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Systematics of the Pacific monkey-faced bats (Chiroptera: Pteropodidae), with a new species of *Pteralopex* and a new Fijian genus

Abstract The fruit-bat genus *Pteralopex* comprises the monkey-faced bats, a group of six endangered species found only in old-growth forests on certain islands in the south-west Pacific (the Solomon Islands and Fiji). The taxonomy of the genus is reviewed in detail and updated accordingly. Two 'cryptic' biological species are shown to occur in sympatry on both Bougainville and Choiseul in the northern Solomon Islands (corresponding to *Pteralopex anceps* Andersen, 1909 and a previously undescribed species) and each is accordingly described and reviewed. A new genus (*Mirimiri*) is erected for the Fijian monkey-faced bat (formerly *Pteralopex acrodonta*), which differs greatly both morphologically and genetically from species of *Pteralopex* in the Solomon Islands. Ecomorphological differences between sympatric *Pteralopex* species are briefly reviewed, including potential differences in functional morphology and feeding ecology. Geographic patterns of occurrence and future survey priorities for monkey-faced bats are also discussed.

Key words biogeography, cryptic species, Fiji, morphometrics, ecomorphology, Melanesia, Papua New Guinea, *Pteralopex*, Pteropodidae, Solomon Islands

Introduction

The monkey-faced bats are a highly distinctive group of medium-sized fruit-bat species endemic to the Solomon Islands and Fiji, previously classified in the single genus *Pteralopex*. In recent years, aspects of the taxonomy, geographical distribution, phylogeny, basic biology and conservation status of *Pteralopex* species have attracted study (Flannery, 1991, 1995; Colgan & Flannery, 1995; Fisher & Tasker, 1997; Bonaccorso, 1998; Parnaby, 2002b; Colgan & da Costa, 2002; Ingleby & Colgan, 2003). However, detailed information remains unavailable for most of these subjects. In particular, species boundaries and taxonomic definitions within the genus (the subject of the current report) have varied over time, obscuring the identity and basic biological attributes of various monkey-faced bat species. On the basis of all known museum material and all available field observations regarding the genus, taxonomic boundaries, geographic distribution and basic biology of the monkey-faced bats are reviewed here.

Materials and methods

Specimens cited here are deposited in the collections of the Australian Museum, Sydney (AM), Bernice P. Bishop Museum, Honolulu (BBM), Natural History Museum, London (BMNH), Field Museum of Natural History, Chicago (FMNH), Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), National Museum and Art Gallery of Papua New Guinea, Port Moresby (PNGM), Senckenberg Museum, Frankfurt (SMF), and the United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

Measurements are abbreviated (and, where necessary, defined) as follows: FA (forearm length); HB (head and body length); E (ear length); WT (mass); CBL (condylobasal length); ONL (orbitonasal length, here defined as the distance from anterior edge of the orbit to the midpoint of the premaxillae); ZYG (greatest bizygomatic width); MTR (length of maxillary toothrow, $C - M^2$); BBM (breadth of braincase at intersection with zygomata); MH (coronoid height of mandible); PL (length from posterior midpoint of palate to anterior midpoint of premaxillae). For wing measurements, digit is abbreviated as 'D', metacarpal as 'M' and phalanx as 'P'; thus, D2P2 refers to the second phalanx of the second digit, etc. For

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dental measurements, terminology and abbreviations follow Hill & Beckon (1978), with incisor abbreviated as 'I', canine as 'C', premolar as 'PM', and molar as 'M', but with upper teeth designated by superscript (e.g. M²) and lower teeth by subscript (e.g. M₂). For more details on the features of soft palate anatomy referred to here, see Andersen (1912). External measurements for museum specimens were recorded by the original collectors in the field. Craniodental variables were measured by the author with hand-held calipers to the nearest 0.01 mm. Single-tooth measurements are measured on the crown. All measurements of length are in millimetres, and measurements of mass are given in grams. In the principal component analyses featured in this paper, components are extracted from a covariance matrix of log-transformed craniodental variables.

Spellings for island names follow Mayr & Diamond (2001). Within the Solomon Archipelago (referred to throughout this paper as the 'Solomon Islands'), the islands of Buka and Bougainville lie within the political boundaries of Papua New Guinea (Northern Solomons Province), while Choiseul, Ysabel, New Georgia and Guadalcanal are politically part of the Solomon Islands.

Previous taxonomic treatments of *Pteralopex*

In 1888, Oldfield Thomas described *Pteralopex atrata*, a new genus and species of medium-sized fruit-bat, based on a series of specimens sent to the British Museum (now the Natural History Museum, London) from Guadalcanal in the central Solomon Islands (Thomas, 1888). Though superficially similar to species of flying-foxes (genus *Pteropus*) in external form, notable traits of this highly distinctive new genus included an unusually robust skull, massive bicuspidate canines, cheekteeth with complex, cuspidate surfaces, and wing membranes attached along the mid-back near the spine, rather than on the sides of the body. Soon after, Matschie (1899) uncritically included *Pteralopex* as a synonym of *Pteropus* (as did Simpson [1945]), but all other authors have correctly acknowledged the distinctiveness of this genus since Thomas' (1888) original description.

Based on the skin and skull of a subadult specimen collected by A.S. Meek in 1904, Knud Andersen (1909b) later described a second species of the genus, *Pteralopex anceps*, from Bougainville in the northern Solomons. Soon after, Andersen (1912) reviewed the morphological attributes of *P. anceps* and *P. atrata* in greater detail. He observed that although the two species are similar in size and coloration (both are black or blackish-brown), they differ both in trenchant aspects of dental morphology and in the texture, length, and distribution of the pelage. Sanborn (1931) later identified a monkey-faced bat specimen from Ysabel as *P. atrata*, presumably on the basis of Andersen's (1912) diagnostic characters.

Nothing was subsequently reported about *Pteralopex* until Laurie & Hill (1954) united *P. atrata* and *P. anceps* as conspecific subspecies in their authoritative checklist of Wallacean and Melanesian mammals. This was presumably done because the two taxa, superficially similar in appearance, were at the time known by very few specimens and were

thought to be allopatric (with *P. atrata* on Guadalcanal and Ysabel, and *P. anceps* on Bougainville). However, this arrangement ignored Andersen's (1912) review of the outstanding dental and pelage differences that distinguish the two taxa (Andersen, 1912).

In 1968, Phillips (1968) reported on newly collected *Pteralopex* specimens from Bougainville and Choiseul, obtained during expeditions by the Smithsonian Institution in Washington and the Bishop Museum in Honolulu. Influenced by Laurie & Hill (1954), he identified these as '*P. atrata anceps*' – apparently on geographic grounds – but he noted that they were more similar in colour and in some dental traits to *P. atrata* (as opposed to *P. anceps*) according to Andersen's (1912) descriptions.

Hill & Beckon (1978) described a newly discovered, small-bodied species of *Pteralopex* (*P. acrodonta*) from the Fijian island of Taveuni, the first record of the genus outside of the Solomon Islands. These authors reviewed in detail how this species differs considerably in cranial, dental and external aspects from the other *Pteralopex* species known at that time. On the basis of their examinations of the type series of *P. atrata* and the holotype of *P. anceps*, Hill & Beckon (1978) again recognized *P. anceps* and *P. atrata* as separate species from Bougainville and Guadalcanal, respectively, though they did not examine the museum specimens from Ysabel, Choiseul or Bougainville that had been reported by Sanborn (1931) or Phillips (1968).

Flannery (1991) described a distinctive new small-bodied species, *Pteralopex pulchra*, from cloud forest at 1230 m on Mt. Makarakomburu, Guadalcanal. He also reported additional monkey-faced bat specimens from Bougainville and Buka (which he identified as *Pteralopex anceps*) and from lowland Guadalcanal (which he identified as *P. atrata*). Subsequently Flannery (1995) reviewed the biology of all species of *Pteralopex* then described (*P. atrata*, *P. anceps*, *P. acrodonta* and *P. pulchra*) as well as that of a newly discovered, unnamed species from the islands of New Georgia and Vangunu in the western Solomons.

Soon after, Fisher & Tasker (1997) reported the results of a detailed field study of the ecology and life history of this then-unnamed species. Parnaby (2002b) named this new species from New Georgia and Vangunu (as *Pteralopex taki*) in a review of the entire genus. He contrasted the attributes of *P. taki* most closely with *P. pulchra*, which he apparently considered to be its closest relative (cf. Ingleby & Colgan, 2003: 21). He also allied *P. atrata* (which he considered to be a Guadalcanal endemic) and *P. anceps* (which he considered to be the only *Pteralopex* species recorded from Buka, Bougainville, Choiseul and Ysabel; *contra* Sanborn, 1931) as immediately related species that differed primarily in body size. Notably, Parnaby (2002b) criticized features used by Andersen (1912) and Hill & Beckon (1978) to diagnose *P. anceps* and *P. atrata*, arguing that these characters are inconsistent. Finally, on the basis of then-unpublished genetic data (Ingleby & Colgan, 2003), Parnaby (2002b) considered the phylogenetic relationship between *P. acrodonta* (from Fiji) and all other *Pteralopex* (from the Solomon Islands) to be rather remote.

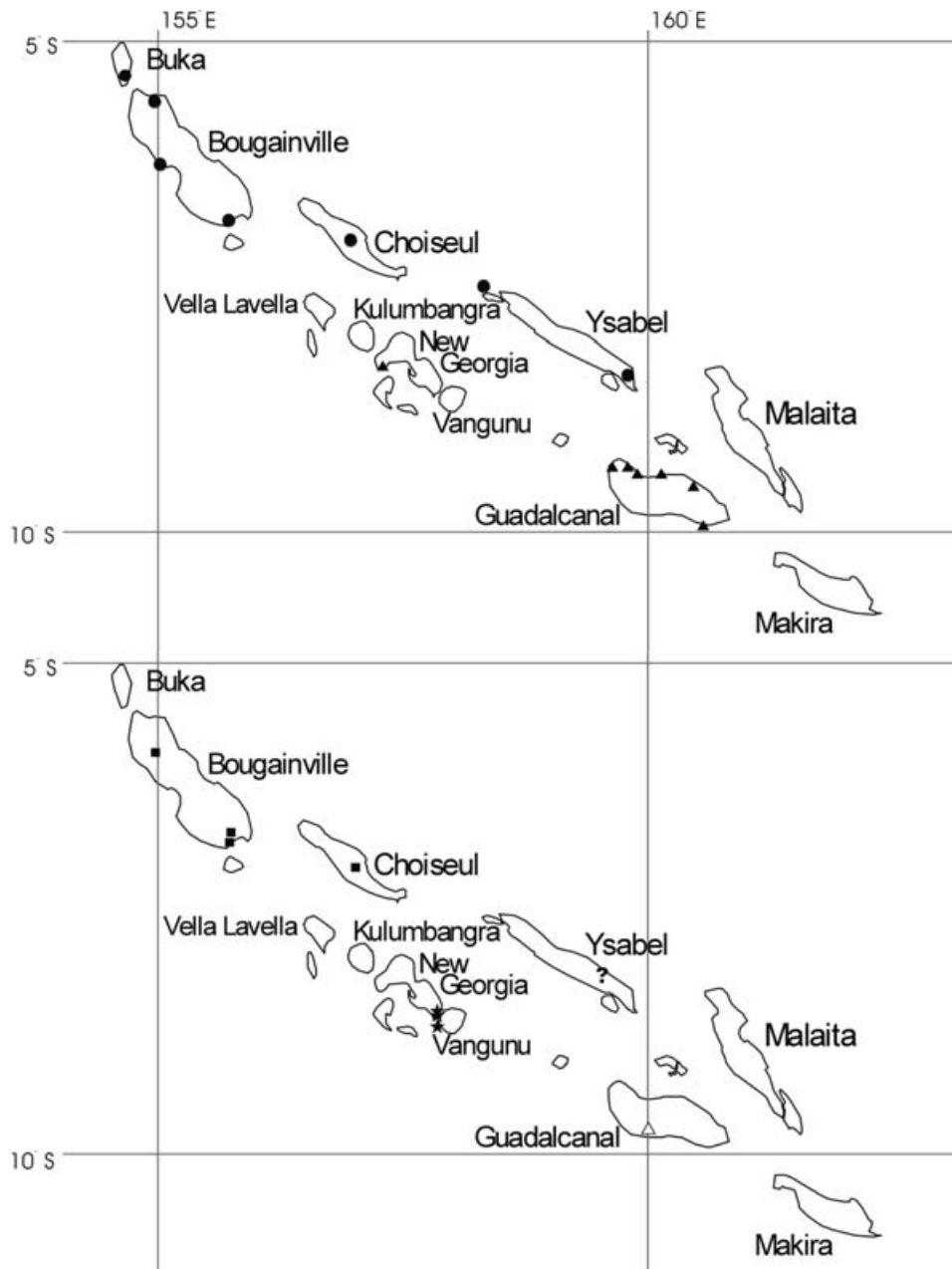


Figure 1 Recorded distribution of *Pteralopex* species in the Solomon Islands. Above, recorded distribution of *P. flanneryi* (●) and *P. atrata* (▲). Below, recorded distribution of *P. anceps* (■ [definite], ? [possible]), *P. taki* (★), and *P. pulchra* (△).

The identity of *Pteralopex atrata* and *P. anceps*

I have recently examined all museum material of *Pteralopex*, including many specimens not seen by Parnaby (2002b). The latter include specimens from Bougainville (at BBM, BMNH and PNGM; see below), Choiseul (at BBM, see below), Ysabel (at FMNH, see below), Guadalcanal (at BMNH, MVZ, and SMF, see below), and New Georgia (at SMF, see below). I have also drawn from field observations of *Pteralopex* recently reported from Choiseul (Bowen-Jones *et al.*, 1997) and Ysabel (Leary & Pita, *in litt.*). Importantly, these examinations clearly demonstrate that two distinct species of *Pteralopex* occur sympatrically on Bougainville, contrary to Parnaby's

(2002b) conclusions. These could be called 'cryptic' species in that they are superficially similar in size and dorsal coloration. However, these taxa differ consistently in body size; cranial size and shape; size, shape, relative proportions, and important occlusal aspects of the teeth; and length, texture, and distribution of the pelage. These two species correspond essentially to diagnoses of *P. anceps* and *P. atrata* as presented by Andersen (1912) and Hill & Beckon (1978), although the *atrata*-like population of Bougainville is much larger-bodied than that of Guadalcanal (the type locality of *atrata*), and differs also in certain other ways (see below). Parnaby (2002b) incorrectly considered diagnostic features previously used to distinguish between *P. anceps* and *P. atrata* (Andersen, 1912; Hill & Beckon, 1978) to be inconsistent because his sample

from Bougainville was composite, consisting of both *P. anceps* and an undescribed species similar to *P. atrata*,¹ described below as *Pteralopex flanneryi* sp. nov.

Examinations reported here further demonstrate that all museum specimens from Buka, Choiseul, and Ysabel reported in the literature as *P. anceps* (e.g. Flannery, 1991, 1995; Bonaccorso, 1998; Parnaby, 2002b) also actually represent *Pteralopex flanneryi*. These taxonomic distinctions and identifications are documented below. Notably, field observations reported by Bowen-Jones *et al.* (1997) confirm that *P. anceps* occurs in sympatry with *P. flanneryi* on Choiseul in addition to Bougainville. Further, *Pteralopex atrata* is recorded for the first time from New Georgia (see below), where it is apparently sympatric with *P. taki*.

The status of '*Pteralopex*' *acrodonta*

'*Pteralopex*' *acrodonta* is a small-bodied species of monkey-faced bat known only from higher altitudes on Mt. Koroturanga on the Fijian island of Taveuni; all other *Pteralopex* species are endemic to the Solomon Islands. Together, Hill & Beckon (1978) and Parnaby (2002b) documented a number of striking morphological differences that separate '*P.*' *acrodonta* from all other *Pteralopex* species. These distinctions led Flannery (1995, p. 237) to presume that '*P.*' *acrodonta* 'has been isolated on Fiji for a very long time'.

An allozyme study (Ingleby & Colgan, 2003) recently revealed that the electrophoretic distance between '*P.*' *acrodonta* and two Solomon Islands *Pteralopex* species (*P. taki* and *P. pulchra*) is equivalent to that between some megachiropteran sister genera. Another recent study drawing from mitochondrial and nuclear sequence data (Colgan & da Costa, 2002) documented considerable sequence divergence between '*P.*' *acrodonta* and *P. atrata* (the only monkey-faced bats included in the study) and was unable to confirm that these species are more closely related to one another than they are to species of other pteropodid genera. On the basis of these studies, Parnaby (2002b) explicitly questioned the monophyly of *Pteralopex* as currently defined.

Monkey-faced bats from the Solomon Islands and from Fiji clearly represent two distinctive lineages, each of which can be diagnosed with respect to the other by a unique combination of morphological apomorphies, as reviewed below. Though I propose that these two groups are indeed sister taxa, I separate them into separate genera below. This taxonomic change better reflects these morphologically and genetically divergent groups' different evolutionary and biogeographic histories, and more accurately portrays phylogenetic relationships among the six species of monkey-faced bats.

¹ Parnaby's (2002b) sample included only two actual specimens of *P. anceps*: AM M6283, which, as he noted, has the dental features of *P. anceps* as diagnosed by Andersen (1912) and AM M6497, which is an old adult with cheekteeth extensively worn, obscuring their occlusal features. All of his other specimens from Bougainville were *P. flanneryi* sp. nov. (compare with the type series, below). On account of his limited sample size, Parnaby did not grasp the significance of variation in pelage and dental traits within the sample.

Systematics

Monophyly of monkey-faced bats

Together, the monkey-faced bats (*Pteralopex* and *Mirimiri* gen. nov.) can be immediately distinguished from all other pteropodid bats by the following combination of distinctive traits:

1. Skull very robust relative to overall size, with thick, heavy zygomata and an unusually high sagittal crest.
2. Mandible with well-developed angular process, prominent masseteric ridge and a very high coronoid process (especially relative to the alveolar margin of the lower tooththrow).
3. Upper canines relatively very large and bicuspidate (bearing a large posterior accessory cusp).
4. Dental formula I2/2, C1/1, PM3/3, M2/3, with PM¹ and I₁ excessively reduced.
5. PM4 and molars bearing a complex pattern of cusps.
6. Iris of eye red/orange in life (verified to date for *pulchra*, *taki* and *acrodonta*).
7. Colour of mantle not markedly contrasting with colour of mid-back.
8. Tail absent.
9. Wings attached to back near the spine, rather than on the sides of the body.
10. Second digit of the wing bearing a claw.
11. Body size medium to large for Pteropodidae (forearm length 117 to 169).
12. Sexually monomorphic (or very weakly dimorphic) in body size.

Of these character states, numbers 1, 2, 3, 4, 5, 6, 8 and 11 are derived relative to the primitive condition in the Pteropodidae (according to my understanding of the distribution of these traits in living and fossil pteropodids). Relative to flying-foxes (*Pteropus* and *Acerodon*), traits 1–6 are more highly derived in monkey-faced bats, traits 8–12 are shared with some or all species of flying-foxes, and 7 is less derived. As *Pteralopex* and *Mirimiri* share a considerable number of apomorphic traits relative to other larger-bodied pteropodid genera, I strongly suspect that they are sister taxa, a point as yet unconfirmed by molecular phylogenetics (cf. Colgan & da Costa, 2002). The more remote phylogenetic relationships of *Pteralopex* and *Mirimiri* are less certain, but probably lie with *Pteropus*, *Acerodon*, and/or other pteropodine bats such as *Dobsonia* and *Aproteles* (Andersen, 1909a, 1912; Hill & Beckon, 1978; Colgan & Flannery, 1995; Colgan & da Costa, 2002).

Hill & Beckon (1978) reviewed in still-useful detail several other features that jointly characterize the monkey-faced bat genera.

Genus *Pteralopex* Thomas, 1888

Revised diagnosis

The genus *Pteralopex* can be distinguished from all pteropodid genera but *Mirimiri* gen. nov. by the distinctive combination of morphological traits listed above. In addition, each of the following eight characters is perfectly diagnostic for *Pteralopex*

with respect to *Mirimiri* gen. nov.:

1. Postorbital processes well-developed and annectent to the zygomata in adults.
2. Interorbital region conspicuously narrowed.
3. M^2 strongly reduced relative to M^1 (less than half the mass).
4. Labial margins of PM^4 and M^1 united in a single elevated cusp.
5. Length of D4P2 conspicuously longer than D4P1.
6. Six divided median ridges in the soft palate.
7. Three serrated supplementary posterior ridges in the soft palate.
8. Sexes identical in coloration.

Of these character states, numbers 1, 2, 3, 5, and 6 are apomorphic with respect to *Mirimiri*. *Pteralopex* can further be considered more highly derived than *Mirimiri* in that three of its five species (*Pteralopex anceps*, *P. flanneryi* and *P. atrata*) are much larger in body size than the small-bodied *M. acrodonta*.

Content

The genus *Pteralopex* comprises five species, all endemic to the Solomon Islands: *P. anceps* Andersen, 1909 (Bougainville, Choiseul); *P. atrata* Thomas, 1888 (Guadalcanal, New Georgia); *P. flanneryi* sp. nov. (Bougainville, Buka, Choiseul, Ysabel); *P. pulchra* Flannery, 1991 (Guadalcanal); and *P. taki* Parnaby, 2002 (New Georgia, Vangunu, and formerly Kulumbangra).

Remarks

The traits of *P. atrata* and *P. anceps* have previously been confused; as a result, the taxonomy of these species is reviewed in detail below in the context of describing a new species, *P. flanneryi*. Systematics and basic attributes of the remaining, small-bodied species (*P. pulchra* and *P. taki*) were recently reviewed adequately by Parnaby (2002b) on the basis of all available museum material; thus these taxa are not treated further here.

Pteralopex flanneryi sp. nov. (Figs 2, 3 lower, 5 upper)

HOLOTYPE. AM M6282, adult male, skin (Figs. 2, 3) and skull (Fig. 5), from Buin District (06°50'S, 155°44'E), 10 miles inland from the coast, altitude 50 m, Bougainville (Northern Solomons Province, Papua New Guinea), collected March 1937 by J.B. Poncelet.

PARATYPES. AM M6498, young adult female, skin and skull, from the type locality, collected September 1937 by J.B. Poncelet. AM M6346, adult male, whole specimen in alcohol, and AM M6347, adult female, skin and skull, from Iula (06°50'S, 155°45'E), 15 miles inland from the coast, altitude 150 m, Bougainville, collected 3 March 1937 by J.B. Poncelet. USNM 276973, adult female, skin, skull, and skeleton, from Cape Torokina (06°15'S, 155°02'E), at sea level, Bougainville, collected 5 August 1944 by D.H. Johnson. USNM 276974, adult male, skull, from Puruata Island opposite Cape Torokina, Bougainville, collected 30 July 1944 by W.L. Necker. USNM 277112, adult male, skin and skull, from Cape Torokina,

Bougainville, collected 22 July 1944 by D.H. Johnson. BBM-NG 61066, adult female, skin and skull, from Pokapa (05°37'S, 154°58'E), altitude 200 m, Bougainville, collected 26 February 1968 by A.B. Mirza.

REFERRED SPECIMENS. FMNH 31561, subadult female, from Tunnabuli (08°24'S, 159°48'E), Ysabel, collected 17 April 1929 by F.C. Wonder (see Sanborn, 1931). BBM-BSIP 23682, adult male, skin and skull, from Malangona (07°01'S, 156°59'E), Choiseul, collected 17 March 1964 by P. Temple (see Phillips, 1968; Parnaby [2002b] erroneously referred to this specimen as USNM 23682). AM M19822, subadult male, skin and skull, from Malasang-Kakalis Hamlet (05°21'S, 154°41'E), Buka, collected September 1987 by S. Wickler. A specimen of *Pteralopex* collected by Leary and Pita (*in litt.*) on Barora Fa (a small island adjacent to Isabel = Barola, 07°30'S, 158°20'E) is also referred to *P. flanneryi* on the basis of its reported measurements. All specimens but the last have been examined by the present author.

Diagnosis

Largest-bodied species of *Pteralopex*, with adult condylobasal length > 71 and forearm greater than or equal to 159; pelage relatively short, with ear exposed, fur of the mid-back and the dorsal surface of the pes adpressed, and the tibia and forearm naked or very sparsely furred; overall colour black dorsally and ventrally with occasional light (yellowish or whitish) tipping to the hairs on the breast (but lacking the expansive white or yellow chest-patch seen in sympatric *P. anceps*). Skull absolutely larger than that of *P. anceps*, with narrower braincase, relatively smaller incisors, larger cheekteeth, and PM_4 , M_1 , and M_2 with lengthened, elevated lingual ridges.

Distribution

Recorded from lowland forest at sea level to 200 m (see specimens above) on the north-eastern Solomon Islands of Bougainville (including the immediately adjacent small island of Puruata), Buka, Choiseul, and Ysabel (including the immediately adjacent small island of Barora Fa). These islands represent land-bridge fragments of a single large Late Pleistocene island (a landmass generally called 'Greater Bukida'; Mayr & Diamond, 2001). *Pteralopex flanneryi* is sympatric with *P. anceps* on Bougainville and Choiseul (Figure 1; see discussion below).

Etymology

For Professor Tim Flannery, current Director of the South Australian Museum in Adelaide, in recognition of his studies of Melanesian mammals, including the mammal fauna of the Solomon Islands. I suggest 'Greater monkey-faced bat' as an appropriate common name.

Description

Pteralopex flanneryi is the largest species of *Pteralopex* (Tables 1, 2). It agrees with *P. atrata* in dental and pelage features as described in detail by Andersen (1912) and Hill & Beckon (1978), including its overall blackish coloration (both dorsally and ventrally). However, in adults of *P. flanneryi* there is occasionally pale tipping to the hairs on the breast (absent in



Figure 2 The Greater monkey-faced bat (*Pteralopex flanneryi*), in life. Painting by Peter Schouten, rendered from the holotype (Flannery & Schouten, 2004).

P. atrata), and the wings always lack mottling (variably present in *P. atrata*; see Flannery, 1991; Parnaby, 2002b). It differs further from *P. atrata* in its absolutely larger skull (Table 1; Figs. 4, 5), body size (Table 2), and teeth (Table 3), and (comparing adults) in its proportionately much more elongate

rostrum ($\text{ONL/CBL} = 0.575\text{--}0.632$ in *P. flanneryi* vs. $0.491\text{--}0.553$ in *P. atrata*).

Several images of this species' skull and external appearance have previously been figured in the literature: Flannery (1995) figured both a skull (p. 450) and the dorsal aspect of a

sample	<i>P. atrata</i> n = 13 ^a	<i>P. flanneryi</i> n = 7 ^b	<i>P. anceps</i> n = 4 ^c
CBL	64.0 ± 1.46 61.80–66.62	74.2 ± 1.42 71.52–75.63	70.1 ± 1.08 68.53–70.96
ONL	19.1 ± 0.80 17.80–20.38	23.0 ± 0.79 21.82–23.94	20.2 ± 0.58 19.50–20.80
ZYG	38.8 ± 0.91 37.00–40.03	43.3 ± 0.95 42.21–44.57	40.3 ± 0.67 39.53–41.12
BBC	23.2 ± 0.91 21.50–24.57	25.1 ± 1.00 23.90–27.20	26.6 ± 0.69 25.90–27.50
MTR	24.6 ± 0.55 23.7–25.22	28.6 ± 0.54 27.63–29.18	25.7 ± 0.66 25.00–26.60
MH	29.8 ± 1.00 28.35–31.11	34.7 ± 1.02 33.05–35.77	29.9 ± 0.59 29.16–30.38
PL	36.2 ± 1.08 34.74–37.67	41.9 ± 1.14 39.99–43.23	38.6 ± 0.89 37.38–39.38

^a AM M3373, AM M19220, BMNH 34.7.2.31, BMNH 88.1.5.9, BMNH 89.4.3.1, MVZ 101673, MVZ 101674, SMF 44786, SMF 48306, SMF 48307, SMF 48308, SMF 48309, SMF 50721.

^b AM M6282, AM M6347, AM M6498, BBM-BSIP 23682, USNM 276973, USNM 276974, USNM 277112.

^c AM M6283, AM M6497, BBM-NG 61213, BBM-NG 61435.

Table 1 Selected skull measurements for *Pteralopex atrata*, *P. flanneryi* and *P. anceps*. Values represent means ± SD, with ranges given below.

sample	<i>P. atrata</i> n = 13 ^a	<i>P. flanneryi</i> n = 11 ^b	<i>P. anceps</i> n = 5 ^c
FA	137.4 ± 5.19 129–147	164.0 ± 4.04 159–169	154.5 ± 9.11 141–160
HB	217.1 ± 12.50 196–237	265.1 ± 12.81 247–285	260.4 ± 7.30 252–270
E	17.5 ± 1.60 15–20	22.5 ± 2.04 20–26	23.8 ± 1.30 22–25
WT	472 438–506 (n = 2)	790 790 (n = 1)	–

^a AM M3373, AM M19220, BMNH 34.7.2.31, BMNH 88.1.5.9, BMNH 89.4.3.1, MVZ 101673, MVZ 101674, SMF 44786, SMF 48306, SMF 48307, SMF 48308, SMF 48309, SMF 50721. Weights (in grams) from AM M19219 and AM M19220.

^b AM M6282, AM M6346, AM M6347, AM M6498, BBM-BSIP 23682, BBM-NG 61066 (subadult with mature external measurements), FMNH 31561 (subadult with mature external measurements), USNM 276973, USNM 276974, USNM 277112, Leary and Pita (*in litt.*). Weight (in grams) from Leary and Pita (*in litt.*).

^c AM M6283, AM M6497, BBM-NG 61213, BBM-NG 61435, PNGM 22824.

Table 2 External measurements for *Pteralopex atrata*, *P. flanneryi*, and *P. anceps*. Values represent means ± SD, with ranges given below.

study skin (p. 239) (as '*P. anceps*') and Parnaby (2002b: 153) figured occlusal aspects of the dentition (as '*P. anceps*').

Representative wing measurements for the adult male holotype and an adult female paratype of *P. flanneryi* (AM

M6347) are as follows, respectively (measured from dry skins): pollex 70.6, 66.5; D1M 22.3, 22.9; D1P1 39.3, 39.6; D2M 90.8, 87.2; D2P1 26.7, 24.8; D2P2 17.4, 22.4; D3M 117.5, 120.1; D3P1 82.3, 81.0; D3P2 123.2, 123.8; D4M 119.2, 118.0; D4P1 64.7, 70.0; D4P2 81.0, 83.6; D5M 126.5, 125.8; D5P1 52.1, 49.4; D5P2 45.1, 47.6; calcar 19.3, 23.5. Representative wing measurements for a nearly-mature subadult (AM M19822) are as follows (measured from dry skin): pollex 62.1; D1M 19.1; D1P1 39.2; D2M 75.1; D2P1 21.3; D2P2 18.9; D3M 109.1; D3P1 72.8; D3P2 99.6; D4M 104.3; D4P1 65.1; D4P2 72.0; D5M 112.7; D5P1 49.0; D5P2 39.2; calcar *circa* 17.

Remarks

In previous literature, the identity of *P. flanneryi* has been confused with both *P. anceps* (with which it is widely sympatric) and *P. atrata* (its allopatric sister species, endemic to Guadalcanal and New Georgia). For example, Phillips (1968), Flannery (1995), Bonaccorso (1998), and Parnaby (2002b) identified some or all museum specimens of *P. flanneryi* as '*P. anceps*', and Sanborn (1931) identified the Ysabel specimen listed above as '*P. atrata*.' Due to this past taxonomic confusion, the morphological traits of *P. flanneryi*, *P. atrata* and *P. anceps* are contrasted in detail below.

External differences between sympatric *Pteralopex flanneryi* and *Pteralopex anceps*

Pteralopex flanneryi and *P. anceps* (the two species of *Pteralopex* sympatric on Bougainville and Choiseul) can be easily identified on the basis of pelage differences. In *P. flanneryi* the pelage is relatively short overall, with the fur on the mid-back and dorsal surface of the pes strongly adpressed, the forearm and tibia naked or only sparsely furred, and the venter dark with occasional pale tipping on the hairs on the breast (all of these features but the last are shared with *P. atrata* of Guadalcanal and New Georgia). In *P. anceps* the fur is long and luxurious, the fur of the mid-back and pes are not at all adpressed, the proximal third of the forearm and the entire tibia are very heavily haired, and ventrally the breast bears an expansive, conspicuous white or yellow patch of fur (Fig. 3). (Each of these traits is an instantly diagnostic feature for *P. anceps* relative to *P. flanneryi*.) The external ear of *P. anceps*, though not actually smaller than that of sympatric *P. flanneryi* (Table 2), is more hidden in the long fur than in the latter species.

Pteralopex anceps and *P. flanneryi* are similar in overall size, though *P. anceps* has a significantly (almost absolutely) shorter forearm (Table 2). Skulls of *P. flanneryi* are absolutely wider and longer than *P. anceps*, suggesting that the former species is heavier than the latter (*P. anceps* has yet to be weighed).

Dental differences between sympatric *Pteralopex flanneryi* and *Pteralopex anceps*

Andersen (1912) accurately described and excellently illustrated the trenchant dental differences that separate the allopatric species *P. atrata* and *P. anceps*. These correspond essentially to the respective dental traits of the two *Pteralopex* species sympatric in the northern Solomons (*flanneryi* and *anceps*). Selected traits include the larger size of the incisors and (vertically) more elongate canines but smaller size of the

	<i>P. atrata</i> n = 12	<i>P. flanneryi</i> n = 5	<i>P. anceps</i>		
			a	b	c
canine length	5.4 ± 0.14 5.26–5.65	6.0 ± 0.23 5.70–6.29	6.00	–	–
canine width	4.2 ± 0.16 4.01–4.47	4.7 ± 0.34 4.17–5.10	4.18	–	–
canine height	7.6 ± 0.31 7.20–8.09	9.3 ± 0.32 8.83–9.61	9.76	–	–
PM³w	4.3 ± 0.25 3.93–4.63	4.6 ± 0.07 4.52–4.71	4.24	4.01	4.7
PM⁴l	5.0 ± 0.21 4.64–5.23	5.8 ± 0.12 5.60–5.89	5.04	4.82	5.8
PM⁴w	4.4 ± 0.24 4.04–4.80	5.0 ± 0.09 4.84–5.09	4.61	4.08	4.8
M¹l	4.4 ± 0.28 4.06–5.00	5.3 ± 0.14 5.02–5.39	4.74	4.68	5.0
M¹w	3.9 ± 0.12 3.69–4.11	4.5 ± 0.08 4.39–4.57	4.01	3.84	4.2
M²l	3.0 ± 0.14 2.80–3.20	3.6 ± 0.16 3.32–3.70	3.13	2.83	3.2
M²w	2.9 ± 0.13 2.68–3.08	3.3 ± 0.15 3.13–3.46	3.16	2.73	3.0
PM₃w	3.4 ± 0.17 3.13–3.60	3.8 ± 0.23 3.50–4.06	3.29	2.97	3.6
PM₄w	3.8 ± 0.13 3.65–4.04	4.4 ± 0.16 4.27–4.60	3.69	3.36	3.9
M₁w	3.8 ± 0.15 3.55–4.04	4.5 ± 0.18 4.23–4.64	3.62	3.43	3.9
M₂w	3.5 ± 0.13 3.25–3.70	4.0 ± 0.19 3.84–4.29	3.52	3.47	3.8
M₃w	2.7 ± 0.15 2.51–3.00	3.1 ± 0.06 3.00–3.16	3.00	2.60	3.0

Table 3 Selected dental measurements for *Pteralopex atrata*, *P. flanneryi*, and *P. anceps*. a = AM M6283; b = AM M6497; c = holotype of *P. anceps* (from Andersen, 1912: 441). Values represent means ± SD, with ranges given below. w = width; l = length.

premolars and molars in *P. anceps* relative to *P. flanneryi*/*P. atrata*, a massive P₄ very long relative to its width in *P. anceps* (more subsquare in *P. flanneryi*/*P. atrata*), heavily-developed anterior cingula on PM⁴ and M¹ in *P. flanneryi*/*P. atrata* (greatly reduced in *P. anceps*), and an unbroken elevated ridge on the lingual edges of PM₄, M₁, and M₂ in *P. flanneryi*/*P. atrata* (interrupted by rising and falling cusps in *P. anceps*). Individuals from Bougainville with the respective pelage traits of *P. anceps* and *P. flanneryi* are also those with the respective dental traits of each species, confirming by this concordance the presence of two different species of *Pteralopex* on the island.

Craniometric differences between sympatric *Pteralopex flanneryi* and *Pteralopex anceps*

A principal component analysis utilizing six cranial and mandibular variables (CBL, ONL, ZYG, BBC, MTR, MH) for all adult *Pteralopex* from Bougainville segregates these individuals into two well-separated groupings (Fig. 4; Table 1).

These two clusters correspond exactly to the distribution of discrete pelage and dental traits as described above, again confirming the distinctness of the two species.

Though superficially similar, the skulls of *P. anceps* and *P. flanneryi* differ consistently in shape. Although the skull of *P. anceps* is absolutely shorter and narrower than that of sympatric *P. flanneryi*, it has a more expansive braincase, both in relative terms (BBC/CBL = 0.375–0.389 in *P. anceps* vs. 0.323–0.363 in adult *P. flanneryi*) and average measurements (e.g. Table 1). In lateral view, the braincase of *P. anceps* is more strongly deflected from the horizontal axis of the palate/toothrow (more pronounced klinorhynch; see Fig. 7: the alveolar line passes above the supraoccipital) than in *P. flanneryi* (in which the alveolar line intersects the supraoccipital). The coronoid process of the mandible is proportionally reduced in *P. anceps* relative to *P. flanneryi* (MH/CBL = 0.410–0.443 in *P. anceps* vs. 0.447–0.484 in *P. flanneryi*), as is the length of the palate (PL/CBL = 0.545–0.557 in *P. anceps* vs. 0.558–0.585 in *P. flanneryi*). In dorsal

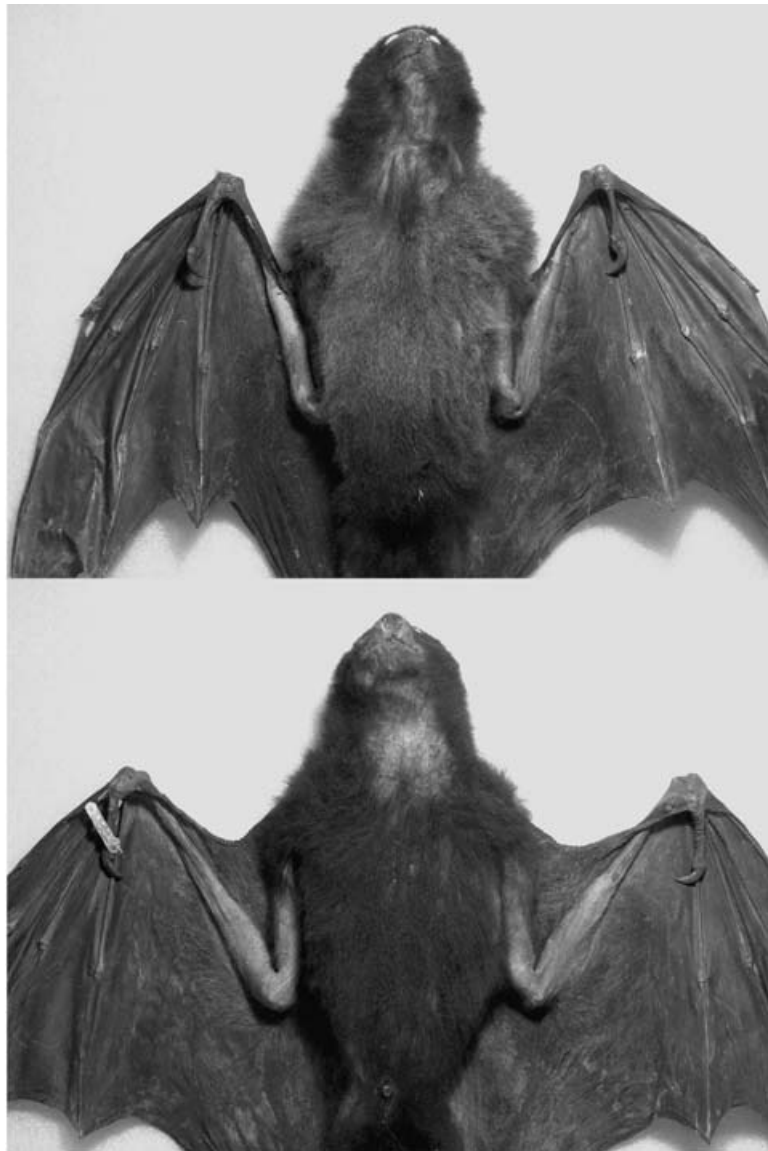


Figure 3 Ventral colouration (seen here in half tone) in sympatric *Pteralopex anceps* (AM M6283, above) and *Pteralopex flanneryi* (AM M6347, below), both from Bougainville.

view, the zygomata of *P. anceps* are more nearly parallel than in other *Pteralopex*, including *P. flanneryi*, in which the zygomata tend to diverge slightly behind the postorbital bar.

Geographic variation in Pteralopex atrata and Pteralopex flanneryi

Pteralopex atrata and *P. flanneryi* are immediately related allopatric species (Fig. 1) that are largely identical in discrete dental and pelage traits, but differ absolutely in body, dental, and cranial size and proportions. These size differences are aptly demonstrated by univariate measurements (Tables 1–3) and by multivariate analysis. For example, a principal component analysis utilizing six cranial and mandibular variables (CBL, ONL, ZYG, BBC, MTR, MH) cleanly separates *P. atrata* and *P. flanneryi* on the basis of overall skull size (Fig. 6), and (importantly) suggests further that geographic variation within each species is minimal. A single skull from New Georgia (see account of *P. atrata* below) is indistin-

guishable in size and shape from adult *P. atrata* skulls from Guadalcanal. Adult skulls of *P. flanneryi* from Bougainville and Choiseul group closely together, and subadult skulls from Ysabel and Buka (entered into the analysis out of geographic interest) also fall near this cluster but differ slightly in shape owing to their incomplete maturity (Fig. 6). Subadults of *P. flanneryi* can be distinguished with confidence even from the largest adult specimens of *P. atrata* by their still-larger overall size and much larger teeth (e.g. Table 3).

Remarks on Pteralopex flanneryi

Pteralopex flanneryi was last collected on Bougainville in 1968, on Choiseul in 1964, and on Buka in 1987. Field surveys in the 1990s failed to record *P. flanneryi* from Bougainville (Bonaccorso, 1998; S. Hamilton, *in litt.*), Choiseul (Bowen-Jones *et al.*, 1997), Buka (Bonaccorso, 1998), and Ysabel (Parnaby, 2002b: 158). However, Leary and Pita (*in litt.*) recently collected an individual on Ysabel (i.e.

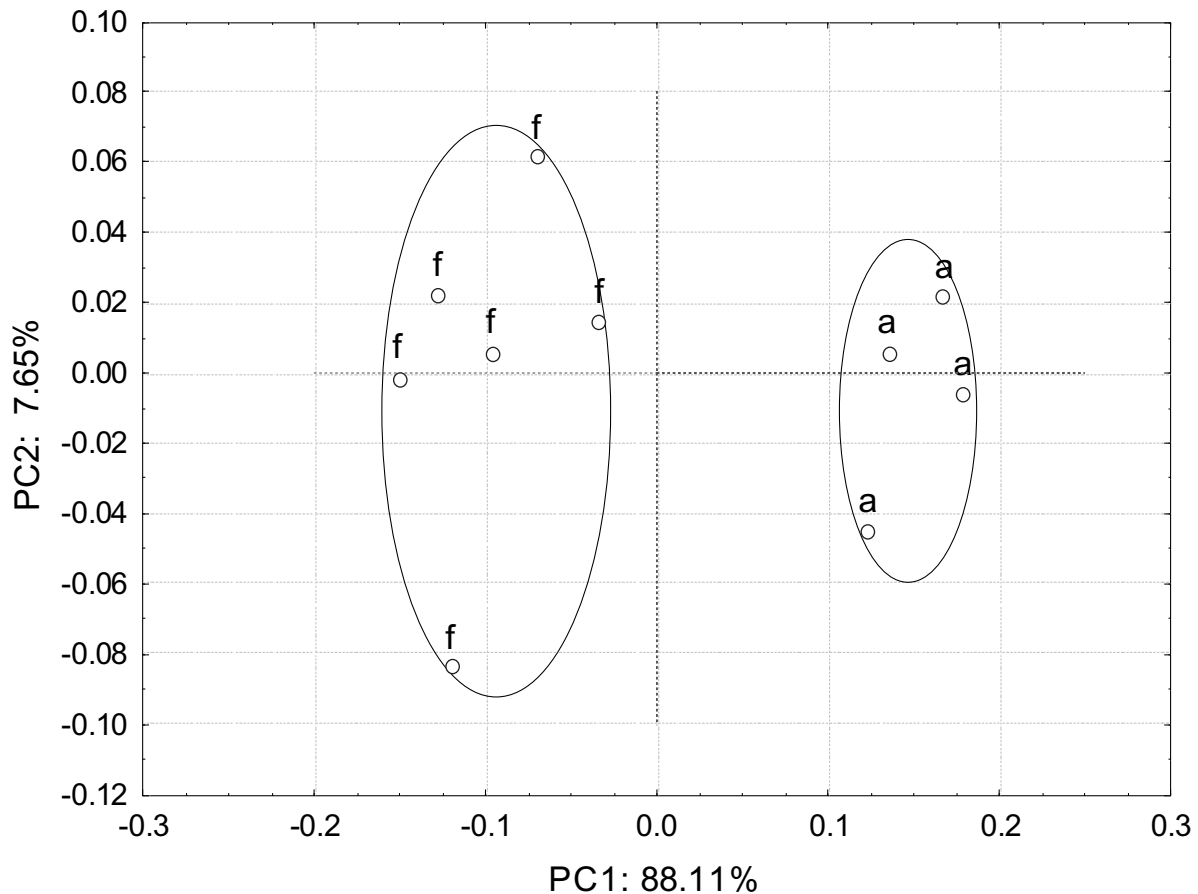


Figure 4 Principal component analysis: adult *Pteralopex* skulls from Bougainville. a = *Pteralopex anceps*; f = *Pteralopex flanneryi*.

Variable	PC1	PC2
CBL	-0.934	-0.141
ONL	-0.991	0.022
ZYG	-0.931	-0.132
BBC	0.552	-0.832
MTR	-0.966	-0.043
MH	-0.977	-0.099
Variance explained	88.11%	7.65%

Table 4 Factor loadings for Fig. 4. Principal components extracted from a covariance matrix of log-transformed craniodontal variables.

Barora Fa) in 2000 (see specimens listed above). *Pteralopex flanneryi* is rarely encountered across its range, is restricted to primary forest, and has apparently declined in recent decades (Troughton, 1936; Flannery, 1995; Bowen-Jones *et al.*, 1997; Bonaccorso, 1998; Parnaby, 2002b; S. Hamilton, *in litt.*). As a very large-bodied bat it is undoubtedly susceptible to continued decline via deforestation and hunting pressure in populated areas. It has previously been classified by the IUCN as ‘Critically Endangered’ (Hilton-Taylor, 2000: as ‘*P. anceps*’), a status it most certainly deserves.

An adult female from Bougainville was lactating when collected in July (Phillips, 1968), and a subadults (forearm

length 145 to 162) have been collected in February, April, and September (see specimens above). Little is known of diet of this species, but one individual was observed eating green coconuts on Ysabel (Sanborn, 1931; see Discussion below), and it is undoubtedly largely frugivorous. The large body size of *P. flanneryi* relative to *P. atrata* may be explained in part by character displacement in the former species relative to the similarly large-bodied *P. anceps* (Table 2), with which it is sympatric on Bougainville and Choiseul (see account of *P. anceps* below).

***Pteralopex atrata* Thomas, 1888** (Fig. 5 lower)

HOLOTYPE. BMNH 1888.1.5.9, adult male, body in alcohol with skull extracted and cleaned, from Aola (09°32’S, 160°29’E), presumably at sea level, Guadalcanal (Central Province, Solomon Islands), collected by C.M. Woodford (Thomas, 1888; Woodford, 1890; Andersen, 1912).

Material examined

I have examined 20 specimens of *P. atrata* (which, as far as I know, constitute all museum material of this species):

1. The type series of *P. atrata* from Aola (09°32’S, 160°29’E), Guadalcanal at BMNH (five specimens; see Andersen (1912) for details), one specimen of which (BMNH 1888.1.5.10) was sent in exchange to Frankfurt (now SMF 44786).

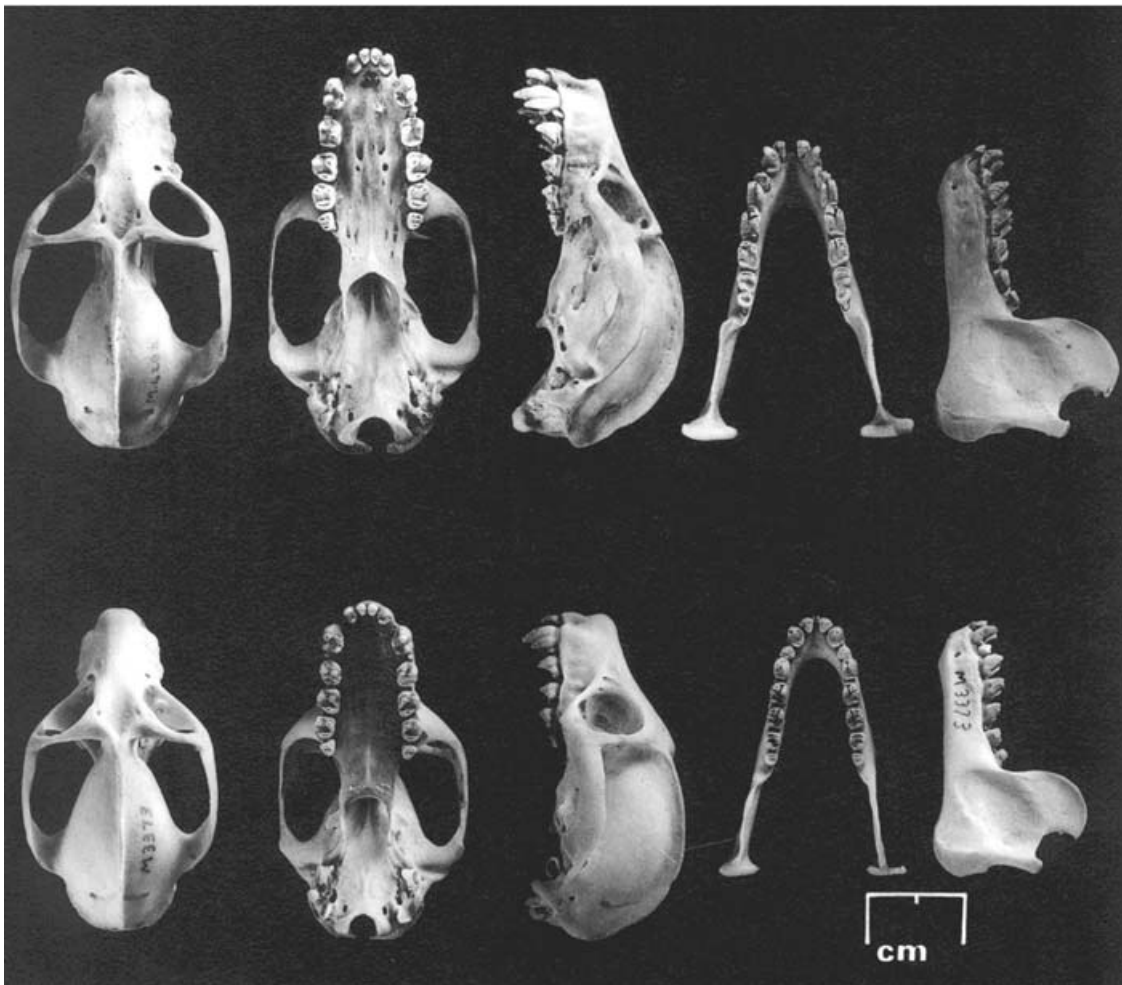


Figure 5 Skulls of *Pteralopex flanneryi* (above: AM M6282, adult male, Bougainville) and *Pteralopex atrata* (below: AM M3373, adult male, Guadalcanal).

2. One specimen (BMNH 1934.7.2.31, adult female, skin and skull), collected on the 'northwest coast' of Guadalcanal in July–August 1927 by C.E. Hart.
3. A total of seven specimens from 'Lavors' (= Lavoro Plantation; 09°19'S, 159°39'E) and the Poha River Valley, 400 m (09°24'S, 159°54'E), Guadalcanal (AM M3373, 3374, 3375, 4218, 4219 [Lavoro]; AM M19219, 19220 [Poha]).
4. Two specimens (MVZ 101673 and 101674, skins and skulls) from the Nalimbiu River (09°24'S, 160°09'E), 1 mile inland, 15 m, Guadalcanal, collected in October 1944 by L. Adams.
5. Four specimens at SMF (skins and skulls) collected on Guadalcanal in 1974 by H.L. Bregulla: SMF 48306 (adult female) and SMF 48307 (adult female) from Vilu; SMF 48308 (adult female) from "Lakalaka and Komambulu" (= Komovaolo? 09°55'S, 160°34'E); SMF 48309 (adult male) from Verawaulu (09°47'S, 159°57'E).
6. A single specimen (SMF 50721, adult female, skull, skin now missing) from "Jericho and Munda Village" (Munda = 08°21'S, 157°13'E), New Georgia (Western Province, Solomon Islands), collected April–May 1975 by Bregulla. This is the first record of *P. atrata* from outside of

Guadalcanal. The skull of this individual does not appear to differ morphologically or morphometrically from skulls of *P. atrata* from Guadalcanal (e.g. Fig. 6). However, it bears an annotation suggesting that it may represent a new species of *Pteralopex* (D. Kock, *in litt.*), which possibly suggests that the skin (now missing) is distinctive relative to Guadalcanal *P. atrata*. Until the skin is rediscovered or additional specimens are collected, I can conclude nothing more about the systematic status of this specimen. Previously, only *P. taki* has been known from New Georgia.

Diagnosis

Pelage variable in length but usually relatively short, with ear exposed, fur of the mid-back and the dorsal surface of the pes adpressed, and the tibia and forearm naked or very sparsely furred; overall colour black dorsally and ventrally (with wings occasionally mottled). Size medium (adult condylobasal length < 67; forearm < 150), but absolutely larger than sympatric *P. pulchra* and *P. taki* (Parnaby, 2002b), with subsquare PM₄, relatively heavy cheekteeth, and PM₄, M₁, and M₂ with lengthened, elevated lingual ridges. Other diagnostic dental traits reviewed by Andersen (1912).

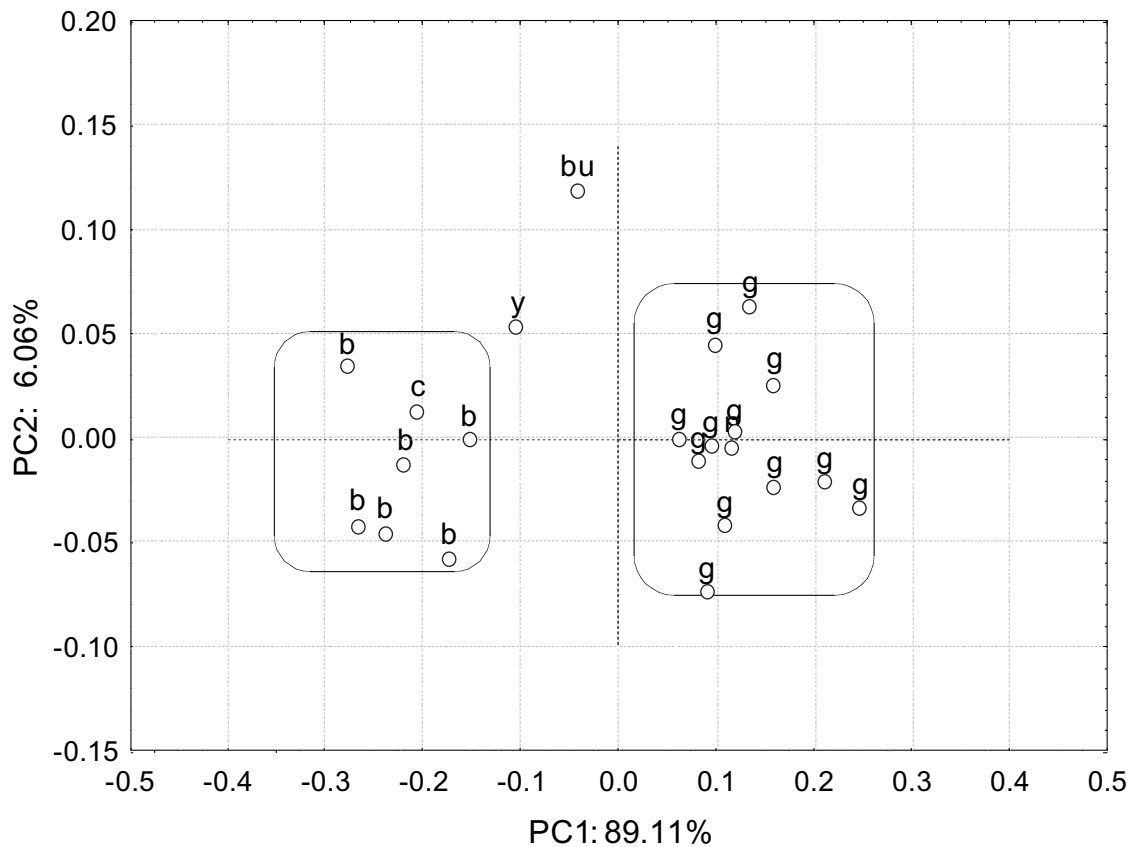


Figure 6 Principal component analysis of skulls of *Pteralopex atrata* (g = Guadalcanal; n = New Georgia) and *Pteralopex flanneryi*. b = Bougainville; c = Choiseul; y = Ysabel (subadult); bu = Buka (subadult).

Variable	PC1	PC2
CBL	−0.982	−0.130
ONL	−0.960	−0.228
ZYG	−0.949	0.003
BBC	−0.776	0.595
MTR	−0.957	0.184
MH	−0.961	−0.004
Variance explained	89.11%	6.06%

Table 5 Factor loadings for Fig. 6. Principal components extracted from a covariance matrix of log-transformed craniodental variables.

Distribution

Recorded from primary lowland forest on Guadalcanal (from sea level to 400 m, but possibly up to 1000–1200 m; Flannery, 1991) and from New Georgia (see above). Most specimens originate from at or near sea level; the mean elevation of all sites where this bat has been collected is 52 m (n = 8; range 0–400 m).

Remarks

Pteralopex atrata was recently reviewed by Flannery (1995) and Parnaby (2002b). Andersen (1912) and Hill & Beckon (1978) reviewed aspects of dental morphology, Thomas (1888)

provided a colour illustration of the head of this species (re-figured by Flannery, 1995), and Flannery (1995) figured a freshly-killed specimen. Andersen (1912), Flannery (1995), and Parnaby (2002b) figured skulls, and Andersen (1912) provided representative wing measurements.

Apart from brief notes presented by Flannery (1991, 1995), little has been recorded of the basic biology of *P. atrata*. Judging from sight records (Flannery, 1995) and museum specimens, it may be more common than other *Pteralopex*, and is apparently distributed in primary lowland forest across the island of Guadalcanal (Fig. 1). However, its IUCN classification of ‘Critically Endangered’ (Hilton-Taylor, 2000; Parnaby, 2002b) probably remains appropriate (Parnaby, 2002b).

P. atrata is regionally sympatric with *P. pulchra* (i.e. both occur on Guadalcanal) but the two species have not been collected syntopically and are probably altitudinally stratified, with *P. atrata* occupying primary lowland forest and *P. pulchra* endemic to cloud forest situated at 1200 m and higher (Flannery, 1991). Interestingly, certain morphometric relationships between these two Guadalcanal species are analogous to those between *P. flanneryi* and *P. anceps* in the north-eastern Solomons. In both cases, the higher-elevation species (*P. pulchra* and *P. anceps*) are smaller-bodied (FA 118 in the only known specimen of *pulchra*), with longer pelage, smaller teeth, proportionally wider braincases (BBC/CBL = 39.8% in *pulchra* vs. 33.6–38.8% in *atrata*), and reduced coronoid processes relative to their respective sympatric lowland congeners.

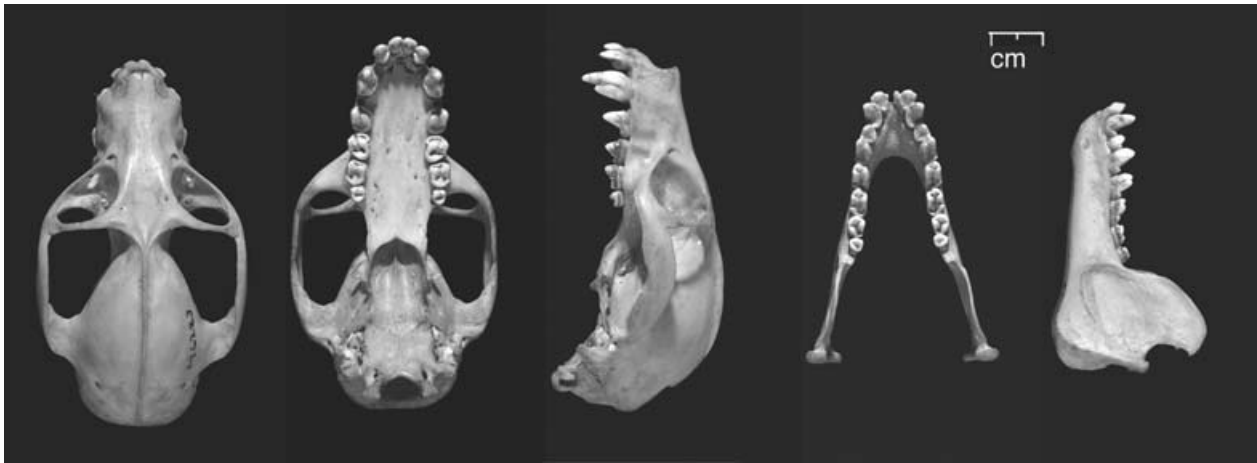


Figure 7 Skull of *Pteralopex anceps* (AM M6283, young adult male, Bougainville). A photograph of the skull of this species has not previously been published.

Both *P. atrata* and *P. taki* are now recorded from New Georgia, where they are likely to occur syntopically in primary lowland forest (see Discussion below).

Maa (1966) correctly recorded the batfly *Cyclopodia macracantha macracantha* Theodor, 1959 as an ectoparasite of this species on Guadalcanal. He also recorded *Cyclopodia solomonarum* Theodor, 1959 from this species (listed from a wide array of localities in the Solomon Islands), but these records appear to be mistaken, based instead on batflies taken from various flying-foxes (*Pteropus* spp.), which *C. solomonarum* certainly parasitizes (Theodor, 1959; Maa, 1966).

***Pteralopex anceps* Andersen, 1909**

(Figs 3 upper, 7)

HOLOTYPE. BMNH 1908.11.16.7, subadult female, skin and skull, from Bougainville (Northern Solomons Province, Papua New Guinea), presumably in coastal lowland forest, collected April 1904 by A.S. Meek.

Other material examined

AM M6283 (adult male, skin and skull) and AM M6497 (adult male, skin and skull), from Buin District (ca. 06°50'S, 155°44'E), 10 miles inland, 150 meters, Bougainville, collected March 1937 and June 1938, respectively, by J.B. Poncelet.

BBM-NG 61435 (adult male, skin and skull), from Mt. Balbi (05°55'S, 154°59'E), 1900 meters ("moss forest" on skin label), Bougainville, collected 15 April 1968 by A.B. Mirza.

PNGM 22824, adult female, skin and skull, from Mutahi (= Muguai, 06°43'S, 155°45'E), 1100 meters ('rainforest' on skin label), Bougainville, collected 10 March 1968 by A.B. Mirza. BBM-NG 61213 (adult female, skin and skull) and BBM-NG 61214 (subadult female, skin and skull), from Mutahi, 1100 m ('rainforest' on skin label), Bougainville, collected 12 March 1968 by A.B. Mirza. Habitat details (in quotations) taken from specimen tags.

Diagnosis

Forearm less than or equal to 160 (vs. 159–169 in sympatric *P. flanneryi*); pelage very long and thick, with ear unreduced

but inconspicuous in the long pelage, the fur of the mid-back not addressed, and the tibia, dorsal surface of the pes, and proximal third of the forearm very densely furred; overall colour blackish brown, but venter with a expansive yellow or white fur patch on the breast. Skull smaller than sympatric *P. flanneryi* (Table 1; Fig. 4), with wider and more horizontally deflected braincase, reduced coronoid process, and less elongate palate; compared to *P. flanneryi*, incisors relatively larger and canines (vertically) longer, but cheekteeth relatively smaller except for a massive, rectangular PM₄ (Table 3); PM₄, M₁, and M₂ without unbroken, elevated lingual ridges along their lengths. Other, lesser diagnostic dental traits were reviewed by Andersen (1912).

Distribution

Pteralopex anceps is known only from Bougainville and Choiseul, where it has a wide recorded altitudinal range. On Bougainville it has been collected in coastal and inland forests at and near sea level, in mid-elevation tall-canopy rainforest at 1100 m, and in mossy montane forest at 1900 m on Mt. Balbi. Notably, *Pteralopex anceps* and *P. flanneryi* have been collected syntopically at 150 m near Buin (series at AM).

This species is recorded from Choiseul on the basis of an unambiguous sight record reported by Bowen-Jones *et al.* (1997) from primary forest at 850 m in the vicinity of Mt. Maetambe (07°05'S, 157°01'E) ('identification of the bats was enabled . . . by the absence of large protruding ears . . . the chest was conspicuously white in colour'). Phillips' (1968) earlier record of this species from Choiseul is based on a misidentified specimen of *P. flanneryi* (see above). *Pteralopex anceps* has not been recorded from Buka (*contra* Flannery [1995], Bonaccorso [1998], and Parnaby [2002b]), or Ysabel (*contra* Parnaby [2002b]); these distributional records are instead also based on misidentified specimens of *P. flanneryi* (see above). However, I suspect that this species does occur on Ysabel, even though there no valid records to date (see Discussion below).

Remarks

The correct identity and unique traits of *P. anceps* have generally been obscured or ignored in the literature since Andersen's

	<i>P. anceps</i>	<i>P. atrata</i> and <i>P. flanneryi</i>
Tibia	heavily furred	naked or sparsely furred
Fur of mid-back	not adpressed	adpressed
Fur of breast	with white or yellow chest patch	without chest patch
Braincase	wider relative to skull length	narrower relative to skull length
I¹ and I²	larger, generally broader than long	smaller, generally longer than broad
PM⁴ and M¹	anterior cingula weak	anterior cingula heavy
PM₄	much longer than broad	subsquare
PM₄, M₁, and M₂	without unbroken lingual ridges	with unbroken lingual ridges

Table 6 Selected qualitative distinctions between *Pteralopex anceps* and *P. atrata*/*P. flanneryi*.

(1909b, 1912) papers; however Hill & Beckon (1978) correctly described characteristic dental and pelage traits of this species on the basis of the holotype. As noted above, Laurie & Hill (1954) arranged *P. anceps* as a subspecies of *P. atrata* without supporting evidence, an arrangement later criticized on morphological grounds by Hill & Beckon (1978). Taxonomic concepts of *P. anceps* employed by Phillips (1968), Koopman (1994), Flannery (1995), Bonaccorso (1998), and Parnaby (2002b) all failed to distinguish between *P. anceps* and *P. flanneryi*, which are sympatric on Bougainville and Choiseul, and thus refer to both of these species. However, a drawing figured by Bonaccorso (1998) correctly depicts the appearance and external diagnostic traits of this species.

Representative wing measurements for an adult male (AM M6497) are as follows (measured from dry skins): pollex 64.4; D1M 19.9; D1P1 41.7; D2M 83.6; D2P1 20.3; D2P2 19.7; D3M 118.9; D3P1 72.4; D3P2 107.7; D4M 112.1; D4P1 64.3; D4P2 74.5; D5M 117.7; D5P1 48.4; D5P2 39.3. Andersen (1912: 440) presented wing measurements for the immature holotype.

Four of the seven known museum specimens of *P. anceps* from Bougainville were collected in high elevation rainforest or mossy montane forest (i.e. cloud forest) at elevations of 1100 m or higher, where the larger-bodied, shorter-furred *P. flanneryi* has never been recorded and may not occur. On Choiseul, *P. anceps* has been observed only in inland primary forest at 850 m (Bowen-Jones *et al.*, 1997), and, on the basis of local interviews, Bowen-Jones *et al.* (1997) suggested that it does not occur in coastal forest there (the mountains of Choiseul rise to 1060 m; Table 8). These observations potentially highlight differences in habitat preference between *P. anceps* and *P. flanneryi*. The long, thick pelage of *P. anceps* (recalling that of *Pteralopex pulchra*, a moss forest endemic from montane Guadalcanal) lends additional support to this supposition. The mean altitude of all sites where *P. anceps* has been collected or observed is 800 m ($n = 5$, range 0 to 1900 m); the mean for *P. flanneryi* is 50 m ($n = 8$, range 0 to 200 m).

Pteralopex anceps has been observed roosting solitarily and in groups (Bowen-Jones *et al.*, 1997: 212). Subadults (forearm 137 to 138.5) have been collected in March and April on Bougainville (see specimens above). Little is known of the diet of this species, but its large incisors and small molars re-

lative to sympatric *P. flanneryi* undoubtedly denote trenchant differences in feeding ecology between the two species; in particular, *P. anceps* may engage in tree-gouging for exudate feeding (see Discussion below). Judging from museum specimens, toothwear in adults is extensive, suggesting hard, abrasive fruits also form part of the diet.

Maa (1968) recorded the batfly *Cyclopodia macracantha longiseta* (taken from AM M6497) from this species on Bougainville.

Anatomically, *P. anceps* is in many ways the most highly-derived species of monkey-faced bat. It differs from other *Pteralopex* in its considerably deflected braincase, expanded incisors, reduced molars, and lack of lingual ridges on the lower first and second molars. These autapomorphies, together with the very close genetic relationship assumed here between *P. flanneryi* and *P. atrata*, and that demonstrated between *P. taki* and *P. pulchra* (Ingleby & Colgan, 2003), may suggest that *P. anceps* is the most basal species of *Pteralopex* (*sensu stricto*). Alternately, the blackish fur and large size of *P. anceps* may betray a sister relationship with *P. flanneryi* and *P. atrata*. No genetic study has yet included samples of all six monkey-faced bat species, but this remains an important priority for resolving the pattern, timing, and geography of diversification in the group.

Museum specimens demonstrate that *P. anceps* has not been collected on Bougainville since 1968, despite some survey efforts (e.g. Flannery, 1995; Bonaccorso, 1998; S. Hamilton, *in litt.*). The species was recorded most recently from Choiseul by Bowen-Jones *et al.* (1997), who observed the species only twice during six months' fieldwork on Choiseul in 1995. Given its limited distribution, apparent rarity, and restriction to old-growth forests, the current IUCN designation of "Critically Endangered" for *P. anceps* (Hilton-Taylor, 2000; Parnaby, 2002b) is still appropriate, despite the present changes in the species' taxonomic definition.

Mirimiri gen. nov.

Diagnosis

The genus *Mirimiri* can be distinguished from all pteropodid genera but *Pteralopex* by the distinctive combination of morphological traits listed above ('Monophyly of monkey-faced bats'). In addition, each of the following eight characters is perfectly diagnostic for *Mirimiri* with respect to

Taxonomic and geographic arrangement of *Pteralopex*: Parnaby (2002b)*Pteralopex atrata*: Guadalcanal*Pteralopex anceps*: Bougainville, Buka, Choiseul, Ysabel*Pteralopex pulchra*: Montane Guadalcanal (1200 m and higher)*Pteralopex taki*: New Georgia and Vangunu, formerly Kulumbangra*Pteralopex acrodonta*: Montane Taveuni (1000 m and higher), possibly Vanua Levu**Taxonomic and geographic arrangement of *Pteralopex* (and *Mirimiri*): this study***Pteralopex atrata*: Guadalcanal, New Georgia*Pteralopex flanneryi*: Bougainville, Buka, Ysabel, Choiseul*Pteralopex anceps*: Bougainville, Choiseul, possibly Ysabel*Pteralopex pulchra*: Montane Guadalcanal (1200 m and higher)*Pteralopex taki*: New Georgia and Vangunu, formerly Kulumbangra*Mirimiri acrodonta*: Montane Taveuni (1000 m and higher), possibly Vanua Levu**Table 7** Changes to *Pteralopex* taxonomy and distribution.*Pteralopex*:

1. Postorbital processes not annectent to the zygomata in adults.
2. Interorbital region of skull not conspicuously narrowed.
3. M² not strongly reduced relative to M¹ (greater than half the mass).
4. Labial margins of PM⁴ and M¹ divided into three distinct cusps.
5. Length of D4P2 subequal to D4P1.
6. Five divided median ridges in the soft palate.
7. Two serrated supplementary posterior ridges in the soft palate.
8. Slight sexual dichromatism in pelage, with the back and rump more strikingly golden in males than females (more khaki-coloured in the latter).

Of these eight traits that distinguish the monkey-faced bat genera, traits 4, 7, and 8 represent character states more highly derived in *Mirimiri* than *Pteralopex*, while (judging from their distribution among the Pteropodidae) the other states are probably more primitive. Parnaby (2002b: 150) illustrated differences in traits 2 and 5 between *Mirimiri* and *Pteralopex* graphically. The palatal ridges (traits 6 and 7) differ from

Pteralopex not only in number, but also in details of structure (Parnaby, 2002b). The cheekteeth of *Mirimiri* differ from *Pteralopex* not only in details of cuspidation along the labial margins of PM⁴ and M¹ (as described above), but also in other features as reviewed in further detail by Hill & Beckon (1978).

CONTENT. Monotypic; comprising only *M. acrodonta* of montane Taveuni (Fiji).

ETYMOLOGY. Fijian, “mist” (Capell, 1968), in allusion to the cloud forests this monkey-faced bat inhabits, and appropriate for such an elusive and endangered animal.

***Mirimiri acrodonta* (Hill and Beckon, 1978)**

(Figs 8, 9)

HOLOTYPE. BMNH 1977.3097, adult male, skin and skull, from Mt. Koroturanga (= Des Voeux Peak, 16°50.5'S, 179°58'W), 1170 m, Taveuni, Fiji, collected 3 May 1977 by W.N. Beckon.

Other material examined

Three specimens from the type locality, collected in May 1990 by Pavel German (AM M24030, adult male, 1190 m; AM

**Figure 8** Skull of *Mirimiri acrodonta* (AM M24030, adult male, Taveuni).

M24031, adult female, 1010 m; AM M24579, adult female, 1010 m). Apart from these three specimens and the holotype, this species is known only by one additional specimen (the paratype, 1190 m) and an individual that was netted but escaped (1170 m); see Hill & Beckon (1978).

Diagnosis

As for the genus.

Distribution

Mirimiri acrodonta is recorded only from mossy montane forest (i.e. cloud forest) on Mt. Koroturanga (= Des Voeux Peak) on the volcanic Fijian island of Taveuni, at altitudes between 1000 and 1200 m (Hill & Beckon, 1978; Flannery, 1995). Aspects of the vegetation and microclimate of this unique forest (Fig. 10) were reviewed in useful detail by Ash (1987) and Mueller-Dombois & Fosberg (1998). This species probably occurs also in high montane forest on the larger, adjacent island of Vanua Levu (especially Delaikoro Peak), where it is recorded by unvouchered observations (Hill & Beckon, 1978; P. German, *pers. comm.*; Flannery, 1995), but this awaits confirmation. The mean elevation of the four sites on Mt. Koroturanga where this bat has been mistnetted (Hill & Beckon, 1978; Flannery, 1995) is 1140 m (range 1010–1190 m).

Remarks

All that is known of the biology of the Fijian monkey-faced bat has previously been reviewed by Hill & Beckon (1978), Flannery (1995), and Parnaby (2002b). Hill & Beckon (1978) provided an excellent descriptive morphological review; Parnaby (2002b) discussed additional museum specimens and figured the species' skull, and Flannery (1995) provided brief biological notes and figured a photograph of the species in life. Using allozymes, Ingleby & Colgan (2003) studied genetic differences between *Mirimiri* and *Pteralopex*, concluding that "the level of separation between *Pt. acrodonta* and its two congeners in the Solomon Islands [fixed differences at 38 % of loci] . . . is about the level found in two other Pacific megachiropteran genera for which electrophoretic data are available [*Nyctimene* and *Paranyctimene*]."

Mirimiri joins a number of other terrestrial vertebrate genera endemic to Fiji, including five living avian genera (*Prosopeia*, *Phigys*, *Trichocichla*, *Lamprolia*, and *Xanthotis*), two extinct avian genera (*Natunaornis*, *Megavitiornis*), one living snake genus (*Ogmodon*), an extinct iguanid genus (*Lapitiguana*), and the extinct mekosuchine crocodylian genus *Volia* (Stattersfield *et al.*, 1998; Worthy, 2000, 2001; Molnar *et al.*, 2002; Pregill & Worthy, 2003). The iguanid genus *Brachylophus* is another near-endemic genus, extending only to Tonga (Gibbons, 1981; Pregill & Worthy, 2003).

Mirimiri acrodonta forms part of a relatively depauperate Fijian bat fauna which also includes two flying-foxes (*Pteropus samoensis* and *P. tonganus*), the blossom-bat *Notopteris macdonaldi*, the sheath-tail-bat *Emballonura semicaudata*, the mastiff-bat *Chaerephon bregullae*, and possibly a species of the vespertilionid genus *Nyctophilus* (Flannery, 1995; Helgen & Flannery, 2002; Parnaby, 2002a; Ingleby & Colgan, 2003). Of these, *M. acrodonta* is the most ancient ele-

ment, and the only endemic taxon in the Fijian bat fauna apart from the flying-fox subspecies *Pteropus samoensis nawaiensis* Gray, 1870.

Mirimiri acrodonta is currently classified as 'Critically Endangered' (Parnaby, 2002b). Though little remains known of its general biology, this is a status it most certainly deserves. Whether this species extends to Vanua Levu or not, its total geographic range is undoubtedly minuscule. As Ash (1987) noted:

The extent of cloud-forest in Fiji is very limited, occupying only the ridges on the highest peaks [above about 900 m altitude]. In Taveuni cloud-forest occurs only along about 10 km of the main range and in the other islands it is restricted to 1–2 km of ridges around isolated peaks which are separated by distances of 30–100 m.

Discussion

Ecomorphological differences between sympatric *Pteralopex* species

Until relatively recently (Hill & Beckon, 1978) all species of *Pteralopex* were thought to be allopatric, but four islands in the Solomons are now known to support two sympatric species of *Pteralopex*. Flannery (1991) reported the first example when he documented the presence of both *P. atrata* and *P. pulchra* on Guadalcanal. There the two species appear to be elevationally stratified, with *P. pulchra* endemic to mossy montane forests at 1200 m and above, and *P. atrata* occupying primary forest at lower elevations (Flannery, 1991). Among many other traits, *P. pulchra* differs from *P. atrata* in its absolutely smaller body size, and longer pelage (Flannery, 1991, 1995).

On New Georgia, both *P. taki* and *P. atrata* have been recorded (this paper), although the latter species is known from that island by a single specimen (collected in 1975) without accompanying elevational data. *Pteralopex taki* is thus far known only from lowland forest on New Georgia and Vangunu (Flannery, 1995; Fisher & Tasker, 1997; Parnaby, 2002b). I suspect that *P. atrata* also occurs in lowland forest on New Georgia, as elsewhere it is recorded only from lowland Guadalcanal. Hence *Pteralopex taki* and *P. atrata* may occur syntopically in lowland forest on New Georgia. If still present there, *P. atrata* is no doubt much the rarer species, given that it was never encountered by Fisher & Tasker (1997) during their survey of pteropodids on New Georgia and adjacent islands. Though ecomorphological distinctions between these taxa remain essentially unstudied, their sympatric occurrence is no doubt facilitated in part by the absolute size difference between the two species: *P. taki* has a forearm length of 112.8 to 122.8 mm and an adult body weight of 225 to 351 grams (Parnaby, 2002b), while *P. atrata* has a forearm length of 129 to 147 mm and an adult body weight of 438 to 506 grams (Table 2).

On Bougainville and Choiseul, where *P. anceps* and *P. flanneryi* both occur, the two species do not simply segregate vertically, as they have been collected together in lowland forest. Nor is the contrast in body size between *P. flanneryi* and *P. anceps* as striking as that between *P. atrata* and



Figure 9 The Fijian monkey-faced bat (*Mirimiri acrodonta*), from Taveuni, in life. Photograph by Pavel German.

P. pulchra on Guadalcanal or between *P. atrata* and *P. taki* on New Georgia. Instead, *Pteralopex anceps* and *P. flanneryi* presumably segregate ecologically, preferentially utilizing both different habitats (see account of *anceps*, above) and different food sources (at least in part; see below). The latter is suggested by their very different dentitions, with, for

example, *P. anceps* having relatively very large incisors and smaller molars and *P. flanneryi* with smaller incisors and larger molars.

Nothing about the diet of *P. anceps* has been recorded in the literature except that individuals have been observed roosting in fig (*Ficus*) trees (Bowen-Jones *et al.*, 1997), and very



Figure 10 Cloud forest on Mt. Des Vouex, Taveuni, Fiji, 1100 m: habitat of *Mirimiri acrodonta*. Photograph by Tim Flannery.

little is known of the diet of *P. flanneryi*. (Feeding ecology of only *P. taki* has been studied in detail: Fisher & Tasker, 1997.) Only two observations relevant to the diet of *P. flanneryi* are available: Sanborn (1931) observed a subadult from Ysabel eating green coconuts, and A.B. Mirza noted on a museum tag that one adult (BBM-NG 61066) was shot at night in a coconut tree on Bougainville. In light of these observations, it is interesting to note Parnaby's (2002b: 158) following comments:

hunters in the Hograno district of Isabel . . . assured [me] that the *Pteralopex* in their region did not feed on coconuts, young or old. A number of people reported that the species chewed bark on the trunk of selected trees. The expectorated pulp of *Pteralopex* could evidently be readily recognized from that of *Pteropus sp.* by shape and greater size. Individuals were said to be equally likely to be encountered in coastal forests as on the higher elevations of the nearby mountains, which reach some 1000 m, the highest mountains on Isabel.

Although only *P. flanneryi* has been recorded to date from Ysabel, given that that species is indeed known to eat coconuts and has never been collected above 200 m, it seems quite likely that Parnaby's local informants were actually describing the behaviour of *P. anceps*. I suspect that the larger, more robust molars of *P. flanneryi* are utilized to break open coconuts and hard fruits with powerful lateral bites (Dumont & Herrell, 2003; Marshall, 1985), while the more strongly-developed incisors, anteriorly expanded braincase, and greater cranial klinorhynch of *P. anceps* (see above) may instead facilitate tree-gouging (as described by Parnaby's informants above), perhaps for exudate feeding – an ecological strategy not uncommon among various small and medium-sized mam-

mals with similar adaptations in other tropical forests (Dumont, 1997; Vinyard *et al.*, 2003). However, the extensively worn cheekteeth of some older specimens of *P. anceps* suggests that harder foods also factor significantly in the diet.

Geography of monkey-faced bats and future survey priorities

Throughout the south-west Pacific, flying-foxes (species of *Pteropus*) are common inhabitants of islands of all sizes, including very small and extremely remote islands. Many aspects of their ecology and physiology are suited to survival on small islands (McNab, 1994; McNab & Bonaccorso, 2001), including predilection for or tolerance of disturbed habitats, such as secondary forest, native gardens, or cyclone-damaged landscapes (Flannery, 1990; Flannery, 1995; Grant *et al.*, 1997). In this regard, basic ecological requirements of flying-foxes contrast strongly with those of monkey-faced bats despite their resemblance in size and external appearance. Across their range, monkey-faced bats (both *Pteralopex* and *Mirimiri*) occur only in old-growth forest – probably necessary both for suitable roosting sites and favoured food plants (Fisher & Tasker, 1997). In the case of *P. atrata*, *P. flanneryi*, and *P. taki* this is primary lowland forest (below about 1000 m), for *P. pulchra* and *M. acrodonta* this is montane forest above 1200 and 1000 m respectively, and for *P. anceps* this is both primary lowland and montane forest (though forests above about 800 m may be most important). Further, monkey-faced bats are not known from any island less than 400 km² in area apart from Barora Fa and Puruata, small islands situated immediately along the respective coasts of Ysabel and Bougainville

Island	km ²	m	Species recorded
Bougainville	8591	2591	2 (fl, an)
Guadalcanal	5281	2448	2 (at, pu)
Malaita	4307	1280	0
Ysabel	4095	1250	1 (fl)
Makira	3090	1040	0
Choiseul	2966	1060	2 (fl, an)
New Georgia	2044	1006	2 (at, ta)
Kulambangra	704	1768	1 (ta: <i>extinct</i>)
Vella Lavella	640	793	0
Buka	611	402	1 (fl)
Vangunu	544	1124	1 (ta)

Table 8 The eleven Solomon Islands (excluding the outlying island of Rennell) greater than 400 km² in area, with area (km²), maximum elevation (m), and number of recorded *Pteralopex* species. an = *P. anceps*; at = *P. atrata*; fl = *P. flanneryi*; pu = *P. pulchra*; ta = *P. taki*. Areas and elevations are from Mayr and Diamond (2001: 60), except for highest elevation for Choiseul (1060 m), taken from Bowen-Jones *et al.* (1997).

(Table 8). This suggests that monkey-faced bats require relatively large areas of old-growth forest to sustain resident populations (although the montane species may be restricted to quite small upland areas on their respective islands). Indeed, *P. taki* has apparently been extirpated on Kulambangra following extensive deforestation (Flannery, 1995; Fisher & Tasker, 1997), which has claimed much of the lowland forest of that island over the last 40 years (Whitmore, 1989).

Of the eleven 'core' islands of the Solomons greater than 400 km² in area (i.e. excluding the outlying island of Rennell), eight are known to support (or to have until recently supported) at least one *Pteralopex* species (Table 8). The three exceptions are the large islands of Malaita, Makira (San Cristobal), and Vella Lavella. Malaita and Makira are large, mountainous islands that have been very incompletely surveyed for mammals, and I suspect future surveys will show these islands to support species of *Pteralopex* (cf. Parnaby, 2002b). Surveys are also needed to determine whether the distribution of *P. taki* extends to Vella Lavella, a poorly-surveyed island seemingly large enough to support a species of *Pteralopex*. In addition, as noted above, I suspect future fieldwork will demonstrate that *P. anceps* (as well as *P. flanneryi*) occurs on the large island of Ysabel.

At 435 km², Taveuni in Fiji is the smallest island that supports a monkey-faced bat (*M. acrodonta*). As noted by Flannery (1995) and Parnaby (2002b), surveys are necessary to establish whether this species extends to cloud forest on the adjacent island of Vanua Levu, which is much larger (5538 km²) but has lower mountains (maximum elevation ca. 1030 m, vs. 1241 m on Mt. Uluinalau on Taveuni [Ash, 1987]).

Finally, because monkey-faced bat genera occur in the Solomon Islands (*Pteralopex*) and Fiji (*Mirimiri*), related species might be expected to occur in the geographically intervening archipelago of Vanuatu (the New Hebrides). Lowland

forests throughout Vanuatu have now been relatively well-surveyed for mammals (Medway & Marshall, 1975; Flannery, 1995; Helgen, *unpubl. data*), and *Pteralopex* does not occur there. However, mammal faunas from the higher peaks in the western part of the largest island of Vanuatu – Espiritu Santo – remain poorly known (Medway & Marshall, 1975). Several of these mountains rise higher than 1000 m (the tallest being Mt. Tabwemasana at 1879 m) and mossy upper montane forests on these peaks (at and above about 1000 m) support an avifauna quite distinct from that of the lowlands, which includes the endemic montane starling *Aplonis santovestris* and the warbler *Cichlornis whitneyi whitneyi* (Bregulla, 1992). If monkey-faced bats are found to occur in Vanuatu, it will probably be in these mountains.

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Appendix

Key to species of monkey-faced bats (*Pteralopex* and *Mirimiri*) (modified from Parnaby, 2002b: 161)

- 1a. Body size relatively small (FA < 130; CBL < 60); post-orbital processes not annectent to the zygomata in adults; M² not strongly reduced relative to M¹ (greater than half the mass); labial margins of PM⁴ and M¹ divided into three distinct cusps; length of D4P2 subequal to D4P1; five divided median ridges in the soft palate; two serrated supplementary posterior ridges in the soft palate
 *Mirimiri acrodonta*
- 1b. Body size small to large (FA 112–170; CBL 52–76); post-orbital processes annectent to the zygomata in adults; M² strongly reduced relative to M¹ (less than half the mass); labial margins of PM⁴ and M¹ united in an elevated cusp; length of D4P2 conspicuously longer than D4P1; six divided median ridges in the soft palate; three serrated supplementary posterior ridges in the soft palate
 genus *Pteralopex* (2)
- 2a. Body size smaller (FA < 125; CBL < 56) 3
- 2b. Body size larger (FA > 128; CBL > 61) 4
- 3a. Dorsal fur dense and long, black; ventral fur dark with yellowish tips; teeth smaller (MTR < 20); second lower incisors separated from each other by at least half the breadth of each tooth *Pteralopex pulchra*
- 3b. Dorsal fur generally sparse, short, overall fur colour light brown, without yellowish venter; teeth larger (MTR > 20); second lower incisors nearly in contact or separated by less than half the breadth of each tooth
 *Pteralopex taki*
- 4a. Body size large (FA 141–160); pelage very long and thick, fur of mid-back not adpressed; tibia, dorsal surface of the pes, and proximal third of the forearm very densely furred; overall colour blackish brown, but venter with a expansive yellow or white fur patch on the breast; incisors and canines relatively very large but cheekteeth relatively small except for PM₄; PM₄, M₁, and M₂ without unbroken, elevated lingual ridges along their lengths
 *Pteralopex anceps*
- 4b. Body size medium to very large (FA 129–169); pelage generally short; fur of mid-back adpressed; tibia, dorsal surface of the pes, and proximal third of the forearm very sparsely furred; overall colour blackish brown above and below; cheekteeth relatively heavy; PM₄, M₁, and M₂ with unbroken, elevated lingual ridges along their lengths . . . 5
- 5a. Size smaller (FA < 150); rostrum less elongate (ONL/CBL = 0.491–0.553) *Pteralopex atrata*
- 5b. Size larger (FA > 158); rostrum more elongate (ONL/CBL = 0.575–0.632) *Pteralopex flanneryi*