

AMERICAN MUSEUM *Novitates*

PUBLISHED BY
THE AMERICAN MUSEUM
OF NATURAL HISTORY

CENTRAL PARK WEST AT 79TH STREET
NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2690

NOVEMBER 2, 1979

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Number 2690, pp. 1-17, fig. 1, tables 1-3

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Zoogeography of Mammals from Islands Off the Northeastern Coast of New Guinea

KARL F. KOOPMAN¹

ABSTRACT

The mammal faunas of seven islands lying off the northeast coast of New Guinea and adjacent to the Bismarck Archipelago have been studied. While a number of characteristic New Guinea elements are lacking, the faunas show a mixture of New Guinea and New Britain (Bismarck) elements. An attempt is

made to explain the presence or absence of various Megachiroptera on these and other islands in the Bismarck area in terms of "incidence functions," but it is evident that the data are inadequate to go very far in this direction.

INTRODUCTION

The American Museum of Natural History received two rather large collections of mammals collected by Jared Diamond from several islands off the northern coast of Papua New Guinea (Karkar, Bagabag, Crown, Long, Tolokiwa, Umboi, Sakar) which has focused my attention on the zoogeography of the Bismarck Archipelago in relation to the mainland of New Guinea. The above-named seven islands (fig. 1) are all off the New Guinea shelf and the quite separate New Britain shelf. They therefore form a link between New Guinea (which is actually an extension of the Australian shelf) with a rich continental fauna, and the Bismarck Archipelago with an insular fauna.

ACKNOWLEDGMENTS

The collections on which this report is chiefly based were made by Dr. Jared Diamond

of the University of California at Los Angeles, and I thank him for donating them to the American Museum of Natural History and for critically reading the manuscript. The late Mr. Hobart Van Deusen initially identified much of the marsupial material and as usual was extremely encouraging in the early stages of the investigation. Dr. Guy Musser of the Department of Mammalogy identified the rodents and critically read the manuscript; both he and Dr. Mary Taylor of the University of British Columbia were very helpful in discussing the distribution of *Rattus* in and around the Bismarcks. Mr. John E. Hill of the British Museum (Natural History), Drs. Hans Hackethal and Renate Angermann of the Zoologisches Museum der Humboldt Universität (Berlin), and Dr. Patricia Freeman of the Field Museum of Natural History (Chicago) made collections available and extended numerous

¹Curator, Department of Mammalogy, American Museum of Natural History.

[illegible]

New Guinea are not *kalubu*, but another species, *E. rufescens*. Both species occur on the New Guinea mainland.

Echymipera kalubu—Diamond obtained specimens from Karkar (32 sets of lower jaws), Bagabag (three skins and skulls, one skin only, 21 sets of lower jaws), Tolokiwa (one skin only), Umboi (one skin and skull, four skulls only), and Sakar (one set of lower jaws). The species is probably widespread throughout the New Guinea-Bismarck area.

ORDER DIPROTODONTA

Three species of diprotodont marsupials are known from New Britain (*Phalanger orientalis*, *Petaurus breviceps*, *Thylogale bruijni*), though only *Phalanger orientalis* goes on to the Solomons (Laurie and Hill, 1954). In addition, *P. maculatus* is known from the Admiralty and Ninigo islands, but apparently not from the main Bismarck Islands. Diamond also obtained a species of tree kangaroo (*Dendrolagus matschiei*) from Umboi, though this species is not known from nearby New Britain.

Phalanger orientalis—Diamond obtained specimens from Karkar (one skull, 363 sets of lower jaws), Bagabag (one skin and skull, one skin only, three skulls only, 152 sets of lower jaws), Long (10 skins only, 14 skulls only, one set of mandibles), and Umboi (one skin and skull, three skins only, five skulls only, one mandible). The American Museum of Natural History also has eight skins and skulls, two skulls only from Long, and one skin and skull from Umboi all collected by W.F. Coultas on the Whitney Expedition in 1933. Two subspecies are currently recognized in the northeast New Guinea-Bismarck area (see Laurie and Hill, 1954), *P. o. vulpecula* on the New Guinea mainland and *P. o. ducatoris* on New Britain. I have been unable to distinguish skulls of these two subspecies, but find that skins of *vulpecula* tend to be redder with the dorsal stripe better defined than in *ducatoris*. On the basis of this color difference, I identify specimens from Karkar and Bagabag as *P. o. vulpecula* and those from Long and Umboi as *P. o. ducatoris*. There is, however, a great deal of individual variation. According to Diamond (*in litt.*), the *Phalanger* of Long was introduced from Tolokiwa in the nineteenth century as attested

to by local residents. This is a very widespread species ranging from Australia, Timor, and the Moluccas to the Solomons (where it is the only marsupial).

Petaurus breviceps—This species was obtained by Diamond only from Bagabag (three skins and skulls). This is another widespread species that ranges from Australia to New Britain, but does not reach the Solomons.

Dendrolagus matschiei—Diamond obtained this species only on Umboi (one skin and skull, one skull only). The late Hobart Van Deusen doubted that tree kangaroos were native to Umboi but thought that they had been introduced, since they are often kept captive in New Guinea villages. Their absence from any islands off the northern coast of New Guinea except Umboi would support this possibility.

Thylogale bruijni—Diamond obtained specimens from Bagabag (one lower jaw) and Umboi (one skin and skull, two skulls only, five mandibles). This is the only wallaby in the Bismarcks and even it does not reach the Solomons.

ORDER CHIROPTERA

Of the five families of bats known from New Guinea, only the Molossidae have not been recorded from the Bismarcks. Even that family may occur there since *Tadarida (Chaerephon) jobensis* is known from both New Guinea and the Solomons (Hill, 1961). Confirmation of its occurrence in the Solomons is provided by two specimens in the American Museum of Natural History from Choiseul. (*Tadarida jobensis solomonis* was previously known only from Ysabel.) There are, however, no records of molossids on any islands off the northeast coast of New Guinea.

FAMILY PTEROPODIDAE

Eight genera of pteropodids are definitely known from the mainland of New Guinea. Of these, only two, the newly described *Aproteles* (Menzies, 1977) and *Paranyctimene*, both monotypic, seem to be confined to the mainland. The other six (*Rousettus*, *Pteropus*, *Dobsonia*, *Nyctimene*, *Macroglossus*, *Syconycteris*) are all known from the Bismarcks, and with the exception of *Syconycteris*, go on at least as far

as the Solomons. Besides these genera, *Melonycteris* (including *Nesonycteris*, see Phillips, 1966) occurs widely in the Bismarcks, but except for one old unconfirmed record, has never been collected on the New Guinea mainland. *Pteralopex* occurs in the Solomons, but has not been found on the Bismarcks or New Guinea. All the Bismarck Archipelago genera are known from one or another of the islands in question off the northeast coast of New Guinea.

Rousettus amplexicaudatus—This is the only species of *Rousettus* in the New Guinea-Bismarck area. Laurie and Hill (1954) recognized a second species, *R. stresemanni*, but after looking over all the Indo-Australian *Rousettus* in the American Museum of Natural History, I cannot distinguish these two alleged species on New Guinea and therefore regard *stresemanni* as a subspecies of *R. amplexicaudatus*. (*Rousettus celebensis* of Celebes and the Sanghir Islands is, however, distinct.) *Rousettus amplexicaudatus* extends from southeastern Asia through the Malay Archipelago, New Guinea, and the Bismarcks to the Solomons. Bagabag is the only one of the seven islands here discussed from which *Rousettus* has been obtained (eight skulls collected by Diamond). It should be mentioned that the Bagabag specimens are clearly referable to the larger *R. a. stresemanni* of mainland New Guinea rather than to the smaller *R. a. brachyotis* of the Bismarcks (including New Britain).

Genus *Pteropus*—This genus has a very wide range in the Old World tropics from the western Indian Ocean east at least as far as the Cook Islands. There are many species currently recognized, some dubiously distinct. Seven species (*hypomelanus*, *melanopogon*, *alecto*, *conspicillatus*, *neohibernicus*, *macrotis*, *pohlei*) have been recorded from the New Guinea mainland. The occurrence of *P. melanopogon* in New Guinea is, however, as will be shown below, based on misidentified *P. neohibernicus*. Two of the remaining species have limited ranges distant from northeastern New Guinea. These are *alecto*, which is known only from a very limited area in southwestern Papua (Tate 1942, p. 337) and *pohlei* which is still recorded only from Japen Island in Geelvink Bay, northwestern New Guinea. Only two of

the remaining five (*hypomelanus* and *neohibernicus*) are known from New Britain, the former on the basis of three immature specimens (AMNH 194302-04) from Kandrian in the western part of the island (see Van Deusen, 1969, p. 2). Two other species have been recorded from New Britain, but do not occur on the New Guinea mainland. These are *temmincki* and the newly described *gailliardi* (Van Deusen, 1969). Two additional species should also be mentioned. *Pteropus admiralitatum* was originally described from the Admiralty Islands, but is also known from the Tabar Islands (AMNH 99841) to the northeast of New Ireland. Furthermore, there are specimens from the eastern end of New Britain in the Berlin Museum. *Pteropus tonganus*, most of whose range is far out in the Pacific, east of the Solomons, occurs also on Karkar. There are still other species of *Pteropus* that occur in the Solomon Islands.

Pteropus hypomelanus—As indicated above, this species is known from both New Guinea and New Britain. Diamond collected 340 mandibles from Karkar, 11 mandibles from Bagabag, a skull from Long, and a mandible from Umboi. The American Museum of Natural History also has the skin and skull of an immature from Long collected by Coultas in 1933. This species appears to be rare on the mainland of New Guinea as is indicated by its absence from any of the extensive mainland New Guinea *Pteropus* collections at the American Museum of Natural History. In the New Guinea region, as elsewhere in its extensive Indo-Australian range, it seems to be chiefly a small island species. Two subspecies are currently recognized in the New Guinea region, *h. luteus*, described from Kiriwina Island in the Trobriands to the east of New Guinea, and *h. vulcanius* from Vulcan (=Manam) to the northwest of Karkar. The latter subspecies was distinguished from *luteus* (Thomas, 1915) solely on the basis of color, a specimen from Dampier (=Karkar) being referred to *luteus*. This character is obviously of no help in allocating the Diamond mandibles to subspecies and I therefore make no attempt to do so.

Pteropus tonganus—As indicated above, the Karkar subspecies (*P. t. basiliscus*) is far re-

moved geographically from the nearest island, Rennell in the southeastern Solomons, where another subspecies (*P. t. geddei*) occurs. Diamond obtained 68 mandibles from Karkar (the only island from which the species had previously been obtained), but none from any other island. This supports the idea that in the New Guinea region *P. tonganus* is restricted to Karkar.

Pteropus temmincki—This species is well-known and widely distributed in the Bismarcks, but has not been recorded from any of the small islands here discussed. It was not obtained by Diamond on any of them, but the British Museum has a specimen from Ruk (=Umboi).

Pteropus neohibernicus—This species is common and widespread in New Guinea and the Bismarcks. Diamond obtained it from Karkar (six mandibles), Umboi (28 skulls, 25 mandibles) and Sakar (one skull, three mandibles). The British Museum also has a specimen from Ruk (=Umboi). At present, specimens from the mainland of New Guinea are allocated to *P. n. papuanus*, whereas those from New Britain are identified as *P. n. neohibernicus*. Andersen (1912, pp. 389-90) distinguished these two forms solely on the basis of color and later in the same work (pp. 823-24) strongly suggested that the color character did not hold and that *papuanus* should be synonymized with *neohibernicus*. I have compared skulls of specimens from northeast New Guinea and New Britain and am unable to find any consistent differences. I am therefore allocating the specimens from Karkar, Umboi, and Sakar only to species. The subspecies from the Admiralty Islands, *P. n. hilli* (Felten, 1961), however, is clearly distinct as shown by the smaller size of three adult specimens in the American Museum of Natural History. Sanborn (1931, p. 14) described a new species, *Pteropus sepikensis*, from the Sepik River in northeastern New Guinea, based on a single skin and skull. (A second skull was later obtained.) *Pteropus sepikensis* was stated to be a member of the *melanopogon* group and was compared only with *P. melanopogon*. Laurie and Hill (1954, p. 35) tentatively listed it as a subspecies of *P. melanopogon*. This has remained the only rec-

ord of *P. melanopogon* from the mainland of New Guinea, the species otherwise being confined to the Moluccas, except for a subspecies from the Aru Islands. I have compared the type and second specimen of *sepikensis* with the very limited material of *P. neohibernicus* available at the Field Museum and have been able to compare the second skull of *sepikensis* with abundant material in the American Museum of Natural History of *P. neohibernicus* from the same part of New Guinea from which the type was obtained (Sepik and Madang districts). I am unable to find any differences between them when tooth wear is taken in to account. When compared with limited material of *P. melanopogon* from Buru and the Kei Islands, the two skulls of *sepikensis* are not only larger but show marked dental differences. The upper canines are longer and more slender, the larger cheek teeth are about as wide as they are long and are practically featureless. On the other hand, *P. melanopogon* has these teeth much longer than wide, and with well-developed cuspidate labial and lingual ridges. I am therefore inclined to regard both *papuanus* and *sepikensis* as synonyms of *P. n. neohibernicus*.

Genus *Dobsonia*—This genus is widely distributed from the Philippines, Celebes, and the Lesser Sundas to Australia and the Solomons. Two species (*moluccensis* and *minor*) occur on the mainland of New Guinea. *Dobsonia moluccensis* also occurs on the Bismarcks along with another species, *D. praedatrix*, which does not occur on the mainland. Bergmans (1975, p. 6) regards the Bismarck representative of *D. moluccensis* (*anderseni*) as a separate species, but, as explained below, I do not agree with him. All three species are found on one or another of the seven islands discussed in this paper.

Dobsonia praedatrix—Although widely distributed in the Bismarck Archipelago, this species has not been recorded outside it. Diamond obtained two skulls from Umboi, however, and the British Museum also has an Umboi specimen.

Dobsonia moluccensis—This species was obtained by Diamond from Karkar (one skull only, four mandibles only), Bagabag (15 skulls only, two mandibles only), Tolokiwa (one skull only), Umboi (10 skulls only, 13 mandibles

only), and Sakar (one skull only). The Karkar specimens are referable to the New Guinea subspecies, *D. m. magna*, but those from the other islands belong to the New Britain form, *D. m. anderseni*. Bergmans (1975, p. 6) considered *anderseni* to be separate species on the basis of its clearly smaller size, but I believe that some intergradation is evident between *magna* and *anderseni* among the islands here discussed. (By intergradation, I mean simply that there are intermediate populations between the two taxa, irrespective of how this intermediacy is maintained.) Due to the nature of the material, I have settled on a modification of condylocanine length, namely, from the posterior edge of the condyle on one side to the anterior edge of the upper canine on the same side. Since many specimens are either immature or badly broken, sample sizes unfortunately are small but I think do show a trend. All specimens measured are in the American Museum of Natural History and all New Guinea mainland specimens are from Morobe and Madang districts, immediately opposite the islands in question. The modified condylocanine measurements (in mm.) are as follows: New Guinea mainland, seven specimens (56.6-58.9); Karkar, one specimen (55.9); Bagabag, three specimens (48.6-49.4); Umboi, seven specimens (49.1-53.9); Bismarcks (New Britain, Tabar Islands, Lihir Islands), five specimens (47.9-50.6). To me this indicates some intergradation on Karkar and Umboi and therefore conspecificity of *anderseni* with *Dobsonia moluccensis*.

Dobsonia minor—Diamond obtained three skulls from Bagabag. This is the only record of *D. minor* known to me from off the mainland of New Guinea and is also unusual in being the easternmost record for the species. Andersen (1912, pp. 461, 825) recorded it from only two localities, both in the western half of New Guinea. Specimens in the American Museum of Natural History (from the Second and Third Archbold expeditions to New Guinea) are either from Indonesian New Guinea (Irian Jaya) or in extreme western Papua (upper Fly River). None of the extensive collections from farther east in New Guinea include *D. minor*. McKean (1972) has, however, recorded *D. minor* from both East Sepik district (northeastern New Guinea)

and Gulf district (Papua). None of the localities is quite as far east as Bagabag.

Genus *Nyctimene*—Four species (*albiventer*, *draconilla*, *cyclotis*, and *aello*) are definitely known from the mainland of New Guinea. *Nyctimene draconilla* was listed as a subspecies of *N. albiventer* by Laurie and Hill (1954), but Greig-Smith (1975) has reported the two forms sympatrically from the Sepik district of northeastern New Guinea. Another sympatric occurrence is in the Western District of Papua (southeast New Guinea), where, among the numerous specimens reported by Tate (1942) as *Nyctimene papuanus* (a subspecies of *N. albiventer*) from the upper Fly River, seven are actually *N. draconilla*. The type locality of *N. major geminus* is given as "South of Huon Gulf, Papua," which would put it on the mainland of New Guinea, but there are no other mainland records for this species and it is doubtful that *N. major* really occurs there. Mayr (1941, p. 168) has indicated that a similar locality for a bird (*Manucodia comrii*) collected by the same man (Dr. P. Comrie) is an error for Fergusson Island. The *N. major* record (the type locality for *N. m. geminus*) is probably a similar error for Fergusson Island, where *N. m. geminus* is known to occur. Of the species mentioned above, only *N. albiventer* and *N. major* are known from the Bismarck Archipelago. Both appear to be widespread there since, on the basis of specimens in the British and Berlin museums, *N. albiventer* is known from New Britain and the Admiralties, *N. major* from New Britain and New Ireland. One additional species in the New Guinea region (*N. cephalotes*) does not occur on the mainland or in the Bismarcks, but does occur on several small islands off the northern coast of New Guinea.

Nyctimene albiventer—Diamond obtained skulls of this species from all of the islands in question but Karkar; one from Bagabag, 15 from Crown, seven from Long, seven from Tolokiwa, 80 from Umboi, and 14 from Sakar. *Nyctimene albiventer* is a wide-ranging common bat from the northern Moluccas through New Guinea and the Bismarcks to the Solomons.

Nyctimene cephalotes—This species has a

fairly extensive western range from Celebes and Timor to the Moluccas, but in the New Guinea region is known from only two islands, Numfoor (in Geelvink Bay, western New Guinea) and Umboi (from which the subspecies *N. c. vizcaccia* was described). Aside from the type specimen of *vizcaccia*, the only specimen known to me from the islands in question is one skull collected by Diamond on Umboi. This is somewhat smaller than the type (7.9 versus 8.7 mm. in maxillary tooth row length) but clearly falls outside the variation in condylobasal length (28.3 vs. 24.8-27.2 mm.) of the large series of *N. albiventer papuanus* from Umboi and the rostrum is narrower in relation to its length. There seems to be no doubt, therefore, that there are two species of *Nyctimene* represented in Diamond's collection from Umboi.

Nyctimene major—Diamond collected two quite distinct forms of *N. major* (*sensu* Laurie and Hill, 1954) on the islands in question. From Sakar, a single skull was collected, which agrees very well with *N. m. major* from the Bismarck Archipelago. On the other hand, 17 skulls from Karkar and two from Bagabag are much smaller than *N. m. major*. Since *N. m. major* is the only subspecies which occurs at all close to Karkar and Bagabag, I have investigated the only other two subspecies of *N. major* in the New Guinea-Bismarck region, namely *geminus* and *lullulae*, both probably confined to islands off the eastern end of New Guinea. Fortunately the American Museum of Natural History has good series of *N. major* from Sudest, Rossel, and Misima in the Louisiade Archipelago and from Normanby, Fergusson, and Goodenough in the D'Entrecasteaux group. These are all referable to the large *N. m. geminus*. Two specimens from Woodlark and one from Kiriwina, however, are smaller and at least the Woodlark specimens are referable to *N. m. lullulae*. These allocations are all in agreement with those of Andersen (1912, pp. 709-13, who, however, called *major*, *geminus*, and *lullulae* separate species) except that Andersen allocated the single Kiriwina specimen in the British Museum to *geminus*. The British Museum also has two skins and skulls from Karkar (obtained

since 1912) and these agree very well with the type of *lullulae* from Woodlark and also, in skull measurements, fall within the variation of Diamond's Karkar series. Skulls of the two Woodlark specimens in the American Museum of Natural History, although a trifle larger (measurements in mm.) than the Karkar and Bagabag skulls (condylobasal length, 32.1, 32.3 vs. 30.2-31.7; width of rostrum just outside molars, 9.6, 9.8 vs. 8.9-9.5) are more like them than to anything else. It is clear, therefore, that populations on Karkar and Bagabag (to the west of New Britain and Sakar) are much more similar to the population on Woodlark, and perhaps Kiriwina (to the south of New Britain and Sakar) than either are to the populations of New Britain and Sakar. It is possible that they can be separated, but I am unable to do so and I therefore allocate the Karkar and Bagabag populations to *lullulae*. The presence of this form on islands on the two sides of New Britain raises the question as to whether *lullulae* should be treated as a separate species from *major*. My initial reaction was to do so, since the size difference between the Karkar and Bagabag specimens on one hand and the Sakar specimen on the other are extreme. However, I have decided to retain these as subspecies for the following reasons. Firstly, there is no evidence of sympatry except on Kiriwina. However, it is probable that the two known specimens from this island are simply large and small individuals of a single variable population, which could therefore show intergradation between *geminus* and *lullulae*. (I find it very difficult to believe that there could actually be two closely related species of *Nyctimene* on such a small low island as Kiriwina.) Secondly, the differences between *lullulae* and smaller individuals of *geminus* are not great and suggest subspecific rather than specific differences. Finally, since *N. major* is an unusually large species of *Nyctimene*, it is probable that the small size of *lullulae* is primitive relative to the larger *major* and *geminus* and also possible that it formerly occupied the adjacent mainland of New Guinea and at that time independently colonized Karkar and Bagabag to the north and Woodlark to the East. All three of these islands were almost certainly

colonized overwater since they are separated from the mainland by water with depths over 200 meters. My present tentative conclusion is to call the populations on Karkar, Bagabag, Woodlark, and possibly Kiriwina *Nyctimene major lullulae*. Obviously more material from Woodlark, Kiriwina, and the islands east of Bagabag would be very useful for determining the true range of *lullulae*-like populations.

Macroglossus lagochilus—This is the only species of its genus in the Australian region and is widely distributed in both New Guinea and the Bismarcks. Diamond obtained specimens from Karkar (three skulls), Crown (12 skulls), Tolokiwa (two skulls), Umboi (20 skulls), and Sakar (one skull).

Syconycteris australis—The genus *Syconycteris* has a rather wide range from Australia through New Guinea (and on many nearby islands) to the Bismarck Archipelago, also west to the Moluccas. Two species have been recognized from the mainland of New Guinea (Tate, 1942, pp. 346-47), *S. australis* (Papua as well as northeastern Australia) and *S. crassa* (New Guinea as a whole as well as the Bismarcks and most of the other smaller islands). These two species were distinguished by Andersen (1912, pp. 775-81) solely on the different proportions of the cheek teeth. After comparing series of *Syconycteris* from a number of areas from northern Queensland through southeastern New Guinea to northeastern New Guinea (including specimens allocated by Tate to both species), I find myself in full agreement with Hill (in Greig-Smith, 1975, p. 119). There is in fact a great deal of individual variation in the proportions of the cheek teeth, but no clearcut dichotomy into broad and narrow toothed forms. Since the few Australian specimens available to me tend to be smaller than those from New Guinea, I would tentatively retain those from the two areas as subspecies, *S. a. australis* of Australia, and *S. a. papuana* of the New Guinea mainland. McKean (1972, p. 9) has synonymized the New Britain subspecies *S. a. finschi* with *S. a. papuana*, but I am inclined to retain it since comparison of a large amount of material (32 specimens) from northeastern New Guinea (Morobe and Madang districts) with two fairly good series from western New

Britain, totaling 12 specimens (all in the American Museum of Natural History) show clear differences in both condylobasal length of skull (23.2-25.7 vs. 22.3-23.9 mm.) and braincase width (10.1-11.7 vs. 9.8-10.8 mm.). Although there is some overlap, this is rather small when the two measurements are plotted against each other. Only six out of 32 specimens from the mainland fall within the New Britain range, and five out of 12 New Britain specimens fall within the mainland range. Diamond collected skulls of *Syconycteris* from six of the seven islands under discussion: Bagabag (eight), Crown (43), Long (97), Tolokiwa (47), Umboi (five), Sakar (seven). I have taken condylobasal lengths and braincase widths on usable adult specimens from all these islands and plotted them in the same way as I have the similar measurements from the New Guinea mainland and New Britain. In the following, the first range is of condylobasal lengths, the second is of braincase widths, both in mm. Bagabag (23.3-23.9; 10.6-10.8). Crown (23.5-25.0; 10.0-11.2); Long (23.3-25.4; 10.0-11.2); Tolokiwa (23.4-25.1; 10.2-11.4); Umboi (23.9; 10.3-10.8); Sakar (23.8-25.1; 10.5-11.2). With the exception of two braincase width measurements from Crown Island, all these measurements fall within the variation of the New Guinea mainland specimens. Since all of the larger series (Crown, Long, Tolokiwa, Sakar) fall mostly outside the range of the New Britain measurements, I am inclined to refer all these small island populations to *S. a. papuana* (the New Guinea mainland subspecies) rather than to *S. a. finschi* (the New Britain subspecies). There is perhaps some indication of intergradation in that the maximum condylobasal length of skulls from the Crown-Long group of islands (25.4) is less than that from the New Guinea mainland (25.7) and that from the Tolokiwa-Umboi-Sakar group is still less (25.1) thus showing a slight approach to that of New Britain (23.9).

Melonycteris melanops—With the exception of an old unconfirmed record from the New Guinea mainland this species has been considered endemic to the Bismarck Archipelago. Phillips (1966), however, referred two species from the Solomon Islands to the genus *Melo-*

nycteris. New Britain specimens in both the British Museum and the Berlin Museum are from the Gazelle peninsula (Keravat and Ralum, respectively) on the northeastern part of the island. The American Museum of Natural History, however, has specimens from both eastern (Wide Bay) and western (Whiteman range and near Kandrian) New Guinea. Diamond also obtained *M. melanops* from Long (three skulls) and Tolokiwa (one skin and skull).

FAMILY EMBALLONURIDAE

Three genera of this family have been recorded from the New Guinea mainland since I agree with Barghorn (1977) that *Saccolaimus* is distinct from *Taphozous*. However, only *Emballonura* reaches the Bismarcks or the islands off the northeast coast of New Guinea, though *Saccolaimus* is known from the Solomons. Although four species of *Emballonura* are known from the New Guinea mainland and two of these plus another species (*E. diana*) occur on the Solomons, only *E. nigrescens* is known from either the Bismarcks (except for the otherwise Solomon Island *E. raffrayana* cor on the Tabar Islands, represented by specimens in the American Museum of Natural History) or the islands off the northeast New Guinea coast.

Emballonura nigrescens—Laurie and Hill (1954) recorded this species from the Bismarcks including New Britain. They also recorded it from Ruk (=Umboi). Diamond did not obtain this species but the American Museum of Natural History does have a series from the Whiteman range in western New Britain. Two quite distinct subspecies are represented in the area, New Guinea being occupied by the small *E. n. papuana*, whereas the larger *E. n. solomonis* occurs on New Britain. Laurie and Hill (1954) referred Umboi material to *E. n. solomonis*.

FAMILY RHINOLOPHIDAE

Of the three New Guinea genera of this family, all are known from the Bismarcks. Though Laurie and Hill (1954) do not record either New Guinea species of *Rhinolophus* in the Bismarcks, the American Museum of Natural History has specimens of both *R. mega-*

phyllus and *R. euryotis* from New Britain and *R. megaphyllus* also from New Ireland. Laurie and Hill (1954) do record the sole New Guinea species of *Aselliscus* (*A. tricuspidatus*) from the Bismarcks. None of these three species are known from any of the seven islands off the northeast New Guinea coast. Of the nine species of New Guinea *Hipposideros* recognized by Hill (1963) in his revision, five (*ater*, *papua*, *muscinus*, *wollastoni*, *semoni*) are unknown in the Bismarcks. Hill does record *H. calcaratus* and *H. cupidus* from Duke of York Island in the Bismarcks and *H. galeritus* from New Ireland. He does not record *H. diadema* from the Bismarcks proper but does list it from Manus. The American Museum of Natural History has no specimens of *H. calcaratus* from off the New Guinea mainland but does have specimens of the other three species from the Bismarcks: *H. cupidus* (New Britain, Duke of York, Tabar Islands); *H. galeritus* (New Britain); *H. diadema* (New Britain; Lihir Islands). It seems probable, therefore, that all four species occur on New Britain. Although some or all of these would be expected on one or another of the seven islands off northeastern New Guinea, only *H. galeritus* is actually known.

Hipposideros galeritus—Diamond obtained two skulls on Karkar and two on Crown. This is a widely distributed Indo-Australian species according to Hill (1963), occurring on both the New Guinea mainland and the Bismarcks.

FAMILY VESPERTILIONIDAE

Ten genera of vespertilionids are known from the New Guinea mainland but only three of these are known from the Bismarcks. *Chalinolobus* (see Van Deusen and Koopman, 1971), *Philetor* (see Hill, 1966, 1971), *Nycticeius* (see Koopman, 1978), *Nyctophilus* (including *Lamingtona*), and *Pharotis* are apparently unknown to the northwest of New Guinea. *Myotis* (including *Anamygdon*, see Phillips and Birney, 1968) is known from both New Guinea and the Solomon Islands, but not as yet from the Bismarcks. As discussed below, *Murina* is known from New Guinea and one of the islands off the northeastern coast but has not been recorded from the Bismarcks.

Pipistrellus tenuis (including *angulatus* and *papuanus*, see Koopman, 1973) is known from several islands in the Bismarcks (including a series in the American Museum of Natural History from New Britain) and the mainland of New Guinea, but has not been recorded from any of the seven islands off the northeastern coast. The genus *Miniopterus* is currently in a state of taxonomic confusion. Dr. R.L. Peterson is revising the genus, but at present, though three species have been recorded from the general Bismarck area, none are known from the seven islands off the northeast coast of New Guinea. In fact, only two species of vespertilionids are at present known from these islands.

Murina florium—Only two specimens of *Murina* are known from east of the Moluccas (Van Deusen, 1961). One of these is from the New Guinea mainland, the other from Ruk (=Umboi). Diamond did not obtain this species, which is otherwise known from Lesser Sundas, the Celebes area, and the Moluccas.

Kerivoula myrella—Hill (1965) has revised the Indo-Australian species of *Kerivoula* and recognizes the Bismarck species (*K. myrella*) as distinct from the New Guinea mainland *K. muscina*. In fact, each species is considered to be more closely related to certain Indo-Malayan ones than to the other species in the New Guinea-Bismarck area. (*K. hardwickei* and *K. papillosa* in the case of *myrella* and *K. whiteheadi* and *K. picta* in the case of *muscina*.) Hill (1965) recorded *K. myrella* from Manus and Duke of York Islands in the Bismarck Archipelago and also from Ruk (=Umboi). The American Museum of Natural History has a series from the Whiteman Range in western New Britain. Diamond did not obtain any specimens of *Kerivoula*. Hill (1965) recognized a second genus related to *Kerivoula*, *Phoniscus* with one New Guinea species (*papuensis*), but I am inclined to treat *Phoniscus* as only a subgenus of *Kerivoula*. In any case, *Phoniscus* is not known from either the Bismarcks or the seven islands off northeastern New Guinea.

ORDER RODENTIA

All rodents in the Australia-New Guinea region belong to the family Muridae. Some 20

genera are known from the New Guinea mainland, including *Xenuromys* (which Laurie and Hill, 1954, inadvertently omitted), but not *Baiyankamys* (which Mahoney, 1968, synonymized with *Hydromys*). However, only five of these (*Pogonomys*, *Rattus*, *Melomys*, *Uromys*, *Hydromys*) are known from the Bismarcks. There are also several species of uncertain generic allocation (related to *Melomys* and *Uromys*) from the Solomons. *Pogonomys*, *Uromys*, and *Hydromys* were all recorded from New Britain by Laurie and Hill (1954). The American Museum of Natural History has specimens of *Rattus*, *Melomys*, *Uromys*, and *Hydromys* from New Britain. *Uromys neobritannicus* and *Hydromys neobritannicus* are both endemic to New Britain and each is the only species of its genus in the Bismarcks. Except for *Rattus*, none of these genera is known from the seven islands off the northeastern coast of New Guinea. Taylor, Calaby, and Van Deusen are currently revising the species of New Guinea *Rattus*, but it is not at present clear how many of these there are. Only two (*exulans* and *praetor*), however, are known from the small islands which are the subject of this paper.

Rattus exulans—This widespread species, occurring in both New Guinea and the Bismarcks, is a well-known commensal of man. It probably, therefore, at present occurs on all islands in this area having human populations. Diamond, however, obtained only one skull from Long, two skulls from Tolokiwa, and none from the other islands.

Rattus praetor—This is the species that Laurie and Hill (1954) called *R. ruber*, but Calaby and Taylor (in press) have shown that the type of *ruber* belongs with another species, making *praetor* the oldest valid name. In any case, *R. praetor* ranges from New Guinea through the Bismarcks to the Solomons. The American Museum of Natural History has specimens from New Britain and Diamond obtained two mandibles from Karkar.

GENERAL ZOOGEOGRAPHY

The seven islands treated in this paper are relatively small and lie more or less between two much larger islands, New Guinea and New

Britain (fig. 1). As would be expected, some species are shared with one, some with the other, and some with both. There are no species endemic to these small islands, but there are a few that have their closest affinities on neither large land mass. In cases where the same species occurs on both New Guinea and New Britain, there may be a marked morphological difference between specimens from the two islands. In such cases, it is possible to determine the affinities of the small island populations by identifying the subspecies involved.

Since these seven islands are not on either the New Guinea or the New Britain shelf, they were almost certainly colonized overwater because they would not have been connected to either island during low water levels at various times in the Pleistocene (see Mayr, 1944, p. 5 for a discussion of this question). The present

biota of Long Island has certainly colonized the island during the past 200 years, since the previous biota had been destroyed by a volcanic eruption (Diamond, 1974).

If we exclude *Dendrolagus matschiei*, *Rattus exulans*, and the Long Island record of *Phalanger orientalis* as probable introductions on the small islands in question, there are 23 native species of mammals which can be considered at present. In nine of these, (*Echymipera kalubu*, *Petaurus breviceps*, *Thylogale bruijnii*, *Pteropus hypomelanus*, *P. neohibernicus*, *Nyctimene albiventer*, *Macroglossus lagochilus*, *Hipposideros galeritus*, *Rattus praetor*) the populations on New Guinea vs. New Britain are either very similar or as yet unanalyzed. *Dobsonia minor* and *Murina florium* occur on New Guinea, but are not known from New Britain. The former occurs on Bagabag, the

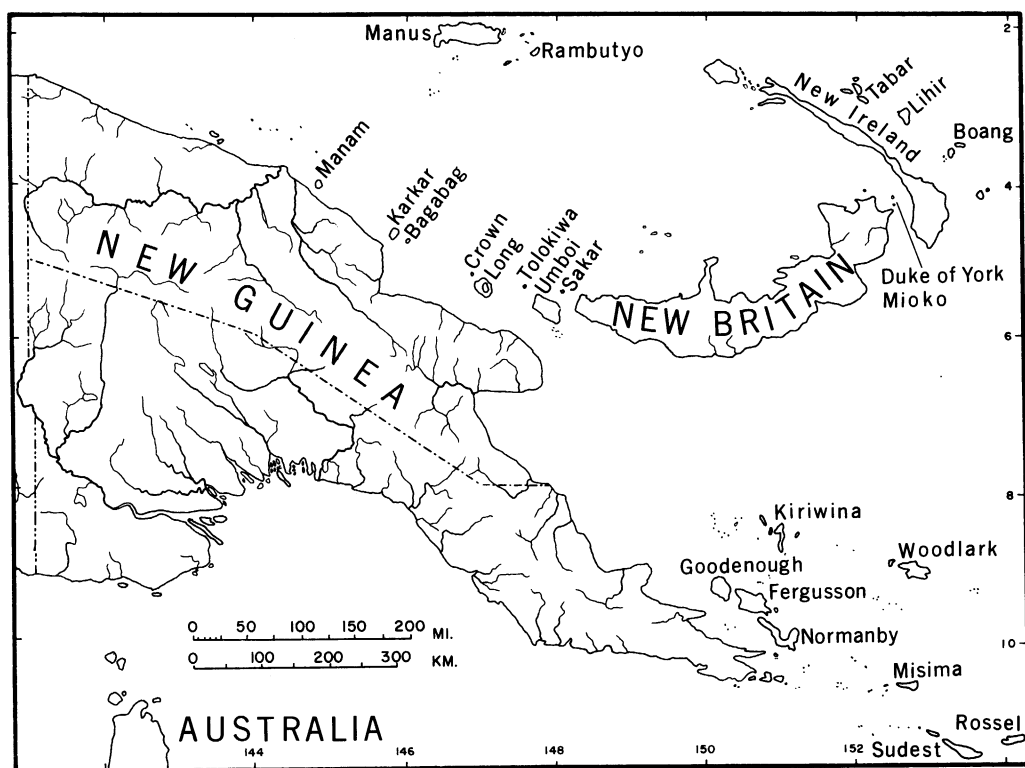


FIG. 1. Map of the eastern half of New Guinea and the Bismarck Archipelago showing most of the islands mentioned in the text. St. Mathias and Emirau are off the map to the northwest of New Ireland and the Solomons are off the map to the east.

latter on Umboi, and both have presumably dispersed overwater from New Guinea. The distribution of *Murina florium* is so poorly known, however, that its apparent absence from New Britain may be an artifact. *Pteropus temmincki*, *Dobsonia praedatrix*, *Melonycteris melanops*, and *Kerivoula myrella* occur on New Britain but probably not on New Guinea. The *Pteropus*, *Dobsonia*, and *Kerivoula* do not get beyond Sakar or Umboi, but *Melonycteris* occurs on both Tolokiwa and Long. For the remaining species a more detailed treatment is necessary.

Phalanger orientalis—Of the two subspecies, *P. o. vulpecula* of mainland New Guinea is found on Karkar and Bagabag, whereas *P. o. ducatoris* occurs on Umboi. Overwater dispersal is clearly indicated from both ends.

Rousettus amplexicaudatus—The New Guinea subspecies, *R. a. stresemanni*, is found on Bagabag. The quite distinct *R. a. brachyotis* occurs on New Britain.

Pteropus tonganus—This is the most puzzling mammal element on these seven islands. *Pteropus tonganus* has an extensive distribution in the Pacific from the Cook Islands in the east to Rennell Island in the west. Although it occurs on most islands within this vast area, it is unknown from the Solomon Islands (except Rennell), the Bismarcks, or the New Guinea mainland. The occurrence of a population of this species on Karkar is completely unexpected. Whether this represents long distance overwater dispersal or a relict distribution is uncertain. At one time, I considered the possibility that the Karkar form (*basiliscus*) actually represented the New Guinea mainland *P. conspicillatus* rather than the Pacific *P. tonganus*. However, J. E. Hill very kindly compared the type (and only complete specimen) of *basiliscus* with specimens of both species in the British Museum and assured me (*in litt.*) that *basiliscus* is indeed a form of *P. tonganus*.

Dobsonia moluccensis—Although, as I have shown above, there is evidence of intergradation on at least two of the seven intermediate islands, only the population on Karkar is referable to the large mainland *D. m. magna*, those on Bagabag, as well as the three eastern is-

lands, being referable to the small *D. m. anderseni*. There has been therefore overwater dispersal from both sides with evidence that some islands have received colonists from both.

Nyctimene cephalotes—This is another species that does not occur on the mainland of New Guinea or in the Bismarcks but is known from one of the seven small islands in question. The main range of *N. cephalotes* is in Celebes and the southern Moluccas. It is also known from Timor and Numfoor Island (in Geelvink Bay, northwestern New Guinea). Its occurrence on Umboi is therefore most surprising. Actually, in this case, there are two significant gaps since it is unknown between Ceram and Numfoor and between Numfoor and Umboi. In this case, a relict distribution is most probable. Possibly, the presence of two other large and medium-sized species of *Nyctimene* (*cyclotis* and *aello*) has displaced it from western and northern New Guinea. Neither species occurs within its present range.

Nyctimene major—This is another species with an unusual distribution pattern. *Nyctimene major* almost certainly does not occur on the mainland of New Guinea, but the Sakar specimen, as expected, agrees with the large *N. m. major* of New Britain. The specimens from Karkar and Bagabag do not, however, but instead agree with the small *N. m. lullulae* of the Trobriands. Again, either long-distance dispersal or a relict distribution (occurring formerly on the New Guinea mainland) may be the explanation. Another possibility is that *lullulae* may represent the primitive condition of *N. major* (a reasonable hypothesis since *N. major* is one of the two largest species of *Nyctimene*). If so, then perhaps the Bismarcks were originally inhabited by a *lullulae*-like form which subsequently became larger, evolving into *N. m. major*.

Syconycteris australis—This is another case in which the small island populations show some intergradation between *S. a. papuana* of New Guinea and *S. a. finschi* of New Britain. All the island populations, however, are more like the New Guinea subspecies, even those from the three islands nearest New Britain. Overwater dispersal from New Guinea has evidently been more active than the reverse,

though the intergradation seen on Long, Crown, and Bagabag suggests some minor dispersal in the opposite direction.

Emballonura nigrescens—In this species there is again one subspecies on New Guinea (*E. n. papuana*) and another on New Britain (*E. n. solomonis*). As would be expected from its position near New Britain, the Umboi population is referable to *E. n. solomonis*.

If we combine the species and subspecies distributions, ignore intergradation, and include only cases where the taxon occurs on either New Guinea or New Britain but not both, then six New Guinea taxa have dispersed westward along the island chain (*Phalanger orientalis vulpecula*, *Rousettus amplexicaudatus stresemanni*, *Dobsonia moluccensis magna*, *D. minor*, *Syconycteris australis*, and *Murina florum*). Likewise, eight New Britain taxa are found on one or another of the small intermediate islands (*Phalanger orientalis ducatoris*, *Pteropus temmincki*, *Dobsonia praedatrix*, *D. moluccensis anderseni*, *Nyctimene m. major*, *Melonycteris melanops*, *Emballonura nigrescens solomonis*, and *Kerivoula myrella*). Of the two species on Karkar, which are relevant to this problem, both (*Phalanger orientalis vulpecula*, *Dobsonia moluccensis magna*) are New Guinea elements. Bagabag, on the other hand, has five relevant elements of which four have come from New Guinea (*Phalanger orientalis vulpecula*, *Rousettus amplexicaudatus stresemanni*, *Dobsonia minor*, and *Syconycteris australis*), but one is a New Britain element (*Dobsonia moluccensis anderseni*). Crown has only one relevant element, *Syconycteris australis papuanus*, from New Guinea. Long has two relevant taxa, one from New Guinea (*Syconycteris australis*) and one from New Britain (*Melonycteris melanops*). Tolokiwa also has three relevant elements, one from New Guinea (*Syconycteris australis papuana*) and two from New Britain (*Dobsonia moluccensis anderseni*, *Melonycteris melanops*). Umboi has seven relevant taxa, of which two have come from New Guinea (*Syconycteris australis papuanus*, *Murina florum*) and five are shared with New Britain (*Phalanger orientalis ducatoris*, *Dobsonia praedatrix*, *D. moluccensis anderseni*, *Emballonura nigrescens solomonis*, and *Kerivoula*

myrella). It should be emphasized again, however, that the distribution of *Murina* in the New Guinea region is so poorly known that its apparent absence from New Britain may not be significant. Finally, Sakar has four relevant taxa of which one (*Syconycteris australis papuanus*) is of New Guinea origin, whereas the other three (*Pteropus temmincki*, *Dobsonia moluccensis anderseni*, and *Nyctimene major major*) are shared with New Britain.

All in all, it is clear that dispersal has taken place from both ends of the small island chain. With the exception of Karkar (at the western end) all islands with more than one relevant element have been colonized from both ends. As would be expected, the three eastern islands have predominantly New Britain elements (8 out of ten taxa). Even here, however, *Syconycteris australis papuanus* and *Murina florum* have evidently dispersed from New Guinea to these islands but have not reached New Britain.

"INCIDENCE FUNCTIONS"

Diamond (1975) has used this term to distinguish various patterns of distribution based on numbers of small islands occupied by various species. He distinguishes a series of arbitrarily defined classes going from the "high-S" species, which occur only on the largest and species-rich islands to "supertramps," which are absent from the largest islands but occur on many small species-poor ones. In between are "A-, B-, C-, and D-tramps" which occur on large islands and also successively larger numbers of small ones. These classes, he believes, reflect both dispersal abilities and (in the case of supertramps) inability to invade large stable communities.

Diamond (1975) based his analysis on the birds of the Bismarck Archipelago area where he had data (unfortunately as yet unpublished) for a great many species on virtually every large and small Bismarck island. Data for mammal distribution is much less adequate, but I will try to make an analysis for the *Megachiroptera*, for which information is best, and all of which are either fruit or flower feeders. This information is based on museum specimens and other records I have been able to cull

from the literature, chiefly Laurie and Hill (1954). The species and their distributions are given in tables 2 and 3. For New Guinea, I have only included the species which occur in the northeastern part of the island. New Britain is the only other island which is here considered "large." Three or more species are known for only 14 islands, and these species are the only ones listed in the body of the table, but in the footnote I have indicated additional islands from which certain species are known. I have combined *Pteropus hypomelanus* and *P. admiralitatum* as the *P. hypomelanus* group because they are closely related and probably allopatric (apparently forming part of a superspecies, *hypomelanus* being known only from western and *admiralitatum* only from eastern New Britain. I am aware that some of the material recorded from Duke of York may have actually been collected on adjacent New Britain or New Ireland. However, I have decided to include all seven species since this is the same number

that occur on Bagabag and Sakar which have roughly the same area. The largest number of species from any one island is 15 from New Guinea (northeast). The species from the largest number of islands are *Pteropus neohibernicus* and *Dobsonia moluccensis*, each known from 12 islands.

Eight species are known only from New Guinea or New Britain; all but one are New Guinea elements, only *Pteropus gaillardi* being a New Britain endemic. The latter species and the New Guinea *Aproteles bulmerae* are both poorly known so it is possible that these two species are not confined to their respective islands. However, these eight should almost certainly be considered "high-S" species. One additional species almost qualifies as a high-S species—*Dobsonia minor*—which is confined to the New Guinea mainland (as far as is known) except for its occurrence on Bagabag. It might be classed as an "A-tramp."

Eight species fall in a middle ground, occur-

TABLE 2
Distribution of Megachiroptera on the Larger Islands of the Bismarck Area, including Northeast New Guinea
(Largest islands to the left, smaller to the right.)

	New Guinea	New Britain	New Ireland	Manus	Umboi	Karkar	Long
<i>Rousettus amplexicaudatus</i>	+	+	+	—	—	—	—
<i>Pteropus hypomelanus</i> gp.	+	+	—	+	+	+	+
<i>Pteropus tonganus</i>	—	—	—	—	—	+	—
<i>Pteropus temmincki</i>	—	+	+	—	—	—	—
<i>Pteropus conspicillatus</i>	+	—	—	—	—	—	—
<i>Pteropus neohibernicus</i>	+	+	+	+	+	+	—
<i>Pteropus macrotis</i>	+	—	—	—	—	—	—
<i>Pteropus gaillardi</i>	—	+	—	—	—	—	—
<i>Aproteles bulmerae</i>	+	—	—	—	—	—	—
<i>Dobsonia predatrix</i>	—	+	+	—	+	—	—
<i>Dobsonia moluccensis</i>	+	+	—	+	+	+	—
<i>Dobsonia minor</i>	+	—	—	—	—	—	—
<i>Nyctimene albiventer</i>	+	+	—	+	+	—	+
<i>Nyctimene draconilla</i>	+	—	—	—	—	—	—
<i>Nyctimene cephalotes</i>	—	—	—	—	+	—	—
<i>Nyctimene major</i>	—	+	+	—	—	+	—
<i>Nyctimene cyclotis</i>	+	—	—	—	—	—	—
<i>Nyctimene aello</i>	+	—	—	—	—	—	—
<i>Paranyctimene raptor</i>	+	—	—	—	—	—	—
<i>Macroglossus lagochilus</i>	+	+	+	+	+	+	—
<i>Syconycteris australis</i>	+	+	—	+	—	—	+
<i>Melonycteris melanops</i>	—	+	+	—	—	—	+

TABLE 3
Distribution of Megachiroptera on the Smaller Islands of the Bismarck Area
(Largest islands to the left, smallest to the right.)

	Lihir	Tabar	Tolokiwa	Duke of York	Bagabag	Sakar	Crown
<i>Rousettus amplexicaudatus</i> ¹	—	+	—	+	+	—	—
<i>Pteropus hypomelanus</i> gp. ²	—	+	—	—	+	—	—
<i>Pteropus tonganus</i>	—	—	—	—	—	—	—
<i>Pteropus temmincki</i>	—	—	—	+	—	+	—
<i>Pteropus conspicillatus</i>	—	—	—	—	—	—	—
<i>Pteropus neohibernicus</i> ³	+	+	—	+	—	+	—
<i>Pteropus macrotis</i>	—	—	—	—	—	—	—
<i>Pteropus gaillardi</i>	—	—	—	—	—	—	—
<i>Aproteles bulmerae</i>	—	—	—	—	—	—	—
<i>Dobsonia praedatrix</i> ⁴	—	—	—	+	—	—	—
<i>Dobsonia moluccensis</i> ⁵	+	+	+	—	+	+	—
<i>Dobsonia minor</i>	—	—	—	—	+	—	—
<i>Nyctimene albiventer</i>	+	—	+	+	+	+	+
<i>Nyctimene draconilla</i>	—	—	—	—	—	—	—
<i>Nyctimene cephalotes</i>	—	—	—	—	—	—	—
<i>Nyctimene major</i>	—	—	—	+	+	+	—
<i>Nyctimene cyclotis</i>	—	—	—	—	—	—	—
<i>Nyctimene aello</i>	—	—	—	—	—	—	—
<i>Paranyctimene raptor</i>	—	—	—	—	—	—	—
<i>Macroglossus lagochilus</i>	—	—	+	+	—	+	+
<i>Syconycteris australis</i>	—	—	+	—	+	+	+
<i>Melonycteris melanops</i> ⁶	—	—	+	+	—	—	—

1 Also Emirau; 2 Also Manam; 3 Also Mioko and Rambuto; 4 Also St. Mathias; 5 Also Boang and Emirau; 6 Also Mioko.

ring on New Britain and in four cases also on New Guinea, and also being known from three to seven of the smaller islands. These may correspond to the "B- and C-tramp" categories. *Pteropus temmincki* occurs on three small islands; *Dobsonia praedatrix* on four; *Rousettus amplexicaudatus*, *Nyctimene major*, and *Melonycteris melanops* on five; the *Pteropus hypomelanus* group and *Syconycteris australis* on six; and *Macroglossus lagochilus* on seven.

Three species occur on both New Guinea and New Britain and also are known from nine (*Nyctimene albiventer*) or 10 (*Pteropus neohibernicus*, *Dobsonia moluccensis*) smaller islands. These would seem to fall into the "D-tramp" category. Finally, two species (*Pteropus tonganus*, *Nyctimene cephalotes*) occur only on small islands, in this region being absent from both New Guinea and New Britain. This would seem to place them in the supertramp category. However, they are pecu-

iar supertramps. The species of birds that Diamond placed in this category occur on many small islands. The two megachiropterans I have tentatively and perhaps erroneously assigned here are known from a single small island in the Bismarck region (though each occurs widely elsewhere). I have no explanation for this peculiar pattern. It is certainly quite different from that seen in the three species I have placed in the D-tramp category.

Diamond (1975) has stated that for birds in the Bismarcks, the smaller the island, the fewer A-tramps and the more (relatively) D-tramps and supertramps it supports. Due probably to the fact that collections on many islands (except for New Guinea and New Britain) have been inadequate, no such relationship can be seen among the Megachiroptera. As can be seen from tables 2 and 3, there is a rough tendency for larger islands to have more species recorded from them. However, even here

New Ireland (the largest after New Britain) and Bagabag (the next to the smallest) have the same number of species (7) recorded from them. Furthermore, New Ireland has six of the medium range (B-C-tramps) and one D-tramp; Bagabag has one A-tramp, four in the medium range, and two D-tramps. Quite obviously, much more distributional data for Bismarck Megachiroptera is necessary before much can be said about incidence functions of this group in this area. This in no way implies that I do not think that interspecific competition is very important, only that I do not think it can be demonstrated with the present data.

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