



Biogeography of mammals on tropical Pacific islands

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ABSTRACT

Aim We examine the influence of geography on species richness and endemism of mammals on tropical Pacific archipelagos to determine the importance of intra- and inter-archipelago speciation in promoting local and regional species richness.

Location Thirty tropical Pacific archipelagos.

Methods A distributional list of mammals on 30 archipelagos was compiled, and values for 10 geographical variables were estimated for each archipelago. Mammal species were placed in three different categories (continental, Pacific and endemic) based on their distribution. The total number of species and numbers of species within each category were related to the geographical variables using Poisson regression analysis.

Results Species richness was related positively to variables describing land area, numbers of large islands and elevation; and negatively to variables describing isolation. Levels of endemism did not differ between volant and non-volant species, but differed between mega- and microchiropterans.

Main conclusions Variation in species richness of mammals in the tropical Pacific region can be accounted for by a combination of intra-archipelago speciation within archipelagos composed of large islands, and inter-archipelago speciation, particularly among more isolated archipelagos. Mammals were less widely distributed throughout the study area than previously found for butterflies, skinks or birds. However, the level of endemism was similar to that of skinks and birds on the same archipelagos, and was higher than that of butterflies.

Keywords

Archipelagos, bats, endemism, island biogeography, mammals, marsupials, Pacific Ocean, rodents, speciation, species richness.

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INTRODUCTION

The distribution and richness of species in insular systems are determined by colonization and extinction events that are largely dependent on geographical characteristics of the islands, particularly size and isolation. Thus the number of species on an island increases with island area and decreases with isolation (Mayr, 1965; MacArthur & Wilson, 1967; Lomolino, 1984; Whittaker, 1998). MacArthur & Wilson (1967) formulated the equilibrium theory of island biogeography to model the influence of island isolation and size on

immigration and extinction rates, respectively. A major shortcoming of the theory, however, is the frequent focus on ecological time-scales, whereas evolutionary time-scales over which speciation may occur have been largely ignored (Lomolino, 2000). Clearly, distribution and richness on islands depend not only on taxon-specific vagility and population persistence, but also on speciation events.

On oceanic islands (particularly large, isolated islands), colonization events may be followed by reduced gene flow and subsequent *in situ* speciation given sufficient time (Brown, 1986; Lomolino, 1994; Ceballos & Brown, 1995). Thus

immigration and extinction events affect the accumulated genetic variance of insular populations. Models based on genetic divergence predict that comparisons between the sequence differences of mainland and island populations will show greater divergence from the mainland in larger and more distant areas, whereas smaller and closer areas will have more newly arrived immigrant alleles, with a consequent decrease in average allelic divergence (Orr & Orr, 1996; Johnson *et al.*, 2000). To a large extent, dispersal capabilities of different taxa will also determine the distribution, richness and endemism of those taxa among oceanic archipelagos. Thus less vagile taxa will be poorly represented within distant archipelagos, but they may also have higher levels of endemism than more vagile taxa in this radiation zone (MacArthur & Wilson, 1963). Extensive genetic data bases do not exist for most island systems and taxa, and therefore the models of Orr & Orr (1996) and Johnson *et al.* (2000) cannot be addressed directly. However, endemism may be used as a proxy for genetic divergence (Johnson *et al.*, 2000).

Insular diversity and endemism of butterflies (Adler & Dudley, 1994; Dudley & Adler, 1996); birds (Adler, 1992); and lizards (Adler *et al.*, 1995) are related strongly to island size and isolation in the tropical Pacific. In the case of mammals, the presence of few non-volant species on oceanic islands is attributed principally to their poor dispersal ability, and thus the low number of colonization events. Richness of non-volant mammals on those islands therefore results from infrequent colonization and subsequent speciation over long periods, resulting in high levels of endemism. In contrast, bats have greater dispersal abilities and have broader distributions across archipelagos because colonization events have been much more frequent (Lawlor, 1986).

The tropical Pacific region contains numerous archipelagos and isolated islands that provide an excellent system in which to examine the influence of geography on insular richness and endemism of mammals with different dispersal abilities. Accordingly, we analyse species richness and endemism of mammals on tropical Pacific islands in relation to the geography of those islands. We also compare mammal diversity and endemism with other animals for which comprehensive data exist.

MATERIALS AND METHODS

We compiled a distributional list of mammals within all oceanic archipelagos and loosely associated island groups of the tropical Pacific, following the definitions of Adler (1992). The presence of each species was recorded for 30 archipelagos, loosely associated island groups, and isolated islands located between 25° N and S and from 120° W westward through the Bismarck and Palau archipelagos (Fig. 1; Table 1). Mammals known to have been introduced through human activities [e.g. *Thylogale browni* (Ramsay, 1877), *Rattus exulans* (Peale, 1848), *Rattus praetor* (Thomas, 1888)] were excluded, but we covered recently extinct native species, including those known only from subfossil remains (Flannery & Wickler, 1990; Flannery, 1995).

We placed each species in one of three groups depending upon its distribution (following Adler, 1992):

- continental species were those found also on continents or land-bridge islands such as New Guinea, the Philippines and the islands of the Sunda Shelf,
- widespread endemics (henceforth called Pacific species) were those found within more than one archipelago, but not on continents or land-bridge islands (*Pteropus mariannus* Desmarest, 1822 also occurred outside the study area in the Ryukyu Islands but we included it here as a Pacific species because it was not found on any continental landmass), and
- endemic species were those restricted to a single archipelago or island group.

We tallied the total number of species within each archipelago, and the numbers of species in each of the three categories.

We estimated 10 variables that characterized the geography of each archipelago, including total land area; area of the largest island; total number of islands; numbers of islands > 100, 500 and 1000 km²; greatest elevation on any island within an archipelago; distance to nearest continental land mass; distance to nearest adjacent land mass; and distance to nearest land mass larger in area than that archipelago (Adler, 1992).

Species–geographical relationships were examined for all, continental, Pacific and endemic species. Numbers of species

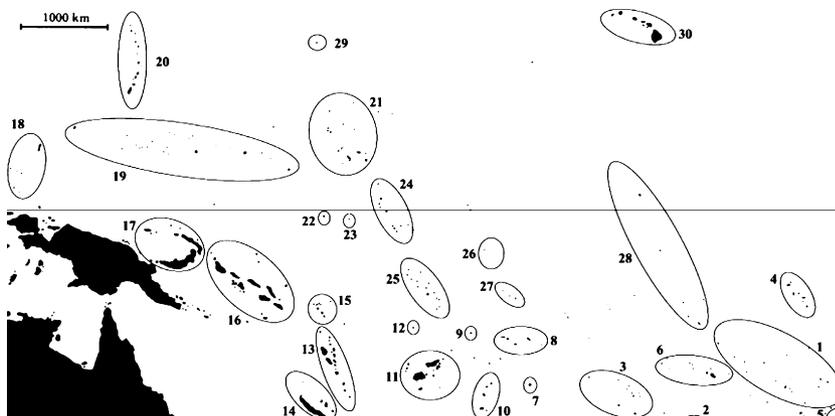


Figure 1 Map of the study area in the tropical Pacific Ocean. Archipelago numbers given in Table 1. New Guinea and eastern Australia appear at lower left, and the Tuamotus (archipelago 2) and Pitcairns (archipelago 5) extend south of the southern boundary of the map.

Table 1 Numbers of species within each archipelago (for species distributional data see Appendix)

Archipelago number	Archipelago name	Number of species			
		Continental	Pacific	Endemic	Total
1	Tuamotus	0	0	0	0
2	Tubuai	0	0	0	0
3	Cooks	0	1	0	1
4	Marquesas	0	0	0	0
5	Pitcairns	0	0	0	0
6	Societies	0	0	0	0
7	Niue	0	1	0	1
8	Samoa	0	3	0	3
9	Wallis	0	1	0	1
10	Tonga	0	4	0	4
11	Fiji	0	5	1	6
12	Rotuma	0	1	0	1
13	Vanuatu	6	4	2	12
14	New Caledonia	2	1	6	9
15	Santa Cruz	4	1	3	8
16	Solomons	18	2	25	45
17	Bismarcks	39	1	12	52
18	Belau	0	1	2	3
19	Carolines	0	2	5	7
20	Marianas	0	2	1	3
21	Marshalls	0	0	0	0
22	Nauru	0	0	0	0
23	Banaba	0	0	0	0
24	Tungaru	0	0	0	0
25	Tuvalu	0	0	0	0
26	Phoenix	0	0	0	0
27	Tokelau	0	0	0	0
28	Lines	0	0	0	0
29	Wake	0	0	0	0
30	Hawaii	1	0	0	1
	Total	42	7	57	106

in each category were not transformed because some archipelagos contained no species but nonetheless contained relevant information. Arguments for the importance of including counts of zero species have been made (Williams, 1995, 1996), and $\log_{10} + 1$ transformations are considered an inferior approach because of unnecessary bias (Russell *et al.*, 2004). Accordingly, we used Poisson regression analysis with a log link (Nelder & Wedderburn, 1972; McCullagh & Nelder, 1994) to model these species–area relationships. Russell *et al.* (2004) suggested that this regression approach is more appropriate than linear regression because counts of species on islands conform to a Poisson distribution, with a long rightward-tending tail. The total number of species and numbers of species in each category were related to the 10 geographical variables using Poisson regression analysis with a log link. All geographical variables except total number of islands and numbers of islands > 100, 500 and 1000 km² were \log_{10} -transformed.

We first constructed Poisson regression models separately for each geographical variable (a total of 40 regression models)

to determine the importance of each such variable alone in explaining variation in species counts. To examine the importance of multiple variables in explaining variation in species richness, we constructed a single multivariable model for each species category. For this purpose, we used a backward elimination procedure whereby we sequentially eliminated the variable with the highest *P* value (the lowest χ^2 value) and stopped the procedure when only variables significant at *P* < 0.05 remained in the model. Correlations among geographical variables were high, and this multicollinearity confounded the importance of the variables in the regression models (Philippi, 1993). Thus multivariable models were unstable in the sense that alternative variables of high statistical significance could have been included in the models in place of the variables that were retained by the backward elimination procedure. Our purpose in constructing multivariable models was simply exploratory, to determine if additional statistically significant variation could be explained that was not explained by simple models.

We compared levels of endemism of non-volant and volant mammals using χ^2 analysis. Numbers of Pacific and endemic species were combined because of the small number of Pacific species. We similarly compared levels of endemism of Megachiroptera (family Pteropodidae) and Microchiroptera (all other families of bats). These two groups of bats differ markedly in size, morphology, brain-visual organization and habits, and may represent two independent lineages of volant mammals (Pettigrew, 1986). We also used χ^2 analysis to compare levels of endemism among mammals and three additional taxa for which similar data were available: butterflies (Adler & Dudley, 1994); skinks (Adler *et al.*, 1995); and birds (Adler, 1992).

RESULTS

The data set consisted of 106 species of mammal, of which 42 species were continental, seven were Pacific and 57 were endemic (Table 1). Marsupials were represented by five species (four continental and one endemic, 20% endemic); rodents by 18 species (four continental and 14 endemic, 78% endemic); and bats by 83 species (34 continental, seven Pacific and 42 endemic, 51% endemic). The most species-rich archipelago was the Bismarcks, with 52 species, followed by the Solomons with 45 species. We could find no records of native mammals within 14 of the 30 archipelagos and island groups (Tuamotus, Tubuai, Marquesas, Pitcairns, Societies, Marshalls, Nauru, Banaba, Tungaru, Tuvalu, Phoenix, Tokelau, Lines and Wake). A single species (bats in all cases) was found within five archipelagos (Cooks, Niue, Wallis, Rotuma and Hawaii). Native marsupials were restricted to the Bismarcks, whereas native rodents were restricted to the Bismarcks and Solomons. No species of rodent was shared by these two archipelagos. The pteropodids were the most successful family, with 49 species occupying 14 archipelagos. The only archipelagos with mammals that lacked pteropodids were Rotuma and Hawaii.

Table 2 Relationships derived from simple Poisson regressions between numbers of species and geographical variables

Geographical variable	Number of species			
	Total	Continental	Pacific	Endemic
Area	+++	+++	+++	+++
Area of largest island	+++	+++	+++	+++
Elevation	+++	+++	+++	+++
Distance to source	---	---	0	---
Distance to archipelago	---	---	-	---
Distance to larger archipelago	--	---	0	---
Number of islands	+++	+++	0	+++
Number of islands > 1000 km ²	+++	+++	+	+++
Number of islands > 500 km ²	+++	+++	+	+++
Number of islands > 100 km ²	+++	+++	++	+++

-,+: $P < 0.05$; --,++: $P < 0.01$; ---,+++ : $P < 0.001$.

Continental bats were present only in Vanuatu, Santa Cruz, New Caledonia, the Bismarcks, Solomons and Hawaii. The most widely distributed species were the Pacific bats *Pteropus tonganus* Quoy & Gaimard, 1830 (10 archipelagos) and *Emballonura semicaudata* (Peale, 1848) (eight archipelagos). Endemic species of mammal were concentrated in the Bismarcks, Solomons, Carolines and New Caledonia. Those four archipelagos contained 48 of the 57 endemic species in the study area.

Numbers of species in each category were related strongly by simple Poisson regression to most of the geographical variables (Table 2). Multivariable Poisson regression models contained from one to five geographical variables (Table 3). In general, species richness was related positively to land area and elevation, and negatively to isolation.

Levels of endemism did not differ between non-volant (65.2% endemic and Pacific) and volant (59.0% endemic and

Pacific) mammals ($\chi^2 = 0.29$, $P = 0.5917$). With marsupials omitted, the level of endemism between rodents and bats still did not differ significantly ($\chi^2 = 2.21$, $P = 0.1368$). However, endemism was higher within the frugivorous megachiropterans (83.7% endemic and Pacific) than within the primarily insectivorous microchiropterans (23.5% endemic and Pacific) ($\chi^2 = 30.02$, $P < 0.0001$). Levels of endemism varied widely among butterflies, birds, skinks and mammals when comparing the distributions of species among continental, Pacific and endemic groups ($\chi^2 = 66.98$, $P < 0.0001$). Butterflies had a lower level of endemism than the other three taxa (Table 4). With butterflies removed from the analysis, there was no significant difference in the distributions of species among continental, Pacific and endemic groups ($\chi^2 = 9.46$, $P = 0.0506$).

DISCUSSION

The tropical Pacific native mammal fauna was dominated by bats derived from the Australopapuan region and Southeast Asia (primarily the Philippines) and, to a lesser extent, by Australopapuan marsupials and rodents (Flannery, 1995). Only the bat *Lasiurus cinereus* (Beauvois, 1796) in Hawaii was derived from North America (Morales & Bickham, 1995). The three orders of mammal represented within archipelagos of the study area differed widely in their vagility and subsequent colonization of archipelagos. Marsupials have colonized only the Bismarcks, which is the nearest archipelago to the source area of New Guinea. Rodents colonized both the Bismarcks and Solomons, but were unable to colonize more distant archipelagos. Despite the ability of bats to fly and to reach even the most remote archipelago (Hawaii), they nonetheless were absent from nearly half the archipelagos, and Australopapuan and Southeast Asian bats were distributed eastward only to the Cook Islands. Most of those archipelagos that contained no

Response variable	Regression model	χ^2	P
All species	-0.5026	0.14	0.7084
	-1.7144(log ₁₀ distance to source)	45.29	< 0.0001
	-0.9957(number of islands > 1000 km ²)	17.52	< 0.0001
	+0.3390(number of islands > 500 km ²)	26.58	< 0.0001
	+1.3735(log ₁₀ elevation)	6.37	0.0116
	+0.8814(log ₁₀ area of largest island)	8.48	0.0036
Continental species	-15.2990	4.23	0.0396
	-3.7542(log ₁₀ distance to source)	24.60	< 0.0001
	-2.2093(number of islands > 1000 km ²)	10.07	0.0015
	+0.6282(number of islands > 500 km ²)	11.70	0.0006
	+9.1750(log ₁₀ elevation)	11.01	0.0009
Pacific species	-1.7898	10.02	0.0015
	+0.6255(log ₁₀ area of largest island)	14.71	0.0001
Endemic species	+1.8377	0.93	0.3361
	+0.6524(number of islands > 500 km ²)	15.75	< 0.0001
	-1.9031(number of islands > 1000 km ²)	11.22	0.0008
	+1.9470(log ₁₀ area of largest island)	12.55	0.0004
	-2.2207(log ₁₀ distance to source)	15.98	< 0.0001

Table 3 Multivariable Poisson regression models relating numbers of species to geographical variables

Table 4 Distributions of four different taxa (numbers of species and percentage in parentheses) among continental, Pacific and endemic groups in the tropical Pacific region

Taxon	Continental	Pacific	Endemic
Butterflies	157 (55.1)	28 (9.8)	100 (35.1)
Skinks	21 (21.0)	13 (10.3)	66 (60.2)
Birds	143 (29.5)	50 (13.0)	292 (66.0)
Mammals	42 (39.6)	7 (6.6)	57 (53.8)

native mammals, including bats, were composed of small, low-lying, sandy islands with low plant diversity (Mueller-Dombois & Fosberg, 1998). It is likely that bats at various times reached at least some of those presently vacant islands, but were unable to maintain persistent populations because of low plant diversity and resource abundance and high extinction rates. Notable exceptions, however, were the Marquesas and Society archipelagos, which contained several large, elevated islands with relatively high plant diversity (Mueller-Dombois & Fosberg, 1998), but no native mammals. Bats may never have established populations on those two archipelagos because of their remoteness (particularly the Marquesas) and the absence of bat populations east of the Cook Islands.

Species richness of mammals within archipelagos is related strongly to geographical variables. In general, richness is related negatively to isolation and positively to land area. The number of islands > 500 km² within an archipelago and greatest elevation are also important predictors of species richness. The most species-rich archipelagos (Bismarcks and Solomons) are also the largest and nearest to continental sources. High species richness within those archipelagos apparently owes its origin to multiple colonizations promoted by proximity to continental sources, relatively low extinction rates promoted by large land area, and subsequent intra-archipelago speciation promoted by multiple large islands. The Bismarcks and Solomons provide several examples of small evolutionary radiations of rodents, including those within the murid genera *Solomys* and *Uromys* (Flannery, 1995). Intra-archipelago speciation has therefore contributed to richness and endemism within those archipelagos.

Smaller and more distant archipelagos composed of fewer large islands apparently have received fewer successful colonists, and the presence of most endemic species is probably the result of inter-archipelago rather than intra-archipelago speciation. Despite the ability of pteropodids to reach distant archipelagos, inter-archipelago speciation has occurred frequently. Thus endemism of pteropodids within the study area is a consequence of intra-archipelago speciation within larger archipelagos and inter-archipelago speciation among both small and large archipelagos. Both types of speciation promote regional species richness, and isolation paradoxically promotes regional richness, despite reducing local richness (Adler, 1994). Among the microchiropterans, however, inter- and intra-archipelago speciation events have not been as common, and the lower levels of endemism may be the result of recent

colonization (e.g. Rhinolophidae and *L. cinereus*) or very conservative, slowly evolving species (e.g. Hipposideridae) (Flannery, 1995; Morales & Bickham, 1995).

Johnson *et al.* (2000) predicted that endemism should be greatest on large, isolated islands (within the radiation zone; MacArthur & Wilson, 1963). Our results support their prediction with respect to island size, but seemingly contradict it with respect to island isolation. Endemism was actually greatest within archipelagos closest to the continental source of New Guinea (the Bismarcks and Solomons), whereas there were no endemic species within the distant archipelago of Hawaii, which contained eight islands > 100 km². However, the radiations of rodents and the large number of endemic pteropodids within the Bismarcks (14 species) and Solomons (five species) suggest that the distances separating large islands within those archipelagos were sufficient to promote speciation. Thus, once those islands were colonized, gene flow was so reduced that genetic divergence and subsequent speciation occurred numerous times. *Lasiurus cinereus* in Hawaii apparently has not had sufficient time to diverge to full-species status from the mainland source populations in North America (Morales & Bickham, 1995). Hawaiian populations of this bat have been accorded subspecies status, and individuals are 45% smaller and have lower wing loading than individuals within mainland populations (Jacobs, 1996). However, molecular analysis reveals a divergence of only 1.8% from North American individuals, thus suggesting relatively recent colonization (Morales & Bickham, 1995).

Patterns in the distribution and endemism of vertebrates among tropical Pacific islands are beginning to emerge. It is perhaps surprising that levels of endemism of skinks, birds and mammals are similar in the tropical Pacific region, despite major differences in vagility. Birds and bats actively disperse by flight, whereas skinks and non-volant mammals can disperse only passively, by rafting. However, once propagules of any of those vertebrate taxa successfully colonize distant islands then speciation often occurs, leading to similar levels of endemism.

Although levels of endemism do not differ among those vertebrate taxa, distributions are strikingly divergent. Birds have colonized all 30 archipelagos and island groups, and skinks are present within 27 of those groups, whereas mammals are present only within 16 groups. Although bats can traverse large expanses of open ocean, as demonstrated by the presence of *L. cinereus* in Hawaii, they have not been able to establish populations east of the Cook Islands by immigrating from the west. In contrast, skinks have colonized the most remote archipelagos, including the Societies, Marquesas and Pitcairns. These distributions suggest that mammals (particularly bats) require large land masses to maintain persistent populations, whereas skinks can maintain populations on even small, low-lying islands.

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BIOSKETCHES

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Gregory H. Adler received his PhD in 1986 from Boston University. Following post-doctoral work at the Harvard School of Public Health, the University of California at Davis, and the Smithsonian Tropical Research Institute, he assumed a permanent position at the University of Wisconsin at Oshkosh. He is currently Curwood Professor of Biology. Adler's research focuses primarily on the ecology of tropical forest mammals, and he is author of approximately 80 publications.

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Appendix 1 Distributions of mammals on tropical Pacific archipelagos. Numbers designate archipelagos, following Table 1. For status, C = continental, P = Pacific and E = endemic. After species names, ep = extinct prehistorically; eh = extinct historically. Compiled from Flannery (1995), Wiles *et al.* (1991), Wilson & Graham (1992) and Wilson & Reeder (1993).

Order/family	Species	Status	Distribution	
Marsupialia				
Peroryctidae	<i>Echymipera kalub</i>	C	17	
Phalangeridae	<i>Phalanger orientalis</i>	C	17	
	<i>Spilocuscus kraemeri</i>	E	17	
	<i>Spilocuscus maculatus</i>	C	17	
	<i>Petaurus breviceps</i>	C	17	
Petauridae	<i>Petaurus breviceps</i>	C	17	
Rodentia				
Muridae	<i>Hydromys neobritannicus</i>	E	17	
	<i>Melomys bougainville</i>	E	16	
	<i>Melomys</i> sp. cf. <i>M. levipes</i>	C	17	
	<i>Melomys matambuai</i>	E	17	
	<i>Melomys spechti</i> (ep)	E	17	
	<i>Melomys platyops</i>	C	17	
	<i>Melomys rufescens</i>	C	17	
	<i>Pogonomys macrourus</i>	C	17	
	<i>Solomys ponceleti</i>	E	16	
	<i>Solomys salamonis</i>	E	16	
	<i>Solomys spriggsarum</i> (ep)	E	17	
	<i>Solomys salebrosus</i>	E	16	
	<i>Solomys sapientis</i>	E	16	
	<i>Solomys imperator</i> (eh?)	E	16	
	<i>Uromys neobritannicus</i>	E	17	
	<i>Uromys porculus</i> (eh?)	E	16	
	<i>Uromys rex</i>	E	16	
	<i>Rattus sanila</i> (ep)	E	17	
	Chiroptera			
	Pteropodidae	<i>Dobsonia anderseni</i>	E	17
<i>Dobsonia inermis</i>		E	16	
<i>Dobsonia praedatrix</i>		E	17	
<i>Macroglossus minimus</i>		C	16,17	
<i>Melonycteris fardoulis</i>		E	16	
<i>Melonycteris melanops</i>		E	17	
<i>Melonycteris woodfordi</i>		E	16	
<i>Notopterus macdonaldi</i>		P	10,11,13	
<i>Notopterus neocaledonica</i>		E	14	
<i>Nyctimene albiventer</i>		C	17	
<i>Nyctimene bougainville</i>		E	16	
<i>Nyctimene cyclotis</i>		C	17	
<i>Nyctimene major</i>		C	16,17	

Appendix 1 *continued*

Order/family	Species	Status	Distribution
	<i>Nyctimene sanctacrucis</i> (eh?)	E	15
	<i>Pteralopex acrodonata</i>	E	11
	<i>Pteralopex anceps</i>	E	16
	<i>Pteralopex atrata</i>	E	16
	<i>Pteralopex pulchra</i>	E	16
	<i>Pteralopex</i> sp.	E	16
	<i>Pteropus admiralitatum</i>	P	16,17
	<i>Pteropus anetianus</i>	E	13
	<i>Pteropus capistratus</i>	E	17
	<i>Pteropus cognatus</i>	E	16
	<i>Pteropus fundatus</i>	E	13
	<i>Pteropus gilliardorum</i>	E	17
	<i>Pteropus howensis</i>	E	16
	<i>Pteropus hypomelanus</i>	C	17
	<i>Pteropus insularis</i>	E	19
	<i>Pteropus mahaganus</i>	E	16
	<i>Pteropus mariannus</i>	P	19,20
	<i>Pteropus molossinus</i>	E	19
	<i>Pteropus neohibernicus</i>	C	17
	<i>Pteropus nitendiensis</i>	E	15
	<i>Pteropus ornatus</i>	E	14
	<i>Pteropus pelewensis</i>	E	18
	<i>Pteropus phaeocephalus</i>	E	19
	<i>Pteropus pilosus</i> (eh?)	E	18
	<i>Pteropus rayneri</i>	E	16
	<i>Pteropus rennelli</i>	E	16
	<i>Pteropus samoensis</i>	P	8,10,11
	<i>Pteropus tokudae</i> (eh?)	E	20
	<i>Pteropus tonganus</i>	P	3,7,8,9,10,11,13,14,15,16
	<i>Pteropus tuberculatus</i>	E	15
	<i>Pteropus ualanus</i>	E	19
	<i>Pteropus vetulus</i>	E	14
	<i>Pteropus woodfordi</i>	E	16
	<i>Pteropus yapensis</i>	E	19
	<i>Rousettus amplexicaudatus</i>	C	16,17
	<i>Syconycteris australis</i>	C	17
Emballonuridae	<i>Emballonura beccarii</i>	C	17
	<i>Emballonura diana</i>	C	16,17
	<i>Emballonura serii</i>	C	17
	<i>Emballonura nigrescens</i>	C	16,17
	<i>Emballonura raffrayana</i>	C	16,17
	<i>Emballonura semicaudata</i>	P	8,10,11,12,13,18,19,20
	<i>Saccolaimus saccolaimus</i>	C	16
Hipposideridae	<i>Anthops ornatus</i>	E	16
	<i>Aselliscus tricuspidatus</i>	C	13,15,16,17
	<i>Hipposideros ater</i>	C	17
	<i>Hipposideros calcaratus</i>	C	16,17
	<i>Hipposideros cervinus</i>	C	13,15,16,17
	<i>Hipposideros demissus</i>	E	16
	<i>Hipposideros diadema</i>	C	16,17
	<i>Hipposideros dinops</i>	C	16
	<i>Hipposideros maggietaaylorae</i>	C	17
Rhinolophidae	<i>Rhinolophus euryotis</i>	C	17
	<i>Rhinolophus megaphyllus</i>	C	17
Vespertilionidae	<i>Chalinolobus neocaledonicus</i>	E	14
	<i>Kerivoula myrella</i>	C	17
	<i>Lasiurus cinereus</i>	C	30

Appendix 1 *continued*

Order/family	Species	Status	Distribution
	<i>Miniopterus australis</i>	C	13,14,16,17
	<i>Miniopterus macrocneme</i>	C	13,14,16,17
	<i>Miniopterus propitristis</i>	C	13,15,16,17
	<i>Miniopterus robustior</i>	E	14
	<i>Miniopterus schreibersii</i>	C	16,17
	<i>Murina florium</i>	C	17
	<i>Myotis adversus</i>	C	13,16,17
	<i>Nyctophilus</i> sp.	E	14
	<i>Philetor brachypterus</i>	C	17
	<i>Pipistrellus angulatus</i>	C	15,16,17
	<i>Pipistrellus papuanus</i>	C	17
Molossidae	<i>Chaerephon bregullae</i>	P	11,13
	<i>Chaerephon solomonis</i>	E	16