AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2747, pp. 1–34, fig. 1, tables 1–3 September 23, 1982

Results of the Archbold Expeditions No. 109. Bats from Eastern Papua and the East Papuan Islands

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ABSTRACT

The bat fauna of eastern Papua, including Central, Northern, and Milne Bay provinces on the mainland and the Louisiade, D'Entrecasteaux, and Trobriand archipelagos, is reviewed. Five families, 23 genera, and 45 species are known from the area. Forty species are known from the mainland or continental islands and 23 from one or another island (or islands) of the three archipelagos. Only six species occur on the islands but not on the mainland and only two of these (*Dobsonia pannietensis, Kerivoula agnella*) are endemic. Most of the insular species for which precise affinities can be determined show closest relationship to mainland populations, but a few have their affinities with those of the Bismarcks or Solomons. Most of the East Papuan mainland species are apparently confined to the lowlands. The East Papuan highland bat fauna is seemingly depauperate compared with that of more extensive highland areas to the northwest. There is only one documented case of altitudinal variation within a species (*Pipistrellus*) and only one of altitudinal replacement among close relatives (*Tadarida*). A new subspecies, *Rhinolophus megaphyllus vandeuseni,* is described.

INTRODUCTION

The eastern end of New Guinea is relatively narrow from north to south and can be regarded as a peninsula of the main part of the island. Off the northern side and eastern end of this peninsula lie several groups of islands, mostly outside of the Australia-New Guinea continental shelf. Known collectively as the East Papuan islands, they include three archipelagos, the Louisiades, D'Entrecasteaux Islands, and Trobriands (fig. 1). I thought it would be interesting to compare the bat faunas of these islands in relation to the bats of the eastern end of New Guinea, since I had earlier made a somewhat similar study of the mammals of the Bismarck archipelago (Koopman, 1979). For the purposes of this paper, I have tried to incorporate the bat records of what are politically the Central, Northern, and Milne Bay provinces of Papua New Guinea.

Four Archbold New Guinea expeditions worked eastern Papua and the East Papuan

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 ISSN 0003-0082 / Price $2.45

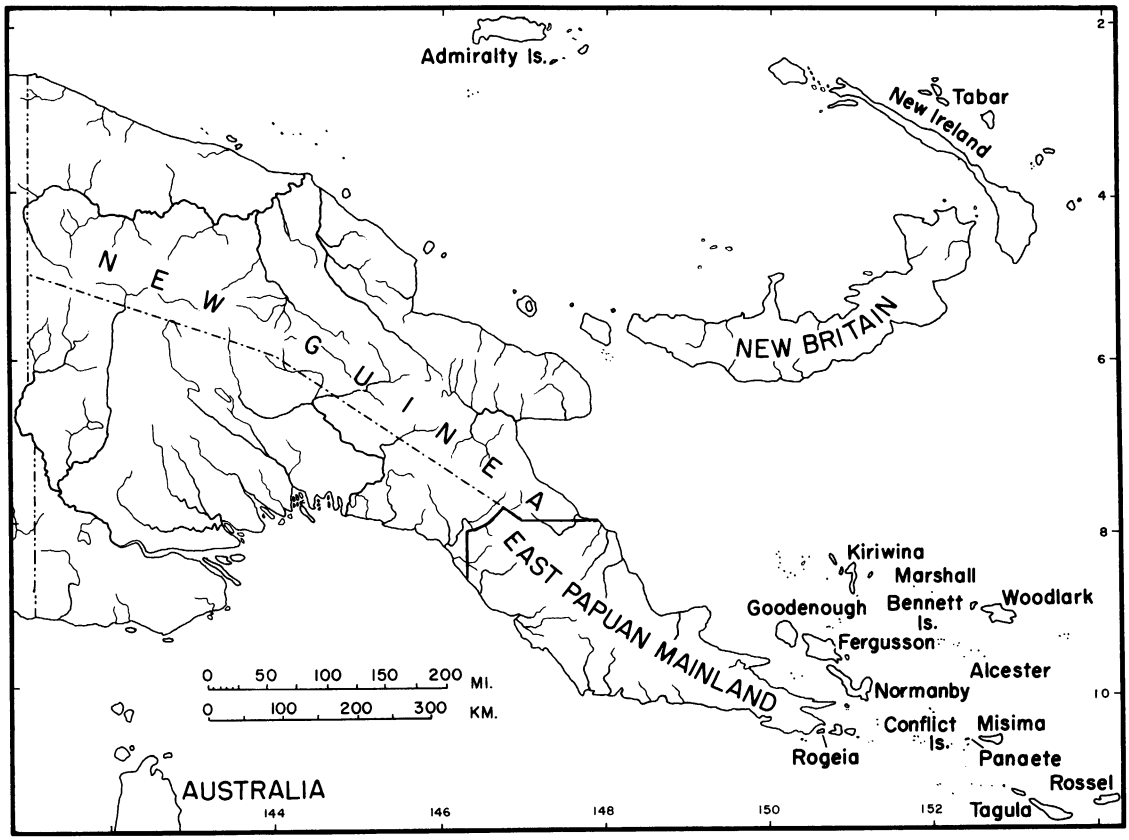

FIG. 1. Map of the eastern half of New Guinea and the Bismarck Archipelago showing most of the areas and islands mentioned in the text. The Solomons are off the map to the east.

islands, the First (1933–1934), the Second (1936–1937), the Fourth (1953), and the Fifth (1956–1957). Information concerning itinerary, history of collecting, and habitats may be found in the reports of each of these expeditions (Archbold and Rand, 1935; Rand and Brass, 1940; Brass, 1956, 1959). Besides these major collections, the American Museum of Natural History has several more limited ones made at various times and I have also culled some records from the literature and from other museum collections. The mountains in the eastern end of New Guinea tend to be lower than those farther west, however, several do rise over 3500 meters and even one of the islands (Goodenough) goes up over 2500 meters. Of the islands off the continental shelf, Goodenough in the D'Entrecasteaux Islands was visited by the Fourth Archbold Expedition, and the Fifth visited Sudest (=Tagula), Rossel, and Misima (=St. Aignan's) in the Louisiades; Normanby and Fergusson in the D'Entrecasteaux; Kiriwina and Woodlark in the Trobriands. The only other East Papuan islands off the continental shelf I know of from which bats have been collected are Panniet (=Pannaete) in the Louisiades, and the Marshall Bennetts and Alcester in the Trobriands (Laurie and Hill, 1954).

Although Tate in a series of papers (1941a, 1941b, 1942a, 1942b; Tate and Archbold, 1939a) reported a number of bats from the Central province of Papua (First and Second Archbold expeditions), none of the bats from the Fourth and Fifth Archbold expeditions and few of the other mammals from these collections have been reported on. Van Deu-

sen (1957) described a new species of macropodid from Goodenough and I (Koopman, 1973) utilized *Pipistrellus* collected on those expeditions though I did not treat them individually. The bats from all these collections are reported on here and literature records and specimens in other museums are included where they supplement American Museum of Natural History specimens.

ACKNOWLEDGMENTS

First of all, I thank the various members of the Mammal Section of the British Museum (Nat. Hist.) for their assistance and for the very pleasant and profitable month I spent there. Most especially, I acknowledge with thanks the help I received from Mr. John Hill, not only for his making available the extensive collections under his care, but also for the stimulating conversations we had on a variety of topics involving New Guinea. My insight into many taxonomic problems would have been much poorer without these extremely fruitful discussions. I thank Mr. John L. McKean of CSIRO for assistance in placing some of his localities. Finally, I acknowledge the inspiration of the late Hobart Van Deusen. Although he died before I initiated this project, I feel that I owe much of my understanding of the background of New Guinea and its mammal fauna to him. His unpublished notes on a number of topics also have been very useful.

SYSTEMATIC SECTION

All five families of New Guinea bats are known from the eastern end of New Guinea and the East Papuan islands.

FAMILY PTEROPODIDAE

There are eight genera of New Guinea mainland pteropodids of which all except the recently described *Aproteles* (Hyndman and Menzies, 1980) are known from the eastern end. With the exception of *Pteropus, Dobsonia,* and *Nyctimene* each is known only by a single species from eastern Papua (including the islands).

Rousettus amplexicaudatus: This species is not known from any of the East Papuan islands but was obtained by the Fourth and Fifth Archbold expeditions at three localities on the mainland of Milne Bay province: Dabora (two skins and skulls, 22 alcoholics), Tapio (six alcoholics), Mornuna (three skins and skulls, three alcoholics). The Dabora specimens were collected by H. M. Van Deusen in 1953, the Tapio material by K. M. Wynn in 1953 and the Mornuna specimens by R. F. Peterson in 1956. As mentioned (Koopman, 1979), I am unable to distinguish *stresemanni* from *R. amplexicaudatus* on the species level and would therefore refer all New Guinea (but not Bismarck or Solomon) *Rousettus* to *R. a. stresemanni.* There certainly is some sexual dimorphism in size (condylobasal length 35.0, 35.8 in the two male skulls, 34.3 in the two female skulls on which this measurement could be taken), but I have been unable to detect geographical variation within New Guinea *Rousettus.* Comparative material consists of 12 usable skulls, the northwesternmost being from Japen Island (a topotype of *stresemanni*), the southeasternmost from the Eastern Highlands province of Papua New Guinea. Unfortunately, the only real series (eight from Bagabag) is unsexed (see Koopman, 1979) so more material might show some geographical variation, but if so, it is slight compared to the differences between *R. a. stresemanni* and *R. a. brachyotis* of the Bismarcks.

GENUS *Pteropus:* Of the seven New Guinea *Pteropus* species (see Koopman, 1979, and Waithman, 1979 for clarification of this), three (*conspicillatus, neohibernicus, macrotis*) are known from the East Papuan mainland and two (*hypomelanus, conspicillatus*) occur on the East Papuan islands. *Pteropus hypomelanus* probably also occurs on the East Papuan mainland since it is known from two localities along the northern coast (Andersen, 1912, p. 128; Sanborn, 1931, p. 12). However, I know of none from the mainland east of Huon Gulf. Of the three other species of New Guinea *Pteropus, P. alecto* and *P. scapulatus* are known only from a small area in western Papua opposite the main distribution areas in northern Australia, whereas *P. pohlei,* as far as I am aware, is only from the Japen Island off northwestern New Guinea. Thus, we are concerned here only with *P. hypomelanus, P. conspicillatus, P. neohibernicus,* and *P. macrotis.*

Pteropus hypomelanus: The American Museum of Natural History has no specimens of this species from the mainland of eastern Papua, but does have 24 skins and skulls, 17 skulls only from Tagula (=Sudest); 10 skins and skulls from Misima (=St. Aignans); eight skins and skulls, one skin only from Normanby; 11 skins and skulls from Fergusson (=Moratau); one lower jaw only, one alcoholic from Goodenough; one skin and skull from Kiriwina; three skins and skulls, two skulls only, from Woodlark. Of these, two from Tagula, one from Misima, and one from Fergusson were collected by H. Hamlin in 1928–1930. One from Goodenough was obtained by H. M. Van Deusen in 1953 and the other by K. J. Quinn in 1964. The remainder were all collected by R. F. Peterson in 1956. Laurie and Hill (1954) also record this species from the Marshall Bennett Islands (between Kiriwina and Woodlark) and from the Conflict Islands which (unlike the others) are on the New Guinea shelf, separated from the mainland only by shallow water. Probably *Pteropus hypomelanus* occurs on most if not all of the East Papuan islands. Andersen (1912) recognized only one subspecies (*P. h. luteus*) in the New Guinea region, the type having come from Kiriwina. Thomas (1915), however, described a second subspecies, *P. h. vulcanius,* from Vulcan island (=Manam) off the north coast of New Guinea. This subspecies was described as differing from *P. h. luteus* by its much darker underparts. The single specimen from Kiriwina (a topotype) is very light in color, both above and below, and agrees very well with Andersen's (1912) description of *P. h. luteus.* There is considerable color variation and most of the specimens from Misima, Normanby, Fergusson, Goodenough, and Woodlark are darker in color than the single skin from Kiriwina; nevertheless, they agree reasonably well with those from the other islands. In varying degrees the remaining five are definitely darker and some (e.g., AMNH 159081 from Tagula) agree more with the original description of *vulcanius* (Thomas, 1915). A specimen in the British Museum from the Conflict Islands likewise is darker than typical *luteus.* Inasmuch as Thomas referred a specimen from Karkar Island (a little east of Manam) to *P. h. luteus,* although this too is darker than typical *luteus,* and Sanborn (1931) referred a specimen from the mainland (a little west of Manam) to *P. h. vulcanius,* it appears that there are probably several populations of *luteus*-like and *vulcanius*-like individuals (with intermediates) in various frequencies interspersed along the northern coast of New Guinea. The fact that *P. hypomelanus* is rare or very local on the mainland and is found chiefly on small islands certainly favors the development of such an erratic distribution, either by local selection or perhaps by genetic drift. In any case, *vulcanius* does not seem to be a useful taxon and I therefore synonymize it with *P. h. luteus.*

Pteropus conspicillatus: The American Museum of Natural History has four skins and skulls from the mainland, one collected at Menapi by Van Deusen in 1953 and three at the Hihilai Plantation (on a small island in Milne Bay) by G. A. Faris in 1944. On the islands, there are five skins and skulls from Sudest (=Tagula); five skins and skulls from Rossel; one skin and skull from Normanby; one skin and skull and one mandible from Goodenough; one skin and skull from Kiriwina; one skin and skull from Woodlark. The two Goodenough specimens were collected by Van Deusen in 1953, the remaining insular material by R. F. Peterson in 1956. Laurie and Hill (1954) also record *P. conspicillatus* from Alcester in the Trobriands (south of Woodlark). The subspecies throughout the area under discussion is *P. c. conspicillatus,* the other New Guinea subspecies, *P. c. chrysauchen* being confined to the western end. The only American Museum specimens of *chrysauchen* are from Geelvink Bay, specimens as far west as the Huon peninsula being referable to the nominate subspecies.

Pteropus neohibernicus: This species is known only from the mainland. The American Museum of Natural History has 11 specimens from the following localities in eastern Papua: Port Moresby (four alcoholics collected by R. F. Peterson in 1959), Brown River (two skins and skulls collected by R. F. Peterson in 1959), Laloki (two skulls only collected by Lawrence Jones in 1952), Mount Dayman at 700 meters (two skins and skulls collected by H. M. Van Deusen in 1953), Mornuna (one skin and skull collected by R.

F. Peterson in 1956). *Pteropus neohibernicus* is widely distributed on the mainland of New Guinea, but although also widespread in the Bismarck archipelago, it apparently does not reach the East Papuan islands. As previously explained (Koopman, 1979), I regard all the mainland and Bismarck populations (except for the ones on the Admiralties) as belonging to one subspecies, *P. n. neohibernicus,* the named forms *papuanus* and *sepikensis* being synonyms.

Pteropus macrotis: This species is also known only from the mainland. The American Museum of Natural History has specimens from Baroka (two skins and skulls, one alcoholic, collected by Archbold and Rand in 1933), Rigo on the Kemp Welch River (one skin and skull collected by L. A. Willis in 1937); the "K. B. Mission" on Milne Bay (two skins and skulls collected by G. A. Faris in 1944), and Menapi (seven skins and skulls collected by H. M. Van Deusen in 1953). The species is probably widely distributed in New Guinea since the American Museum has specimens from northern as well as southern New Guinea. All mainland populations are referable to *P. m. epularius,* the nominate subspecies being on the Aru Islands.

GENUS *Dobsonia:* Laurie and Hill (1954) recognized three species in the New Guinea region, *D. moluccensis, D. minor,* and *D. remota. Dobsonia minor* is a very distinct species, now known from several localities in western and central New Guinea (see Koopman, 1979). However, none are reported from the eastern end of New Guinea. The only other form of *Dobsonia* on the mainland is *D. moluccensis magna.* Laurie and Hill allocate *pannietensis* from the East Papuan islands to *D. moluccensis,* but I am inclined to agree with Bergmans (1979) that they should be retained as separate species, albeit closely related allopatric ones (probably members of a superspecies). As explained below, I regard *remota* as a subspecies of *D. pannietensis,* although Bergmans (1979) keeps them separate.

Dobsonia moluccensis: The American Museum of Natural History has a great deal of eastern Papuan material of this widespread mainland species. This may be summarized as follows: Mafulu (one skin and skull collected by Archbold and Rand in 1933), Iawareri on the Musgrave River (13 skins and skulls collected by Archbold and Tate in 1937); Menapi (14 skins and skulls, one alcoholic, collected by H. M. Van Deusen in 1953); Baniara (two alcoholics collected by H. M. Van Deusen in 1953); Dabora (three skins and skulls and one alcoholic collected by H. M. Van Deusen in 1953); Mt. Dayman at 700 m. (two skins and skulls collected by H. M. Van Deusen in 1953); Mornuna (one skin and skull collected by R. F. Peterson in 1956). All New Guinea mainland populations are referable to *D. moluccensis magna.* Measurements of some of the eastern Papuan specimens are given below in the *D. pannietensis* account.

Dobsonia pannietensis: This species appears to be endemic to the East Papuan islands and was obtained by the Fourth (H. M. Van Deusen, 1953) and Fifth (R. F. Peterson, 1956) Archbold expeditions on all the islands they visited. The numbers of specimens from the various islands are as follows: Tagula (eight skins and skulls, one skull only), Rossel (10 skins and skulls, two skulls only), Misima (five skins and skulls, two of which were obtained by the Whitney Expedition in 1930), Normanby (five skins and skulls), Fergusson (11 skins and skulls), Goodenough (12 skins and skulls, seven mandibles only), Kiriwina (four skins and skulls, three alcoholics), Woodlark (14 skins and skulls, one alcoholic). The type locality is Panniet (=Pannaete), a small island just west of Misima. *Dobsonia remota* was originally described (Cabrera, 1920) from Kiriwina, as most closely related to *D. peroni* of the Lesser Sunda Islands. The reason for this placement was the presence of a well-marked anterointernal cusp on the first lower molar. Study of the small series in the American Museum from Kiriwina, however, shows that this character is inconstant. It is present and fairly well developed on AMNH 159152 (though not as strong as in *D. peroni*), completely absent in AMNH 159151 and 159154, and intermediate in AMNH 159153. Likewise, in the three British Museum specimens from Kiriwina, there is a definite trace in BM 96.11.5.6 but not in BM 96.11.5.7 or 96.11.5.8. I am therefore combining *remota* with *D. pannietensis,* though, as shown below, I am using the name for the small sub-

species from Kiriwina and Woodlark. McKean (1972, p. 8) has also recorded *remota* from Bougainville in the Solomons, but Bergmans (1979) is convinced that this record is based on misidentified *D. inermis.* Laurie and Hill (1954, p. 42) treated *pannietensis* as a subspecies of *D. moluccensis,* but I am inclined to agree with Bergmans (1975, p. 6) that the size difference is too great to retain them in the same species and I see no evidence of intergradation. The following ranges of condylobasal measurements (in mm.) for adult skulls from the mainland of extreme eastern Papua (Milne Bay province) and for the various islands from which these measurements are available show these differences: Mainland, four males (59.5–61.8), five females (59.8–61.3); Tagula, four males (47.8–50.1), two females (47.3, 48.1); Rossel, one male (51.3), one female (47.9); Misima, one female (47.3); Normanby, three males (50.0–53.1); Fergusson, two males (49.1, 50.9); Goodenough, two males (50.4, 51.1), one female (50.3); Kiriwina, three females (43.1–44.9); Woodlark, one male (45.6), three females (44.2–44.7). Although the number of intact adult skulls (many are immature or broken) is small and there is clearly some sexual dimorphism, it is evident that there is a marked hiatus between the sizes of mainland and island populations and also that the specimens from Kiriwina and Woodlark stand somewhat apart from the other insular population samples. The mainland sample is therefore allocated to *D. moluccensis magna,* the Louisiade and D'Entrecasteaux samples to *D. pannietensis pannietensis,* and the Trobriand samples to *D. pannietensis remota.* Although Bergmans (1979) keeps *remota* as a distinct species, he allocates all four American Museum specimens from Kiriwina to *pannietensis.* Bergmans disagrees with my conclusions, but it seems to me that all his evidence is consistent with mine. It is not clear what evidence would cause him to combine *remota* with *pannietensis.* In my opinion it is extremely improbable that such a small, low island as Kiriwina would support two such similar species.

The above conclusions were reached by comparison of the East Papuan mainland specimens with those on the East Papuan islands. A different picture emerges in comparison of *pannietensis* from the Louisiades and D'Entrecasteaux islands with *anderseni* from the Bismarcks to the north. The resemblance between the two named forms is so close that I know of no way to distinguish them, in spite of the fact that they are well separated by the broad and deep Solomon Sea. Laurie and Hill (1954) treat both *pannietensis* and *anderseni* as subspecies of *D. moluccensis,* whereas Bergmans (1975, 1979) considers them as distinct species, both from *moluccensis* and from one another. I previously (Koopman, 1979) considered *anderseni* to be a subspecies after finding intermediates with *D. m. magna* on two small islands (Karkar and Umboi) lying between the New Guinea mainland and the Bismarcks. I therefore find myself in the peculiar position of treating as separate species two very similar entities and, moreover, considering one of these as a subspecies of the quite distinct *D. moluccensis* and the other as a separate species. From a phyletic point of view, it is possible that *pannietensis* and *anderseni,* in spite of their close resemblance to one another, are independently derived from populations on the New Guinea mainland. It is also quite possible that the resemblance between the two island forms (small size) is simply a shared primitive character, that a similar primitive population formerly occurred on at least eastern New Guinea, and that it evolved into the larger derived *magna* after colonizing both the Bismarcks and the East Papuan islands. Under the circumstances, therefore, it is possible that the East Papuan populations (*pannietensis*) have and Bismarck populations (*anderseni*) have not developed reproductive isolation from the present New Guinea populations (*magna*). I have therefore decided to recognize *pannietensis,* but not *anderseni,* as a species distinct from *D. moluccensis* in spite of their similarity with one another, at least until Bergmans finishes his revision of *Dobsonia.* I admit that part of my peculiar reasoning is based on the existence of the still smaller Trobriand subspecies *remota,* which is geographically, but not morphologically, intermediate between *pannietensis* and *anderseni.*

GENUS *Nyctimene:* Laurie and Hill (1954) recognized five species of *Nyctimene* in the

New Guinea region. Since then, Greig-Smith (1975) has treated *draconilla* as a species distinct from *N. albiventer* and I (Koopman, 1979) have determined that part of Tate's Fly River series (Tate, 1942b, p. 342) is referable to *N. draconilla.* However, of these six species *N. cephalotes* is known no closer to eastern Papua than Western province (Waithman, 1979) and Umboi island (lat. 148°E, long. 6°S) and neither Greig-Smith's nor Tate's records of *N. draconilla* are east of 144°E. Of the remaining four species, three (*N. albiventer, N. cyclotis, N. aello*) are known from the East Papuan mainland, but *N. major* is confined to the islands, the alleged mainland locality, "South of Huon Gulf," being apparently an error for Fergusson island (see Koopman, 1979, p. 6). All four species are treated in the accounts below.

Nyctimene albiventer: The only East Papuan specimens of this species in the American Museum of Natural History are two skins and skulls, one each from the Fourth and Fifth Archbold expeditions. These are from Biawa (Moi Biri Bay) collected by H. M. Van Deusen in 1953, and from Mornuna collected by R. F. Peterson in 1956, both on the mainland. The only subspecies of *N. albiventer* in the New Guinea region is *N. a. papuanus.*

Nyctimene major: This species was collected by the Archbold expeditions from every East Papuan island visited. With the indicated exceptions, all specimens were collected by R. F. Peterson in 1956. The numbers of specimens were as follows: Tagula (21 skins and skulls, two skulls only, one alcoholic); Rossel (12 skins and skulls, two alcoholics, one of which was collected by H. F. Osborne in 1960); Misima (two skins and skulls); Normanby (13 skins and skulls); Fergusson (six skins and skulls); Goodenough (seven skins and skulls, six collected by H. M. Van Deusen in 1953, the other by H. Hamlin in 1928, one alcoholic by R. H. Beck in 1924); Kiriwina (one skin and skull, one alcoholic); Woodlark (two skins and skulls). Two subspecies of *N. major* are currently recognized in the East Papuan islands, *m. geminus* and *m. lullulae,* the latter previously recorded only from Woodlark. *Nyctimene major geminus* has been recorded from Fergusson, Goodenough, Kiriwina, and Heath (=Rogeia). This last island, unlike the others, is on the New Guinea shelf just south of the eastern end of Papua. The two subspecies have been distinguished solely on the basis of size. This may be seen in the following skull measurements (in mm.) of adults in the American Museum of Natural History and the British Museum for all islands represented except Kiriwina. Since there seems to be little if any sexual dimorphism, males and females are combined. Condylobasal length: Tagula, 21 (34.9–36.6); Rossel, five (34.3–36.3); Misima, two (34.0, 34.2); Normanby, six (34.6–36.4); Fergusson, seven (33.9–35.4); Goodenough, six (34.0–36.3); Woodlark, two (30.8, 32.6). Maxillary tooth row length: Tagula, 23 (12.0–12.9); Rossel, seven (11.5–12.9); Misima, two (12.0); Normanby, seven (11.8–12.5); Fergusson, eight (11.5–12.4); Goodenough, eight (11.5–12.6); Woodlark, three (10.7–11.2). Width across molar alveoli at widest point: Tagula, 22 (10.0–11.3); Rossel, seven (9.9–10.9); Misima, two (10.7); Normanby, seven (10.1–10.9); Fergusson, seven (10.3–10.6); Goodenough, eight (10.1–11.1); Woodlark, three (9.0–9.5). The Woodlark specimens clearly stand apart from those of the Louisiade and D'Entrecasteaux islands. Kiriwina presents special problems. Andersen (1912, p. 710) had only four specimens which he referred to *geminus* and one (the type) of *lullulae.* Of the four referred to *geminus,* one was from Goodenough, one from Fergusson, one (the type) from "S. of Huon Gulf, B. New Guinea" (presumably also from Fergusson), and one from Kiriwina. Unfortunately, in his tables of measurements (Andersen, 1912, pp. 718, 720), he does not separate the Kiriwina specimen from the other three. Of the two specimens R. F. Peterson obtained from Kiriwina, one is immature and the other has a broken skull. It was therefore impossible to obtain a condylobasal measurement, but I could get measurements of the maxillary tooth row and width across molars. These are 11.0 and 10.0, respectively which fall within the *lullulae* range as far as the maxillary tooth row is concerned but within the *geminus* range in width across molars. The Kiriwina skull is of a very aged individual with some suggestion of palatal spreading. This is shown by the presence of secondary bone deposition lateral to the molars and by a peculiar irreg-

ular palatal fenestration in the hard palate near the midline between the molars exposing part of the vomer. Examination of a number of aged skulls of *N. m. geminus* shows nothing really comparable with these modifications. The skull seems therefore somewhat pathological and determination of the Kiriwina population difficult. I have therefore borrowed Andersen's skull but, unfortunately, the status of the Kiriwina population is still far from clear. The skull is of an adult female with the teeth in good condition and without any of the pathological modifications of Peterson's Kiriwina skull. The posterior end is missing, however, so no overall skull length measurements can be taken. The maxillary tooth row length is 11.6 mm. and the width across the molars is 10.2 mm. The skull in the British Museum, therefore, though evidently quite similar to that in the American Museum, is somewhat larger. The British Museum skull, unlike the one in the American Museum, falls within the variation of *N. m. geminus,* though smaller than most specimens of this subspecies. More and better material of the Kiriwina and Woodlark populations is necessary before a confident allocation can be made. Meanwhile, I tentatively identify Kiriwina specimens as *N. m. geminus,* though there is some indication of intergradation with *N. m. lullulae.* It should be noted, however, that the type of *lullulae* is the smallest of the three Woodlark specimens measured, whereas the Kiriwina specimen referred to *geminus* by Andersen is the larger of the two Kiriwina specimens measured. Thus the effect of adding the American Museum specimens is to reduce the observed difference between the Kiriwina and Woodlark populations.

Nyctimene cyclotis: The American Museum of Natural History has no specimens of this species from eastern Papua. Andersen (1912, p. 828), however, recorded two specimens of the eastern subspecies, *N. c. certans* from the upper Aroa River. This is in the Central province of Papua, a little to the northwest of Port Moresby.

Nyctimene aello: The American Museum of Natural History has no eastern Papuan specimens of this species. However, Milne Bay is the type locality of the eastern New Guinea *N. a. aello.*

Paranyctimene raptor: The only eastern Papuan specimens in the American Museum are two skins and skulls collected by Peterson at Mornuna in 1956. It is known only from the mainland of Papua New Guinea, but is probably widespread throughout New Guinea. There are no records from the East Papuan islands.

Macroglossus lagochilus: The American Museum of Natural History has only two East Papuan specimens, one mainland, the other insular. The first is an alcoholic obtained by H. M. Van Deusen at Menapi in 1953. The second is a skin and skull collected by R. F. Peterson on Fergusson island in 1956. All populations of this species from New Guinea and the Bismarcks are currently referred to *M. l. nanus.* The single (adult male) skull from Fergusson has been compared with available adult skulls from the mainland of New Guinea and differs by its shorter rostrum. However, there is considerable variation on New Guinea as McKean (1972, pp. 12, 13) has noted. (In fact on this basis McKean synonymizes the Australian *pygmaeus* and the Solomon Island *microtis* with *M. l. nanus.*) Some of this variation is sexual, but unfortunately most of the available skulls are either immature or unsexed. I am reluctant to name the Fergusson Island specimen and therefore give only a few comparative skull measurements (in mm.) of the Fergusson skull and the only other available adult male skull from New Guinea, collected at Lae in Morobe province. In each case, the measurement for the Fergusson skull is given first, then the Lae skull: Condylobasal length (23.8, 25.3); palatal length in the midline from the posterior border of the hard palate to the anterior end of the premaxillary (12.7, 14.2); rostral width just in front of the lacrimal (5.8, 6.0). Obviously, more material from the mainland and the East Papuan islands will be needed to substantiate this as a population difference.

Syconycteris australis: Laurie and Hill (1954) recognize three species of *Syconycteris* in the New Guinea area, but as I have previously pointed out (Koopman, 1979, p. 8), *S. crassa* cannot be separated on a specific level from *S. australis* and as I show below, the same is true of the third "species," *S. naias.* The American Museum of Natural

History has 10 specimens from the East Papuan mainland. Three skins and skulls are from Central province (Mafulu, Mt. Tafa, and Kagi) and were reported on by Tate (1942b, p. 346). Later specimens are all from Milne Bay province. Van Deusen collected two skins and skulls from Menapi, three skins and skulls and one alcoholic from Mount Dayman (at both 700 m. and 2230 m.). Peterson collected one skin and skull from Mornuna. There is a great deal more material from the islands in the American Museum. Peterson collected six skins and skulls from Tagula; 28 skins and skulls and four alcoholics from Rossel (and there is another alcoholic from Rossel collected by H. F. Osborne); 23 skins and skulls and five alcoholics from Misima; two skins and skulls from Fergusson; one skin and skull from Kiriwina; seven skins and skulls and five alcoholics from Woodlark. Strangely enough, there seem to be no records of *Syconycteris* from either Normanby or Goodenough. Andersen (1912) recognized three taxa from eastern Papua and the East Papuan islands: *crassa papuana* on the mainland; *crassa crassa* on Fergusson and Kiriwina; *naias* on Woodlark. *Syconycteris c. crassa* was distinguished from *c. papuana* solely on the basis of its larger size. *Syconycteris naias* was compared with *S. australis,* which it was said to resemble on the basis of its narrower cheek teeth, but was distinguished by its reduced number of molars (1/2 vs. 2/3). I have previously (Koopman, 1979) discussed the cheek tooth proportion character and found that it does not distinguish *crassa* from *australis* on the mainland of New Guinea where Tate (1942b, p. 346) recorded them as virtually sympatric. Comparison of the three intact adult skulls from Woodlark with the three adults from Kiriwina and Fergusson shows that the cheek teeth of the Woodlark specimens are indeed narrower, but there is considerable variability and the character is difficult to use because of the small size of the teeth and the changes in their appearance due to wear. Lidicker and Ziegler have discussed the dental formula character (1968, pp. 33, 34). Of the skulls of *Syconycteris* in the American Museum of Natural History from eastern Papua and the East Papuan islands, most have the molar formula 2/3. However, one from the mainland (AMNH 104025) has 2/4; one from Rossel (AMNH 159191) has 2/4, another (AMNH 159197) 1/3, another (AMNH 159187) 1/2, and still another (AMNH 159192) 2/2 on one side and 1/2 on the other; from Misima, one (AMNH 159169) has 2/4, another (AMNH 159177) has 1/3. Although all four intact skulls from Woodlark have the usual 2/3, it is evident that molar number is not a good species character. However, I disagree with Lidicker and Ziegler's (1968) interpretation of the two specimens in which there are a larger than usual number of lower cheek teeth (retention of an additional premolar). In both 104025 and 159191, the premolars are all quite typical of the lower molars of *S. australis,* but the last tooth is like a reduced third lower molar. I think that what has happened is a duplication of this last molar. Phillips (1971, p. 6) has discussed this phenomenon in another group of nectar-feeding bats. The remaining character to consider is that of size. This is probably best expressed by the condylobasal length. I can see no clear-cut sexual difference in this measurement and therefore pool males and females in the following numbers of intact adult skulls from both the American Museum and the British Museum (the latter all seen by Andersen): East Papuan mainland, nine (23.2–25.7); Tagula, five (23.8–26.0); Rossel, 18 (23.1–25.0); Misima, 12 (24.0–26.1); Fergusson, two (25.4, 26.3); Kiriwina, three (25.5–26.0); Woodlark, three (23.9–24.3). The three specimens from Woodlark (the type locality of *naias*) are clearly smaller than the five from Fergusson and Kiriwina (the two islands included by Andersen (1912) within the range of *crassa*). Two skulls from the mainland, one from Tagula, and nine from Rossel are as small or smaller than the three skulls from Woodlark. Likewise, there are rather marked differences between other populations, such as the one on Rossel which tends to be considerably smaller than the one on Misima. In view of the small number of specimens known from the three islands to which Andersen restricted *crassa* and *naias,* it is difficult to decide the status of these named forms. Under the circumstances, though I am rather dubious about the taxonomic distinction of either *crassa* or *naias* from *papuana,* I am inclined to retain both

of them at present within the ranges as given by Andersen (1912). In the case of *naias,* this relies in part on its narrower cheek teeth. For the three Louisiade populations, known from much more material, assignment must be somewhat arbitrary. Specimens from Tagula and Misima agree well with mainland *papuanus,* but those from Rossel average smaller (with a great deal of morphological overlap) and agree better in size with *naias,* though far removed geographically from that subspecies. There is, as usual, a great deal of individual variation in cheek tooth width in the Rossel series and also molar number (as enumerated above). Tentatively, I allocate the mainland and Louisiade populations to *S. australis papuanus,* the Fergusson and Kiriwina populations to *S. australis crassa,* and the Woodlark population to *S. australis naias.*

FAMILY EMBALLONURIDAE

There are three genera of emballonurids in the New Guinea region (*Saccolaimus* here considered a valid genus, following Barghoorn, 1977) and all three are known from eastern Papua. For *Taphozous* and *Saccolaimus,* only a single species of each is known from this area, but three species of Emballonura are known.

GENUS *Emballonura:* Four species of *Emballonura* occur in New Guinea, but I can find no indication that *furax* occurs in eastern Papua, though McKean (1972, p. 21) does record a specimen from Putei in Gulf province, just west of eastern Papua. Each of the other three are known from at least the East Papuan mainland and in two cases from its islands. Since I have reidentified one of the specimens mentioned by Tate and Archbold (1939a, p. 11), some statement about the characters of two of the New Guinea species (*beccarii* and *raffrayana*) is in order. The paper by Tate and Archbold was the first of a series reporting on bats in the Archbold collection and in the year 1939, available material in the American Museum of these two species from New Guinea was extremely limited. Tate and Archbold mention a single specimen from Mafulu (Central province of Papua) which they identify as *beccarii meeki* and two specimens of *raffrayana raffrayana* from the Weyland Mountains in Irian Jaya (then Dutch New Guinea). The skull of the Mafulu specimen (at least at present) consists only of the posteroventral portion of the cranium and the mandibles. However, the diagnostic basicranial region of this fragment, both in size and morphology shows much closer resemblance to the only Weyland Mountain specimen of *raffrayana* showing this part of the skull than to a series also from Irian Jaya identified by Tate as *beccarii meeki.* These had already been collected at the time Tate and Archbold's paper was published, but were evidently not available for study when the paper was prepared. I therefore identify the Mafulu specimen as *raffrayana* rather than as *beccarii.*

Emballonura beccarii: The British Museum of Natural History has a single specimen of this species from the mainland of eastern Papua (Dinawa in the Owen Stanley Mountains). The American Museum of Natural History has no East Papuan mainland specimens and only two (skins and skulls) from the islands, one each from Kiriwina and Woodlark, both collected by R. F. Peterson in 1956. Kiriwina is the type locality of *E. b. meeki* and the mainland and Woodlark specimens are clearly referable to the same subspecies.

Emballonura raffrayana: To my knowledge, the only record of this species from eastern Papua is the above-mentioned specimen from Mafulu, Central province, obtained by Archbold and Rand in 1933. Although the species is also known from the Solomon Islands (*E. r. cor*), it has not been recorded from any of the East Papuan islands.

Emballonura nigrescens: The American Museum of Natural History has specimens of this species from both the mainland and one of the islands. Mainland specimens are from Oro Bay, Northern province (Robert R. Horton, 1945, one skin and skull), Biniguni, Milne Bay province (Van Deusen, 1953, one skin and skull, one alcoholic), and Peria Creek, Milne Bay province (H. M. Van Deusen, 1953, five skins and skulls). From Woodlark (the only East Papuan island from which *E. nigrescens* has been recorded), there are four skins and skulls and two alcoholics col-

lected by R. F. Peterson in 1956. Currently two subspecies are recognized in the East Papuan area (Laurie and Hill, 1954), mainland specimens belonging to *E. n. papuana,* those from Woodlark being referable to *E. n. solomonis.* These are distinguished by Tate and Archbold (1939a, p. 7), who treat them as separate species, by the shorter and broader skull of *papuana.* This character will certainly not distinguish the three usable adult Woodlark skulls from the 10 available East Papuan mainland adults (including specimens in the British Museum). Using condylocanine length (in mm.) as the best measure of skull length we get the following: mainland, 10 adults (10.1–10.8); Woodlark, three adults (10.4–10.9). Evidently the three Woodlark specimens largely fall within the variation of those from the East Papuan mainland, and they also fall largely within the variation of eight specimens of *solomonis* from the Solomon Islands (including the type) in the British and American Museums (10.5–11.4). There is evidently some overlap between East Papuan mainland specimens and typical *solomonis* from the Solomons. It is possible that the Woodlark population is an intergrade one, but obviously more study of individual and geographical variation of *E. nigrescens* throughout its range is necessary before the true relationship of *solomonis* and *papuana* can be determined.

Taphozous australis: To my knowledge, the only New Guinea record of this species is still the one from Port Moresby in the Central province of eastern Papua (Laurie and Hill, 1954, p. 51). Since this is a common northeastern Australian species, the record is almost certainly either erroneous or accidental.

Saccolaimus mixtus: Although two species of *Saccolaimus* are recognized from New Guinea, there are no records of *S. saccolaimus* (=*nudicluniatus,* following Goodwin, 1979, p. 102) from eastern Papua as far as I know. The other species, *S. mixtus,* was originally described from Port Moresby. The American Museum of Natural History has no specimens of this species from either the mainland or islands of eastern Papua, though both *mixtus* and *saccolaimus* are represented by specimens from elsewhere in Papua New Guinea, and *saccolaimus* reaches the Solomons.

FAMILY RHINOLOPHIDAE

Since I include the hipposiderines in this family I recognize three New Guinea genera, all of which are known from eastern Papua. *Aselliscus* has only a single New Guinea species, *Rhinolophus* has two, but there are a number of New Guinea species of *Hipposideros.*

Rhinolophus megaphyllus: From the East Papuan mainland, the American Museum of Natural History has eight alcoholics collected by Van Deusen in 1953 at Dabora, Milne Bay province. From the islands, there are eight skins and skulls and 13 alcoholics from Misima collected by R. F. Peterson in 1956; also five skins and skulls and one alcoholic collected by H. M. Van Deusen on Goodenough in 1953. The species is not known from any of the other East Papuan islands, but does have an extensive range in the eastern Australia from Victoria to Cape York (at least as far north as 12°30′). Here it is a common bat, at least in the northern part of its range, judging by the large number of specimens from the Cape York peninsula in the American Museum of Natural History. McKean and Price (1967, p. 109) also indicate a large number of specimens from southern Queensland and New South Wales. Records from New Guinea are much fewer, however, and as far as I am aware restricted to the eastern half of the island. Besides the specimens listed above, I am aware of only three New Guinea mainland records. These are the type locality of *R. m. fallax* at Ighibierei in Central province (Andersen, 1906), Putei in Gulf province (McKean, 1972), and three specimens in the American Museum of Natural History from Oomsis Creek in Morobe province. The American Museum also has specimens from both New Britain and New Ireland in the Bismarcks. I should point out that much farther to the west, in the Moluccas and Lesser Sundas, there are several forms which Tate and Archbold (1939b) include along with *megaphyllus* in their "*simplex* subgroup." These western forms are included by Laurie and Hill (1954) in two

species, *simplex* and *keyensis* (including *truncatus, nanus,* and *annectens*). *Rhinolophus keyensis annectens,* unfortunately omitted by Laurie and Hill, was described by Sanborn (1939, p. 37) from Wetar in the eastern Lesser Sundas. All these western forms are quite similar and are allopatric to *megaphyllus* and to each other. They may well be western subspecies of *R. megaphyllus* but are, I believe outside the scope of this paper. In Australia, two subspecies are currently recognized, the northern *R. m. ignifer* and the southern *R. m. megaphyllus.* These were distinguished by Allen (1933) solely on the basis of color. McKean and Price (1967) show that this character is not valid, but distinguish the two subspecies on the basis of size. Although some overlap is indicated for forearm length (the only measurement they give), the northern *ignifer* is shown to average smaller than the southern *megaphyllus.* My inspection of skulls shows just the opposite. Most of my material is clearly within the geographical range of *ignifer* as given by McKean and Price (1967) and though I am unsure as to whether any are true *megaphyllus* because of uncertainty as to its northern boundary, the four skulls from between Townsville and Rockhampton in central Queensland (which Hall and Richards, 1979, p. 27, imply are typical *megaphyllus*) are clearly smaller than the 51 usable skulls from the vicinity of Cairns north. (The southern skulls have condylocanine lengths of less than 17.0.) Clearly, the picture in New Guinea is more complex, but the amount of available material is much less. Two forms have been named, *fallax* from the mainland in Central province and *monachus* from Misima in the Louisiades. Both were described by Andersen (1905a, 1906) but whereas *monachus* was described as a subspecies of *R. megaphyllus, fallax* was recognized as a distinct species, based on the possession of a broader horseshoe in the noseleaf and a larger skull with broader braincase. McKean (1972, p. 23) found that horseshoe width would not separate Australian and New Guinea specimens, but suggested that New Guinea individuals had a lower connecting process on the noseleaf. I can see no clear distinction in this character and therefore agree with Laurie and Hill (1954) and McKean (1972) in treating *fallax* and *monachus* as subspecies of *R. megaphyllus.* The available material does not entirely agree with a two subspecies picture. The specimens from Dabora on the mainland of Milne Bay province are relatively large (forearm length 45–48; condylocanine length 17.5–17.8; maxillary tooth row length 7.6–7.9; width across last molars 6.8–7.1; mastoid width 8.9–9.2). The specimens from Oomsis creek on the mainland of Morobe province are, however, considerably smaller (forearm length 45–46; condylocanine length 16.3–16.8; maxillary tooth row length 7.0–7.1; width across last molars 6.3–6.6; mastoid width 8.9–9.2). The island populations further complicate the picture. Goodenough specimens are similar to the ones of Milne Bay mainland, but are even larger (forearm length 46–49; condylocanine length 17.8–18.2; maxillary tooth row length 7.7–8.0; width across last molars 6.9–7.1; mastoid width 9.7–9.8). Specimens from New Britain and New Ireland are similar to those of Morobe province, but are even smaller (forearm length 41–46; condylocanine length 16.2–16.3; maxillary tooth row length 6.6–6.8; width across last molars 6.1–6.4; mastoid width 8.7–9.0). Finally, specimens from Misima are virtually indistinguishable from those from Morobe province (forearm length 40–45; condylocanine length 16.6–17.0; maxillary tooth row length 7.1–7.3; width across last molars 6.3–6.9; mastoid width 9.0–9.3). In my opinion, the best way to express this pattern of geographic variation is by recognizing three subspecies. The isolated relatively small form on Misima would be one. The relatively large mainland form from Gulf, Central, and Milne Bay provinces would constitute a second with the very large Goodenough population an extreme variant. The very small Bismarck form would be a third with the Morobe province population a somewhat larger and probably intergrading variant. It would also be possible to recognize five subspecies with the Goodenough population distinguished from that of the Papuan mainland and with the Morobe province population distinguished from the Bismarck one. However, in my opinion, these additional two are not distinct enough to be recognized as separate subspecies. The Misima subspecies (*R. m. monachus*) and the Gulf–

Central–Milne Bay–Goodenough subspecies (*R. m. fallax*) have already been named. The Morobe-Bismarck subspecies, however, is as yet unnamed and therefore must be described as new.

Rhinolophus megaphyllus vandeuseni, New Subspecies

HOLOTYPE: AMNH 196648, a female obtained by John H. Huon de Navrancourt (original number 3) on June 3, 1960 in a coastal cave at Bululogon plantation on the east coast of New Ireland, Bismarck Archipelago, Papua New Guinea. (According to Dr. J. D. Smith, who has recently collected on New Ireland, this "locality" is a combination of two adjacent plantations, Bulo and Lokon. The co-ordinates of the type locality are lat. 3°22′S, long. 152°8′E). The holotype consists of an entire specimen preserved in alcohol with the skull extracted and cleaned.

DIAGNOSIS: An unusually small subspecies of *R. megaphyllus.* In its typical form it is smaller than either of the other two subspecies in the New Guinea region (*R. m. fallax* and *R. m. monachus*) and is also smaller than either of the two Australian subspecies (*R. m. ignifer* and *R. m. megaphyllus*). Specimens from New Ireland and New Britain measure: forearm (41–46), condylocanine length (16.2–16.3), maxillary tooth row length (6.6–6.8), width across third upper molars at widest point (6.1–6.4), mastoid width (8.7–9.0). If the specimens from Morobe province on the mainland of Papua New Guinea (Oomsis creek) are included, the condylocanine length is extended to 16.8, the maxillary tooth row length to 7.1, the width across the third upper molars to 6.6, and the mastoid width to 9.2. I regard these Morobe province specimens as intergrades, presumably with *R. m. fallax.*

ETYMOLOGY: I am naming this subspecies after the late Hobart Van Deusen, colleague, co-author (Van Deusen and Koopman 1971), and friend. Although he published relatively little, his contributions to New Guinea mammalogy and ecology were great, both as a collector and as one who freely gave whatever information about the area he could. As far as I am aware, he never visited the Bismarck archipelago and did not collect any of the typical material of this subspecies, but he did collect the Oomsis creek specimens and also all the comparative material I have seen of *R. m. fallax.*

LOCALITY RECORDS: NEW IRELAND: Bululogon plantation: AMNH 196648 (alcoholic, extracted skull); Hilalon: AMNH 196647 (alcoholic, extracted skull). NEW BRITAIN: Keravat: AMNH 193726–193732, 221851 (alcoholics, 2 skulls extracted); Mount Talawe: AMNH 221450 (skull only). NEW GUINEA (*Morobe province*): Oomsis creek: AMNH 191324–25 (skins and skulls), AMNH 192848 (alcoholic, extracted skull).

Rhinolophus euryotis: From the East Papuan mainland the American Museum of Natural History has one skin and skull and 10 alcoholics from Dabora in Milne Bay province collected by H. M. Van Deusen in 1953. There are also two skins and skulls and one alcoholic from Kiriwina collected by R. F. Peterson in 1956. New Guinea specimens have been referred by various people (Tate and Archbold, 1939b, p. 9; McKean, 1972, p. 22) with some hesitation to *R. e. timidus.* The type localities of all subspecies of *R. euryotis* are in the Moluccas and Aru islands, from which the American Museum has little material. However, there are specimens from several parts of New Guinea. Besides the Dabora and Kiriwina specimens mentioned above, there is also material from Morobe province, and from two well-separated parts of Irian Jaya, Jayapura (=Hollandia) in the northeast and the Weyland Mountains south of Geelvink Bay, as well as a specimen from New Britain. Although these are all single specimens or small series (at least as far as skulls are concerned), I fail to see any clear evidence of overall geographical variation except as noted below. However, there does seem to be a fairly pronounced difference in skull size between males and females, a fact which as far as I am aware has not been previously noted. The few Kiriwina specimens seem to be definitely smaller than those from Dabora, as can be seen from the following measurements (number of specimens in parentheses). Forearm length: Dabora males, 57–58 (7); Dabora females, 56–57 (4); Kiriwina males, 52 (1). Condylocanine length: Dabora males, 22.2, 22.3 (2); Dabora females, 22.1 (1); Kiriwina males, 20.4 (1); Kiriwina females, 20.1 (1). Maxillary tooth

row length: Dabora males, 9.7, 9.9 (2); Dabora females, 9.7, 9.8(2); Kiriwina males, 9.1, 9.2(2); Kiriwina females, 8.8(1). Width across third upper molars at widest point: Dabora males, 8.6, 8.8(2); Dabora females, 8.6, 8.7(2); Kiriwina males, 8.3, 8.4(2); Kiriwina females, 8.1(1). Mastoid width: Dabora males, 11.4, 11.5(2); Dabora females, 11.3(1); Kiriwina males, 10.9(1); Kiriwina females, 10.7(1). Actually, the specimens from Dabora are unusually large in relation to other New Guinea mainland localities, condylocanine lengths for which are 21.1–21.9 (males) and 20.6–21.2 (females). The mainland variation is not clinal since the next largest specimens are from the Weyland Mountains (the westernmost locality from which I have seen specimens). A more reasonable source for the Kiriwina population might well be New Britain since the single male is considerably closer in measurements than are those from Dabora. These measurements are as follows: forearm length (51), condylocanine length (21.1), maxillary tooth row length (9.5), width across third upper molars at widest point (8.5), mastoid width (11.4). In view of the small number of specimens, the uncertainty of the application of the name *R. e. timidus,* and the pattern of relationships in the New Guinea region, I see no utility in describing additional subspecies. Tentatively, both mainland and Kiriwina specimens may be allocated to *R. e. timidus.* I might add, however, that I have compared series of skulls in the British Museum pertaining to two of the Moluccan subspecies (*e. euryotis* from Amboina and Ceran; *e. praestens* from the Keis) and see little, if any, difference between them. I am therefore skeptical of the validity of the currently recognized subspecies.

GENUS *Hipposideros:* Of the nine species of *Hipposideros* known from New Guinea (Hill, 1963; Smith and Hill, 1981) two (*H. papua* and *H. wollastoni*) appear to be known only from the western half (Irian Jaya). Seven species (*H. ater, H. maggietaylorae, H. calcaratus, H. galeritus, H. muscinus, H. semoni, H. diadema*) are represented by East Papuan mainland specimens in either the American Museum of Natural History or the British Museum (Nat. Hist.) and four are also known from the East Papuan islands.

Hipposideros ater: The American Museum of Natural History has specimens of this species from Western province to the southwest and Morobe province to the northwest but none from the East Papuan mainland. However, the British Museum has a single specimen from Bara Bara on the mainland of Milne Bay province. The American Museum does have three skins and skulls and one alcoholic from Woodlark collected by R. F. Peterson in 1956. Although the Woodlark population is geographically distant from any of the mainland ones and there seems to be some geographical variation in New Guinea, I can see no significant differences that will clearly set off the Woodlark from the mainland populations. I therefore refer the Woodlark population to *H. ater aruensis,* which is widely distributed in New Guinea and northeastern Australia. However, neither this subspecies nor any other of the species is known from either the Bismarcks or the Solomons.

Hipposideros maggietaylorae: The American Museum of Natural History has abundant material of this species from the East Papuan mainland. Archbold and Tate obtained seven skins and skulls from Iawareri, Musgrave River (Central province) in 1937. Hobart M. Van Deusen collected two skins and skulls and two alcoholics from Budumaga, three skins and skulls and 10 alcoholics from near Maneroa, eight skins and skulls and six alcoholics from Opaigwari. All three localities are in Milne Bay province and were obtained in 1953. It should be pointed out that with the exception of one series from northeastern New Britain, all specimens of *Hipposideros maggietaylorae* in the American Museum are from the mainland of New Guinea. This is the species that until recently was called *H. calcaratus,* but I heartily agree with Smith and Hill (1981), having come to almost the same conclusion independently, that the name *calcaratus* belongs with the following species, and that this one is correctly renamed. There are no records of *H. maggietaylorae* from any of the East Papuan islands.

Hipposideros calcaratus: The American Museum of Natural History has five skins and skulls from Iawareri, Musgrave River (Central province) collected by Archbold and Tate in 1937, but these are the only East Pap-

uan mainland specimens in the collection. There is one skin and skull and one alcoholic (with extracted skull) from Misima as well as five skins and skulls and 10 alcoholics (one with extracted skull) from Kiriwina. These insular *calcaratus* were all collected by Peterson in 1956. It is immediately apparent that there is a marked size difference between the mainland and island specimens when they are compared. This may be seen by the condylocanine lengths of the skulls, 16.8–17.3 (mainland) vs. 18.1–19.2 (Misima and Kiriwina). Since the type locality of the named form *cupidus* is Eaga in Chimbu province, not far from eastern Papua, it is evident that the East Papuan mainland specimens are typical of *cupidus,* now, I think correctly, regarded as a subspecies of *calcaratus.* The Misima and Kiriwina specimens, on the other hand, approach *maggietaylorae* in their larger size (*maggietaylorae* from the East Papuan mainland having condylocanine lengths of 19.6–20.5). However, the Misima and Kiriwina skulls agree with mainland *calcaratus* in the characters given by Hill (1963) in his key (p. 24) to distinguish the two species (breadth of the sphenoidal bridge and degree of development of the sphenoidal depression). Incidentally, a character mentioned by Hill in his species accounts but not in his key, i.e., the greater height of the jugal projection does not seem to hold, being quite variable in both *calcaratus* and *maggietaylorae.* The character of the relative massiveness of the upper canines holds for the two species on the mainland, but not on Misima and Kiriwina, suggesting that it may be a function of size. In any case, mainland specimens of the two species are very distinct on the basis of size and the sphenoidal characters, but the size difference (not the sphenoidal differences) are less when East Papuan island *calcaratus* are compared with mainland *maggietaylorae.* Before the appearance of Smith and Hill's (1981) paper, I had already concluded that the type of *calcaratus* (from the Bismarcks) was basically similar to the smaller rather than to the larger New Guinea species as previously believed. Fortunately, Smith and Hill (1981) have demonstrated conclusively that the names *calcaratus* and *cupidus* refer to the Bismarck and New Guinea representatives of the same species and have treated them, correctly, I believe, as subspecies. Bismarck specimens, like those from the East Papuan islands, are larger than those from the New Guinea mainland and Smith and Hill have placed both in the same subspecies. Thus the East Papuan mainland populations are referred to *H. c. cupidus* and the East Papuan island ones to *H. c. calcaratus.* Although there are minor differences between the specimens from Bismarcks and the East Papuan islands, I am inclined to concur. The New Guinea mainland populations, previously erroneously associated with the name *calcaratus,* have been allocated by Smith and Hill (1981) to their new species *H. maggietaylorae.*

Hipposideros galeritus: This species is evidently extremely abundant on the East Papuan mainland, all American Museum specimens having been collected by H. M. Van Deusen in 1953. The localities with numbers of specimens are as follows: Dabora (two skins, one alcoholic), Gwariu River, 1 mi. S Binigone (one skin and skull), 1 mi. N Maneau (one skin and skull, 155 alcoholics), Mount Dayman, 700 m. (one skin and skull), Peria River, 2 mi. NE Opaigwari (six skins and skulls). There are also a number of specimens from the East Papuan islands: Rossel (13 skins and skulls, 21 alcoholics, collected by R. F. Peterson in 1956; eight alcoholics collected by H. Osborne in 1960); Misima (eight skins and skulls, five alcoholics, collected by R. F. Peterson in 1956); Fergusson (eight skins and skulls, 10 alcoholics, collected by R. F. Peterson in 1956); Goodenough (three skins and skulls collected by H. M. Van Deusen in 1953); Kiriwina (one skin and skull collected by R. F. Peterson in 1956). Hill (1963, p. 58) also recorded *H. galeritus* from Kiriwina. I can detect no significant differences among the various mainland and island populations and therefore refer all to *H. q. cervinus,* which has a very wide range from Waigeo and the Kei islands to the west of New Guinea to the New Hebrides and northeastern Australia.

Hipposideros muscinus: The only East Papuan specimens in the American Museum of Natural History were collected by Archbold and Tate in 1937 on the mainland (Central province). These are Astrolabe Range, Baruari resthouse, 520 m. (two skins and skulls)

and Sogeri, 450 m. (four skins and skulls). I know of no records from the East Papuan islands.

Hipposideros semoni: The only record I know of from the East Papuan mainland is a single specimen in the British Museum from Avera, Aroa River in Central province. I know of no record from the East Papuan islands.

Hipposideros diadema: This is evidently a common bat in East Papua, at least on the mainland. The American Museum of Natural History has one alcoholic from near Sogeri (Central province) obtained by J. Huon de Navrancourt in 1960. Specimens from the mainland of Milne Bay province were all collected by H. M. Van Deusen in 1953; three skins and skulls, 24 alcoholics, from Dabora; five alcoholics from Tapio. The East Papuan island specimens were all obtained by R. F. Peterson in 1956: eight skins and skulls, eight alcoholics, from Misima; three skins and skulls, one alcoholic, from Kiriwina. Two subspecies have been described from the New Guinea area, *H. d. pullatus* from the mainland (Central province) and *H. d. trobrius* from Kiriwina. These were distinguished by Troughton (1937) by the shorter forearm, longer third metacarpal, wider and heavier zygomatic arches, and narrower anteorbital width (evidently as defined by Andersen, 1905, p. 497) of *trobrius.* Troughton had two specimens of *trobrius,* both males, but it is not clear what *pullatus* he was comparing them with. All my Kiriwina specimens are females and while it is true that with some exceptions their forearms are shorter than those of the mainland females from Central and Milne Bay provinces (including the type and other specimens of *pullatus* in the British Museum (72–75 vs. 70–83), I cannot see that their third metacarpals are longer (54–57 vs. 54–64); if anything, I see the reverse. As far as heavier zygomatic arches and narrower anteorbital widths are concerned, I cannot see any differences and know of no accurate way of measuring the characters involved. For the zygomatic width, however, a real difference certainly seems to exist (taking apparent sexual dimorphism into account), the three Kiriwina female skulls being 17.7–17.8, whereas for the mainland ones, the four female skulls measure 17.1–17.3, the five males 17.0–17.8. Condylocanine lengths for these same skulls show less difference: Kiriwina females (27.0–27.7), mainland females (25.9–27.0), mainland males (26.3–27.4). The Kiriwina population, in any case, seems only slightly distinct from those of the East Papuan mainland and the subspecies *trobrius* to be of dubious validity. The Misima specimens cannot be associated with either *pullatus* or *trobrius.* The four measurements used above are as follows for the Misima series: Forearm length, males (67–72), females (65–72); third metacarpal length, males (51–53), females (49–54); condylocanine length, males (24.8–25.7), females (24.4–25.5); zygomatic breadth, males (16.5–17.1), females (16.5–17.1). It is evident that specimens from Misima are smaller than those from either the mainland or Kiriwina and therefore represent a differentiated population of small size. It is clear from Phillips (1967) and Hill (1968) that there is a mosaic of larger and smaller populations of *H. diadema* in the New Guinea–Bismarck–Solomon area. Clearly, the Misima population is a small one like *mirandus* (Manus), *malaitensis* (Malaita, but see Hill, 1971b, pp. 575–576), and *demissus* (San Cristobal), but separated from them by the larger *pullatus* (New Guinea), *trobrius* (Kiriwina) and *oceanitis* (main Solomon islands from Bougainville to Guadalcanal). While I have considered describing yet another small subspecies of *H. diadema* (as did Phillips, 1967), instead I have decided to refrain as did Hill (1968), when confronted with an unusually large population from Rennell. I am therefore leaving the Misima population unnamed.

Aselliscus tricuspidatus: I know of no records of this species from the East Papuan mainland nor does the American Museum have any. It does have specimens from the Huon peninsula in Morobe province and McKean (1972, p. 27) records the species from Gulf province. All specimens in the American Museum from the East Papuan islands were collected by R. F. Peterson in 1956 and are as follows: Misima (eight skins and skulls, 24 alcoholics); Kiriwina (two skins and skulls, one alcoholic); Woodlark (18 skins and skulls, 34 alcoholics). This is a widespread species ranging from the Moluccas through New Guinea, the Bismarcks, Sol-

omons, and Santa Cruz islands to the New Hebrides. The type locality is Amboina in the Moluccas (from which I have studied only the type which is in the Leiden Museum). The species was regarded as monotypic until Sanborn and Nicholson (1950, pp. 331, 332) described *A. t. novehebridensis* from the New Hebrides on the basis of larger size. Their measurements show a clear size difference but unfortunately they do not indicate the localities of their comparative material allocated to *A. t. tricuspidatus.* A skull from the Santa Cruz Islands in the American Museum of Natural History (AMNH 75182), however, clearly falls in the range of *novehebridensis* (condylocanine length 13.2). Hill's (1956, 1968) specimens from Rennell island in the extreme southeastern Solomons seem to be intermediate between Sanborn and Nicholson's *t. tricuspidatus* and *t. novehebridensis.* Probably the basis for Sanborn and Nicholson's typical *tricuspidatus* measurements are the specimens from the central Solomons (New Georgia, Banika) recorded by Sanborn and Beecher (1947, p. 390) since the comparable measurements given are identical. Specimens from the East Papuan islands are likewise small (condylocanine 12.1–12.6). McKean (1972) points out that his measurements of New Guinea mainland specimens (Gulf and East Sepik provinces) are large (approaching *novehebridensis*), his condylocanine lengths being 13.0–13.8. The mainland skulls I measured (from northeastern Irian Jaya) are also rather large, the condylocanine lengths running 12.6–13.4. A single skull from New Britain in the American Museum of Natural History is intermediate in size between the large New Guinea and small Solomon Island populations (condylobasal 12.6). The picture that emerges therefore seems to be one of a group of large populations in the New Hebrides and Santa Cruz Islands (including the type of *novehebridensis*), another group of large populations on the New Guinea mainland, and a group of small-sized populations in between. These three might well rank as subspecies, but the type of *tricuspidatus* falls in none of these groups but rather in the Moluccas where, to my knowledge, nobody has assessed the population characteristics. I have measured the skull of the type as best I could (a wooden peg has been driven into the foramen magnum) and get a condylocanine length of 12.7 mm., which falls in the lower part of the Irian Jaya range. Until a complete revision is done, it seems fruitless to recognize formal subspecies in the New Guinea–Bismarck–Solomon area, though it is probably safe to include New Guinea populations in *A. t. tricuspidatus.*

FAMILY VESPERTILIONIDAE

Of the 10 genera of vespertilionids known from the mainland of New Guinea (not including *Lamingtona* which is here considered a synonym of *Nyctophilus*), only *Murina* is unknown from eastern Papua or its islands. *Murina* is actually so poorly known from the New Guinea region (see Van Deusen, 1961, pp. 531–533) that it could well also be found in eastern Papua.

GENUS *Myotis:* Only two species of *Myotis* have been recorded from New Guinea and neither is at all well represented in eastern Papua. Tate (1941b, p. 564) records what Laurie and Hill (1954, p. 68) call *M. mystacinus ater* (but which Findley (1972) separates from *M. mystacinus* as part of *M. muricola*) from Sogeri, which is in Central province, eastern Papua. However, I am unable to find any trace of a specimen in the American Museum collections to substantiate this record and am inclined to doubt it. In fact, there are no New Guinea specimens of *M. muricola* in the American Museum and aside from Tate's, I know of no published records from New Guinea. I am therefore inclined to doubt whether the species really occurs east of the Moluccas. The other species, *M. adversus* is abundant in some parts of New Guinea but is also poorly known from eastern Papua.

Myotis adversus: Although McKean (1972, p. 31) records this species from both East Sepik and Gulf provinces, I know of no East Papuan mainland records. The American Museum of Natural History does have an alcoholic from Tagula, received from the Queensland Museum and obtained by an unknown collector (probably Albert C. English, see Van Deusen and Koopman, 1971, p. 2) in 1891; also a single skin and skull collected by R. F. Peterson on Normanby in

1956. Currently all populations of this species from Celebes to the New Hebrides (but not those from Australia) are referred to *M. a. moluccarum.* I have no reason for treating the Tagula and Normanby specimens as anything else.

Pipistrellus tenuis: This is evidently a common species in eastern Papua and at least on the mainland is represented by two quite distinct subspecies which replace each other altitudinally. In listing the localities of American Museum specimens, I will (within one island or mainland province) give localities in altitudinal order from low to high. I will give elevations only when they are over 500 meters. For Central province, these are Rigo, Kemp Welch River (one skin and skull, L. A. Willis, 1937); near Ufafa River on boundary between Mekoo plain and Tapala valley (one alcoholic, J. H. de Navrancourt, 1955); Sogeri (13 skins and skulls, one skin only, Archbold and Tate, 1937); Tapini, *ca.* 1000 meters (one alcoholic, J. H. de Navrancourt, 1956); upper Kunimaipa River, near Gru-Gruk creek, *ca.* 1700 meters (three alcoholics, two with extracted skulls, J. H. de Navrancourt, 1955); upper Kunimaipa River, between Mt. Strong and Mt. Chapman, *ca.* 1900 meters (three alcoholics, one with extracted skull, J. H. de Navrancourt, 1955); upper Kunimaipa River, foot of Mt. Chapman, 2000 meters (one alcoholic with extracted skull, J. H. de Navrancourt, 1955); Mt. Tafa, west slope, 2400 meters (skin and skull, Archbold and Rand, 1933); Mt. Albert Edward, *ca.* 2450 meters (skin and skull, J. M. Diamond, 1959). In Milne Bay province, we have Menapi (10 skins and skulls, 34 alcoholics, H. M. Van Deusen, 1953); Mornuna (one skin and skull, R. F. Peterson, 1956); Peria Creek (one skin and skull, H. M. Van Deusen, 1953); Dabora (one alcoholic, H. M. Van Deusen, 1953); Gwariu River, 1 mile S of Binigoni (one skin and skull, H. M. Van Deusen, 1953); Mt. Dayman, north slopes, 700 meters (one skin and skull, H. M. Van Deusen, 1953); Mt. Dayman, north slopes, 1540 meters (six skins and skulls, four alcoholics, H. M. Van Deusen, 1953); Mt. Dayman, north slopes, 2230 meters (five skins and skulls, H. M. Van Deusen, 1953). From Northern province, there is only a single alcoholic from Oro Bay collected by Robert L. Horton in 1945. From the Louisiades, there is only a single series of six alcoholics (two with extracted skulls) from Tagula collected in 1881 and received from the Queensland Museum; the precise locality is unknown but is evidently in the lowlands. From Normanby there are 10 skins and skulls and 24 alcoholics from Waikaiuna (R. F. Peterson in 1956) and one skin only from Sawatait plantation (K. M. Wynn in 1954). From Fergusson, the localities are: Deidei (seven alcoholics, R. F. Peterson, in 1956); Mapomoiwa (three skins and skulls, H. M. Van Deusen in 1953 and R. F. Peterson in 1956); Iamele No. 1 (nine skins and skulls, seven alcoholics, R. F. Peterson, 1956); Agamoia (three alcoholics, R. F. Peterson, 1956). The specimens from Goodenough were all collected by H. M. Van Deusen in 1953 and come from the following localities: Bolu Bolu (one skin and skull); Wakonai (two skins and skulls); east slopes at 1600 meters (one skin and skull, one alcoholic with extracted skull). As I have pointed out (Koopman, 1973), that there are two very different subspecies of *P. tenuis* in New Guinea, which had previously been put in different species groups. The small *P. t. papuanus* occurs in the lowlands and *P. t. collinus* in the highlands. In 1973, I discussed this general pattern, showing that in some areas (specifically Central province), the two subspecies were quite distinct, in others, extensive intergradation occurs. Here I would like to consider the specific distributional and intergradational pattern which can be seen in eastern Papua and its islands. Since the condylobasal measurement seems to be better than any other for discriminating between *papuanus* and *collinus,* I would like to concentrate on it and since there seems to be no sexual dimorphism in this measurement, sex will be disregarded. I will use the same three altitudinal categories I used in my 1973 paper (0–1000 m., 1000–1800 m., 1800–3000 m.) and will utilize a few Central and Milne Bay province specimens in the British Museum (Nat. Hist.) which were studied after the graphs in Koopman (1973) were made, namely from Port Moresby, Kamali, and Dinawa (*ca.* 1200 m.) in Central province; Dinner Island and Chad's Bay in Milne Bay province. I will consider the mainland localities in Central and Milne Bay provinces

first (there is not enough material from Northern province to say much) and then take up the special situation on the East Papuan islands. For Central province specimens the condylobasal lengths are as follows: below 1000 m. (10.0–11.9), 1000–1800 m. (11.7–12.6), above 1800 m. (12.3–13.0). It should be noted that the two lowland specimens with condylobasal lengths of more than 10.7 were supposedly collected at Port Moresby before 1891 and may actually have come from well above Port Moresby since the mountains there are fairly close to the sea. Of the three skulls from the 1000–1800 m. range, those measuring 12.5 and 12.6 are from upper Kunimaipa River near Gru-Gruk creek (1700 m.) whereas the one measuring 11.7 is from Dinawa (1200 m.). The picture in Central province therefore is of typical *papuanus* in the lowlands, typical *collinus* in the highlands and a few specimens (interpreted by me as intergrades) in between. For Milne Bay province the condylobasal lengths are as follows: 0–1000 m. (10.3–12.0), 1000–1800 m. (11.8–12.1), above 1800 m. (12.1–12.3). All skulls with condylobasal lengths of more than 11.5 come from Mount Dayman, the one lowland skull being from 700 meters. I interpret its large size as resulting from gene flow from the populations higher up on the same mountain. If in this area, gene flow has also gone from the lowlands to the highlands, this could explain why even the population from the highest collecting locality on this northern mountain (2230 m.) is of relatively small size compared with those from somewhat lower altitudes (1700–2000 m.) on the upper Kunimaipa River (12.5–13.0 mm.). In any case, highland and lowland populations are not as well differentiated as in Central province. Tentatively, I would allocate all the Mount Dayman specimens to *P. t. collinus* and the others from Central province to *P. t. papuanus*. As I pointed out in 1973, the distinction between the two subspecies becomes even less clear in northeastern Irian Jaya. From the East Papuan islands, the specimens from Tagula, Normanby, and Fergusson were all collected in the lowlands and appear to be typical *papuanus,* the condylobasal lengths being 10.8, 11.5 (Tagula); 10.8–11.5 (Normanby); 10.6–11.2 (Fergusson). On Goodenough, however, the few specimens were obtained both near sea level and at 1600 meters. Condylobasal lengths are 11.0–11.1 (lowlands) and 11.9, 12.0 (highlands). Although the highland skulls are as large as those from low and intermediate elevations on Mount Dayman, I am allocating all Louisiade and D'Entrecasteaux material to *P. t. papuanus,* recognizing that the Goodenough highland specimens certainly do approach *P. t. collinus* in size. I previously (Koopman, 1973) pointed out a somewhat similar situation on the isolated highlands of the Huon peninsula. It is possible that *papuanus* and *collinus* are better considered ecotypes rather than subspecies in the strict sense.

Philetor brachypterus: This is the species which was formerly called *P. rohui,* but Hill (1971a) has shown that it is conspecific with *brachypterus* (which is an older name), a Malaysian species. Hill (1966) had previously recorded the species from several mainland localities in Central and Milne Bay provinces. All American Museum of Natural History specimens from Eastern Papua were collected by H. M. Van Deusen in 1953 at two mainland localities in Milne Bay province. These are Biniguni (two skins and skulls, 53 alcoholics, one with extracted skull) and Opaigwari (three skins and skull, 18 alcoholics). The species is known from Malaya, Sumatra, and Borneo as well as New Guinea, the New Guinea subspecies being *P. b. rohui,* which is unknown from any of the East Papuan islands.

Chalinolobus nigrogriseus: There is little to add to what was said previously (Van Deusen and Koopman, 1971). The American Museum of Natural History has four skins and skulls and six alcoholics from Port Moresby (Central province) collected by J. I. Menzies in 1969. There is also a single alcoholic with extracted skull obtained by R. C. English on Fergusson Island in 1891. The only other record of *C. nigrogriseus* is from East Cape, Milne Bay province. The species thus occurs on both the East Papuan mainland and on Fergusson Island but is not known from any of the other East Papuan islands. As Van Deusen and Koopman (1971) made clear, this is the only species of *Chalinolobus* known from New Guinea.

Nycticeius balstoni: As I have previously shown (Koopman, 1978), this is the only

species of *Nycticeius* in New Guinea, records referred to by Laurie and Hill (1954) under the names *greyi* and *sanborni* being referable to *N. balstoni.* The American Museum of Natural History has no East Papuan specimens, but there are specimens in the Field Museum of Natural History and the British Museum (Nat. Hist.) from Port Moresby and Kamali in Central province. The type locality of *sanborni* (East Cape) is on the mainland of Milne Bay province, but there are no records of the species from any of the east Papuan islands. The only New Guinea subspecies is *N. b. sanborni.*

GENUS *Miniopterus:* This genus is at present in a state of taxonomic confusion. Laurie and Hill (1954) recognized only three species in New Guinea (*australis, schreibersi, tristis*), but Hill (1971) recognized a fourth, which he called *medius.* Dr. R. L. Peterson of the Royal Ontario Museum, Toronto, is currently revising this genus but except for the *tristis* group (Peterson, 1981a) this is largely unpublished. However, he has very kindly given me identifications for a great many specimens which he had borrowed. Using these identifications as a guide, I have examined all skulls of *Miniopterus* in the American Museum collection and have come up with an arrangement for New Guinea which is basically in agreement with Peterson's, but also not too far from Hill's. I would recognize five species in New Guinea and the East Papuan islands, which are here briefly characterized on skull measurements. The picture is, however, somewhat complicated by geographical variation even within the New Guinea region and the measurements below apply to eastern Papua (or in the case of *magnater* to northcentral Papua New Guinea). From smallest to largest, they are as follows: *paululus,* condylobasal length not more than 13.3, width across molars at widest point less than 5.5; *australis,* condylobasal length 13.0–13.7, width across molars at widest point 5.5–6.0; *schreibersi,* condylobasal length 14.0–14.8, width across molars at widest point 6.2–6.8; *magnater,* condylobasal length 16.5–17.3, width across molars at widest point 7.5–7.7; *tristis,* condylobasal length 16.5–18.3, width across molars at widest point 7.3–8.2 (it should be mentioned that although both measurements overlap with those of *magnater,* the width across the molars at widest point is always narrower in relation to condylobasal length in *tristis*). Of the five species, only *magnater* appears to be absent from eastern Papua, though the American Museum has specimens from as close as Morobe province. *Miniopterus australis, schreibersi,* and *tristis* are known from both the mainland and the islands, but *M. paululus* is known only from Misima, Kiriwina, and Woodlark. All pairs of species are found sympatrically somewhere in the East Papuan area except that *paululus* and *australis* do not occur together, the latter being known only from the mainland and Tagula. Strangely enough, the genus *Miniopterus* appears to be absent from Rossel and all three of the D'Entrecasteaux islands.

Miniopterus paululus: The American Museum of Natural History has nine skins and skulls, 26 alcoholics from Misima; two skins and skulls, seven alcoholics from Kiriwina; eight skins and skulls, 19 alcoholics from Woodlark. All were collected by R. F. Peterson in 1956. To my knowledge, these are the only records of *paululus* from the New Guinea area, but outside it, the species is known from islands both to the east (e.g., New Hebrides) and the west (e.g., Timor, see Goodwin, 1979, p. 120, who called this species *australis*). The identity of the subspecies in the East Papuan islands is highly uncertain at present.

Miniopterus australis: The American Museum of Natural History has two skins and skulls from Sogeri in Central province, collected by Archbold and Tate in 1937; one alcoholic from the Port Moresby area in Central province, collected by L. J. Jones about 1950. All specimens from the mainland of Milne Bay province were collected by H. M. Van Deusen in 1953. These include one skin and skull, 126 alcoholics from Dabora; four skins and skulls, five alcoholics from Menapi; one skin and skull from Peria creek. Finally R. F. Peterson collected six skins and skulls and 15 alcoholics from Tagula in 1956. This is a common and widespread species in New Guinea, judged by specimens in the American Museum. I can see no differences between north Queensland (Australia), East Papuan mainland and Tagula specimens, although all appear to be somewhat smaller

than specimens farther west in New Guinea and would refer all East Papuan material to *M. a. australis,* since Peterson (1981b) has corrected the type locality from the Loyalty islands to eastern Australia. In view of the close similarity of *australis* to *paululus* and their allopatry in the Indo-Malayan and Australian regions (though forming an odd checkerboard pattern), I am strongly tempted to treat them as conspecific, even though I had seen no actual intergradation. Dr. R. L. Peterson, however, has unpublished data indicating that close relatives of both species are sympatric on Madagascar. I therefore reluctantly keep them separate.

Miniopterus schreibersi: Although by far the most widespread of the species of *Miniopterus* and one of the commonest bats in Australia, the only New Guinea mainland specimens I have seen are two alcoholics collected at Dabora (Milne Bay province) by H. M. Van Deusen in 1953, and one in the British Museum from Port Moresby (Central province). However the specimen from Gulf province (Putei), which McKean (1972, pp. 32, 33) identified as *medius* seems, on the basis of his measurements to be referable to *schreibersi.* It certainly seems to be much commoner on some of the East Papuan islands, all specimens that I have seen from these having been collected by R. F. Peterson in 1956. These include four skins and skulls, five alcoholics from Tagula; seven skins and skulls, seven alcoholics from Misima; two skins and skulls, one alcoholic from Woodlark. I cannot distinguish mainland skulls from island skulls or skulls from the three islands from one another, though all are clearly smaller than specimens from eastern Australia. Since Dr. R. L. Peterson is currently revising the group, I will refrain from describing any subspecies.

Miniopterus tristis: Peterson (1981a) has recently revised this group and separates what has hitherto (e.g., Hill, 1971b) been considered a single species extending from the Philippines to the New Hebrides into two. *Miniopterus tristis* is restricted to Celebes and the Philippines, populations from New Guinea eastward being allocated to *M. propritristis* with three subspecies. I have read Peterson's (1981a) paper and have checked his characters on all the specimens in the American Museum and I find that in at least some respects the western (Philippines, Celebes) material does separate from specimens farther east, however, I cannot see these two groups as separate species and therefore include all in *M. tristis.* From Central province, the American Museum has 10 skins and skulls from Iawareri collected by Archbold and Tate in 1937 and one alcoholic from near Sogeri collected by J. Huon de Navrancourt in 1960. From the mainland of Milne Bay province, there is one skin and skull, 34 alcoholics from Dabora, all collected by H. M. Van Deusen in 1953. Specimens from the East Papuan islands were all collected by R. F. Peterson in 1956. They include eight alcoholics from Misima; two skins and skulls, four alcoholics from Kiriwina; two skins and skulls from Woodlark. This is the only species of *Miniopterus* for which there is clear evidence of geographical variation within the Papuan area (assuming that *australis* and *paululus* are distinct species. There is certainly geographical variation on the New Guinea mainland (as Peterson, 1981, indicated by naming subspecies) judging by the larger size of the few Irian Jaya specimens examined (*M. t. grandis*) compared with material farther east (*M. t. propritristis*). However, there is somewhat (in my opinion) greater difference between East Papuan mainland and East Papuan island specimens as may be seen from comparing ranges of condylobasal measurements. These are in millimeters with the number of skulls in parentheses. Mainland (12) 17.5–18.4; Misima (3) 15.9–16.9; Kiriwina (3) 16.5–17.1; Woodlark (1) 17.0. It is clear that the East Papuan island populations are subspecifically distinct from those of the mainland, and were therefore allocated by Peterson to *M. t. insularis,* which also occurs in the Bismarcks, Solomons, and New Hebrides. It should be mentioned that Peterson saw some of the Trobriand but none of the Louisiade material.

GENUS *Kerivoula:* Laurie and Hill (1954) recognize four species in the New Guinea region, including *myrella* which is confined to the Bismarcks and at least one of the small islands off the northeast coast of New Guinea. Hill (1965) revised the Indo-Australian kerivoulines and recognized two genera, *Kerivoula* and *Phoniscus, myrella* together

with the New Guinea mainland *muscina* and the East Papuan island *agnella* being retained in *Kerivoula,* whereas the New Guinea mainland (and northeastern Australian) *papuensis* is included in *Phoniscus.* There has been considerable difference of opinion regarding the characterization of these two taxa. Aside from a tragus character, which I cannot judge because of lack of comparably preserved material, the distinctions that Hill (1965) makes involve the skull. According to him, *Phoniscus* may be distinguished from *Kerivoula* by its grooved upper canines, its shorter and wider narial and anterior palatal emarginations, its broader (unconstricted) "interorbital" (really postorbital), and its more reduced posterior upper incisor. These differences can all be seen, just as Hill describes them when the skull of AMNH 157475 (*papuensis* from Peria creek on the East Papuan mainland) is compared with that of AMNH 105081 (*muscina* from Fly River, examined by Hill (1965, p. 535). However, AMNH 159560 (*agnella* from Fergusson Island) is somewhat intermediate, though closer to *muscina.* In its constricted postorbital and unreduced posterior upper incisor, it is very much like *muscina.* However its upper canine is faintly grooved, and though the anterior palatal emargination is as in *muscina,* its narial emargination is intermediate in width and as short as in *papuensis.* In view of the somewhat intermediate nature of *agnella* and the fact that the same incisor character can differ among closely related species in *Pipistrellus,* I am inclined to treat *Phoniscus* only as a subgenus of *Kerivoula,* as was done by Laurie and Hill (1954). Within this genus (*s.l.*), *agnella* is known from the East Papuan islands and *papuensis* from the East Papuan mainland. *Kerivoula muscina* may also occur in eastern Papua, but so far the only known localities are in Western province (American Museum specimens) and East Sepik province (McKean, 1972, p. 33).

Kerivoula (*Kerivoula*) *agnella:* Hill (1965, p. 536) recorded this species from both Tagula and Misima. The American Museum of Natural History has a single skin and skull from Fergusson collected by R. F. Peterson in 1956. To my knowledge, these are the only places where it is known to occur. As Hill indicated, it is probably the East Papuan island representative of the mainland *muscina,* but I do not think there is any question of their being distinct species.

Kerivoula (*Phoniscus*) *papuensis:* Originally described from Port Moresby in Central Province, the American Museum of Natural History has a single skin and skull collected by H. M. Van Deusen at the Peria River on the mainland of Milne Bay province.

GENUS *Nyctophilus:* Laurie and Hill (1954) record two species of this genus in New Guinea, one of which they described as new. As explained below, they overlooked a third, but first we must consider the status of a new genus and species (*Lamingtona*) later described by McKean and Calaby (1968). This genus has since been shown to be a synonym of *Nyctophilus microtus* (Hill and Koopman, 1981) and is treated under that species. As mentioned above, Laurie and Hill (1954) listed only two species of *Nyctophilus* for New Guinea, *microtus* and *microdon.* However, Tate (1952, pp. 601, 602) referred to a specimen of *bifax* from Irian Jaya (admittedly in a very obscure fashion). I have studied this specimen as well as a second one, which Tate overlooked, from the Western province of Papua. These specimens agree well with *bifax* from northern Queensland (Australia), though near the upper end of the size range. They are clearly much larger than *microtis* or *microdon* (condylobasal 15.4 mm. vs. 13.5–13.6). *Nyctophilus bifax,* unlike *microtis,* has the ears connected by a high band (though not as high as that of *microdon*). This difference is also reflected by ear length (from notch) as follows (in mm.): *microtis* (15–17), *bifax* (21), *microdon* (24–28). On the other hand, the posterior nasal projection (behind the true noseleaf) is low and undifferentiated in both *bifax* and *microtis,* whereas in *microdon* it is higher and clearly divided into two parts. As mentioned above, *bifax* in New Guinea is known only from Irian Jaya and the Western province of Papua. The American Museum has specimens of *microdon* from Eastern Highlands province which constitutes a slight eastward extension of range from the type locality in Western Highlands province. Hill and Pratt (1981) have recently discovered a fourth species of *Nyctophilus* in New Guinea, *N. timoriensis* from Morobe

province. I have seen one of the specimens (BM 80,498) and it is clearly larger than any of the other New Guinea species (condylobasal length 17.1). However, neither *timoriensis, bifax,* nor *microdon* is known from eastern Papua. The occurrence of *microtis* on the East Papuan mainland is discussed below. The only record I know of *Nyctophilus* from the East Papuan islands is that of DeVis (1892, p. 94) from Tagula (=Sudest). This was identified as *timoriensis,* but could well have been *microtis* or another species, since in the late 19th century, following Dobson (1878, pp. 172–175), only a single species (*timoriensis*) was generally recognized. Since DeVis was at the Queensland Museum, it is possible that the specimen(s) from Tagula may still be there. I am indebted to the late Hobart Van Deusen, whose notes led me to this obscure reference. I know of two other records of "*timoriensis*" from eastern Papua (Kamali and Kapa Kapa), both in Central province. These were recorded by Thomas (1897, p. 608) and were presumably not *microtis* since that species was separately recorded by Thomas in the same paper. However, Thomas later (1914, p. 382) described at least some of these specimens as a new genus and species, *Pharotis imogene.*

Nyctophilus microtis: The American Museum of Natural History has two specimens, both from the Central province of eastern Papua. One alcoholic was collected by Archbold and Rand at Kabuna in 1933; a skin and skull was obtained by Tate at Sogeri in 1937. Unfortunately, both are immature but the American Museum has five adult specimens from elsewhere in Papua New Guinea (Western, Morobe, and East Sepik provinces). Hill and Koopman (1981) are agreed that *Lamingtona lophorhina* cannot be distinguished even specifically from *Nyctophilus microtis.* Furthermore, with the type localities of all three New Guinea named forms of the *microtis* group (*microtis, bicolor, lophorhina*) on the mainland of eastern Papua and with such paucity of material from this area, I don't think it would be profitable to try to evaluate the taxonomic validity of these three named forms.

Pharotis imogene: The American Museum of Natural History has a single alcoholic specimen collected by Loria in 1890 at Kamali (Central province) on the East Papuan mainland. The specimen is from the original series of this monotypic New Guinea genus (Thomas, 1914). I know of no subsequent records.

FAMILY MOLOSSIDAE

Of the two genera currently recognized from New Guinea, *Otomops* is known by two species, neither of which has been recorded from eastern Papua, though either may occur there. *Otomops papuensis* was described from Gulf province (just to the west of our area) and as far as I am aware is still only reported from the type locality. *Otomops secundus* was described from Madang province, but the American Museum has a single specimen from Eastern Highlands province. Thus, of the two species, one occurs on the southern side of Papua New Guinea, the other on the northern side but neither is recorded from eastern Papua. All four species of *Tadarida* currently recognized from New Guinea occur in eastern Papua and are treated below.

Tadarida (*Chaerephon*) *jobensis:* The American Museum of Natural History has no New Guinea material of this species except for two topotypes from Japen (=Jobi) island in western Irian Jaya. The British Museum, however, has a specimen from Deva Deva (near Mafulu at 770 meters) in Central province. This species was listed as a subspecies of *T. plicata* by Laurie and Hill (1954) but see Hill (1961). *T. jobensis* is not known from the East Papuan islands, but a subspecies (*T. j. solomonis*) is known from the Solomons.

Tadarida australis: The American Museum of Natural History has two specimens of this species from the East Papuan mainland, an alcoholic from the upper Kunimaipa River at *ca.* 1900 meters in Central province, collected by Huon de Navrancourt in 1955, and a skin and skull from 2230 m. on Mount Dayman, Milne Bay province, by Van Deusen. Laurie and Hill (1954) recorded *T. australis* (as a monotypic) species from both Australia and New Guinea. McKean and Calaby (1968), however, described a new species, *T. kuboriensis* from Chimbu province in Papua New Guinea and suggested that

all New Guinea specimens previously referred to *australis* were really *kuboriensis.* The latter was distinguished from the former by its smaller ear and antitragus, its absence of a white flank stripe, and in the skull, shorter length, less inflated rostrum, less-developed supraorbital and sagittal crests, and narrower upper molars. Measurements were listed for the type and paratypes of *kuboriensis* but none are given of *australis* for comparison. Furthermore, it is evident that both the skull McKean and Calaby figure and a paratype in the American Museum are immature, as is evident from the open basicranial sutures. Fortunately, the Mount Dayman skin and skull are of an adult and can be compared with five specimens of *australis* from Queensland and Western Australia. The ear length (from notch) of the Mount Dayman specimen is 21 vs. 26–29 mm. for those from Australia, but I am unable to see any difference in the antitragus, though this is not ruled out. The Mount Dayman specimen does indeed lack the white flank stripe that can be seen in the five Australian skins. Comparing skulls of the two adults of *kuboriensis* with the only two intact adult *australis* available, the skull is indeed shorter (20.5, 20.9 vs. 22.9, 23.9) and the upper molars are narrower in proportion. I am, however, unable to see any difference in rostral inflation or the supraorbital and sagittal crests. The validity of *kuboriensis* as distinct from *T. australis* must therefore stand or fall on its smaller size and lack of a white flank stripe. To me, this difference is best expressed by recognizing the two forms as subspecies, *T. a. australis* for the Australian, and *T. a. kuboriensis* for the New Guinea subspecies.

Tadarida (*Mormopterus*) *planiceps:* The specific name of the smallest species of New Guinea *Tadarida* has been the subject of much disagreement. Originally described as a separate species, *loriae,* this was listed by Laurie and Hill (1954) as *T. norfolkensis loriae.* Hill (1961) separated *norfolkensis* as a separate species but treated *loriae* as a subspecies of the southern Australian *planiceps.* Finally, Felten (1964), separated both *loriae* and *planiceps* as separate species and recognized two subspecies of *loriae* in tropical Australia, to one of which (*T. l. ridei*) he referred specimens from northeastern Queensland that Tate (1952) had allocated to two different species, namely *norfolkensis* and *loriae.* The problem is further complicated by uncertainty concerning the type localities of both *norfolkensis* and *planiceps.* The American Museum has no authentic material of either *norfolkensis* or typical *loriae* and with the exception of two from Victoria and two from southern Western Australia, all its material of this complex comes from northeastern Queensland. The Queensland series is somewhat heterogeneous but probably all belongs to one species (in agreement with Felten and not with Tate). However, I am not as impressed with the differences between these northern Queensland specimens with those from southern Australia as is Felten and therefore consider them all to be conspecific. I am not in a position to say whether or not *norfolkensis* is also conspecific, but for the present would be inclined to follow Hill (1961), in considering *loriae* a subspecies of *T. planiceps.* It should be mentioned, however, that Hall and Richards (1979) agree with Felten and map these as sympatric in southeastern Queensland. As indicated above, the American Museum has no New Guinea specimens of this species and indeed I know of no published records from New Guinea aside from the original material collected in Central province on the East Papuan mainland. However, the British Museum does have additional Central province specimens.

Tadarida (*Mormopterus*) *beccarii:* The only East Papuan specimen in the American Museum of Natural History is a skin and skull from Fergusson Island collected by R. F. Peterson in 1956. The species is probably widespread on the New Guinea mainland, including eastern Papua. Besides the two localities mentioned by Laurie and Hill (1954, p. 64) in Irian Jaya and Madang province, Waithman (1979) has recorded it from Western province, and the American Museum has three specimens from Kanganaman, East Sepik province. The Fergusson specimen, a male, has a skull with a condylobasal length of 17.8 mm., whereas the single male from East Sepik province measures 18.4 mm., and two females from the same place measure 16.8 and 17.0 mm. However, three specimens in the British Museum (at least one of which is a male) measure 16.6–16.9. This

suggests both geographical variation and sexual dimorphism, but the number of specimens is obviously too small to be sure. The subspecies, at least on the mainland, is *T. b. astrolabiensis.*

DISCUSSION

There are obviously several ways in which the data (presented above) can be analyzed. The three that I have chosen to consider are the East Papuan mainland species that do and those that do not occur on the various East Papuan islands, the affinities of the East Papuan island bat species with those of the New Guinea mainland, the Bismarcks, and the Solomons, and finally the altitudinal distribution of bat species on the East Papuan mainland. Finally, some general ecological and zoogeographical conclusions are in order.

The East Papuan Mainland Species

The 44 species that are known or inferred to occur on the East Papuan mainland are listed in table 1. Of these, 20 species are not known to occur on any of the East Papuan islands and one is only questionably recorded. Of the remaining 23 species, all but two occur on one or more of the islands, *Dobsonia moluccensis* is represented by the closely related allopatric *D. pannietensis, Kerivoula muscina* by the closely related allopatric *K. agnella,* and *Miniopterus australis* (in part) by the closely related *M. paululus.* Again, of the 23 species, 16 are known or are represented on the Louisiades, 13 are known or represented on the D'Entrecasteaux, and 16 on the Trobriands. Thus there seems to be no tendency for a greater number on the nearby Louisiades and D'Entrecasteaux than on the more distant Trobriands. Only six species are known or represented on all three island groups, four species from the Louisiades and D'Entrecasteaux but not the Trobriands, six from the Louisiades and Trobriands but not the D'Entrecasteaux, none from the Louisiades and D'Entrecasteaux but not the Trobriands, none known only from the Louisiades only, but three from the D'Entrecasteaux only (in each case only from Fergusson island), and four from the Trobriands only. More will be said of the species localized in a part of the East Papuan islands in the following section, but it does seem strange that nothing is shared between New Guinea and the Louisiades alone. It should be pointed out, however, that in the *Miniopterus australis* group, one of the Louisiade populations (from Tagula) belongs to the mainland *M. australis* rather than to *M. paululus* which occurs in Misima and the Trobriands. It is also strange that there is a greater affinity of the bats of the Trobriands with those of the more distant Louisiades than with the nearer D'Entrecasteaux. Perhaps the greater distance between the mainland and the larger Louisiades has given them a more oceanic aspect (along with the Trobriands) than the nearer D'Entrecasteaux.

Affinities of the East Papuan Island Species

The East Papuan island bat species are enumerated in table 2. It may be seen that all 24 species occur or are represented on the mainland (or at least continental islands of New Guinea). For three of the four species of *Miniopterus* the systematics is so confused that it is uncertain whether or not they occur on the Bismarcks or Solomons and are not considered further. Of the remaining 21, only six are absent from both the Bismarcks and Solomons. (The genus *Kerivoula* occurs in the Bismarcks, but its species, *K. myrella,* is not at all closely related to *K. agnella,* though the New Guinea mainland *K. muscina* is (see Hill, 1965.) These six species are not considered further since their affinities are clearly with New Guinea and not with the Bismarcks or Solomons. The remaining 15 species, however, must be taken up in more detail.

Pteropus hypomelanus: This is a widespread species of spotty distribution, known from limited parts of all three of the areas surrounding the East Papuan islands. All appear to be referable to *P. h. luteus* and I see no basis for choice among the three areas.

Dobsonia pannietensis: The *Dobsonia moluccensis* group is represented in both New Guinea and the Bismarcks but not in the Solomons so the choice is between the first two areas. In the above systematics section, I have treated the Bismarck form (*anderseni*) as a subspecies of *D. moluccensis* but have

TABLE 1

The East Papuan Mainland Bat Species and Their Distribution in the East Papuan Islands

Mainland Species	Louisiades	D'Entrecasteaux	Trobriands
Rousettus amplexicaudatus	–	–	–
Pteropus hypomelanus[a]	+	+	+
Pteropus conspicillatus	+	+	+
Pteropus neohibernicus	–	–	–
Pteropus macrotis	–	–	–
Dobsonia moluccensis	(+)[b]	(+)[b]	(+)[b]
Nyctimene albiventer	–	–	–
Nyctimene major[c]	+	+	+
Nyctimene cyclotis	–	–	–
Nyctimene aello	–	–	–
Paranyctimene raptor	–	–	–
Macroglossus lagochilus	–	+[d]	–
Syconycteris australis	+	+	+
Emballonura beccarii	–	–	+
Emballonura raffrayana	–	–	–
Emballonura nigrescens	–	–	+[e]
Taphozous australis	–	–	–
Saccolaimus mixtus	–	–	–
Rhinolophus megaphyllus	+	+	–
Rhinolophus euryotis	–	–	+[f]
Hipposideros ater	–	–	+[e]
Hipposideros maggietaylorae	–	–	–
Hipposideros calcaratus	+	–	+
Hipposideros galeritus	+	+	+
Hipposideros muscinus	–	–	–
Hipposideros semoni	–	–	–
Hipposideros diadema	+	–	+
(*Aselliscus tricuspidatus*)[g]	+	–	+
(*Myotis adversus*)[g]	+	+	–
Pipistrellus tenuis	+	+	–
Philetor brachypterus	–	–	–
Chalinolobus nigrogriseus	–	+[d]	–
Nycticeius balstoni	–	–	–
Miniopterus australis	+	–	(+)[b]
Miniopterus schreibersi	+	–	+
Miniopterus tristis	+	–	+
(*Kerivoula muscina*)[g]	(+)[b]	(+)[b]	–
Kerivoula papuensis	–	–	–
Nyctophilus microtis	?[h]	–	–
Pharotis imogene	–	–	–
Tadarida jobensis	–	–	–
Tadarida australis	–	–	–
Tadarida planiceps	–	–	–
(*Tadarida beccarii*)[g]	–	+[d]	–

[a] Not actually known from the East Papuan mainland but does occur on the continental Conflict Islands.

[b] Parentheses around a plus sign indicates that the listed species does not occur but is represented by a closely related allopatric species.

[c] Not actually known from the East Papuan mainland but does occur on continental Rogeia Island.

[d] Fergusson Island only.

[e] Woodlark Island only.

[f] Kiriwina Island only.

[g] Species in parentheses have not been reported from the East Papuan mainland but probably occur there since they are known from elsewhere on the mainland of New Guinea and from East Papuan islands.

[h] *Nyctophilus* is known from Tagula but it may not be this species.

TABLE 2
The East Papuan Island Bat Species and Their Distribution in Adjacent Areas

East Papuan Island Species	New Guinea	Bismarcks	Solomons
Pteropus hypomelanus	+	+	+
Pteropus conspicillatus	+	–	–
Dobsonia pannietensis	(+)[a]	(+)[a]	–
Nyctimene major	+	+	+
Macroglossus lagochilus	+	+	+
Syconycteris australis	+	+	–
Emballonura beccarii	+	–	–
Emballonura nigrescens	+	+	+
Rhinolophus megaphyllus	+	+	–
Rhinolophus euryotis	+	+	–
Hipposideros ater	+	–	–
Hipposideros calcaratus	+	+	+
Hipposideros galeritus	+	+	+
Hipposideros diadema	+	+	+
Aselliscus tricuspidatus	+	+	+
Myotis adversus	+	+	+
Pipistrellus tenuis	+	+	+
Chalinolobus nigrogriseus	+	–	–
Miniopterus paululus	(+)[a]	?	?
Miniopterus australis	+	?	?
Miniopterus schreibersi	+	?	?
Miniopterus tristis	+	+	+
Kerivoula agnella	(+)[a]	–	–
Tadarida beccarii	+	–	–

[a] Parentheses around a plus sign indicates that the listed species does not occur but is represented by a closely related allopatric species.

noted the much greater resemblance between the East Papuan *D. pannietensis* and *D. m. anderseni* than between *D. pannietensis* and *D. m. magna* of the New Guinea mainland. On the face of it, this would imply derivation of the East Papuan island *Dobsonia* from the Bismarck form of *D. moluccensis.* However, as I have indicated, if this were true I would expect *D. m. anderseni* of the Bismarcks to be more like *D. p. remota* of the Trobriands than like *D. p. pannietensis* of the Louisiades and D'Entrecasteaux. If, on the other hand, New Guinea has been the source area for the East Papuan island populations, then there is a (stepped) cline from the large mainland *magna* through the smaller *pannietensis* of the Louisiades and D'Entrecasteaux to the smallest *remota* of the Trobriands. In my opinion, the question is still open.

Nyctimene major: The placement of this species on the New Guinea "mainland" is based entirely on its presence on continental Rogeia Island, which is most reasonably explained by secondary colonization from the Louisiades. However, forms of *N. major,* as currently constituted, do occur on both the Bismarcks and Solomons as well as throughout the East Papuan islands. Four subspecies are currently recognized in this area, *major* in the Bismarcks, *scitulus* in the Solomons, *geminus* in the Louisiades and D'Entrecasteaux, and *lullulae* on Woodlark (and perhaps Kiriwina). However, except for *lullulae* which is clearly smaller, the characters Andersen (1912, p. 697) gives do not hold. There is broad overlap in size and the palatal character Andersen gives to separate *scitulus* from *geminus* and *major* (free edge more acutely angular vs. evenly concave) is quite variable within populations and clearly cannot distinguish subspecies. Andersen also separates *scitulus* on the basis of ear length but unfortunately very few ear length measurements are available. The subspecies situation is further complicated by the presence of *lullulae*-like populations on Karkar and Bagabag to the

west of New Britain (see Koopman, 1979, p. 7). This presents the picture of a checkerboard of large- and small-sized populations and no clear geographical trend. It is not even clear whether small or large size is primitive in this particular complex, though small size is probably primitive for the genus as a whole. Since the mainland of New Guinea is probably the center of origin for the subtribe Nyctimenina (*Nyctimene* plus *Paranyctimene*), it is clear that New Guinea is the ultimate source, but whether all the populations of the *major* group from the Louisiades to Karkar represent a single invasion or multiple invasions and what additional dispersals have occurred subsequently is still obscure.

Macroglossus lagochilus: Laurie and Hill (1954), following Andersen (1912) referred New Guinea and Bismarck specimens to *M. l. nanus* but Solomon Island ones to *M. l. microtis.* McKean (1972) synonymized *microtis* with *M. l. nanus,* thus recognizing only a single subspecies in the area under consideration. In view of this fact, the small number of specimens available from any of the four areas involved, and the presence of sexual dimorphism, it seems futile to attempt to determine which is the most likely source area for *Macroglossus* from the East Papuan Islands.

Syconycteris australis: Syconycteris is absent from the Solomons, so only New Guinea and the Bismarcks would seem to qualify as source areas for the East Papuan island populations. As discussed above, the chief character separating the various East Papuan populations from one another is size. East Papuan island *Syconycteris* are either similar in size or larger than East Papuan mainland populations. Bismarck specimens, however, tend to be smaller than those from the New Guinea mainland (see Koopman, 1979, p. 8). It is therefore improbable that the East Papuan island populations are derived from those on the Bismarcks and are far more likely to be derived from the New Guinea mainland.

Emballonura nigrescens: Currently, populations from the New Guinea mainland are allocated to *E. n. papuana* and those from the Bismarcks, Solomons, and Woodlark are identified as *E. n. solomonis.* As indicated above, the differences between these two subspecies are not great but East Papuan mainland specimens do tend to have shorter skulls than those from the Solomons. Bismarck specimens (as represented by two skulls in the American Museum from western New Britain) clearly agree much better with *solomonis* (condylocanine length 11.4, 11.6 vs. 10.5–11.4 for Solomon Island skulls and 10.1–10.8 for East Papuan mainland ones). As pointed out above, the few Woodlark skulls fall largely in the overlap zone between the two subspecies (condylocanine length 10.4–10.9). No definite decision can be made, at present between New Guinea vs. Bismarck or Solomon Island derivation.

Rhinolophus megaphyllus: Rhinolophus is apparently absent from the Solomons, but *R. megaphyllus* does occur on the Bismarcks as well as New Guinea, Misima, and Goodenough. For both, derivation, albeit independent, from New Guinea is reasonably certain. The Misima subspecies (*monachus*) is most like a New Guinea population (though not the one on the adjacent mainland). The Goodenough population is most like the one on the adjacent mainland and differs in the opposite direction (larger vs. smaller) from the one on the Bismarcks.

Rhinolophus euryotis: As mentioned above, the specimens from Kiriwina (the only East Papuan island from which *R. euryotis* is known) agree better with the only known Bismarck specimen than it does with East Papuan mainland specimens. Derivation of the Kiriwina population from the Bismarcks is, therefore, most likely, though the number of specimens (particularly in view of sexual dimorphism) is too small to be at all positive.

Hipposideros calcaratus: As explained above, the East Papuan island representatives of this species agree better with the Bismarck and Solomon *H. c. calcaratus* than with the New Guinea mainland *H. c. cupidus.* There is not a great deal to choose from between Bismarck and Solomon derivation but Solomon Island specimens tend to depart farther from East Papuan island ones in larger average size and also show some approach to *H. maggietaylorae* in canine and post-palatal characters. I would therefore favor a derivation from the Bismarcks.

Hipposideros galeritus: In this species, there is a single subspecies on the New

Guinea mainland, East Papuan islands, Bismarcks, and Solomons. There is therefore no basis for postulating which of the three possible source areas functioned as such in this case.

Hipposideros diadema: This species occurs on the New Guinea mainland, Bismarcks, and Solomons as well as Misima and Kiriwina in the east Papuan islands. Although Hill (1963) does not record this species from the Bismarcks (except for *H. d. mirandus* from the Admiralties), the American Museum has 18 specimens from New Britain and one from Lihir. Most of the Solomon Island populations have been referred to *H. d. oceanitis.* This name was published in the same paper as *pullatus* but they were not directly compared and it is not clear to me how they differ, especially after comparison of specimens from Bougainville and Vella Lavella in the Solomons with specimens from the East Papuan mainland. New Britain specimens overlap both the New Guinea and Solomon island ranges in forearm length (69–74 vs. 70–83 and 72–78), third metacarpal length (51–55 vs. 54–64 and 54–58), condylobasal length (26.0–27.8 vs. 25.9–27.4 and 26.1–28.3), and zygomatic breadth (16.6–17.8 vs. 17.0–17.8 and 16.6–18.1) respectively. The small Kiriwina sample also falls out in the same area (forearm 72–75, third metacarpal 54–57, condylobasal 27.0–27.7, zygomatic breadth (17.7–17.8). I can see no basis for choosing among any of the three larger areas as a source for the Kiriwina population and indeed see little basis for distinguishing either *trobrius* or *pullatus* from *oceanitis* as subspecies, though I would hesitate to synonymize them at the present time. By far the most distinct population in the area is the unnamed one from Misima. However, in view of the slight geographical variation among the source areas, its derivation is uncertain, though the East Papuan mainland is certainly most likely on geographical grounds. In summary, there seems to be no basis for determination of the source for either of the two East Papuan island populations of *Hipposideros diadema.*

Aselliscus tricuspidatus: As seen above, New Guinea mainland populations tend to be large (tentatively identified as *A. t. tricuspidatus*), the single New Britain skull measured was intermediate, whereas Solomon Island populations are small. Since East Papuan Island populations are likewise small, a Solomon Island derivation of these populations seems most likely, though the pattern of geographical variation in this species is still imperfectly understood.

Myotis adversus: This species is probably widespread throughout the New Guinea-Bismarck-Solomon region, though to my knowledge, the only record from the Bismarcks is a single specimen in the American Museum from Tabar Island (northeast of New Ireland). All these populations have been referred to *M. a. moluccarum.* There is, therefore, no basis for choice among the three source areas.

Pipistrellus tenuis: As discussed above, two subspecies (*papuanus* and *collinus*) occur on the New Guinea mainland. The subspecies in the Bismarcks is *P. t. angulatus* and on the Solomons is *P. t. ponceleti.* East Papuan island populations (Tagula and all three of the D'Entrecasteaux) have been allocated to the New Guinea lowland subspecies (*P. t. papuanus*) even though Goodenough highland specimens approach the New Guinea highland *P. t. collinus.* I have made this allocation because all East Papuan island specimens (with the exception of the two from the Goodenough highlands) fall within the variability of East Papuan mainland *papuanus* for all measurements I have taken with the exception of a single Goodenough lowland specimen whose width across last molars measurement (4.7) falls just below the lowest for bats from the East Papuan mainland (4.8). There is also overlap between measurements of East Papuan island specimens and those of *Pipistrellus* from the Bismarcks (*angulatus*) and the Solomons (*ponceleti*), but this is not complete. Thus (excluding the two from the Goodenough Highlands) we have forearm length: East Papuan island (28–31), New Britain (28–30), Solomon (31–33); condylobasal length: East Papuan island (10.6–11.5), New Britain (11.3–11.6), Solomon (11.1–11.8); maxillary tooth row length: East Papuan island (3.7–4.0), New Britain (4.0–4.2), Solomon (3.9–4.2). There is thus better agreement between East Papuan island and East Papuan mainland populations than between the former and those of the Bismarcks and

Solomons. It is significant, however, that the differences among all these populations are less than that between lowland and highland populations on the East Papuan mainland.

Miniopterus tristis: This species occurs in all three source areas. However, two well-marked subspecies are represented. East Papuan island specimens belong to the small *M. t. insularis* (which also occurs in the Bismarcks and Solomons) rather than the larger *M. t. propritristis* which occurs on the East Papuan mainland. I have no basis for choosing between the Bismarcks and the Solomons as a source area for East Papuan island populations.

Summing up, besides the six that are shared only by the New Guinea mainland and the East Papuan islands, three other species (*Syconycteris australis, Rhinolophus megaphyllus, Pipistrellus tenuis*) probably also have closest affinity between those two areas. Two species (*Rhinolophus euryotis, Hipposideros calcaratus*) seem to show closest affinities with the Bismarcks and finally *Aselliscus tricuspidatus* shows closest affinity with the Solomons. *Dobsonia pannietensis* shows affinity with either New Guinea or the Bismarcks but not the Solomons; *Miniopterus tristis* closer affinity with either the Bismarcks or Solomons, but not the New Guinea mainland. For the remaining 10 species, no decision is possible at this time. The New Guinea mainland has clearly been the most important source area for the East Papuan island bats.

Altitudinal Distribution of East Papuan Mainland Bats

The known or presumed altitudinal distributions of the 40 species of bats recorded from the East Papuan mainland are listed with their known (or, in a few cases, presumed) occurrence in the three altitudinal zones recognized for *Pipistrellus*. In a number of instances the data are too incomplete to say very much. Two of the species (*Pteropus hypomelanus, Nyctimene major*) are not actually known from the East Papuan mainland but only on offshore islands which are separated from the mainland only by shallow water and were therefore connected to the mainland 10,000 years ago. They are listed only for the sake of completeness but if they do at present occur on the mainland, they are

TABLE 3
Altitudinal Distribution of East Papuan Mainland Bats

	Below 1000 m.	1000–1800 m.	Above 1800 m.
Rousettus amplexicaudatus	+	–	–
Pteropus hypomelanus	(+)[a]	–	–
Pteropus conspicillatus	+	–	–
Pteropus neohibernicus	+	–	–
Pteropus macrotis	+	–	–
Dobsonia moluccensis	+	+	–
Nyctimene albiventer	+	–	–
Nyctimene major	(+)[b]	–	–
Nyctimene cyclotis	–	?[c]	–
Nyctimene aello	+	–	–
Paranyctimene raptor	+	–	–
Macroglossus lagochilus	+	–	–
Syconycteris australis	+	+	+
Emballonura beccarii	–	+	–
Emballonura raffrayana	–	+	–
Emballonura nigrescens	+	–	–
Taphozous australis	+	–	–
Saccolaimus mixtus	+	–	–
Rhinolophus megaphyllus	+	–	–
Rhinolophus euryotis	+	–	–
Hipposideros ater	+	–	–
Hipposideros maggietaylorae	+	–	–
Hipposideros calcaratus	+	–	–
Hipposideros galeritus	+	–	–
Hipposideros muscinus	+	–	–
Hipposideros semoni	–	?[c]	–
Hipposideros diadema	+	–	–
Pipistrellus tenuis	+	+	+
Philetor brachypterus	+	+	+
Chalinolobus nigrogriseus	+	–	–
Nycticeius balstoni	+	–	–
Miniopterus australis	+	–	–
Miniopterus schreibersi	+	–	–
Miniopterus tristis	+	–	–
Kerivoula papuensis	+	–	–
Nyctophilus microtis	+	+	–
Pharotis imogene	+	–	–
Tadarida jobensis	+	–	–
Tadarida australis	–	–	+
Tadarida planiceps	+	–	–

[a] Conflict Islands (on the continental shelf, not yet recorded from the mainland), surely does not occur above 1000 m.

[b] Rogeia Island (on the continental shelf, not yet recorded from the mainland), surely does not occur above 1000 m.

[c] Upper Aroa River, elevation not certain.

almost certainly confined to the lowlands (below 1000 m.). Information concerning two other species (*Nyctimene cyclotis, H. semoni*) is clearly inadequate since in each case, it is based on a single old record of indeterminate altitude. Of the remaining 36 species, all except three are known from the lowlands. This is not very significant for *Emballonura beccarii* and *E. raffrayana,* however, since, on the east Papuan mainland, each is known from a single mid-mountain locality. *Tadarida australis* is known from two localities in eastern Papua, both above 1800 meters. Of the remaining 33 species, 28 are known only from the lowlands. Of the five remaining species, two (*Dobsonia moluccensis, Nyctophilus microtis*) are not known above 1800 meters, and only three (*Syconycteris australis, Pipistrellus tenuis, Philetor brachypterus*) are known from above 1800 meters, together with *Tadarida australis,* mentioned above. On the face of it, the highland bat fauna appears to be very depauperate (four out of 32 species). Some of this may well be an artifact since there has certainly been a good deal more collecting in the lowlands than in the highlands. However, the absence of such highland species as *Aproteles bulmerae, Miniopterus magnater, Murina florium, Nyctophilus timoriensis, N. microdon,* and *Otomops secundus* may be real. Not only do the mountains tend to be higher to the northwest, but, probably more important, the highland areas are considerably larger so that they would be expected to be able to support a larger number of highland species.

A species which occurs both in the lowlands and the highlands might be expected to show altitudinal variation. I have discussed this for *Pipistrellus tenuis* above. Unfortunately, for the other two species for which such a phenomenon might be expected (*Syconycteris australis, Philetor brachypterus*), there is not enough material from the East Papuan mainland to show this one way or the other. The *Pipistrellus* case, therefore, apparently stands alone. The only case which can be interpreted as altitudinal replacement of one species by another related one is to be seen in the Molossidae. Here, there are two species (*Tadarida jobensis, T. planiceps*) that appear to be restricted to the lowlands and a third (*T. australis*), which is only known from the highlands. However, there are too few East Papuan localities for any of these species to be sure.

General Conclusions

Eastern Papua represents a peninsula of New Guinea with several groups of islands off its eastern end. Some 46 species are known from this area but a number of these are represented by very inadequate material. Thus, though eastern Papua was worked by three Archbold expeditions, supplemented by a fair amount of American Museum material from other sources, eight species which are known to occur in eastern Papua are not represented in the American Museum collections from that area. Undoubtedly a number of additional New Guinea species will eventually be found in eastern Papua. Nevertheless, some general conclusions can be made.

The East Papuan mainland is poor in highland species, probably because the highland area is relatively small and discontinuous compared to highland areas to the northwest. Of the 40 East Papuan mainland species, 18 also occur on one or more of the East Papuan islands and another is represented by a very closely related species. In regard to the relationships from the other side, nine of the 12 species of East Papuan island bats whose affinities are reasonably clear, agree best with populations on New Guinea as opposed to two for the Bismarcks and one for the Solomons. Another factor to be considered is that the level of endemism among East Papuan island bats is low. There are only two endemic species (*Dobsonia pannietensis, Kerivoula agnella*) out of a total of 24. Thus the East Papuan peninsula bat fauna is largely a depauperate sample of the main New Guinea fauna and the East Papuan island bat fauna largely a depauperate sample of the East Papuan peninsula bat fauna. In neither case can I discern any pattern as to what drops out and what remains.

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