; Richmond et al., 1998; Thomson et al., 1998, 2002; Brooke et al., 2000; Nelson et al., 2000; Webb et al., 2000; Brooke, 2001; Banack and Grant, 2002, 2003).

A LECTOTYPE FOR *PTEROPUS SAMOENSIS* PEALE, 1848

As discussed above, Peale (1848) did not designate a type specimen for *Pteropus samoensis* in the original description of that

TABLE 5
Underlying Statistics for Discriminant
Function Analysis

Correlations, canonical correlations, eigenvalue, cumulative proportion of variance contrast eight log-transformed measurements for adult skulls identified as *Pteropus samoensis* (25 skulls), *P. anetianus* (15 skulls), and *P. coxi* (2 skulls) (see fig. 14, where specimen scores are plotted)

	CV1	CV2
ONL	0.2255	-0.6424
ZYG	-0.5093	-0.5915
MTR	-0.1682	-0.7728
CC	-0.1113	-0.5118
M2M2	-0.0032	-0.1207
ML	-0.2695	-0.7578
MH	-0.6815	-0.2677
LTR	-0.2631	-0.7630
Canonical correlation	0.7628	0.5841
Eigenvalue	1.3915	0.5178
Cumulative proportion of variance	0.7288	1.0000

species (and did not discriminate specimens of *P. tonganus* and *P. coxi* from the remainder of the Samoan *Pteropus* specimens referred to *P. samoensis*). Accordingly, all Samoan *Pteropus* collected during the U.S. Exploring Expedition must be regarded as syntypes of *P. samoensis*, including those specimens included here in the type series of *P. coxi*. Lyon and Osgood (1909: 258) (followed by Poole and Schantz, 1942: 142) regarded the series of specimens of *P. samoensis* from Tutuila as "typical", based on Peale's statement that "this species was first discovered on Tutuila, and subsequently on all the islands of the Samoan group; we obtained numerous specimens." This act by Lyon and Osgood formally restricted the type locality of *P. samoensis* to Tutuila, but no lectotype was designated.

The syntype series of *P. samoensis* is composite (table 4), comprising specimens of three biological species (nine specimens of the taxon traditionally identified as *P. samoensis*, three specimens of *P. tonganus*, and two specimens of *P. coxi*; table 4). Selection of a lectotype for *P. samoensis* is required to preserve what can be regarded as the traditional association of the name, as established most authoritatively by Andersen's (1912) description and overview of *P. samoensis*. (Unfortunately, in preparing his account,

Andersen did not have access to the entire syntype series collected by the U.S. Exploring Expedition, and in particular he did not examine the type series of *P. coxi*.)

Included within the syntype series of *P. samoensis* at USNM are three specimens marked as coming from Tutuila, which has been regarded as the type locality following Lyon and Osgood (1909) and Poole and Schantz (1942). Each of these three specimens represents the biological species corresponding to Andersen's understanding and usage of the name *Pteropus samoensis* Peale, 1848. The first of the three specimens listed by Lyon and Osgood (1909: 142), an unsexed adult, USNM 8594/22562 (the latter number misquoted as 25562 by Lyon and Osgood), was at some point "turned over to the Dep[artment of] Comp[arative] Anat[omy]", and it now consists only of a skull with the basicranial region broken. The second, an adult female, USNM 8596/37862, consists of a study skin and accompanying skull with the back of the braincase sawn off and the left upper molar row smashed. The third, USNM 8597/37860, an unsexed adult, comprises a study skin and skull, both in reasonably good condition. It is this last specimen, figured here (figs. 12, 13), that we choose as the lectotype of *Pteropus samoensis* Peale, 1848.

THE SYNONYMY OF *PTEROPUS* *SAMOENSIS* PEALE, 1848

In the context of designating a lectotype for *P. samoensis*, it is profitable to briefly review the nomenclatural synonymy of the species. So far as we can ascertain, the first name ever applied to a flying fox from Samoa appears in the narrative account of the U.S. Exploring Expedition published by Wilkes (1844). Wilkes (1844: 128) wrote, "there are no traces among these islands of any native quadruped, nor any other of the mammalia, except a species of bat (*Pteropus ruficollis*), which is very destructive to the bread-fruit." This name (*ruficollis*), introduced without description, must be regarded as a nomen nudum, and can be taken to apply to all flying foxes that Wilkes and his crew may have seen in Samoa (at least four species at the time of their voyage) or collected in Samoa (at least three

species; table 4). Wilkes' nomen nudum is probably a lapsus for *Pteropus rubricollis* E. Geoffroy, 1810 (a synonym of *P. subniger* (Kerr, 1792), an extinct flying fox endemic to the Mascarenes), a taxonomic epithet widely applied to flying foxes in the early to middle 19th century (see Andersen, 1912). Andersen (1912) and subsequent systematic workers (e.g., Wilson and Engbring, 1992; Simmons, 2005) overlooked Wilkes' usage of *ruficollis* and attributed the original use of the name to Nicoll (1908), also as a nomen nudum, in his book *Three Voyages of a Naturalist*. Nicoll (1908) also employed another lapsus, *rufficollis*, in the index of his book, and yet another, *fuscicollis*, in an earlier publication (Nicoll, 1904). It is clear to us that in each case Nicoll's names were used for Samoan flying foxes in the same general sense as employed by Wilkes (1844). Both of these additional nomina nuda can be regarded simply as incorrect subsequent spellings of Wilkes' original nomen nudum, *ruficollis*; all of these are partial synonyms of *Pteropus samoensis* Peale, 1848.

A scientific name that deserves careful consideration in light of the discoveries reported in this paper is *Pteropus whitmeei* Alston, 1874. Alston (1874: 96) discussed a small collection of bats received from the Rev. S.J. Whitmee in Samoa, which consisted of four specimens—one individual of *Emballonura semicaudata*, two individuals of *Pteropus tonganus* (reported at the time as "*P. flavicollis*"), and one specimen that Alston judged to be an undescribed species, introduced under the new name *Pteropus whitmeei*. The collector of the holotype of *whitmeei* indicated that this latter species was "very common in Samoa" and that he "once saw a number together ... estimated at over a thousand" in an inland crater on Savai'i (Whitmee, 1874b). Alston's description of *whitmeei* is cursory and based on a single specimen preserved intact (i.e., with skull in situ) in alcohol (such that only color, external measurements, and the comparative size of the first upper premolar are discussed). This type specimen was deposited in the personal collection of "the Rev. Canon Tristram" (Alston, 1874: 96), and we do not know its current whereabouts. This specimen was not available to Andersen (1912), who, while based in London, attempted to examine all megachir-

opteran type specimens for his signal treatise on pteropodid systematics, and this specimen is apparently not in the BMNH today. Andersen (1912) argued that the type of *whitmeei* must be an incompletely grown specimen of *P. samoensis*, and we agree. Alston noted that *whitmeei* "is most nearly allied to *P. vitiensis* Gray (= *Pteropus samoensis nawaiensis* Gray, 1870, the Fijian subspecies), of which it may probably be regarded as the Samoan representative", and he distinguished it from typical *P. samoensis* (which he knew only on the basis of Peale's original description) by its smaller size alone. Alston's description of the pelage and the excellent accompanying color plate of the type specimen match the coloration of many skins of *Pteropus samoensis samoensis* at USNM and elsewhere. Its forearm length (113 mm) falls within the range of subadult *P. samoensis*. This forearm length also compares favorably with the nearly mature holotype of *Pteropus allenorum* (116 mm). It is not possible that *whitmeei* is an earlier name for *P. allenorum*, however, as Alston mentioned that the first upper premolar in *whitmeei* is heavier than in *P. s. nawaiensis*, itself a much larger-toothed bat than *P. allenorum*. We suggest that *Pteropus whitmeei* is unlikely to be an earlier name for *P. coxi* because of the very small size of the holotype, which instead matches subadult *P. samoensis* in size and corresponds precisely in its coloration to the most common color variant of *P. samoensis*. As long as its holotype remains unavailable to systematists, the name *whitmeei* should rest within the synonymy of *P. samoensis*, where Andersen (1912) and all subsequent authors have placed it, and where we judge that it is best arranged on the basis of information provided in the original description (Alston, 1874). Whitmee's (1874b) comments about the abundance of "*P. whitmeei*" further suggest that he was referring to one (or both) of the more commonly collected bats of Samoa (i.e., *Pteropus samoensis* and/or *P. tonganus*), and probably indicate his inability to distinguish the two (or more) *Pteropus* species extant in the archipelago at that time. Other flying fox specimens sent to BMNH by Whitmee from Samoa represent both *P. samoensis* and *P. tonganus* (Andersen, 1912: 188, 287).

Apart from *whitmeei* and *ruficollis* and its various lapsed nomenclatural manifestations,

the synonymy of *Pteropus samoensis* also includes the names *nawaiensis* and *vitiensis*, taxonomic names applied to Fijian populations of *P. samoensis* by Gray (1870). We follow all recent authors in recognizing the Fijian *P. s. nawaiensis* as a subspecies of *P. samoensis* (e.g., Wodzicki and Felten, 1975; Wilson and Engbring, 1992; Flannery, 1995; Ingleby and Colgan, 2003; Simmons, 2005). *Pteropus s. nawaiensis* differs from the nominate subspecies of Samoa in its smaller body size (in average terms; see table 1; body weight averages 353 g in seven adults from Fiji [AM] versus 383 g in three adults from Samoa [USNM]), but without concomitant differences in cranial size (table 1), and in its less variable coloration—most Fijian animals are dark brown with a paler, straw-colored mantle, in contrast to the greater chromatic variability evident in museum samples of *P. samoensis* (fig. 11).

The synonymy of *Pteropus samoensis* (including synonyms from Fiji) can thus be delineated as follows:

- Pteropus ruficollis* Wilkes, 1844: 128. Type locality “Samoa”. Part; nomen nudum.
- Pteropus samoënsis* Peale, 1848: 20. Type locality “Tutuila ... and, all islands of the Samoan Group.” Part; type series including specimens referred here to *Pteropus tonganus* Quoy and Gaimard, 1830, and *Pteropus coxi*, n. sp. Type locality restricted to Tutuila (American Samoa) by Lyon and Osgood (1909: 142). Clarification of composite type series and lectotype designation provided above.
- Pteropus whitmeei* Alston, 1874: 96. Type locality “Samoa”.
- Pteropus nawaiensis* Gray, 1870: 107. Type locality “Nauai” and “Ovalau” (Fiji). Lectotype designation and restriction of type locality to Nauai by Andersen (1912: 283–284).
- Pteropus vitiensis* Gray, 1870: 109. Type locality “Ovalau” (Fiji).
- Pteropus fuscicollis* Nicoll, 1904: 413. Part; nomen nudum and incorrect subsequent spelling of *P. ruficollis* Wilkes, 1844: 128.
- Pteropus rufficollis* Nicoll, 1908: 245. Part; nomen nudum and incorrect subsequent spelling of *P. ruficollis* Wilkes, 1844: 128.

DISCUSSION

RELATIONSHIPS AND BIOGEOGRAPHY

In his classic monograph on the Pteropodidae, Andersen (1912) subdivided the large genus *Pteropus* into 17 species groups. No

single reviewer has reviewed the content of the entire genus in detail since, although some authors have provided important partial revisions (e.g., Musser et al., 1982; Bergmans, 1990, 2001; Koopman, 1994; Giannini et al., 2008). It is becoming clear, especially from molecular studies, that species groups of *Pteropus* as currently constituted will require substantial revision and rearrangement before these groupings effectively portray evolutionary relationships (Kirsch et al., 1995; Colgan and da Costa, 2002; Giannini and Simmons, 2003, 2005; Giannini et al., 2008), and for now we suggest these should be employed only as “groupings of convenience”.

Andersen (1912) united *P. samoensis* (including the Fijian subspecies *P. s. nawaiensis*, then recognized as a distinct species) and *P. anetianus* of Vanuatu into a unique species group, designated as “the *Pteropus samoënsis* Group.” These species share a skull that is not particularly large, but that is extremely robust, with a relatively short rostrum, heavy mandible, and large teeth. Based on these same morphological features, we tentatively add *P. coxi* to this species group, which may constitute an older Pacific lineage in the genus (Ingleby and Colgan, 2003; Giannini et al., 2008).

Andersen (1912) classified the other common species of Samoa, *P. tonganus*, in the *marianus* species group, which includes *P. mariannus* from the Mariana Islands, *P. pelewensis* from the Palau, *P. ualanus* from Kosrae, and *P. yapensis* from Yap, a group of closely related allopatric species of the remote central Pacific (Simmons, 2005). This group of species is united by a rather uniform color pattern that includes a pale yellowish mantle contrasting with a blackish back, and dark brown underparts with scattered silver hairs. More recently, especially through genetic studies (Colgan and da Costa, 2002; Ingleby and Colgan, 2003), it has become clear that *P. tonganus* is most closely related to *P. conspicillatus* of the Moluccas, New Guinea, and Australia, a species that it closely resembles morphologically, but that Andersen (1912) instead placed within a separate species group (the *conspicillatus* group). As noted, ongoing studies such as these provide an indication that previously recognized species groupings

within *Pteropus* are united out of geographic convenience or primarily by features that are variably plesiomorphic in nature or convergently derived. These will eventually require comprehensive revision, ideally drawing from united anatomical and molecular comparisons (see Giannini et al., 2008).

If we were to place *P. allenorum* within the species group framework advocated by Andersen (1912) and Koopman (1994), it would be within the *chrysoproctus* species group (cf. Simmons, 2005). Other members of this group include *P. chrysoproctus* from the Moluccas, *P. rayneri* from the Solomon Islands, and *P. fundatus* from Vanuatu. These species share a dentition characterized by relatively small cheekteeth, with somewhat more robust incisors and canines. However, based on our own preliminary examinations, we suggest that the *chrysoproctus* group (with or without inclusion of *P. allenorum*) is unlikely to be monophyletic, and we advocate further study of the immediate relationships of *P. allenorum* in particular.

ECOLOGY AND EXTINCTION

With the advent in recent decades of rigorous zooarchaeological excavations in Pacific archipelagos, and the resulting systematic studies of osteological remains, it is now well established that both insular extirpations and global extinctions of vertebrate species have been widespread and severe throughout the region since the first arrivals of human settlers to many island groups in recent millennia (e.g., Steadman, 1993, 1995, 1997, 2006a, 2006b; Steadman and Kirch, 1990; Pregill, 1993; Pregill and Dye, 1989; Balouet and Buffetout, 1987; Mead et al., 2002; Molnar et al., 2002; Helgen, 2004b). Documented prehistoric vertebrate extinctions in the Pacific primarily concern birds, lizards, and land crocodiles; relatively few examples concerning mammals are known (Flannery, 1995). Mammalian examples of Holocene extinction events documented with recourse to insular subfossil records (each extinction possibly dating to either prehistoric times or to recent centuries) thus far include rodent extinctions in the Bismarck Archipelago and Solomon Islands (Flannery and Wickler, 1990;

Flannery and White, 1991), bat extinctions in Hawaii and on Lord Howe Island (Ziegler, 2002; McKean, 1973), insular extirpations of bats in Tonga and the Cook Islands (Hill, 1979; Wodzicki and Felten, 1981; Tiraa, 1992; Flannery, 1995; Koopman and Steadman, 1995; Weisler et al., 2006), and insular extirpations of marsupials and rodents anthropogenically transported to islands in Northern Melanesia and West Polynesia (Flannery et al., 1988; White et al., 2000). Closer study of zooarchaeological material already excavated from various Pacific islands will probably document additional examples of mammalian extinction and insular extirpation in the broader region, particularly for bats (see Steadman, 2006b: 68; Steadman, in litt.), as undoubtedly will future zooarchaeological fieldwork. In West Polynesia, detailed studies of subfossil vertebrates of Fiji and Tonga have been published (Molnar et al., 2002; Pregill, 1993; Pregill and Dye, 1989; Steadman, 2006b and references therein), but excavations in Samoa have not yet revealed an extensive Holocene vertebrate record. Prehistoric vertebrate extinctions in that archipelago, if they have occurred, remain to be documented (Green and Davidson, 1969, 1974; Jennings et al., 1976; Nagaoka, 1993; Steadman and Pregill, 2004; Steadman, 2006b).

Other Pacific vertebrate extinctions, not clearly associated with the initial colonization of Pacific islands by humans, have happened more recently—within the past 200 years. This is demonstrated by the discovery (and deposition of representative specimens in museum collections) of a number of locally endemic species, mainly birds, that were encountered during the period of early, pioneering biological exploration of the Pacific by European sailors and scientists (primarily between the late 17th and early 20th centuries), but that are no longer to be found in the archipelagos where they were collected. Avian examples of historical extinctions are recorded especially from New Zealand (Tennyson and Martinson, 2006; Worthy and Holdaway, 2002) and Hawaii (Pratt, 1994; Ziegler, 2002), but also from the Solomon Islands, New Caledonia, the Society Islands, Guam, and the Micronesian island of Kosrae (Mayr and Diamond, 2001; Steadman, 2006b and references there-

in). As far as we are aware, there is only one previously documented case of an historical vertebrate extinction in Samoa. This concerns the large flightless gallinule *Pareudiastes pacificus*, a Samoan endemic that occurred historically on Savai'i (Hartlaub and Finsch, 1871), probably also on Upolu (Whitmee, 1874a), and perhaps on other islands in American Samoa (Armstrong, 1932). Known by a handful of specimens collected between 1869 and 1873 on Savai'i, it probably became extinct in the late 19th or early 20th century (Hartlaub and Finsch, 1871; Stair, 1897; Olson, 1975; DuPont, 1976; Reed, 1980; Merlin and Juvik, 1983; Pratt et al., 1987; Taylor, 1998), although some authorities are convinced that it may still survive in upland Savai'i as a critically endangered species (Bellingham and Davis, 1988; Stattersfield et al., 1998). Whether extinct or critically endangered, as a Samoan endemic known with certainty only from a small number of 19th-century specimens, and not definitively recorded during the 20th century, *Pareudiastes pacificus* offers a close analogy to the two flying foxes described in this paper. We suggest that *Pteropus allenorum* and *P. coxi* are probably best regarded as extinct, as neither species has been definitively encountered in the past 150 years. However, as with *Pareudiastes pacificus*, it would not be surprising if exhaustive searching in the archipelago, perhaps especially on remote islets (cf. Freifeld et al., 2001) and in upland habitats, revealed that a population of one or both species of these large bats still persists.

Pteropus allenorum and *P. coxi* coexisted into modern times with at least three other bat species definitively recorded in the contemporary fauna of Samoa—the small, insectivorous emballonurid *Emballonura semicaudata* (mass averaging 7 g) and the large fruit-eating pteropodids *Pteropus samoensis* and *Pteropus tonganus*. *Pteropus allenorum* and *P. coxi* are the only endemic chiropteran species known in the Samoan fauna; the ranges of these other bats extend (or extended) beyond Samoa at least to Fiji and Tonga (although *Pteropus samoensis* is extinct in Tonga today; Koopman and Steadman, 1995), and two of them (*E. semicaudata* and *P. tonganus*) are comparatively widespread in the broader Pacific region

(Flannery, 1995; Helgen and Flannery, 2002). Additionally, a species of the vespertilionid genus *Myotis* may also have been present in the 19th-century fauna of Samoa, although this is disputed (see below).

Specimens retained in museum collections today reveal that naturalists who visited Samoa between 1839 and 1856 encountered four species of *Pteropus* in the archipelago: *P. samoensis* (many specimens, 1839 and later), *P. tonganus* (three specimens, 1839–1841), *P. coxi* (two specimens, 1839–1841), and *P. allenorum* (one specimen, 1856). Members of the U.S. Exploring Expedition visited Samoa for about two months over the years 1839–1841, collecting at least nine specimens of *P. samoensis*, but only two specimens of *P. coxi* and three of *P. tonganus* (table 4). This provides a possible indication that *P. samoensis* was more common than *P. tonganus* in Samoa 170 years ago, although interspecific differences in behavior (*Pteropus samoensis* is diurnal and less skittish than *P. tonganus*) may also explain these differences. In any case, *Pteropus tonganus* is today the most common pteropodid in Samoa, *P. samoensis* is much less common, and *P. allenorum* and *P. coxi* are probably extinct (Wilson and Engbring, 1992). With these disruptions over the past century and a half in taxonomic (and trophic) diversity (and possibly in relative abundance) in the flying fox component of Samoa, we speculate that the tropical ecology of Samoan forests has probably changed in tandem. Flying foxes have been characterized as “strong interactors” in remote insular tropical forest ecosystems (Cox et al., 1991) because they are important pollinators and seed dispersers in these vertebrate-depauperate environments (Cox, 1982, 1984b; Marshall, 1983; Fujita and Tuttle, 1991; Whittaker and Jones, 1994; Banack, 1998; Shilton et al., 1999; Cox and Elmquist, 2000; Webb et al., 2000; Nelson et al., 2000, 2005; Elmquist et al., 2002; Meehan et al., 2002, 2005; McConkey and Drake, 2002, 2006, 2007; Parsons et al., 2007). The extinction of Samoa's largest and smallest flying foxes may have had particularly acute effects on forest ecology, with the remaining, intermediate-sized *Pteropus* species unlikely to replicate all of their ecological interactions. Many Samoan plants may have depended on

Pteropus coxi and *P. allenorum* as key pollinators and seed dispersers, and would have coevolved with them. We encourage future studies contrasting cranial and dental morphologies of the four modern *Pteropus* of Samoa in greater detail. In light of previous studies of chiropteran craniodental features and their ecological correlates, research along these lines may further illuminate ecological differentiation in these four presumably sympatric congeners (cf. Aguirre et al., 2002; Campbell et al., 2007; Dumont, 1997, 2004, 2006; Dumont and O'Neal, 2004; Freeman, 1988, 1995; Steadman, 1997).

Ultimately, recourse to extensive subfossil deposits will provide the only means to definitively characterize the complete prehuman and pre-European content of the Samoan bat fauna, should such deposits prove eventually to be available (Steadman, 2006b). The elucidation of *P. allenorum* and *P. coxi* demonstrates that the large-bodied bat fauna of Samoa was twice as diverse in historical times (comprising four species larger than 200 g) than previously suspected. Other lines of evidence lead us to suspect that the small-bodied chiropteran fauna of Samoa may also have been more species-rich than indicated by the single insectivorous species known from the archipelago today (*E. semicaudata*). The molossid *Chaerephon bregullae* and the small pteropodid *Notopterus macdonaldi* are both known from the modern faunas of Vanuatu and Fiji, to the west of Samoa, and from the subfossil fauna of Tonga, to the south (Koopman and Steadman, 1995). Other species of *Chaerephon* are represented in the modern oceanic insular faunas of Northern Melanesia (Flannery, 1995), and a second species of *Notopterus* (*N. neocaledonica*) occurs in the modern oceanic fauna of New Caledonia. Clearly, representatives of *Chaerephon* and *Notopterus* (like *Pteropus* and *Emballonura*) crossed extensive oceanic barriers repeatedly during their histories of dispersal throughout the Pacific; their scattered distribution across multiple remote insular archipelagos suggests to us that *Chaerephon* and *Notopterus* could conceivably have colonized and occurred in Samoa in the past. Both *Chaerephon* and *Notopterus* (like *Emballonura*) are reliant on caves as roosting sites, which

may render them more susceptible to decline and extinction in the face of intensive exploitation or cave disturbances than forest-roosting bats (Flannery, 1995). As in Tonga, these elements of the fauna might have become extinct in Samoa either before or soon after European exploration and impacts in the region began, before any modern museum specimens were (or, perhaps, could be) obtained. Alternatively, *Chaerephon* and *Notopterus* could occur today in remote cave systems in Samoa, remaining undetected to date. Similarly, the vespertilionid genus *Nyctophilus* is represented in the modern faunas of Northern Melanesia (Flannery, 1995), New Caledonia (Parnaby, 2002a), and Vanuatu (P. Bouchet, personal commun.; Steadman, 2006b), and persisted into the 19th century in Fiji, at least if the record presented by Dobson (1878: 174–175) is to be accepted (e.g., see Miller, 1907; Parnaby, 2002a). On remote Pacific islands, species of *Nyctophilus* are associated with montane forest habitats (Bonaccorso, 1998; Parnaby, 2002a; P. Bouchet, personal commun.), and we suggest that the mountains of Samoa, little surveyed for small bats, might well harbor a representative of the genus, or have done so into the recent past. Montane forests in Fiji are the place to search for the continued occurrence of the genus in that archipelago, as well.

Another indication of a potentially richer Samoan “microchiropteran” fauna was provided by Dobson (1878), who described the vespertilionid taxon *Myotis insularum* (initially under the name combination *Vespertilio insularum*), the holotype of which was said to have been collected in the “Navigators’ Islands” (i.e., Samoa). According to Dobson (1878: 313), the holotype was collected by a “Mr. Schmeltz”. This was most likely Johannes Dietrich Eduard Schmeltz, custodian of the Godeffroy Museum in Hamburg, which sold natural history specimens collected throughout the Pacific region to many European museums during the 19th century (see Evenhuis, 2007). Our understanding is that Schmeltz organized Godeffroy specimens in Hamburg, but was not a field collector himself. If the holotype of *M. insularum* originated from Samoa, it was likely received

from Dr. Eduard Gräffe, a Godeffroy representative based in Apia for a decade beginning in 1861, who was apparently responsible for the collection of most Godeffroy specimens from Samoa (Hoffman, 1999; Evenhuis, 2007). The collectors Andrew Garrett and Franz Hübner also collected in Samoa for the Godeffroy trading company and museum (Evenhuis, 2007: 20).

Because no further specimens of *Myotis* have been obtained in Samoa, most authors have regarded the occurrence as probably erroneous (Tate, 1941; Findley, 1972; Cox, 1983; Koopman, 1994; Helgen and Flannery, 2002). Nevertheless, *insularum* has never been firmly equated with any other species in the genus; its taxonomic status remains indeterminate (Simmons, 2005). The discovery of *P. allenorum* and *P. coxi* amongst Samoan museum material collected in the mid-19th century suggests to us that the status of *M. insularum* as a rare or now-extinct Samoan bat deserves consideration and renewed study. The natural presence of *Myotis* in Samoa would hardly be surprising, as *Myotis* is the most geographically widespread chiropteran genus on earth (Findley, 1972; Ruedi and Mayer, 2001). Like all chiropteran genera present in the modern and subfossil faunas of Fiji, Samoa, or Tonga apart from the endemic montane genus *Mirimiri* (i.e., *Pteropus*, *Notopterus*, *Emballonura*, and *Chaerephon*), *Myotis* also occurs in the relatively remote archipelago of Vanuatu (Medway and Marshall, 1975; Hill, 1983; Flannery, 1995; Helgen and Flannery, 2002). Comprehensive systematic study of Old World *Myotis* will be requisite to establish whether the holotype of *insularum* is truly morphologically or genetically distinctive relative to phenetically similar *Myotis* taxa (cf. Findley, 1972), as would be expected if the holotype originated (and not as a vagrant) from such a remote archipelago. In the meantime, we concur with Simmons (2005) that *M. insularum* should be provisionally ranked as a Samoan taxon in need of clarifying study. In this light we note that Krämer (1903) listed two native names applied to small insectivorous bats in Samoa—*pe'ape'avai*, said to apply to "*Emballonura semicaudata*", and *apa'auvai*, said to apply to "*Emballonura fuliginosa*" (a

synonym of *E. semicaudata*). We presume this to be an error of interpretation on Krämer's part, and that both of these Samoan names (if indeed they are truly different names) apply to *Emballonura semicaudata*. We mention Krämer's account simply to reference his apparent impression that more than one kind of small insectivorous bat was traditionally recognized by Samoans in historical times (see also Cox, 1983: 519).

The case of *Myotis insularum* warns that careful consideration is needed before accepting the geographic provenance of specimens from possibly "unlikely" (or subsequently unverified) localities, perhaps especially when associated label or catalog data provide a general locality only (such as the "Navigators' Islands" in the case of *insularum*). Notable errors have been made in the past in attributing bats to Pacific archipelagos on the basis of incorrect locality data. *Emballonura semicaudata* was mistakenly recorded from the Marshall Islands by Tate and Archbold (1939) (see Sanborn, 1953; Lemke, 1986). The syntypes of *Phyllorhina taitensis* Fitzinger, 1861, a synonym of the horseshoe-bat *Hipposideros speoris* (Schneider, 1800), endemic to the Indian subcontinent, were supposedly collected in Tahiti, far outside the natural distribution of *Hipposideros*, and they are undoubtedly incorrectly localized (Dobson, 1877). An early record of *Notopterus* from Ponapé in the Caroline Islands, based on two immature specimens at the Naturalis Museum in Leiden (Jentink, 1887, 1888), is probably erroneous (Helgen, *in* Simmons, 2005). A particularly relevant case of misattribution is that of *Pteropus laniger*, a species described by Harrison Allen in 1890 (originally as *Pteropus lanigera* [sic]) on the basis of two specimens, located today at USNM and MCZ (Allen, 1890; Helgen and McFadden, 2001). The type series of *P. laniger*, purchased from Ward's Natural Science Establishment in Rochester, New York (a well-known supplier of natural history specimens), was supposedly collected in the "Samoa Islands", but Andersen (1912) established that the lectotype of *laniger* (designated by Helgen, *in* Helgen and McFadden, 2001: 98–99) is morphologically indistinguishable from *Pteropus insularis*

Hombron and Jacquinot, 1842, a small flying fox known only from Micronesia. Indeed, Allen (1890) based his description more on geography than anything else; he recognized that his new taxon *laniger* was more or less identical to *Pteropus phaeocephalus* (a synonym of *P. insularis*), and he did not offer any features to distinguish the two nominal forms. We have independently verified Andersen's conclusions regarding *laniger* based on direct comparisons of the lectotype of *laniger* and series of *insularis* (at USNM) and through multivariate craniometric analyses involving different insular populations of *P. insularis*, based on specimens at AMNH, ANSP, BMNH, MNHN, USNM, and ZMB (our results, not shown here, suggest to us that the type series of *laniger* likely originated from islands in the Chuuk group of the Carolines). Certainly, misattribution of the type locality in the description of *Pteropus laniger* should give pause for thought in a paper in which we describe two species of *Pteropus*, both credited to Samoa, on the basis of incomplete 19th century museum specimens. In contrast to the situation with *laniger*, however, for both new species described here (*P. allenorum* and *P. coxi*), our type material is associated with firm sources (ANSP associates working on Upolu in the case of *allenorum*, and the U.S. Exploring Expedition in the case of *coxi*), rather than natural history dealers. Furthermore, in contrast to Allen's description of *laniger*, we describe *P. allenorum* and *P. coxi* because both taxa are distinguishable from all previously described *Pteropus* species, from Polynesia and beyond.

In summary, based on the recorded historical distributions of bat genera across remote Pacific archipelagos, we can easily envision a prehuman bat fauna in Samoa's tropical rainforests that might have included representatives of *Emballonura*, *Chaerephon*, *Myotis*, and *Nyctophilus* as insectivores, *Notopteris* and *Pteropus allenorum* as nectarivores or flower and smaller fruit feeders, and *Pteropus samoensis*, *P. coxi*, and *P. tonganus* as large frugivores, with the latter group of three species perhaps dominating in inland, montane, and coastal landscapes, respectively. Of these, only *Emballonura* and the four *Pteropus* are confirmed members of Samoa's Holocene

fauna, and only *Emballonura* and two of the *Pteropus* (*P. samoensis* and *P. tonganus*) persist today.

We interpret currently available evidence from museum specimens and published accounts to suggest that, apart from *Pteropus allenorum* and *Pteropus coxi*, at least five taxonomically valid species of bats have become extinct during the past 200 years. Four of these are species of *Pteropus*: *Pteropus subniger* (Kerr, 1792) of Réunion and Mauritius in the Mascarene archipelago, last recorded in the latter part of the 19th century (Cheke and Dahl, 1981; Moutou, 1982; Bergmans, 1990); *P. pilosus* Andersen, 1908, of Palau, last recorded in the mid-19th century (Andersen, 1912; Flannery, 1995); *P. brunneus* Dobson, 1878, of coastal northern Australia (recorded only from Percy Island), still known only by the holotype (Dobson, 1878; Andersen, 1912); and *P. tokudae* Tate, 1934, of Guam, last recorded in the late 1960s or early 1970s (Perez, 1973a, 1973b; Wiles, 1987; Flannery, 1995). Apart from these flying foxes, the mystacinid *Mystacina robusta* Dwyer, 1962, of New Zealand, last recorded in 1967 (Hill and Daniel, 1985; Flannery, 1987, 1995), is the only other bat that can be definitively regarded as becoming extinct in recent centuries, although it is likely that *Nyctophilus howensis* McKean, 1973, an extinct bat recorded only by a subfossil skull from Lord Howe Island, also survived into historical times (to the late 19th century; McKean, 1973). Some bats often considered to be extinct are actually taxonomically invalid or problematic (e.g., *Acerodon lucifer*, *Pipistrellus sturdeeii*; see Simmons, 2005). In the western Pacific, this category includes "*Pteropus loochooensis*" of Japan, which we regard as a synonym of *P. mariannus* based on independent study (K.M. Helgen, personal obs.), and *Nyctimene sanctacrucis* Troughton, 1931 (of the Santa Cruz Islands), which may be indistinguishable from populations of *Nyctimene major* elsewhere in the Solomon Archipelago (K.M. Helgen, personal obs.). Other bats often considered to be extinct have been recently rediscovered as living animals (e.g., *Dobsonia chapmani*, *Myotis planiceps*; see Simmons, 2005). Several mormoopid and phyllostomid species from the West Indies

also became extinct during the Holocene and may have persisted into historical times, but as far as we know these taxa remain known solely from subfossil remains rather than historical museum specimens (Simmons, 2005; see also Tejedor et al., 2004, 2005).

Thus, of the seven to eight bat species that probably became extinct within the past 200 years, six are species of *Pteropus*, and all but one of these extinctions (*P. subniger* of the Mascarenes) took place in the Pacific region. These extinctions are not well understood, and they have been tentatively linked to overhunting and habitat destruction especially (Flannery and Schouten, 2001). As oceanic island specialists, many species of *Pteropus* are especially vulnerable to natural population perturbations, such as tropical storms and epidemic disease (Flannery, 1989; Elmqvist et al., 1994; Pierson et al., 1996; McConkey et al., 2004; Esselstyn et al., 2006), and human impacts such as hunting and deforestation for agriculture can severely amplify the effects of these natural impacts (Wiles and Payne, 1986; Mickleburgh et al., 1992; Craig et al., 1994b; Brooke and Tschapka, 2002; Struebig et al., 2007). Any of these factors may have been involved in the decline to extinction of these various insular flying foxes. A more extensive (and speculative) review of possible factors underlying the extinction of *P. allenorum* and *P. coxi* is beyond the scope of the present paper, but the elucidation of these new Samoan species points to the need for further study in this direction. In any case, the apparent disappearance of these two *Pteropus* species parallels the extinction of at least one flightless bird, *Pareudiastes pacificus*, and the decline and extinction of many elements in the Samoan land snail fauna (Cowie, 2001; Cowie and Cook, 2001; Cowie and Robinson, 2003), declines that have progressed in the face of ongoing deforestation, growing human populations, and introductions of non-native species in the Samoan fauna and flora over the past century (Evans et al., 1992; Whistler, 1992; Mueller-Dombois and Fosberg, 1998; Stattersfield et al., 1998; Cox, 1999). These anthropogenic perturbations underscore the ecological fragility of many oceanic insular ecosystems, and they remind us of the role of conservation biology

in documenting and understanding extinctions so that further losses can be prevented.

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