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Taxonomic and Distributional Notes on Tropical Australian Bats

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ABSTRACT

The bats of tropical Australia are reviewed with some 51 species recognized, though a few are very poorly known. A new subspecies, *Pipistrellus tenuis westralis* is described and *Rhinolophus megaphyllus ignifer* is synonymized with *R. m. megaphyllus*. The two previously recognized subspecies of *Macroderma gigas* are also synonymized. A majority of tropical Australian bats are restricted to mesic areas, but a number are more or less arid tolerant. Only one species (*Taphozous hilli*) actually avoids mesic areas. The Cape York Peninsula has the greatest number of species with a falling off in numbers to the west and south. Of

the three areas adjacent to tropical Australia, New Guinea shares a large number of species, whereas temperate Australia and the Lesser Sunda Islands share relatively few. New Guinea has probably been an important source area for tropical Australian bats, particularly those confined to the Cape York Peninsula. The low level of endemism among Australian bats strongly implies that there were no bats in Australia prior to the Miocene, when Australia drifted far enough to the north to be able to receive species occurring on the extended Malay archipelago. Since then some low level endemism and adaptive radiation has developed in Australia.

INTRODUCTION

More than three decades have passed since Tate (1952a) published on the bats of the Cape York Peninsula. During that period, the American Museum has obtained numerous tropical Australian bat specimens, not only from already well-represented northern Queensland but also from the Northern Territory and Western Australia. The most im-

portant of these collections are those made by G. Neuhauser (1937–1938), and J. Roberts (1949–1969) in northern Queensland; R. F. Peterson (1959) in northern Queensland and northeastern Northern Territory; Rosen, Nelson, and Butler (1969) in northwestern Northern Territory and Western Australia; and by W. H. Butler (1963–1966, 1973) in

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Western Australia. With recent quickening interest in bat systematics among Australian mammalogists (see Hall, 1981, and references therein), this seems a propitious time to put on record this additional, largely unpublished material. Specimens from the Museum of Comparative Zoology (Cambridge), National Museum of Natural History (Washington), Field Museum of Natural History (Chicago), and British Museum (Natural History—London) are referred to where they provide additional taxonomic and distributional information.

I define tropical Australia in this paper as Australia north of the tropic of Capricorn, thus approximately the northern two-thirds of Queensland, all but the southernmost portion of the Northern Territory, and about the northern three-fifths of Western Australia. About 22 genera and 51 species of bats are known from within this area. This is depauperate compared to a number of other tropical areas, but it can probably be explained by three factors, the peripheral position of Australia, the small portion occupied by rain forest, and the absence of high mountains and extensive highland areas, thus contrasting markedly with New Guinea to the north. Although most species of Australian bats do occur in the tropical portion, extra-tropical species and populations are discussed only as they throw light on those to the north.

The most important ecological division of tropical Australia is the Great Dividing Range. These mountains separate a fairly narrow strip of relatively mesic habitat (with patches of rain forest) along the Pacific Ocean from the dryer areas farther west. Many species appear to be confined to this strip east of the Great Dividing Range (see maps in Hall and Richards, 1979). West of the Great Dividing Range, there are a few relatively mesic areas in the extreme north of the Northern Territory and Western Australia, but conditions become increasingly arid to the south.

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SYSTEMATICS

All six bat families known from Australia occur in the tropical north and are discussed in turn. All specimen measurements are in millimeters unless otherwise stated.

FAMILY PTEROPODIDAE

Five genera of pteropodids are known from Australia and occur north of the Tropic of Capricorn. With the exception of *Pteropus*, each is known by only a single species, at least as represented by American Museum material.

GENUS *Pteropus*: All the Australian species occur in the tropical north. Four species are well known and are treated below. The fifth (*P. brunneus*) is of uncertain status. Still known only from the type collected on Percy Island off east central Queensland, it has always constituted a problem. It is clearly

very distinct from any other Australian *Pteropus*, and, unlike any of them, is a member of the *subniger* group (called by Andersen, 1912, the *hypomelanus* group). Hall and Richards (1979, p. 13) suggest that the type of *brunneus* was an accidental windblown waif from the Louisiades, which would make the name a senior synonym of *P. hypomelanus luteus*. However, I have compared the type of *brunneus* (at the British Museum) with Louisiade specimens of *h. luteus* and the two taxa are clearly distinct, the characters Andersen (1912) gives appear to hold. The only other members of the *subniger* group, which occur on islands bordering the Coral Sea (and therefore the only members which could reasonably be blown to Percy Island) are *admiralitatum solomonis* (Solomons), *sanctae-crucis* (Santa Cruz Islands), and *o. ornatus* (New Caledonia). Of these, *ornatus* is much too large (forearm 145–152 vs. 118). Judged by Troughton's (1930) description, *sanctae-crucis* is the right size (forearm 112–121), but the dorsal side of the tibia is hairless, unlike *brunneus*, a character which Andersen (1912, pp. 90, 91) emphasized; although it should be mentioned that the species *P. admiralitatum* as presently constituted (Laurie and Hill, 1954, p. 33) contains subspecies which have tibiae either hairy (*solomonis*) or relatively hairless (*admiralitatum*, *colonus*, *goweri*). Of these members of the *subniger* group around the Coral Sea, *solomonis* seems most like *brunneus*, agreeing in hairiness of the tibia, but was keyed out by Andersen (1912, p. 91) on the basis of shorter forearm (110 vs. 118) and shorter maxillary tooth row (less vs. more than 22). Since 1912, several published (Sanborn, 1931; Sanborn and Beecher, 1947; Hill, 1971) and unpublished (American Museum series from Malaita) records of *solomonis* have appeared and these have considerably extended the range of forearm measurements, which now stands at 104–116, its upper end now closely approaching the forearm length (118) of the single specimen of *brunneus*. None of the above cited papers give any maxillary tooththrow measurements, but I have checked the American Museum material and all specimens have maxillary tooth row measurements of considerably less than 22 mm., much less than that of the type of *brunneus* (23.7). Although the Solomon

Islands appear to be the most probable source area for *brunneus* (whether regarded as the single known representative of a population or as based on an individual waif), I am unwilling to synonymize *brunneus* with *admiralitatum solomonis* since it falls outside its known size range. I am particularly reluctant to do this because *brunneus* (Dobson, 1878) is an older name than *solomonis* (Thomas, 1904) or even *admiralitatum* (Thomas, 1894) and would therefore become the name for both the subspecies and species.

Pteropus alecto: This is a widespread species, going all the way across tropical Australia from eastern Queensland to Western Australia. All Australian populations are referable to *P. a. gouldi*, which also barely gets into extreme southern New Guinea (Waithman, 1979). Other subspecies occur on various islands to the northwest of Australia. Tate (1952a, p. 610) recorded specimens from five localities on Cape York. The American Museum also has a single specimen from Normanton, northwestern Queensland, taken by R. F. Peterson in 1959. There are also numerous specimens collected by W. H. Butler (1964–1966, 1973) from five localities in northern Western Australia (Kalumburu; Mitchell River; Parry Creek; Tunnel Creek; Tambrey). The last locality is near the southern limit of the range in the west as given by Ride (1970, p. 180), but Kitchener and Vicker (1981) record the species from considerably farther south.

Pteropus conspicillatus: This is primarily a New Guinea species. The nominate subspecies (to which Australian populations belong) occupies at least the eastern half of New Guinea, another subspecies occurs in the northwest and also in the Moluccas. In Australia, *P. conspicillatus* is confined to northeastern Queensland. Two other New Guinea *Pteropus* species (*P. neohibernicus*, and *P. macrotis*) occur in Western Province, just north of Torres Strait, but do not reach Australia. Tate (1952a, p. 610) recorded *P. conspicillatus* from nine localities on the Cape York Peninsula, and the American Museum of Natural History has specimens from four other localities in the same region: Babinda Creek (H. C. Raven in 1921), Lake Barrine (G. Neuhauser in 1937); Coen (G. Neuhauser in 1938), Cooktown (J. Roberts in 1949).

Pteropus poliocephalus: This species is endemic to eastern Australia, though closely related to *P. macrotis* and *P. pohlei* of New Guinea. It is chiefly a temperate species only reaching the southeastern corner of tropical Australia (Hall and Richards, 1979, p. 11). The American Museum of Natural History has no tropical Australian specimens, the northernmost being a series from Mundubera in southeastern Queensland.

Pteropus scapulatus: This is a widespread species almost endemic to Australia, though there are relatives in the Bismarcks and Solomons. However, it is now known from extreme southern New Guinea (Waithman, 1979, p. 321) and has even been recorded as an accidental from New Zealand (Daniel, 1975). Tate (1952a, pp. 610, 611) reported this species from 10 localities in northeastern Queensland, from the northern part of the Cape York Peninsula to the southern edge of the tropical zone. Specimens were collected by J. Roberts in 1949 and 1950 from Cooktown, Flaggy, and Green Hills in the same region. There are also numerous specimens from Western Australia collected by W. H. Butler in 1963, 1965, and 1973 from the following localities: Ningbing; Parry Creek; Stockade Creek; Frazier Downs. All are in the extreme north, though the species is widely distributed in Western Australia.

Dobsonia moluccensis: The subspecies *D. m. magna* has an extensive distribution in New Guinea and other subspecies occur in the Moluccas and Bismarcks. Australian populations, which are confined to the Cape York Peninsula, also belong to *D. m. magna*. Tate (1952a, p. 611) recorded it from three localities, all in the northern part of the Cape York Peninsula. The American Museum of Natural History has no other Australian material.

Nyctimene robinsoni: Ride (1970, pp. 182, 205) has recorded *N. albiventer* from three localities in eastern Australia. However, McKean (1972b) has shown that the New South Wales record is in error and Winter and Allison (1980) have shown that this is also almost certainly true for the Queensland records. If so, then the only Australian species of *Nyctimene* is *N. robinsoni*. This bat is endemic to eastern Queensland, though the species has close relatives in the East Papuan

islands, Bismarcks and Solomons. Tate (1952a, p. 611) recorded a single specimen from the northern part of the Cape York Peninsula (Portland Roads) but the American Museum of Natural History now also has specimens from Shipton's Flat (collected by J. Roberts in 1967 and 1969), Mission Beach (by J. L. McKean in 1968), and Captain Billy Creek—"Heathlands" (by F. R. Allison in 1971). The first locality is also on the Cape York Peninsula, but I have not been able to find either of the other two localities.

MacroGLOSSUS minimus: Until recently this species was called *M. lagochilus*, but it has been recently shown (Lekagul and McNeely, 1977) that the species should be called *M. minimus*. Its range extends from the Malay Peninsula to the Solomons and south to northern and northeastern Australia. With the reallocation of the name *minimus*, there are apparently two (*m. minimus* and *m. lagochilus*) in the western part of the range (see Hill, 1983), but in the east, where it is the only species of *MacroGLOSSUS*, three subspecies were recognized by Andersen (1912). These were *microtus* in the Solomons, *nanus* in the Bismarcks and New Guinea, and *pygmaeus* in the Murray Islands of Torres Straits. The genus was then unknown from the Australian mainland. Iredale and Troughton (1934, p. 92) listed another Australian locality (Sunday Island, Western Australia) for *nanus*. Tate (1952a, p. 612) identified specimens from the Cape York Peninsula as *nanus* but gave no reasons for ignoring *pygmaeus*. McKean (1972a), noting a great deal of variation in this species in various eastern parts of its range, synonymized both *microtus* and *pygmaeus* with *nanus*. I have previously (Koopman, 1982, p. 8) discussed this problem in New Guinea and am inclined to agree with McKean's decision, though I am not at all certain that only one subspecies is present in the region. As I pointed out in (1982), some of the variation seems to be sexual (male skulls larger than females) though the small number of skulls of sexed adults makes this somewhat uncertain. In any case, if we recognize a single subspecies in Australia, in Queensland this subspecies is confined to the Cape York Peninsula east of the Great Dividing Range and west of Queensland; it is only known from very restricted areas in the far north of North-

ern Territory and Western Australia. Hall and Richards (1979, p. 19) shows the range of the species extending south to Mackay, but the Mackay specimen is actually referable to *Syconycteris australis* (see Andersen, 1912, p. 781). The only eastern Australian specimens of *Macroglossus minimus* that the American Museum of Natural History has are from the single locality (Seagren's Farm) on the Cape York Peninsula on which Tate (1952, p. 612) reported. However, from Western Australia, there are three specimens from Mitchell River collected by W. H. Butler in 1973.

Syconycteris australis: This species, as now constituted (see Koopman, 1982, pp. 8–10) is centered in New Guinea but reaches the Moluccas, Bismarcks, and Australia east of the Great Dividing Range. The nominate subspecies, the only one in Australia, though restricted to a narrow band along the coast extends well beyond the southern edge of the tropics. Tate (1952a) did not record this species, but previously (1942b, p. 346) Tate recorded six skulls only from "northern Queensland." These were collected by G. Neuhauser, probably in 1938. The American Museum of Natural History has since acquired two additional *Syconycteris* from Queensland, one obtained by J. Nelson in 1962 at Nambour, another by J. Roberts at Shipton's Flat in 1969. The first locality is in southeastern Queensland, a little to the south of the Tropic of Capricorn; the second in the southern part of the Cape York Peninsula.

FAMILY EMBALLONURIDAE

A single genus, *Taphozous*, has in recent years been recognized from Australia, but I agree with Barghoorn (1977) in treating *Saccolaimus* as a separate genus, based on distinctive skull characters and even a distinctive external one. Each genus has several Australian species and has its share of taxonomic problems.

GENUS *Taphozous*: Until recently (e.g., Ride, 1970, p. 170), two Australian species were recognized in this genus (*sensu stricto*), *T. australis* and *T. georgianus*. Tate (1952a, p. 607), however, had regarded the types of the two species in the British Museum as indistinguishable and described what earlier authors (e.g., Troughton, 1925) had called

georgianus as a new species (*T. troughtoni*). I shared this view until, after reading McKean and Price (1967), I reviewed all the Australian *Taphozous* in the American Museum of Natural History with both Troughton (1925) and McKean and Price (1967) in hand. I now agree with McKean and Price that *georgianus* is indeed conspecific with *troughtoni* rather than with *australis*. I believe that the reason why Tate (and initially I) went wrong was because in northern Queensland where the two species are in close proximity and where virtually all of Tate's material came from, the two species are most readily distinguished by size, particularly if skins and skulls are studied. *Taphozous troughtoni* was based on these large northern Queensland specimens. However, as McKean and Price (1967) pointed out, the species becomes smaller as one goes west and south and, as a result, the types of *georgianus* from southern Western Australia are much smaller than northern Queensland *troughtoni*, but agree well in size with *australis*. Recently, the problem has become much more complicated with the description of two new species, *T. kapalgensis* (McKean and Friend, 1979) from Northern Territory and *T. hilli* (Kitchenner, 1980) from Western Australia and Northern Territory. *Taphozous hilli* was compared with all previously described Australian species, but *T. kapalgensis*, though compared with *georgianus* and the Lesser Sunda *leucopleurus* (a subspecies of *T. longimanus*) was not compared with what seems to be the more closely related *T. australis*. The American Museum of Natural History has no specimens of *T. kapalgensis*, but Dr. Calaby has kindly lent me three topotypes (including the holotype) from the CSIRO collections, which I have been able to compare with American Museum specimens of the three other species. I have found four characters that are useful for distinguishing these four species and I here give the character states in what could be regarded as a random access key. Gular sac, present (*australis*, *kapalgensis*, *hilli*) vs. absent (*georgianus*); skull size, small (*hilli*) vs. medium (*australis*, *kapalgensis*) vs. medium to large (*georgianus*); sphenoid pits, narrow (*hilli*) vs. medium (*georgianus*, *kapalgensis*) vs. broad (*australis*); anterior mandibular emargination, strong

(*australis*, *georgianus*, *hilli*) vs. weak (*kapalgensis*). I believe that all four species are distinct from one another and consider them so in the following accounts.

Taphozous australis: Except for one old record from southeastern New Guinea, which is probably either accidental or erroneous, this species is endemic to Australia. Although the map in Hall and Richards (1979, p. 21) shows *T. australis* extending across the Great Dividing Range into northwestern Queensland (and apparently on into Northern Territory), all American Museum material is from northeastern Queensland (east of the Great Dividing Range) and I suspect that the more western records represent another species (probably *georgianus*). Tate (1952a, p. 609) listed nine localities for *australis*, but, using the characters that Troughton (1925, pp. 331, 332) gives, I would allocate the specimens from Quamby and Chillagoe to *T. georgianus*. The American Museum of Natural History also has specimens of *T. australis* from Cowie Bay (locality not found) collected by J. Roberts in 1950.

Taphozous georgianus: As outlined by McKean and Price (1967), Ride (1970), Parker (1973), and Hall and Richards (1979) this species has an extensive distribution across northern Australia and extends some distance south of the Tropic of Capricorn. However, the records on which this distribution was based were all published before the description of *T. kapalgensis* and *T. hilli*, so many of these records should be reexamined. Tate (1952a, pp. 605, 608) recorded this species (as *troughtoni*) from three localities in northern and eastern Queensland south of the Cape York Peninsula. However, I believe the specimens he allocated to *australis* from two localities (Quamby and Chillagoe) to be *T. georgianus*, just as McKean and Price (1967, p. 107) suspected. The American Museum of Natural History also has specimens from two other localities in Queensland (Lappa Junction and Mungana) collected by R. F. Peterson in 1959. Specimens from Lappa Junction, Chillagoe, and Mungana are interesting since they lie only a little to the west of Cooktown and Cardwell where Troughton (1925, p. 336) recorded *T. australis*. The two species here appear to have parapatric distributions corresponding to wet coastal (*aus-*

tralis) and dry interior (*georgianus*) habitats. From Northern Territory, the American Museum of Natural History has specimens from 18 mi. w. Wollogorang (collected by R. F. Peterson in 1959) and from 3 mi. n. Katherine (collected by P. Spaulding and W. Hosmer in 1960 and by A. J. Coventry in 1963). The American Museum of Natural History also has a great deal of material collected by Rosen, Nelson, and Butler in 1969 and by W. H. Butler in 1963–1965 and 1973 from the following localities in Western Australia: Kalumburu; King Edward River; Ningbing; Parry Creek; Manning Creek; Inglis Gap; Tunnel Creek; Napier Downs; Mt. Anderson; Black Elvire River; 20 mi. n. Callowa; Peawah Mundabullangana; Whim Creek; Barrow Island; Tambrey; Woodstock; 6 mi. ne. Yardie Homestead; Wittenoom Gorge; Willie Wollie Spring (ca. 20 mi. wnw. Poonda). McKean and Price (1967) tentatively recognized two subspecies, though they were evidently uncertain as to where to draw the boundary. The type locality of *T. g. trougtoni* is Mt. Isa in northwestern Queensland and that of *T. g. georgianus* is King George Sound in southwestern Western Australia (but I know of no recent records from anywhere near the alleged type locality). Although there is considerable variability, specimens in the American Museum from Queensland and Northern Territory tend to be large, thus agreeing with *troughtoni* and those from Western Australia, regardless of latitude, tend to be smaller, thus agreeing with typical *georgianus*; I allocate specimens to the two subspecies accordingly. It should be pointed out, however, that the smallest *T. georgianus* I have seen are three specimens in the National Museum of Natural History from Oenpelli in the Northern Territory. These have forearm lengths of 58–69 and condylocanine lengths of 18.5–19.4. Condylocanine lengths of the five Northern Territory skulls of *g. trougtoni* in the American Museum of Natural History are 21.2–21.7. At first I thought that these Oenpelli skulls belonged to one of the other species of Australian *Taphozous*, but except for their small size, they agree with *T. georgianus* in the characters enumerated above. Obviously more work needs to be done on geographical variation of *T. georgianus*, particularly in the Northern Territory.

Taphozous kapalgensis: McKean and Friend (1979) made no mention of *T. australis* when describing this species, and the American Museum has no specimens. However, as indicated above; after studying borrowed specimens of this species, it seems to me to be perfectly distinct.

However, it appears to be confined to what seems to be an unusually mesic area of north-western northern Territory. The dryer area between this limited area and the mesic range of *australis* is occupied only by the more arid-adapted *T. georgianus*.

Taphozous hilli: This species was described by Kitchener (1980) from a number of localities in Western Australia but was also recorded from Tennant Creek in Northern Territory from which the American Museum of Natural History also has a specimen collected by W. Hosmer in 1960. *Taphozous hilli* appears to be a perfectly good species, particularly well differentiated from the sympatric *T. georgianus*. The species is much less common than *georgianus*, since among all the Western Australian specimens in the American Museum of Natural History none are *T. hilli*. From the distribution given by Kitchener it is the most arid adapted of the Australian *Taphozous* and straddles the Tropic of Capricorn.

GENUS *Saccolaimus*: There are three Australian species of this genus, all occurring in the tropical portion and two of which are confined to it. There appear to be no taxonomic problems involving this genus within Australia.

Saccolaimus mixtus: This is chiefly a New Guinea species, but Tate (1952a, p. 606) recorded it from a single locality in the northern part of the Cape York Peninsula. There seem to be no other published Australian records.

Saccolaimus saccolaimus: In Australia until recently this species was called *S. nudicluniatus*. I agree with Goodwin (1979), however, in treating *nudicluniatus* as a subspecies of *S. saccolaimus*. The species has a wide range from India to the Solomon Islands. While the pattern of geographical variation in this species is poorly understood, New Guinea and Australian populations, together with the single Solomon Island record, may be included in *S. s. nudicluniatus*. Until recently, the species in Australia was known

only from northeastern Queensland, east of the Great Dividing Range, but McKean, Friend, and Hertog (1980) have recorded it from the same limited area of the Northern Territory from which *Taphozous kapalgensis* was described. Tate (1952a) recorded a single specimen from Babinda Creek in northern Queensland. There are no other Australian specimens in the American Museum of Natural History.

Saccolaimus flaviventris: This is a widespread endemic Australian bat, occurring both in the tropics and well to the south of the tropic of Capricorn. The map in Hall and Richards (1979, p. 21) indicates the species' occurrence throughout the Cape York Peninsula, but they show no actual records from the wet eastern coast and there are no specimens in the American Museum of Natural History from there. (A specimen was referred to by Winter and Allison, 1980, p. 34.) Tate (1952a, p. 606) recorded *S. flaviventris* from two localities in northern Queensland south of the Cape York Peninsula. The only other specimens of this species in the American Museum are from northernmost Western Australia (Ningbing and Inglis Gap), collected by W. H. Butler in 1965.

FAMILY MEGADERMATIDAE

There is only one Australian member of this small, widespread Old World tropical family. The genus is endemic to Australia.

Macroderma gigas: This species occurs across the whole of tropical Australia and also somewhat south of the Tropic of Capricorn, particularly in Western Australia. Tate (1952a) recorded this species from one central Queensland locality. The American Museum also has a specimen from the northeastern Northern Territory (18 mi. w. Wollongorang) collected by R. F. Peterson in 1959. There are a number of specimens from northern Western Australia collected by W. H. Butler in 1964, 1965, and 1973 (Kalumburu; Koolan Island; Tunnel Creek; 20 mi. s. Marble Bar). Two subspecies have been recognized, *M. g. gigas* originally described from Mt. Margaret on Wilson's River in southwestern Queensland and *M. g. saturata* from Kalumburu in northern Western Australia. The two subspecies were distinguished

(Douglas, 1962) entirely on the basis of color, among American Museum specimens only the specimens which Tate reported (from near Rockhampton) being of the dark (*saturata*) type. One of the light-colored specimens is a topotype of *saturata*. It has been in alcohol since 1964, but is much lighter than Rockhampton specimens which have been in alcohol since 1948 and agrees well with a Koolan Island specimen that has been in alcohol since 1973. Although it is indeed likely that desert populations tend to be lighter in color than those from more mesic areas, I cannot see these two color phases as distinct subspecies. Since there seem to be no other characters that correlate with the color difference I cannot see the utility of recognizing subspecies.

FAMILY RHINOLOPHIDAE

Since I include the Hipposiderinae in this family, there are three Australian genera. *Rhinonycteris* is monotypic, there are two well-marked species of *Rhinolophus*, but there are five Australian species of *Hipposideros*.

Rhinolophus megaphyllus: This, by far the commoner of the two Australian species, occurs from the Bismarck archipelago through eastern New Guinea and its islands and Eastern Australia (for the most part east of the Great Dividing Range) to Victoria. There are three quite distinct subspecies in the New Guinea region (Koopman, 1982), but Australian populations are much more uniform and (as shown below) probably only a single subspecies can be recognized. Tate (1952a) recorded the species from 19 localities in northern and central Queensland, and the American Museum of Natural History has obtained a great deal more material. With a few exceptions it likewise comes from north of the Tropic of Capricorn. First, there is a great deal of material collected by J. Roberts from 1948 to 1951 which add the following localities: Collingwood; Home Rule; Grass Tree; Helenvale; Boiling Springs, Mt. Poverty; Stucky's Gap; Wyalla; Green Hills; Aytton; Middle Normanby; Mt. Amos, Phoenician; Endeavor Bridge; Mc Ivor; Mt. Cook. I have not been able to find most of these localities but those that I have are all in the general vicinity of Cooktown or immediately

to the south of it, and I have assumed that all are in that area. In 1958 and 1959, J. L. Harrison collected specimens from Innisfail. Finally, in 1959, R. F. Peterson collected this species from Chillagoe and Lappa Junction at the base of the Cape York Peninsula and from Lyndhurst Station to the south of it. This last locality is unusually far inland, actually being on the west side of the Great Dividing Range. Two Australian subspecies have, since 1933, been recognized in this species, *R. m. megaphyllus* described from southern New South Wales, and *R. m. ignifer* from Coen in northern Queensland. The original description of *ignifer* (Allen, 1933) distinguished it entirely on the basis of color. McKean and Price (1967) have shown quite convincingly that the color characters do not hold but felt that they could distinguish the two subspecies on the basis of size (as determined by forearm length). In the course of determining the pattern of geographical variation in the New Guinea region (Koopman, 1982), I compared the two alleged subspecies in Australia and found that if anything *R. m. megaphyllus* was smaller (based on skull size) than *R. m. ignifer* (*contra* McKean and Price). My problem, however, was uncertainty as to whether I had any genuine *R. m. megaphyllus*. McKean and Price give the range of *R. m. ignifer* as Bramston Beach north and of *m. megaphyllus* as Brookfield south. Bramston Beach is near Innisfail at the base of the Cape York Peninsula but I have been unable to find Brookfield. Hall and Richards (1979), however, place the boundary at about Townsville. I have therefore done a more thorough analysis using, besides the specimens from north of the Tropic of Capricorn which I have listed, also a few from southern Queensland, northern New South Wales, and Victoria. These temperate zone specimens are all alcoholics from which I have extracted some representative skulls. I have grouped the specimens geographically as follows from north to south: Area 1 (Portland Roads, Iron Range, Pascoe River, Wenlock); Area 2 (Coen, Nesbit River, Peach River); Area 3 (Cooktown area, Laura, Mt. Finnigan, Shipton's Flat); Area 4 (Cairns, Jullattan-Mossman Road, Mt. Carbine); Area 5 (Walter Hill Range, Irvine Bank, Lappa Junction, Chillagoe, Innisfail); Area 6 (Mt. Etna, Cromarty,

Lindhurst Station); Area 7 (southern Queensland, New South Wales, Victoria). Areas 1–5 are regarded as typical *ignifer*, Area 6 as *megaphyllus* but perhaps showing intergradation with *ignifer*, Area 7 as typical *megaphyllus*. Unfortunately, the vast majority of the specimens are from Areas 1–3; the areas farther south (some of which of necessity cover great distances) are much more poorly represented. In the following, the ranges of forearm and condylocanine lengths are given for each area, forearm first and condylocanine second: Area 1 (44–48, 16.9–17.8); Area 2 (44–48, 16.8–17.5); Area 3 (44–48, 16.8–17.4); Area 4 (44–48, 17.3–17.8); Area 5 (45–47, 16.9–17.6); Area 6 (43–47, 16.6–17.0); Area 7 (47–49, 17.1–18.0). The discrepancy between my earlier (Koopman, 1982) and McKean and Price's (1967) conclusions are explained. My "typical *megaphyllus*" consisted only of Area 6 and it is apparent that this central Queensland sample tends to be smaller than populations either to the north or to the south, particularly in condylocanine length. Most if not all of McKean and Price's material of *m. megaphyllus* is from my Area 7 and does tend to run somewhat larger than their *ignifer* from Areas 1–5. Evidently there is some geographical variation along the almost 2000 mi. range of the species in Australia. However, the magnitude of this interpopulational variation is small in relation to intrapopulational variation, and morphological ranges broadly overlap. I therefore see little utility in recognizing two subspecies and would synonymize *ignifer* with *R. m. megaphyllus*.

Rhinolophus philippinensis: This species is known from several areas from the northern Philippines to northeastern Australia. In the latter country, its known distribution is restricted to a rather small area in the southeastern Cape York Peninsula, where it is represented by the endemic *R. p. robertsi*. This was as yet unknown to Tate (1952a), but was described a few months later (Tate, 1952b). Tate only mentions the type locality (Mt. Amos), but one of the original series is from Helenvale, which is probably also in the Cooktown region. The American Museum has no other Australian material of this species.

GENUS *Hipposideros*: Five species of this genus are known from Australia and all are

confined to the tropical portion. Nine species are known from New Guinea, four being shared.

Hipposideros ater: This is a widespread species of the Indo-Malayan and Australian regions. Two subspecies, *albanensis* (from Cape York) and *gilberti* (from the northern part of the Northern Territory) have been described from Australia. Both have been synonymized with *H. a. aruensis*, the New Guinea subspecies (Hill, 1963, p. 33; McKean and Price, 1967, pp. 110, 111). I have seen no specimens from the Aru Islands (the type locality of *aruensis*), but specimens from the Western Province of Papua should be quite similar. Specimens from this latter area have been compared with those from Cape York and I can see no consistent differences. I would agree that *albanensis* should be retained in the synonymy of *aruensis*, but I am not at all certain whether I can agree with McKean and Price in synonymizing *gilberti* with *aruensis*. The western subspecies was distinguished on both size and color. Hill (1963) believed that the two subspecies could not be separated on size and his histograms of forearm measurements (p. 32) support this. McKean and Price (1967) believe that the variation of their northern Queensland material overlapped *gilberti* in both size and color and again, at least as far as size is concerned, their histograms of forearm measurements bear this out. I find this puzzling since the specimens I have seen do not show this. A series of 11 Queensland forearms (from three localities, including Bramston Beach where McKean and Price's specimens came from) have lengths of 38–41. Four skulls, including one from the smallest of these have condylocanine lengths of 13.5–14.2. In contrast, seven forearms from the Northern Territory (including specimens in the National Museum of Natural History and CSIRO, one of them the type of *gilberti*) measure 35–38 and available skulls have condylocanine lengths of 13.2 to 14.1. So far, this shows considerable overlap and would support McKean and Price. Western Australian specimens I have seen, including those at the Field Museum of Natural History, show greater difference from Queensland specimens. Their forearm lengths are 35–37 and condylocanine lengths are 12.2–12.6. I can-

not judge the color difference since most specimens in the American Museum of Natural History are or have been in alcohol for a significant length of time (though the few I have seen do indicate a color difference). The size difference (at least as far as Western Australian specimens are concerned) is great enough so that I considered the possibility that *gilberti* is actually a representative of the Indo-Malayan *H. cineraceus*. Hill (1963, pp. 24, 35–36) distinguishes *ater* from *cineraceus* by two characters, the presence of a dorsal process on the zygomatic arch and the extrusion (more or less) of the anterior upper premolar from the toothrow. The former character seems to hold, though in many skulls the delicate zygomatic arch is broken at that point, but not the latter character. Comparing *cineraceus* skulls from Malaya with *ater* from Australia and New Guinea, I see a great deal of variation in the placement of the anterior upper premolar, but no clear-cut difference between the two species. All *gilberti* skulls available, which have the zygomatic arch intact, do have a small but definite dorsal process and should therefore be referred to *H. ater*. This then is the problem. If I knew only the Queensland and Northern Territory populations, I would be inclined to follow McKean and Price (1967) in synonymizing *gilberti* with *H. a. aruensis*. On the other hand, if *gilberti* had never been described, I would have no hesitation in recognizing the Western Australian populations as a different subspecies from those of Queensland and considering the Northern Territory populations as intergrades. The Northern Territory and Western Australian populations are probably continuous, whereas the Queensland populations (not known from west of the Great Dividing Range) are geographically separate. Rather than synonymizing *gilberti* with *aruensis* and then describing the Western Australian populations as a separate subspecies, I tentatively associate these with *gilberti*, recognizing that the typotypical population is in the intergrade area between *H. ater gilberti* and *H. ater aruensis*. Tate (1952a) recorded *H. ater* (under the name of *H. bicolor albanensis*) only from Lockerbie at the tip of Cape York. The American Museum also has specimens of *H. a. aruensis* from Shipton's Flat collected by J. Roberts in 1950, 1952,

and 1967 and from Bramston Beach collected by J. L. Harrison, all in Queensland. There are specimens of *H. a. gilberti* from near Katherine in the Northern Territory (collected by W. Hosmer in 1960) and from Koolan Island in Western Australia (collected by W. H. Butler in 1965). In Western Australia, the species is only known from the far north (Kimberley).

Hipposideros cervinus: This is the species which until recently was called *H. galeritus*. However, Jenkins and Hill (1981) have demonstrated sympatry between two members of this complex in Borneo and have therefore separated the more eastern species as *H. cervinus*, which still has a wide range extending from Sumatra to the New Hebrides. Virtually the entire range in the Australian region is included in *H. c. cervinus* which, however, in Australia is confined to the Cape York Peninsula and adjacent islands. Tate (1952a) recorded this species from five localities in the Cape York region. The American Museum of Natural History has no other specimens from Australia.

Hipposideros semoni: Tate (1952a) listed this as a subspecies of the New Guinea *muscinus*, but Hill (1963, pp. 82, 86) separates them on the specific level and I am inclined to agree with him. The main distribution is in New Guinea where it has a wide range. In Australia, however, it is confined to northern Queensland east of the Great Dividing Range. Tate (1952a) recorded it from four localities and the American Museum has no material from any others.

Hipposideros stenotis: This species is endemic to Australia but is closely related to and allopatric with *H. semoni* so the two could be included in the same superspecies. (I agree with Hill, 1963, that they should be retained as separate species.) The species occurs across the dryer portions of tropical Australia from northwestern Queensland to northeastern Western Australia. Tate (1952a) did not record it but the American Museum of Natural History has four specimens collected by R. F. Peterson from 18 mi. w. Wollongorang in the northeastern Northern Territory in 1959 which are the basis for one of Parker's (1973, p. 35) records.

Hipposideros diadema: This is another widespread species ranging from southeast-

ern Asia to the Solomon Islands. Two Australian subspecies have been described, *H. d. reginae* from the Cape York Peninsula and *H. d. inornatus* (McKean, 1970a; McKean and Hertog, 1979) from the northwestern Northern Territory. The American Museum has no specimens of the latter subspecies but Dr. John Calaby has very kindly lent me two paratypes. Comparison of these with *d. reginae* shows that whereas *reginae* is one of the larger subspecies, *inornatus* is one of the smallest (condylobasal length 26.4–28.7 vs. 23.9). I have previously (Koopman, 1982, p. 16) discussed the problem of the patchwork of large and small subspecies in this species. Although its subspecific taxonomy is chaotic, the two Australian subspecies seem well differentiated from each other. Neither has any close affinity with the still larger *H. d. diadema* of the Lesser Sundas. Tate (1952a) recorded *H. diadema reginae* from three localities on the Cape York Peninsula. The American Museum of Natural History also has specimens from Shipton's Flat (collected by J. Roberts in 1951 and S. Breeden in 1962) and from Chillagoe (collected by R. F. Peterson in 1959).

Rhinyonycteris aurantius: This (for emended spelling see Hill, 1982) is one of the only two endemic Australian genera (the other being *Macroderma*). Confined to tropical Australia but, like *Hipposideros stenotis*, *R. aurantius* is absent from the east coast yet avoids the desert. Like *H. stenotis*, *R. aurantius* ranges from northwestern Queensland to northeastern Western Australia, but also occurs farther to the southwest in Western Australia (Pilbara). Tate (1952a) did not record this species, but the American Museum of Natural History has specimens from near Katherine in the Northern Territory collected by P. E. Aitken in 1966 and from Koolan Island in Western Australia collected by W. H. Butler in 1965.

FAMILY VESPERTILIONIDAE

Nine genera of this cosmopolitan family have been recorded from Australia and all are known from north of the Tropic of Capricorn. All but *Murina* and *Kerivoula* have more than a single Australian species and must be discussed as genera before individual species are taken up.

GENUS *Myotis*: Two species of *Myotis* have been recorded from Australia, the well-known *adversus* (treated below) and *australis* (known only by the type specimen that was supposed to have been collected near Sydney, New South Wales). The latter (unlike *adversus*) is a member of the subgenus *Selysius*. Except for *insularum* of Samoa (likewise known only from the type and of dubious status), the only species of *M. (Selysius)* known from Celebes and the Lesser Sundas eastward is *M. muricola* (formerly erroneously included in *M. mystacinus*, but see Koopman, 1982, p. 17; Hill, 1983, also recognizes *ater* as a distinct species in Celebes and the Mentawai Islands). This species probably does not occur east of the Moluccas (see Koopman, 1982, p. 17) which makes the status of *australis* (and *insularum*) highly uncertain. I previously believed that both were based on mislabeled material. However, the Field Museum has a single specimen (FMNH 120121) collected at Geikie Gorge (Kimberley region), 3 December 1976, by L. E. Schiller. The specimen is a female, in alcohol with the skull removed, with the following measurements: forearm (35), hindfoot (9), ear from notch (13), condylobasal length (11.9), maxillary tooth row (4.5), width across last molars (4.8). These skull measurements compare with an unusually small specimen of *M. m. muricola* from Bali (AMNH 107523), the most similar specimen I could find, with the following: condylobasal length (12.6), maxillary tooth row (5.0), width across last molars (5.3). The two skulls also differ in the less-reduced middle upper premolar and relatively more inflated braincase of the Geikie Gorge skull as compared with that of the Bali skull. This is shown by the mastoid width, which in spite of the considerable difference in skull length is only slightly smaller (6.8 vs. 6.9). A comparison of the Geikie Gorge specimen with information concerning the type specimen of *australis* (Dobson, 1978, pp. 317, 318; Tate, 1941a, p. 555; Husson in McKean, 1970b) is obviously in order. (Hill, 1983, regards *australis* as a possible synonym of *M. ater*.) In qualitative characters (post-calcaneal lobe on the calcar, tragus shape, size and position of the middle upper premolar) the two are quite similar. However, in the few measurements that can be taken on the type of *aus-*

tralis (the skull is in fragments) the specimen is clearly considerably larger than that from Geikie Gorge: forearm (39 vs. 35), maxillary tooth row (5.8 vs. 4.5). I am therefore reluctant to refer the Geikie Gorge specimen to *M. australis*, though, if the type of the latter did come from New South Wales, the Geikie Gorge specimen could represent a small northwestern geographical variant. Without more material I hesitate to describe it as new. The specimen was identified in the field as *Eptesicus douglasi*, so *Eptesicus* from northern Western Australia (and elsewhere) should be scrutinized with care. In this paper the Geikie Gorge specimen is henceforth referred to as *Myotis* sp. (near *australis*).

Myotis adversus: This species (a member of the subgenus *Leuconoe*) has an extensive range from Sumatra to the New Hebrides and its subspecies, *M. a. macropus* (confined to Australia) likewise has a broad distribution from extreme northeastern Western Australia around the northern and eastern coasts to southeastern South Australia but apparently nowhere extending far inland. Tate (1952a) recorded it from Cairns on the Cape York Peninsula. The only other American Museum material of this species from Australia is a series collected by W. H. Butler in 1973 at Mitchell River in the Kimberley region of Western Australia.

GENUS *Pipistrellus*: Three species have been recorded in Australia. By far the most distinctive is the large *P. tasmaniensis*, one of the few species of bats which appears to be confined to the southern half of Australia. Its northernmost known occurrence is in extreme southeastern Queensland and all American Museum specimens are from southwestern Western Australia. *Pipistrellus tenuis* is now fairly well known from tropical Australia and is discussed below. The third species, *P. javanicus*, has an extensive distribution from southeastern Siberia to Java, Celebes, and perhaps the Aru Islands (see Hill, 1983), but the only Australian record is provided by two specimens in the British Museum without definite locality. I have examined these specimens and can vouch for their identity as *P. javanicus*. However, the status of this species in Australia (assuming that the two specimens are not mislabeled as to locality) is not clear.

Pipistrellus tenuis: I have previously (Koopman, 1973) discussed my concept of this species and indicated its distribution in a general way. It has an extensive range from southeastern Asia to the New Hebrides, but there are only a few records from Australia. Tate (1952a, p. 598) recorded the species (under the name *papuanus*) from three localities, all in the northern part of the Cape York Peninsula. Hall and Richards (1979, p. 41) show the species extending south to Townsville. The American Museum of Natural History also has a few specimens collected at Cape Bossut in northern Western Australia by Nelson, Butler, and Rosen in 1969. McKean and Price (1979) mention another northern Western Australian locality and give measurements for another Cape York specimen. Most importantly, they record *P. tenuis* from two localities in the Northern Territory. One (Port Essington) is on the northern coast, approximately equidistant from the Cape York and Western Australian records. The other (Thring Creek) according to the coordinates they give should be in the arid southern part of the Northern Territory. Dr. John Calaby, however, assures me that this is in error and that Thring Creek is actually just south of Van Diemens Gulf (12°14'S, 131°54'E) and therefore also in coastal Northern Territory. The skulls of the American Museum specimens fall into two rather different morphological groups, according to whether they come from Queensland (given as the first range of measurements) or Western Australia (as the second range as given below). I see no difference in the condylobasal lengths (10.9–11.1 vs. 10.7–11.2), but for maxillary tooth row lengths (3.9–4.1 vs. 3.6–3.7) and widths across the last molars (5.1–5.2 vs. 4.6–4.9), there is clearly a difference. Thus, it would appear that the Western Australian specimens differ from those in Queensland by their relatively smaller rostra (fig. 1). McKean and Price (1978) give skull measurements for one specimen from Cape York and two from Thring Creek (the Port Essington specimen unfortunately is represented only by external measurements). Measurements for their Cape York specimen agree well with those in the American Museum. Dr. John Calaby has very kindly lent me the two Thring Creek skulls from the CSIRO col-

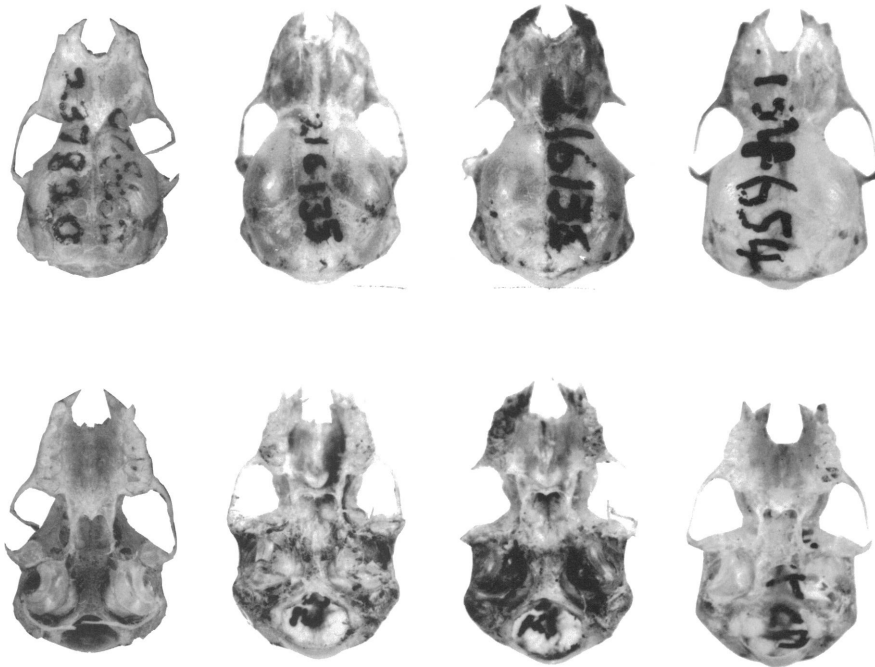


FIG. 1. Skulls of *Pipistrellus tenuis*, dorsal (above) and ventral (below) views from left to right: AMNH 237820 (adult male from Taibesse, Timor); AMNH 216135 (adult male from Cape Bossut, Western Australia, holotype of *westralis*); AMNH 216136 (adult female from Cape Bossut, Western Australia); AMNH 154654 (adult male from Brown's Creek, Queensland). Approximately $\times 3$.

lections and my measurements for both are: condylobasal length (10.8), maxillary tooth length (3.7), width across last molars (5.0). As with those from Queensland and Western Australia, there is no difference in condylobasal length, but in maxillary tooth row length, they clearly agree with those from Western Australia, whereas in width across the last molars, they are intermediate. Therefore the Queensland specimens (fig. 1) are clearly referable to *P. t. papuanus* and have New Guinea affinities. Those from Northern Territory are probably intergrades but agree better with those from Western Australia. These in turn, however, most closely resemble in their skull proportions specimens from the lowlands of Timor (Dili and Djamplong) as represented in the American Museum of Natural History, the Rijksmuseum van Natuurlijke Historie in Leiden, and the Zoologisches Museum der Humboldt Universität in Berlin. Finally, these intergrade with the subspecies in Celebes, Lombok, and the Timor

highlands (Bonleo) to which the name *P. t. sewelanus* is applicable. I believe that the Western Australian population is most closely related to *P. t. sewelanus*, but it is much smaller and therefore should not be included in this subspecies. I believe that the best way to express the phenetic and phylogenetic relationships of this form is to describe it as new.

***Pipistrellus tenuis westralis*,
new subspecies**

HOLOTYPE: AMNH 216135, an adult male collected by Gareth J. Nelson, W. H. Butler, and Donn E. Rosen on 15–16 April 1969 at Cape Bossut (ca. 18°40'S, 121°30'E), Western Australia. The holotype consists of an entire specimen preserved in alcohol with the skull extracted and cleaned.

DIAGNOSIS: A small subspecies of *Pipistrellus tenuis* (forearm length 27–30; condylobasal length 10.7–11.2), thus being smaller

than *P. t. collinus* or any but intergrade (lowland Timor) populations of *P. t. sewelanus*. It differs from *P. t. murrayi*, *P. t. nitidus*, *P. t. sewelanus*, *P. t. angulatus*, and *P. t. poncetii* in its shorter (3.6–3.7) maxillary tooth row. It differs from the vast majority of *P. t. papuanus* (including those from Cape York) in its combination of a shorter maxillary toothrow with a narrower width across the last molars (4.6–5.0). I know of no way to distinguish *P. t. westralis* from the geographically distant *P. t. tenuis*. Specimens from the lowlands of Timor (forearm length, 27–29; condylobasal length, 10.6–11.4; maxillary tooth row length, 3.8–4.2; width across last molars, 4.9–5.2), while probably best referred to *P. t. sewelanus*, show intergradation with *P. t. westralis*. Specimens from the Northern Territory (see measurements above) are probably best referred to *P. t. westralis* but show intergradation with *P. t. papuanus*.

ETYMOLOGY: The name refers to Western Australia.

LOCALITY RECORDS: I have only seen the type and three topotypes from near the type locality: AMNH 216134–216137, alcoholics, skulls extracted and cleaned for 216135 and 216136. Almost certainly the specimen from Roebuck Bay (referred to by McKean and Price, 1978), however, *ca.* 60 mi. ne. Cape Bossut is referable to this subspecies, as are those from the Pender area of the Dampier Peninsula (see McKenzie, 1983, p. 50). I would also refer specimens from Smith Point and Thring Creek in the northern part of the Northern Territory to *P. t. westralis*, but they show intergradation with *P. t. papuanus*.

GENUS *Eptesicus*: Prior to 1976, only one species of *Eptesicus* had generally been recognized in Australia (e.g., Ride, 1970). However, in the next two years (Kitchener, 1976; McKean, Richards, and Price, 1978), two new species were described and two additional named forms that had been put in the species synonymy of *E. pumilus* were resurrected as full species. The five species now recognized are all closely related and confined to Australia (including Tasmania and Lord Howe Island) and are widely separated geographically from the nearest other *Eptesicus* in southern Thailand, *E. demissus*. (The Malayan species that Kitchener (1976) refers to has since been transferred to *Philetor*; see Hill,

1966.) Furthermore, none of the southeastern Asian *Eptesicus* seem to be particularly closely related to any of the Australian *Eptesicus*, which can be viewed as constituting an endemic radiation. While there have been several subsequent papers which have dealt with these species (Kitchener and Halse, 1978; Carpenter, McKean, and Richards, 1978; Hall and Richards, 1979), the distinctions are none too clear and indeed seem to be rather subtle. Fortunately, the American Museum has at least some material of each of these five species and this has been of great help in evaluating their differences. Unfortunately, the American Museum has no *Eptesicus* from southeastern New South Wales, the one area where apparently four of the species occur in close proximity. I have been forced to use widely allopatric specimens which I am assuming represent these four species in southeastern New South Wales. As a result I have tried to evaluate them using the following skulls: one *vulturinus* from Victoria; eight *regulus* from southwestern Western Australia; one *sagittula* from Tasmania; 13 *pumilus* from northeastern Queensland (Cooktown area). Besides size, the principal skull character used by McKean, Richards, and Price (1978) and Carpenter, McKean, and Richards (1978) is the slope of the forehead, distinguishing a “cave dweller” (with an abrupt forehead) from a “forest dweller” (with a gradually sloping forehead). *Eptesicus pumilus* (along with the Western Australian *E. douglasi*) has the “cave dweller” skull, whereas *sagittula*, *regulus*, and *vulturinus* have “forest dweller” skulls. Comparing actual skulls of the four species, I find the slope character quite subtle, but nevertheless see fairly marked differences in skull shape between these two types. To me, however, this is better shown by rostral proportions, best seen in palatal view. *Eptesicus vulturinus*, *E. regulus*, and (to a lesser extent) *E. sagittula* have long narrow rostra, whereas *E. pumilus* (and also *E. douglasi*) have shorter, broader rostra. This is probably associated with differences in feeding habits, the “forest” type being better equipped for feeding on soft insects (such as moths) and the “cave” type for hard insects (such as beetles). (See Freeman, 1979, for a discussion of some of the associated adaptations.) Within the “forest” group

the single *vulturinus* skull is smaller than any of my *regulus* skulls, whereas the *sagittula* skull is near the maximum size for the *regulus* series. Outside of southeastern mainland Australia, there are rarely more than two sympatric species and in each case they are clearly different in size. Thus in Tasmania, the large *sagittula* occurs with the small *vulturinus*, in southern Western Australia, the larger *regulus* occurs fairly close to, and perhaps in contact with, the small *pumilus caurinus*, though Kitchener and Vicker (1981) also list the small *vulturinus*. The relationship between the large *douglasi* and the small *pumilus caurinus* in northern Western Australia and Northern Territory is discussed below. Of the five Australian species, *vulturinus*, *regulus*, and *sagittula* are all confined to the southern part, south of the Tropic of Capricorn, though *vulturinus* has recently been recorded (Thompson, 1982) from just south of it in the Northern Territory. Only *pumilus* and *douglasi* require separate treatment.

Eptesicus pumilus: This is by far the most widespread of all the Australian *Eptesicus*, extending over the entire continent except for the southern edges. Even though it reaches the tip of Cape York near Somerset (AMNH 155012), *Eptesicus* has never been recorded in New Guinea. Neither McKean (1972) nor Waithman (1979) record *Eptesicus* from there and I have checked all specimens identified as *Pipistrellus* (the genus most likely to be confused with *Eptesicus*) from Western province (Papua New Guinea) and southeastern Irian Jaya (the parts of New Guinea closest to Cape York) and all are indeed *Pipistrellus tenuis*. Over most of tropical Australia, *E. pumilus* is the only *Eptesicus*. Tate (1952a, p. 599) recorded this species from eight localities (the Pentland and Quamby specimens having been collected by G. Neuhauser in 1948). However, Tate omitted another locality (Lockerbie) which was worked by Tate and Van Deusen in 1948, though this is the northernmost locality for *Eptesicus* in Australia. In 1950 and 1951, J. Roberts collected specimens from Helenvale and China Camp, two localities south of Cooktown. Finally, in 1959 R. F. Peterson collected specimens at Lappa Junction, Mungana, and Koombooloomba Creek (30 mi. s. Ravenshoe). From the Northern Territory, the American Mu-

seum has a number of specimens collected from the vicinity of Katherine by Spalding and Hosmer (1960), J. Owen (1962), and A. J. Coventry (1963). W. H. Butler collected numerous specimens from tropical Western Australia at the following localities: Kalumburu (1965); Parry Creek (1965); Koolan Island (1973); King Edward River (1973); Inglis Gap (1965); Napier Range (1973); Tunnel Creek (1973); 20 mi. north of Callowa (1973); Peawah, Mundabullangana (1963); Whim Creek (1963); Woodstock Station (1963); Tambrey (1964, 1973); Wittenoom Gorge (1973); Nodswell Creek (1963); Yardie Homestead (1963); Barrow Island (1964, 1966, 1967); Hermite Island, Montebello Group (1966). Two subspecies of *E. pumilus* are currently recognized (McKean, Richards, and Price, 1978), *p. pumilus* in eastern Queensland (and New South Wales), *p. caurinus* in western Queensland, Northern Territory, and Western Australia. These are distinguished on size and bacular form. Judged by the distribution map in McKean, Richards, and Price (1978), only the Quamby and Mount Isa specimens among the Queensland material at the American Museum are referable to *E. p. caurinus*. All others are *E. p. pumilus* and I have listed them accordingly. I have not examined any bacula, but I do note that among these eastern Queensland specimens referred to *p. pumilus* there is considerable variation in size, some of which is geographical. The largest specimens (which I have used in the above-mentioned comparisons with other species) are from the Cooktown area (condylobasal length 11.9–12.7). Specimens from localities farther south (and mostly farther inland (Koombooloomba Creek, Mungana, Pentland) are clearly smaller (condylobasal length 11.2–11.9) and closely resemble specimens from Mount Isa and Quamby referred to *E. p. caurinus* (condylobasal length 11.2–11.7). This suggests intergradation between the two, but it must also be pointed out that the few specimens from north of Cooktown (Iron Range, Lockerbie) are also small (condylobasal length 11.0–11.7) and it is difficult on geographical grounds to interpret these as intergrades. In any case, most of the Cooktown specimens were evidently not available to Tate (1952a) when he wrote his paper, therefore it is not surprising

that he referred all northern Queensland material to *E. p. caurinus*. The specimens from Northern Territory (Katherine, together with specimens at the National Museum of Natural History from Groote Eylandt, Oenpelli, and 170 mi. e. of Darwin) are typical *caurinus* (condylobasal length 10.8–11.5) as are specimens from northeastern Western Australia (Parry Creek, Inglis Gap, Kalumburu, Koolan Island, Tunnel Creek, Napier Range). These specimens are, in fact, unusually small (condylobasal length 10.3–11.0) and are important in two respects; they come from the region of the type locality of *caurinus* (Drysdale), and they are more or less sympatric with *E. douglasi* (see below for details). Specimens from the Pilbara area to the southwest (Peawah, Tambrey, Woodstock) are larger (condylobasal length 11.0–11.6) as are the few that I have seen from south of the Tropic of Capricorn (Kurara) in Western Australia (condylobasal length 11.6–11.8). By far the largest Western Australian specimens I have allocated to *E. pumilus*, however, come from extreme northwestern Western Australia (Yardie Homestead on the Northwest Cape, Barrow Island, and Hermite Island in the Montebello group). With condylobasal lengths of 11.5–12.5, I thought it necessary to compare these with the three other relatively large Australian *Eptesicus* outside of southeastern Australia; they are *regulus* from southern Western Australia, *douglasi* from northeastern Western Australia (Kimberley), and *p. pumilus* from eastern Queensland (particularly the Cooktown area). The large northwestern Western Australian population is clearly not *regulus*, using the character mentioned above. However, I cannot distinguish it from either *douglasi* or *p. pumilus*. These two taxa have never been satisfactorily distinguished. Kitchener (1976), compared three bacula of *douglasi* with five bacula identified as *p. pumilus*, three from the eastern Pilbara and two from Yardie Homestead (one of which was figured). McKean, Richards, and Price (1978), on the other hand, do not agree that these five specimens are *p. pumilus* since their bacula are somewhat different from eastern Australian specimens and imply that Kitchener's *pumilus* are all *p. caurinus*. I would agree that this is probably true for the eastern Pilbara specimens but not for those

from Yardie Homestead. In view of the fact the Kitchener (1976) referred Yardie Homestead specimens to *E. pumilus* and because Pilbara specimens (and those from farther south) seem to show intergradation, I am allocating specimens from Northwest Cape, Barrow, and the Montebello Islands to *E. pumilus*, but leave them unidentified as to subspecies. I cannot fit them into *p. caurinus*, allocation to *p. pumilus* seems ruled out on the basis of geography and bacular morphology, and description of a new subspecies should only be done after a thorough revision of *E. pumilus* (and perhaps all Australian *Eptesicus*) throughout the continent. I am not in a position to do this because of inadequate material from many areas.

Eptesicus douglasi: This recently described species (Kitchener, 1976) has only been recorded from the Kimberley area (northeastern Western Australia), but the National Museum of Natural History has two specimens from northeastern Northern Territory that I would refer to this species. These were identified by Johnson (1964) as *E. pumilus caurinus* but the condylobasal lengths (11.9, 12.1) lie well outside the range of Northern Territory *p. caurinus*, but within that of Western Australian *douglasi*. All American Museum specimens were collected by W. H. Butler at only four localities: Inglis Gap (1965), Mt. Anderson (1965, 1973), Derby (1973), Langey Crossing (1965). At Inglis Gap it was found sympatric with *E. pumilus caurinus*, but at Mt. Anderson, Derby, and Langey Crossing it occurred alone. Kitchener (1976) recorded *E. douglasi* from Tunnel Creek (the type locality), but the two American Museum *Eptesicus* from this locality are clearly *E. pumilus caurinus*. Specimens of *E. douglasi* (including the two National Museum specimens from Cape Arnhem) are clearly larger than Kimberley *pumilus caurinus* (condylobasal length 11.5–12.1 vs. 10.3–11.0), but there is some overlap with *pumilus* from farther to the southwest and complete overlap with the Northwest Cape and island populations. My only reason for associating the latter populations with *E. pumilus* specifically, rather than with *E. douglasi*, is that these northwest populations intergrade with *pumilus caurinus* (in the Pilbara), but *E. douglasi* occurs sympatrically (without inter-

gradation) in the Kimberley. The two species may also be sympatric in the Northern Territory, but the known localities are quite separate. Thus the picture as I see it is of two species of *Eptesicus* in tropical Australia. *Eptesicus pumilus* extends across the entire continent with marked geographical variation, but with the large far eastern and far western infraspecific forms connected by intergrades with a small subspecies that spans the intervening area. *Eptesicus douglasi* has a limited range clearly distinct from the populations of *E. pumilus* sympatric with it, but probably not distinguishable from the species as a whole. How this situation arose is unclear to me at present.

GENUS *Chalinolobus*: In the restricted sense, this genus is confined to Australia, southern New Guinea, Norfolk Island, New Caledonia, and New Zealand. However, I have previously (Koopman, 1971) treated the African *Glauconycteris* as a subgenus of *Chalinolobus*. Of the six currently recognized species of the subgenus *C.* (*Chalinolobus*), only the New Zealand *tuberculatus* does not occur in Australia. Of the remaining five, only *dwyeri* (of which I have seen no specimens) fails to reach tropical Australia (though *pictus* barely gets across the Tropic of Capricorn). These four species are therefore the ones treated below.

***Chalinolobus nigrogriseus*:** There is little to add to what has already been said by Van Deusen and Koopman (1971). Tate (1952a) recorded this species (under the name of *rogersi*) from two localities. The American Museum has specimens from two other Queensland localities, 24 mi. s. Burketown collected by R. F. Peterson in 1959 and Karumba by G. Pawlowski in 1961. Two Northern Territory localities are also represented, 18 mi. w. Wollagorang by R. F. Peterson in 1959 and 12 mi. e. Coolibah by Nelson, Butler, and Rosen in 1969. In tropical Western Australia, W. H. Butler collected the species at three localities, Ningbing and Parry Creek (1965), and with Nelson and Rosen at North Creek (1969), all in the Kimberley region. Van Deusen and Koopman (1971) combined western *rogersi* with eastern *nigrogriseus* (which had previously been treated as a subspecies of *C. pictus*) and drew the line between the two subspecies at the southwestern

base of Cape York (as is done here). However, they pointed out that all specimens from northwestern Queensland could be regarded as intergrades. Van Deusen and Koopman (1971) believed that the gap in the recorded range of *C. n. nigrogriseus* between northern and extreme southeastern Queensland was an artifact of collecting, but the map in Hall and Richards (1979) shows the gap still essentially unfilled and they imply that the species is now extinct in this isolated southeastern portion of its range.

***Chalinolobus pictus*:** Again, there is little to add to the information in Van Deusen and Koopman (1971) except that the species is now also known from South Australia (Hall and Richards, 1979). Confined to eastern Australia, west of the Great Dividing Range, it is known from four localities just north of the Tropic of Capricorn. The only specimens in the American Museum of Natural History, however, are from farther south in southwestern Queensland (Birdsville) and northwestern New South Wales.

***Chalinolobus morio*:** The overall distribution of this species (which is confined to Australia, including Tasmania) is unclear to me. Hall and Richards (1979) show the species with a fairly extensive range in eastern Australia (mostly east of the Great Dividing Range) as far north as the Townsville area. Parker (1973) shows the distribution in the Northern Territory as confined to the far south, not extending north of the Tropic of Capricorn. Hamilton Smith's (1966) map shows it confined to localities south of 30 degrees in Western Australia, but he maps only cave occurrences and in some parts of its range it is a tree-dwelling bat. Ride (1970) gives the range only as "Southern Australia, including Tas.," but none of the localities listed by Kitchener and Vicker (1981) are north of 28 degrees. Therefore, I know of no records north of the Tropic of Capricorn except for the central Queensland ones given by Hall and Richards (1979). All American Museum specimens are from farther south in southeastern Queensland (Bunya Mountains), Tasmania, and southwestern Western Australia (Busselton, Contine).

***Chalinolobus gouldii*:** This is the most widespread species in the subgenus *Chalinolobus*, occurring over most of continen-

tal Australia, Tasmania, Norfolk Island (Troughton, 1967), and New Caledonia (Koopman, 1971). Tate (1952a) does not record this species, whose distribution stops just short of the Cape York Peninsula. The American Museum has specimens collected by G. Neuhauser in 1938 from two localities in northcentral Queensland (Pentland; Malbon). From Western Australia there are specimens collected by W. H. Butler from La Grange Dam (1963) and Inglis Gap (1965) and in 1969 Nelson, Butler, and Rosen collected specimens from Cape Bossut. All specimens I have seen from tropical Australia belong to the small northern *C. g. venatoris*, and the contrast in size between northern Queensland specimens on one hand and those from New South Wales and South Australia on the other is striking. I have seen only three specimens from the Northern Territory all in the National Museum of Natural History, but Parker (1973, p. 37) refers specimens from the northern part of the territory to *C. g. venatoris*, and quotes McKean to the effect that those from the southern part are intergrades with *C. g. gouldii*. The single specimen I have seen from Darwin (USNM 237954) in the far north is referable to *g. venatoris* (condylobasal length 14.1). On the other hand, specimens from near Alice Springs (USNM 284187) and the Horsehoe Bend of the Finke River (USNM 284188), both in the far south, are indistinguishable from southern Australian specimens of *g. gouldii* (condylobasal length 14.7, 15.4). In Western Australia, specimens from the three northern localities are definitely *venatoris*. The largest of these (a skull extracted from the largest of the alcoholics from Cape Bossut) has a condylobasal length of 14.2. This is the same as the smallest skull I have seen from southern Western Australia (150 mi. n. Geraldton), which was likewise extracted from the smallest of a large series of alcoholics. Other Western Australian localities for *C. g. gouldii* (as represented by American Museum material) are Lake Nabberu and Gandak. I have seen no specimens of *C. gouldii* from between Cape Bossut and Lake Nabberu. If *C. gouldii* occurs in this intervening area (as according to Bannister, 1969, pp. 67, 69, and Kitchener and Vicker, 1981, it does) this is where intergrades would be expected.

GENUS *Nycticeius*: I have previously (Koopman, 1978) discussed the status of this genus and its species in Australia. Except for one species that also occurs in New Guinea, all are endemic to Australia (not including Tasmania) and are widely separated geographically from other species of the genus in Africa (including extreme southwestern Asia) and North America (including Cuba). The Australian species fall into two groups, the large *rueppelli* (subgenus *Scoteanax*) and the smaller taxa (subgenus *Scotorepens*). There has never been any problem as to the identity of *rueppelli* on a species level, but there has been much disagreement as to how many species of *N. (Scotorepens)* to recognize. Estimates have gone from five (McKean, 1966) to two (Ride, 1970). In 1978, I examined this problem (Koopman, 1978) and came to the conclusion that three should be recognized. In view of continued disagreement with this point of view, I have reexamined the pattern of species and population relationships to see how, if possible, the problems can be resolved.

Perhaps the best way to approach this problem is geographically, starting in Queensland, where the greatest complexity exists, particularly if one adopts the five species hypothesis (Hall and Richards, 1979). The largest taxon is *inflatus*, which I previously (Koopman, 1978) recognized as one of three valid species. I have seen only two specimens, both males from central Queensland, the type from Prairie in the British Museum (BM) and one from 20 mi. s. Mt. Isa borrowed from the Commonwealth Scientific and Industrial Research Organization (CSIRO) in Canberra. The skulls have condylobasal lengths of 14.8 and 15.2 and since females tend to be larger than males in *N. (Scotorepens)*, females would be expected to be even larger. Hall and Richards (1979) map additional localities from both north (Cooktown area) and south (southcentral Queensland) of Prairie and Mt. Ida. The next largest named species is *balstoni*. I have seen only two Queensland specimens (CSIRO), both from Mt. Pluto (near Tambo). The male has a condylobasal length of 14.4, the female, 14.5, both significantly smaller than the two *inflatus* I have measured. Hall and Richards (1979) state (p. 51) that *balstoni* reaches the

coast near Rockhampton, but their map shows this taxon confined to the area west of the Great Dividing Range and south of the Tropic of Capricorn. McKean (1966) suggests that *inflatus* is conspecific with *balstoni*. This hypothesis should be quite testable since the maps in Hall and Richards (1979) show the two species in close proximity in southern Queensland, where they should intergrade if conspecific. Currently recognized in coastal Queensland are two taxa, which are smaller than typical *balstoni* but larger than *greyi*. These are *sanborni* (originally described from New Guinea) and *aquilo*, originally described as a subspecies of the coastal New South Wales (and perhaps Victoria, see p. 53 of Hall and Richards, but not their map) *orion*. These two coastal Queensland taxa have never been clearly distinguished. Hall and Richards (1979) indicate slight size and color differences, but it would appear that these are weak subspecies at most. The critical area would seem to be the Tully-Innisfail region with *sanborni* to the north and *aquilo* to the south. Hall and Richard's text implies allopatry, but their maps suggest contact. To me, the distinction between *aquilo* and true *orion* seems much clearer. Hall and Richards (1979) state that *aquilo* occurs from Rockhampton north and imply that specimens from extreme southeastern Queensland are true *orion*. The specimens I have seen in the American Museum (AMNH), Museum of Comparative Zoology at Cambridge in Massachusetts (MCZ), CSIRO, BM, and Los Angeles County Museum of Natural History (LACM) show otherwise. Those from Cooktown north have condylobasal lengths as follows: single male (12.8), five females (12.9–13.6); from the Tully-Townsville area, two males (12.9), three females (12.9–13.4); from Southport in extreme southeastern Queensland, a single female (13.2); from Dorrigo in northeastern New South Wales, two females (14.3, 14.4). Southport and Dorrigo are only about 170 mi. apart. This means that either the transition from *aquilo* to *orion* is sharp or else that the Southport and Dorrigo specimens happen to fall at the two extremes of a highly variable population. Obviously, northeastern New South Wales and southeastern Queensland is a critical area for understanding the *orion-aquilo* relationship. Another interest-

ing possible contact is between *orion* and *balstoni*. These are apparently separated by the Great Dividing Range, although Hall and Richards (1979, p. 51) imply sympatry with *aquilo* near Rockhampton. The most important difference between *orion* and *balstoni* appears to be the broader skull of the former, though the difference is not great. Comparison of the two females from Dorrigo (*orion*, MCZ) with the female from Mt. Pluto (*balstoni*, CSIRO) shows less difference in condylobasal length (14.3, 14.4 vs. 14.5) and maxillary tooth row length (5.1, 5.2 vs. 5.2) than in width across the last molars (6.8 vs. 6.6). Obviously, more skulls from in and around the Great Dividing Range in northern New South Wales should be compared. The British Museum has two relevant specimens. An unsexed skin and skull from the Liverpool Range has a maxillary tooth row length of 5.0 and a width across the last molars of 6.6, thus agreeing better with *balstoni* than with *orion*. An alcoholic female from 40 mi. s. Moree had been identified as *orion*, but the skull was not available to me. The smallest species of *Nycticeius* in Queensland is *N. greyi*, which also has the broadest range within the state, being absent only from Cape York and most of the Pacific coast. It extends as far north as the Gregory River near the Gulf of Carpentaria, reaches the Pacific coast (at least in the Townsville-Tully area), and extends well to the south of Queensland west of the Great Dividing Range. Over much of this area it is sympatric with *inflatus*, *balstoni*, or *aquilo*. In Queensland, the condylobasal length measures 11.6–12.2 in males and 11.8–12.8 in females, which means that *greyi* is everywhere (at least in Queensland) distinct in skull size from any other population of *Nycticeius* with which it is sympatric. The above is my rationale for recognizing, in Queensland and New South Wales, three species; *N. inflatus*, *N. balstoni* (including *orion*, *aquilo*, and *sanborni*), and *N. greyi*.

I have seen no specimens of *Nycticeius* from Victoria and very little from South Australia so I will proceed to the Northern Territory. Since Parker (1973) does not distinguish between *greyi* and *balstoni*, it is difficult to determine the distribution of the three named forms which have been recorded from the

territory. However, I have seen a fair amount of material (USNM, MCZ, BM, CSIRO) from which the following pattern emerges. All specimens from south of the Tropic of Capricorn (Finke River, Horseshoe Bend; Hermannsburg; Charlotte Waters) are large (condylobasal length 13.9–14.6 in males, 14.2–15.0 in females) and agree well with typical *balstoni*. All specimens from north of 19°S and east of 134°E (18 mi. w. Wollogorang; Black Waterhole, Nicholson River; Upper Gorge, Fish River; Alexandria) are small (condylobasal length 11.8–12.6 in males, 12.2–12.6 in females) thus agreeing well with Queensland *greyi*. Parker's map (1973, p. 39) shows five localities south of 22°S (two slightly north of the Tropic of Capricorn), which presumably are typical *balstoni* and four localities north of 20°S and east of 134°E, which are presumably *greyi*. Thus, there appears to be a gap between the two ranges where no *Nycticeius* occurs. Material from the northwestern Northern Territory presents more of a problem. I have seen nine intact skulls from this area and only five of these come from the most critical portion of it (Cobourg Peninsula; Deaf Adder Creek; Darwin) which includes the type locality of *greyi* at Port Essington. I previously (Koopman, 1978) allocated one of the Cobourg Peninsula specimens and those from Deaf Adder Creek and Darwin to *balstoni caprenus* and left unallocated a topotype of *greyi* (also from the Cobourg Peninsula). I did this because four of the specimens agreed better with Western Australian *caprenus* than with Western Australian *greyi*. However, I am now dubious that *caprenus* really occurs in the Northern Territory. The condylobasal length measurements of these extremely northern Northern Territory specimens are 12.6 (for the single male) and 12.7–13.0 (for the four females), which straddles the size hiatus between *greyi* and *caprenus* as I have determined it in Western Australia. While more material from this area is necessary for a definite decision, I am inclined to treat these as unusually large *greyi*. Specimens from a little farther south (12 mi. e. Coolibah; Montejinni area; Wave Hill), with condylobasal lengths of 12.0 (two males) and 12.2–12.3 (two females) agree better with *greyi* from farther east (and farther west).

Passing on to Western Australia, first we

have the type series of *balstoni* from Laverton in the southern part of the state, constituting the only material of nominate *balstoni* I have seen from Western Australia. These Laverton specimens are smaller than most specimens of nominate *balstoni* from the Northern Territory and Queensland (condylobasal length of the three female skulls, including the type in the British Museum, 13.9–14.0). The other two named forms in Western Australia are *caprenus* and *greyi*, and this has been a major point of disagreement between me and Western Australian mammalogists. The most important material by far is a series in the American Museum of Natural History from Cape Bossut, to which I have added specimens that have since become available from Frazier Downs and La Grange, two closely adjacent localities. The suggestion has been made that this all represents one species, in which case it would be extremely variable. The condylobasal length of the entire series would be 11.3–13.4 (males) and 11.6–14.2 (females). In my opinion, the series is much better segregated into two species: *greyi* (males 11.3–12.1, females 11.6–12.3) and *balstoni caprenus* (males 12.8–13.4, females 13.0–14.2). The female with a condylobasal length of 14.2 is interesting because it falls well within the variation of *N. b. balstoni* and is in fact larger than any of the type series of *balstoni* (also females). Most of the remaining specimens I have seen from Western Australia fall into the variability of either *greyi* or *caprenus* as known from the Cape Bossut area. The only Western Australian specimen of *Nycticeius* that has given me difficulty is a skull from Parry Creek, which is no longer available to me. It is of a male with a condylobasal length of 12.5, well below that of the smallest male of *caprenus* from Cape Bossut. The skull is closer in size to that of *greyi* of Western Australia and since that is so, it is strange that it is larger than any of the female *greyi* from Western Australia. Since Parry Creek is quite far north and fairly close to the Northern Territory border, I have considered the possibility of allying the Parry Creek specimen with the large *greyi* occurring around Van Diemen's Gulf in northwestern Northern Territory. However, I have seen two specimens, one female and one unsexed from Ningbing, which is also far to the north and

even closer to the Northern Territory boundary. With condylobasal lengths of 13.0 and 13.2, they fall within the Cape Bossut *caprenus* range. More material from extreme northeastern Western Australia is necessary to determine the *greyi-caprenus* limits in that area. Besides the Parry Creek skull, I have seen skulls of four males and one female *greyi* from this area (Kununurra; Lissodell homestead; Carranya homestead) in two museums (CSIRO and FMNH). Condylobasal lengths are 12.0–12.3 for males and 12.4 for the female. These lie at the upper end or slightly beyond the upper end of the Cape Bossut *greyi* series. They agree better with specimens in the Northern Territory immediately to the east (Coolibah; Montejinni, Wave Hill) than to those to the northeast (Darwin; Deaf Ad-der Creek; Cobourg Peninsula).

To sum up this survey, I still believe that there are three species of *N. (Scotorepens)*: *greyi*, *balstoni* (including *sanborni*, *aquilo*, *orion*, and *caprenus*), and *inflatus* but have indicated several critical areas where this theory might be tested. The only important departure from the conclusions in my previous (Koopman, 1978) paper is that I no longer believe that *balstoni caprenus* reaches the Northern Territory, but would confine it to the northern and western portions of Western Australia.

Nycticeius greyi: As I now conceive this species, it extends from the Pacific coast near Townville south to the Victorian border, and west across the northern part of the Northern Territory to northeastern Western Australia at least as far as Cape Bossut. Tate (1952a, p. 601) recorded this species from Pentland and Malbon. From Queensland, the American Museum of Natural History now has two additional specimens from between Camooweal and Mt. Isa collected by P. Kraus in 1967 and 24 mi. s. Burketown by R. F. Peterson in 1959. From the Northern Territory, there are specimens from 18 mi. w. Wollgorang by R. F. Peterson in 1959 and 12 mi. e. Coolibah by Nelson, Butler, and Rosen in 1969. From Western Australia, there is a large series from Cape Bossut by Nelson, Rosen, and Butler in 1969; W. H. Butler in 1973). As indicated above, *N. greyi* is smallest in eastern Queensland (where it is in contact with *N. balstoni aquilo*) and in Western

Australia (where it is in contact with *N. balstoni caprenus*), larger in western Queensland and most of the Northern Territory, and largest in the extreme northwestern Northern Territory. It was from this usually large population, on the Cobourg Peninsula and just south of Van Diemen Gulf that the type of *greyi* was drawn, and I believe that the uncertainty as to where this population should be allocated taxonomically has caused much of the confusion.

Nycticeius balstoni: This is another widespread Australian species (according to my concept) which also occurs in southeastern New Guinea. In northern Queensland it occurs only east of the Great Dividing Range, but farther south it extends from the Pacific Ocean across Victoria, New South Wales, southern Queensland, southern Northern Territory and throughout much of Western Australia. The two southern subspecies, *b. orion* and *b. balstoni*, are large, but the three northern subspecies, *b. sanborni*, *b. aquilo*, and *b. caprenus*, are small. *Nycticeius b. orion* does not occur north of the Tropic of Capricorn and *N. b. balstoni* extends at most slightly north of it in the Northern Territory. The three small subspecies, however, all occur extensively north of the Tropic of Capricorn. *Nycticeius balstoni sanborni* and *N. b. aquilo* are found only to the east of the Great Dividing Range, meeting at about the southeastern base of the Cape York Peninsula (if indeed they are distinct). *Nycticeius balstoni caprenus* (as I now conceive it) is confined to Western Australia, extending from its northeast corner southwest at least to Yanarrie River (22°50'N, 115°E). I erroneously thought that one of these specimens came from Barrow Island. The only specimen of *b. caprenus* I have seen from farther south is a single female skull (no longer available to me) which came (Bannister, 1969) from Contine (32°50'S, 116°50'E). It is a perfectly typical *caprenus* (condylobasal length 13.1) and shows no indication of intergradation with *b. balstoni*, although, as indicated above, some specimens from farther north do show such intergradation. Tate (1952a, p. 601) recorded *N. b. sanborni* from two localities in the Cooktown area of northern Queensland. All the remaining material of this species that we have is from Western Australia and belongs

to *N. b. caprenus*. This includes specimens from Frazier Downs (W. H. Butler in 1963), La Grange (W. H. Butler in 1963), Ningbing (W. H. Butler in 1965), Yanarrie River (W. H. Butler in 1965), Cape Bossut (Nelson, Butler, and Rosen in 1969, W. H. Butler in 1973), Yeeda Creek (Nelson, Butler, and Rosen in 1969).

Nycticeius influatus: This species is confined to Queensland, where (according to Hall and Richards, 1979, p. 51) it has an extensive distribution from the southern parts of the Cape York Peninsula to just south of the Tropic of Capricorn. The American Museum of Natural History has no specimens.

Nycticeius rueppellii: Hall and Richards (1979) give as the range of this species "coastal eastern Australia from southern New South Wales to Ingham, Queensland." However, specimens in the American Museum and the Museum of Comparative Zoology carry the distribution somewhat farther north to Lake Barrine, definitely onto the Cape York Peninsula. Tate (1952a) did not record this species, but the American Museum has a specimen from 30 mi. s. Ravenshoe collected by R. F. Peterson in 1959.

GENUS *Miniopterus*: As previously discussed (Koopman, 1982), this genus is in taxonomic confusion with no two investigators agreeing on what species to recognize or what to call them. Many of the respective points of view have not been published but as of the end of 1981, it was evident that Hill (1971) and Peterson (1981a) differed rather sharply. Since then, Maeda (1982) has published a classification of all the *Miniopterus* of the Palearctic, Indo-Malayan, and Australian regions which differs rather radically from those of either Hill or Peterson. This is perhaps best shown in their treatments of the *Miniopterus tristis* group which all have published on. Ignoring subspecies and also the status of *robustior* of the Loyalty Islands, which all three authors recognize as a separate species, we have the following alternative treatments. Hill (1971, pp. 578–580) recognized a single species, *M. tristis* extending from the Philippines to the New Hebrides. Peterson (1981a) recognized two species, *M. tristis* from the Philippines (and also Celebes, from which neither of the other authors has seen specimens) and *M. propritristis* from

New Guinea, New Britain, Admiralties, Solomons, and New Hebrides. Maeda (1982) recognizes three species, *M. tristis* in the Philippines, New Guinea, and New Britain, *M. bismarckensis* from the Admiralties, and *M. melanesiensis* from the Solomons and New Hebrides (though in a footnote, p. 47, he synonymized *melanesiensis* with Peterson's *propritristis insularis*). While both the Peterson and Maeda arrangements can be derived from Hill's by simple splitting, Peterson's and Maeda's are irreconcilable.

Maeda's procedure (1982, p. 17 and personal commun.) seems to be as follows. Within the main Japanese islands, where Maeda's earlier work was done and where his material is most adequate, there is little geographical variation. From this observation, he has drawn the conclusion that this pattern exists throughout the genus. He therefore interprets any morphological change in going from one area to another as a species change. Numerous species are therefore recognized (19 in the area he covers), but these tend to have spotty, discontinuous ranges since similar appearing forms, even though widely separated geographically (with other species in between) are combined into the same species. Needless to say, my method is quite different and I will try to summarize it here (though I use it for determining species in general, not just for *Miniopterus*). I first look for as many places as I can where sympatry occurs between closely related species. From study of these areas, I try to determine the kind and degree of difference which distinguishes the most similar pairs of sympatric species in the group under consideration (in this case, *Miniopterus*). Then, in trying to interpret the specific status or its absence between related allopatric forms (usually separated by a marked barrier), I compare their kind and degree of difference with what I have found between the related sympatric species. A phenotypic break between populations on the two sides of a barrier is therefore not automatically treated as indicating a species difference, but only if it is of such a nature that it compares well with differences between related sympatric species. I do not claim that this method is infallible, but I do believe that it is the most objective and efficient way to make such a decision. But whatever the method,

decisions are subject to change when new data become available.

Taking up Maeda's treatment of Australian *Miniopterus* we get the following pattern. The larger *Miniopterus* of eastern Australia (usually regarded as a form of *M. schreibersi*) is described as a new species *M. oceanensis* (type locality Cape York), but to it are also referred specimens from San Cristobal in the Solomons, St. Matthias in the Bismarcks, southeastern New Guinea, Amboina in the Moluccas, and a small area in Yunnan (southwestern China), and upper Burma. Maeda's Australian material of *oceanensis* came from Queensland and New South Wales. He saw no specimens from Victoria, but from South Australia, he had four specimens from the Flinders Range. These he allocated to another new species (*M. macrodens*, type locality in Borneo) to which he also allocated specimens from Timor (presumably the species Goodwin, 1979, called *M. magnater*), Moluccas (where apparently sympatric with *oceanensis*), Java, and several areas in southeastern Asia. I have looked at all *Miniopterus* skulls in the American Museum of Natural History which seem relevant to the problem at hand. Specimens from Hainan (China), Burma, Malaya, Bali, and Timor are all from within or near areas where Maeda allocated specimens to his *macrodens* (and seem to agree with his concept of that species), but I have seen no specimens from the Flinders Range. I have also looked at typical *magnater* from New Guinea. Also from New Guinea but from localities farther to the south and east, I have seen specimens which I previously (Koopman, 1982) referred to *M. schreibersi*, but without allocation to subspecies. Maeda saw one of these southeastern New Guinea specimens (as well as typical *magnater*) and referred it to *oceanensis*. However, as I previously (Koopman, 1982) stated, these southeastern New Guinea (including East Papuan Island) specimens are smaller than those from eastern Australia and I therefore would not refer them to *oceanensis*. (Hill, 1983, has also recorded two specimens from southwestern Irian Jaya.) From study of the extensive series of eastern Australian *oceanensis* in the American Museum, I note that some specimens approach *macrodens* from Timor closely, though obviously simply large-

er individuals of *oceanensis*. This is particularly true of a single skull from Panmure in southwestern Victoria. I therefore believe that the Flinders Range specimens that Maeda referred to *macrodens* are simply unusually large *oceanensis*. However, a study of geographical variation of *Miniopterus* in its limited South Australian range would certainly be instructive. The third large species of *Miniopterus* that Maeda recognized in Australia was *eschscholtzi* (type locality in the Philippines), with which he synonymizes *oriana* (type locality in the Northern Territory). To *eschscholtzi* he also allocated specimens from South Australia and from San Cristobal in the Solomons. I have not seen any Solomon Islands material and suspect that the South Australian record is in error (see Aitkin, 1975, for a discussion of this problem in a different species), but again careful study of South Australian material would be rewarding. I have compared true *eschscholtzi* from the Philippines with *oriana* from Northern Territory and Western Australia and can see no special resemblance. To me they are as different from one another as either is from European *schreibersi* (which Maeda puts in a different species group) and would put them all in the same species for which the oldest name would be *M. schreibersi*. As explained below, I regard *oceanensis* as conspecific with *oriana* and would regard both as subspecies of *M. schreibersi* (and thus in agreement with Hill, 1983). Summing up, I would recognize the following taxa of larger *Miniopterus* from Australia and surrounding areas: *M. magnater magnater* from northern and western New Guinea; *M. magnater macrodens* from Timor (in agreement with Hill, 1983, as to status, but not as to allocation of these specimens); *M. schreibersi oceanensis* from eastern Australia; *M. schreibersi* ssp. from southern New Guinea; *M. schreibersi oriana* from Northern Territory and Western Australia.

Maeda (1982) recognized only one additional Australian species of *Miniopterus*, *M. australis*. He accepted the now conventional view that the type locality is in the Loyalty Islands, but also allocated specimens from New Caledonia, New Hebrides, eastern Australia, "New Guinea," Amboina (including the type of *tibialis*), and Borneo (including the type of *witkampii*). Maeda recognized

another species, *M. paululus* from the Philippines, Java (including the type of *shortridgei*), and Rennell Island in the Solomons. This is essentially the arrangement of names that Peterson (1982b) adhered to, but he has concluded that the type of *australis* actually came from eastern Australia and that *M. australis* does not occur in either New Caledonia or the Loyalty Islands. Hill (1983) disagrees with these conclusions, but I still see problems. If we follow Peterson, then *M. a. australis* occurs in eastern Australia, southeastern New Guinea, and on Tagula Island in the Louisiade archipelago; *M. australis* of uncertain subspecies occupies northern and western New Guinea; *M. paululus* is in Timor. The third species in Timor (besides *magrater*, *macrodens*, and *paululus*) is *M. pusillus*, which does not occur in either Australia or New Guinea, but does range from India to the Aru Islands (southwest of New Guinea) and perhaps occurs on some islands east of New Guinea and Australia.

Miniopterus schreibersi: Tate (1952a) recorded this species from seven localities (based on American Museum specimens) in northeastern Queensland. There is also Queensland material in the American Museum from a number of other localities. In 1937–1938 G. Neuhauser obtained specimens from Cunjeboi, Pentland, Port Stuart (probably = Port Stewart), and Somerset. Tate and Van Deusen also collected specimens from Lockerbie, but they were omitted from Tate's (1952a) account. In 1950–1951 J. Roberts collected specimens from Mt. Amos (Phoenician), Ayton, Cooktown, and Green Hills (south of Cooktown); J. L. Harrison in 1958–1959 from Bramston Beach and Ingham; R. F. Peterson in 1959 from Koombooloomba Creek (south of Ravenshoe) and Lyndhurst Station; R. M. Ryan and L. Wassell from 5 mi. se. Coen. From the Northern Territory, there is a single specimen from north of Katherine collected by A. J. Coventry in 1963. All Western Australian specimens were obtained by W. H. Butler, either in 1965 (Ningbing; Parry Creek) or 1973 (Mitchell River; Port Warrender). All specimens from eastern Australia are *M. s. oceanensis*, which has a wide distribution from islands off the northern end of Cape York to Victoria and southeastern South

Australia. *Miniopterus s. orianae*, on the other hand (if the alleged South Australian record is ignored), is confined to northwestern Northern Territory and northeastern Western Australia. Though *M. s. oceanensis* extends slightly west of the Great Dividing Range at Lyndhurst Station, there is still a wide gap between the ranges of the two subspecies. While the subspecies remain distinct, the difference is not great and there is even a little overlap. Thus five skulls from Pentland and Lyndhurst have condylobasal lengths of 15.1–15.8 and the skull from north of Katherine has a condylobasal length measuring 14.8. Furthermore, the largest of a series of 25 skulls from Darwin in the National Museum of Natural History (USNM 248203) has a condylobasal length of 15.2. As indicated above, both subspecies are probably endemic to Australia.

Miniopterus australis: Tate (1952a) recorded this species from four localities (based on American Museum material) in eastern Queensland north of the Tropic of Capricorn. There are also specimens from Port Stuart (G. Neuhauser in 1938); Cowie Bay (J. Roberts in 1950); Innisfail (J. L. Harrison in 1959); Chillagoe, Mt. Garnet, and Mungara (R. F. Peterson in 1959). Like *M. s. oceanensis*, *M. a. australis* extends slightly west of the Great Dividing Range but does not extend as far south (only to northeastern New South Wales). Also unlike *M. s. oceanensis*, it occurs in New Guinea, but has no representative in the Northern Territory or Western Australia.

Murina florum: This species has recently (Richards et al., 1982) been recorded from near Atherton on the Cape York Peninsula, Queensland. The species is distributed from the Lesser Sundas to New Guinea. Though three subspecies are recognized by Laurie and Hill (1954), their type localities are all in the Lesser Sundas and Moluccas and it is uncertain what subspecific name should apply to material from New Guinea and Australia. It should be pointed out, however, that the measurements (supported by the scale of their photographs) that Richards et al. (1982) give are unusually large for *Murina florum*. Thus for their specimen vs. the largest of the Celebes and New Guinea *florum* skulls in the American Museum, we obtain: condylobasal

length (15.8, 14.2); maxillary tooth row length (5.8, 5.2) and the latter measurement is also larger than that for the types of *lanosa* and *toxopei* (5.6, as given by Tate, 1941), which are currently considered to be conspecific with *M. florum*. Hill (1983), however, gives a condylobasal length of 15.7 and a maxillary toothrow of 5.6 for a skull from Goram in the Moluccas. The American Museum has no Australian material of *Murina*.

Kerivoula (Phoniscus) papuensis: Although Hill (1965) and others (e.g., Hall and Richards, 1979) have treated *Phoniscus* as a separate genus, I have given reasons for including *Phoniscus* in *Kerivoula* as a subgenus (Koopman, 1982, p. 22). The only species of this subgenus in the Australian region (see Hill, 1955) is *K. (P.) papuensis*, known only from tropical Queensland and eastern New Guinea. Tate (1952a) did not record it, but the American Museum of Natural History has a single specimen obtained by J. Roberts in 1950 at Shipton's Flat. Hall and Richards (1979) record it from two additional localities in eastern Queensland and also (surprisingly) in northwestern Queensland. This unusual distribution suggests that *papuensis* may also occur farther west. Hall and Richards (1979) suggested that it may be extinct, but I see no basis for this statement. Like other members of its subgenus (see Hill, 1965), it is indeed rare in collections from throughout its range. Besides the Shipton's Flat specimen mentioned above, the American Museum has only two specimens, both from Papua New Guinea, one from Milne Bay province, the other from Morobe province. Hill (1965) saw only two specimens, the type from Central province in Papua New Guinea and another specimen from Rockhampton in Queensland. Whether the species is genuinely rare in nature or whether its habits have prevented it from being collected efficiently is as yet uncertain.

GENUS *Nyctophilus*: This genus is virtually confined to Australia and New Guinea, though the type of *N. timoriensis* is supposed to have come from Timor, and McKean (1975) has described a (?subfossil) species from Lord Howe Island. This species (*N. howensis*) is larger than any species known living. The condylobasal length measurement McKean gives (21.4) contrasts with that

of the largest *Nyctophilus* skull I have measured (18.0 for a specimen of *N. timoriensis major* from southwestern Western Australia). There has been considerable confusion in the past as to what species to recognize in Australia and, as will be seen, my arrangement is somewhat different from any proposed in the past. Starting with the smallest species that lacks a highly modified postnasal elevation (not to be confused with the true noseleaf that is anterior to it), thus corresponding to degrees 1 and 2 of Thomas (1915), we have *N. walkeri*. In the past considerable uncertainty has existed concerning this species (e.g., Ride, 1970, p. 165), but it is perfectly distinct with at least one good series referred to it. Next in size is *N. arnhemensis*, which is also quite distinct. The larger populations with the less derived nasal elevation are treated by Ride (1970) as belonging to two species, *bifax* and *timoriensis*. Hall and Richards (1979), however, separate *N. gouldi* (previously regarded as the southeastern mainland subspecies of *N. timoriensis*) as a separate species and after studying all the *Nyctophilus* material at the British Museum, I agree, and believe that at least near sympatry can be demonstrated. However, there is complete allopatry between *gouldi* and *bifax* and comparison of their skulls shows close resemblance. There are other characters which Thomas (1915) pointed out, but, as I will explain below, these do not seem to be of sufficient magnitude to characterize species. The last Australian *Nyctophilus* species to be considered, *N. geoffroyi*, differs from the rest in having the postnasal elevation much more highly developed (degree 3 of Thomas, 1915). Whereas there are several names which have been applied to variants, there seems to be general agreement, at least since Thomas (1915), that only a single species is represented. I therefore recognize five species of *Nyctophilus* in Australia, *walkeri*, *arnhemensis*, *gouldi*, *timoriensis*, and *geoffroyi*, all of which are known north of the Tropic of Capricorn. I have previously (Koopman, 1982) discussed the four species of *Nyctophilus* that occur in New Guinea. Two of them, *gouldi* (previously called *bifax*) and *timoriensis* also occur in Australia. Of the other two, *microtis* is obviously very closely related to *arnhemensis* and their relationship will be dis-

cussed in the *N. arnhemensis* account. The other species, *microdon*, is much more distinct. I believe that it is most closely related to *N. geoffroyi*, albeit considerably more primitive. Like *gouldi*, *timoriensis*, and *geoffroyi*, *N. microdon* has the ears connected by a high band. However, the postnasal elevation is considerably better developed than in *gouldi* or *timoriensis*, though not as highly developed as in *geoffroyi*. *Nyctophilus microdon* resembles *N. geoffroyi* and differs from *N. arnhemensis* and *N. gouldi* in its smaller molars and less massive rostrum, suggesting that *microdon* and *geoffroyi* are adapted for feeding on softer (and perhaps smaller) insect prey than are other *Nyctophilus* (with the possible exception of *walkerii*).

Nyctophilus walkeri: Until fairly recently, this species was known only from the holotype, collected in northwestern Northern Territory. More recently, the species has been recorded from two areas in northeastern Western Australia (Kimberley) and the National Museum of Natural History (USNM) has a series of 11 specimens from Jim Jim Creek (150–160 mi. se. Darwin). The USNM series is sympatric with a series of *arnhemensis* from the same localities, showing that they are perfectly distinct species (condylobasal length 11.4–12.5 vs. 13.4–14.1). Though the American Museum has no specimens of this species, clearly it is well established at least in northwestern Northern Territory and northeastern Western Australia.

Nyctophilus arnhemensis: This species was described (Johnson, 1959) after Tate's (1952a) paper appeared. The American Museum has a single specimen from northwestern Queensland (24 mi. s. Burketown) collected by R. F. Peterson in 1959. There is also a single specimen from northwestern Northern Territory (Adelaide River, Tortilla flats) collected by Bolton and Parker in 1967 and a series from Cape Bossut in northern Western Australia collected by Nelson, Butler, and Rosen in 1969. The Queensland and Western Australian localities are the easternmost and westernmost known for the species. As Johnson (1959, p. 185; 1964, p. 481) made clear, no comparison was made between *arnhemensis* and the New Guinea *microtis*. This I have done using specimens in the American Museum and measurements of specimens in

the National Museum of Natural History and the British Museum from several localities in northern Australia and Papua New Guinea. From this comparison, it becomes evident that the most important difference is in ear length, *arnhemensis* clearly having longer ears (19–22 vs. 14–17) and this is also reflected in the slightly better development of the band connecting the ears (Hill and Koopman, 1981) and the larger bullae (which I have not tried to measure). I would therefore retain *arnhemensis* as a species distinct from *N. microtis*. Perhaps they could be included in the same superspecies.

Nyctophilus gouldi: Tate (1952a) recorded this species (under the name *bifax*) from three localities on the Cape York Peninsula. The specimen from Ravenshoe, which he identified as *N. geoffroyi pallescens*, however, is also referable to *N. gouldi*. Furthermore, the American Museum has a specimen obtained on the Atherton Tableland (9 mi. sse. Ravenshoe) by H. C. Raven in 1922, and three from Jackaroo collected by J. Roberts in 1950. The only other tropical Australian specimens in the American Museum are two from Willie Wollie Spring (ca. 20 mi. wnw. Poonda) in the Pilbara region of Western Australia collected by Nelson, Butler, and Rosen in 1969. Hall and Richards (1979) showed a marked hiatus in eastern Queensland between the ranges of *gouldi* (not extending north of the Tropic of Capricorn) and *bifax* (south to about Ingham), amounting to some 600 mi. The only specimen I have seen from western Queensland is one in the British Museum from Cloncurry, which Thomas (1915) referred to *bifax*, though in its great condylobasal length (16.0), it agrees better with Northern Territory *daedalus* (15.1–16.2) than with eastern Queensland *bifax* (14.7–15.4). All Northern Territory *daedalus* I have seen and all records I know of (Parker, 1973) are from the extreme northwestern portion. I have seen no specimens I would refer to *N. gouldi* from South Australia and only two additional ones from Western Australia (besides the two from Willie Wollie Spring mentioned above). One is from a place called Eureka (which I have not been able to find); the specimen (British Museum) tag gives as additional locality information "N. Territory W. A." which I would interpret as meaning the northeastern

(Kimberley) portion of Western Australia. The other, also in the British Museum, is from Swan River in the southwest. All these specimens are females and the two from Willie Wollie Spring have the same forearm and ear measurements. I have extracted the skull from one of the Willie Wollie alcoholics and compared this specimen with those from Eureka (first) and Swan River (last), thus in north to south order: forearm length (44, 42, 40); ear from notch (—, 24, 27); condylobasal length (15.6, 15.7, 15.4); width across last molars (6.9, 7.0, 6.5); maxillary tooth row length (6.3, 6.1, 5.8). When these Western Australian specimens are compared with *N. gouldi* from southeastern Australia and with *N. daedalus* from the Northern Territory, it becomes evident that in forearm length, the Eureka and Willie Wollie Spring specimens agree better with *daedalus* (38–44) than with *gouldi* (38–41), whereas in ear length and width across last molars, the Swan River specimen agrees better with *gouldi* (24–28, 6.5–7.0) than with *daedalus* (20–25, 6.7–7.2). I am therefore inclined to identify the Eureka and Willie Wollie Spring specimens as *N. g. daedalus* and the one from Swan River as *N. g. gouldi*. However, this decision is based on very few specimens and it is obvious that much more material from southern and Western Australia will have to be analyzed before these relationships can be anything more than tentative. It should be possible to do so now that it is clear that *gouldi* is not conspecific with *N. timoriensis*. Thomas (1915) characterized *gouldi* as having the postnasal elevation medium (degree 2), whereas *daedalus* and *bifax* were characterized as having it poorly developed (degree 1). However, if the Willie Wollie specimens are *daedalus*, then in this respect they are intermediate between northeastern Queensland *bifax* and southeastern Australian *gouldi*. *Nyctophilus bifax* was originally distinguished from both *gouldi* and *daedalus* primarily on the basis of its bifurcate baculum. However, I know of no study of the bacula of the various species of *Nyctophilus* that has taken variation into account so that it is certainly not clear to me how constant the bacular difference is between *bifax* and *daedalus*. The only published records I know from Western Australia of the species I have called

N. gouldi are of a single male from the Drysdale River (McKenzie et al., 1977) and one male and three females from the Dampier Peninsula (McKenzie, 1983, p. 47). At least the Drysdale River specimen was identified as *bifax* on the basis of its bifurcate baculum although this Western Australian locality is on the other side of *daedalus* geographically. Kitchener and Vicker (1981) list three specimens as *bifax* (all from north of 18°) and 24 Western Australian specimens as cf. *gouldi* (all south of 31°). Obviously, there is still much to be learned about the precise relationships of *bifax* and *daedalus*. For the present I recognize a single species, *N. gouldi*, with three subspecies; *N. g. gouldi* across southern Australia, *N. g. daedalus* in northwestern and northcentral Australia, and *N. g. bifax* in northeastern Australia. The first and last are most distinct from one another, with *N. g. daedalus* being somewhat intermediate in morphology between *N. g. gouldi* and *N. g. bifax*.

Nyctophilus timoriensis: With the removal of *gouldi*, the characterization of this species as the largest living species of the genus becomes clearer. Two subspecies are recognizable in southern Australia, the very large *major* in the west and the somewhat smaller *sherrini* in the east. Although the implication of Hall and Richards's (1979, pp. 59, 61) maps are that *sherrini* (described from Tasmania) belongs to *N. gouldi*, I have seen the type in the British Museum and it belongs in *N. timoriensis*. (On inspection, it is clear that the type of *sherrini* is somewhat immature and its resultant smaller measurements have evidently been responsible for its association with *gouldi*.) Hall and Richards (1979) showed *N. timoriensis* as being confined to the area west of the Great Dividing Range. However, the only eastern Australian mainland specimen in the British Museum is from the Richmond River in extreme northeastern New South Wales. I know of no record of *N. timoriensis* in eastern Australia north of the Tropic of Capricorn. The only specimens in the American Museum are from southwestern Western Australia and all but one of the Western Australian specimens in the British Museum are from the same area. The one exception is unfortunately immature (a male from Margaret River in southern Kimberley).

Kitchener and Vicker (1981) list a number of Western Australian specimens (under the name of *major*), all but two of which are from south of the Tropic of Capricorn. The two localities (Mount Bruce and "Weeli Wooli Spring") are in the Pilbara and if correctly identified would constitute additional tropical Western Australian records. In view of the fact that the two Willie Wollie Springs specimens I have seen are *N. gouldi*, I am somewhat skeptical of these records. However, in the British Museum there is also an adult female from Port Essington in northwestern Northern Territory and Hill and Pratt (1981) recorded two specimens from New Guinea, which they tentatively referred to *N. t. timoriensis*. I am inclined to refer the two northern Australian specimens (Margaret River and Port Essington) also to *N. t. timoriensis*, leaving open the question as to whether or not the type of *timoriensis* actually came from Timor.

Nyctophilus geoffroyi: Tate (1952a) recorded this species from two localities, but as explained above, the Ravenshoe specimen was misidentified and only the Pentland specimen is actually *N. geoffroyi*. The only other tropical Australian specimen in the American Museum of Natural History was collected by W. H. Butler at Yarraloola in Western Australia. Unlike the other Australian species of the genus, whose ranges are more or less confined to the periphery of the continent, *N. geoffroyi* occurs across its center (see Hall and Richards, 1979, p. 61; Parker, 1973, p. 41) and this makes the delimitation of subspecies more difficult. Thomas (1915) recognized three subspecies, *g. geoffroyi* in southwestern Western Australia, *g. pallescens* in Northern Territory and northwestern Queensland, and *g. pacificus* in southeastern Australia (including Tasmania) and he has been generally followed. Tate (1941b, p. 504), however, on the basis of tooth size of the types, believed that the type of *pacificus* (described from "Islands of the Pacific") originated from northeastern rather than southeastern Australia. What would appear to be the consequence of this would be to make *pacificus* a senior synonym of *pallescens*, with *unicolor* then becoming the oldest name for the southeastern subspecies. Although I am unable to detect any relative size difference

in molar teeth between the single American Museum skull from northern Queensland and the four from southern Queensland, New South Wales, and Victoria, the type of *pacificus* (a male) is smaller in condylobasal length than any of the southeastern Australian males I have measured (14.2 vs. 14.4–15.4). Unfortunately, I have only seen one male skull from northeastern Australia, the type of *pallescens* from Alexandria, Northern Territory, which has a condylobasal length of 14.1. It should be noted that in *N. geoffroyi*, males tend to be smaller than females, though as far as I know this has not been pointed out before. In view of Tate's earlier (1941) remarks, it is odd that in his later (1952a) paper, he made no mention of the name *pacificus* in reference to northern Queensland material. I am therefore inclined to follow Thomas in using the name *pallescens* rather than *pacificus* for the subspecies in northern Queensland and the Northern Territory. I would be inclined to place the geographical boundary between *pallescens* and *pacificus* in eastern Australia somewhere between Pentland and the southeastern corner of Queensland. Hall and Richards (1979, p. 61) allocated not only inland Queensland but even inland New South Wales material to *pallescens*, but it is not clear where they would put specimens from coastal localities, since they mention *unicolor* only from Tasmania. All Western Australian specimens I have seen I have allocated to *N. g. geoffroyi*, though my basis for doing this is very shaky. Thomas (1915) distinguished *g. geoffroyi* from *g. pallescens* only on color ("rather dark" vs. "much paler"). All American Museum material of *g. geoffroyi* (mostly from southwestern Western Australia) is either in fluid or as a skeleton only). The only dry skins of *N. geoffroyi* in the American Museum are the one from Pentland (identified as *g. pallescens*) and one from Mandurama (near Blayney) in New South Wales (identified as *g. pacificus*). These should be very different in color since Thomas (1915) characterized *g. pacificus* as "dark." Yet I see very little difference in color between these two specimens. I have borrowed two skins from the Field Museum which come from the Kimberley region (northwestern Western Australia). They too are very similar in color to the Pentland and Mandurama

skins. Thomas (1915) also gave the condylobasal length of *g. geoffroyi* as 14 and that of *g. pallescens* as 15.3. My measurements of southern and central Western Australian skulls give condylobasal measurements of 13.3–14.1 for males and 13.8–15.2 for females. Specimens from the Kimberley region (borrowed from the Field Museum) have condylobasal lengths of 13.8–14.5 for eight males and 14.3 for the single female. None of my condylobasal measurements of *g. pallescens* approaches 15.3, the largest being a female from Killalpanima (east of Lake Eyre and one of the specimens seen by Thomas), which measures 14.7 (the male type from Alexandria which Thomas also saw measuring only 14.1). It seems evident that much work remains to be done to elucidate the subspecies of *N. geoffroyi*, assuming that subspecies can usefully be recognized.

FAMILY MOLOSSIDAE

During the last two decades, all Australian molossids have generally (e.g., Ride, 1970) been included in one genus, *Tadarida*. Freeman (1981), however, has made a good case for dividing it into several of which three (*Mormopterus*, *Tadarida*, *Chaerephon*) are recognized in Australia. There is but a single species each in *Tadarida* (*australis*) and *Chaerephon* (*jobensis*) and few taxonomic problems exist for either of these within Australia. *Mormopterus*, however, presents several serious taxonomic problems involving Australian populations, which are still not resolved.

GENUS *Mormopterus*: I have previously (Koopman, 1982) discussed some of the problems involving this genus in the Australian region, but I have since studied the situation in Australia in considerably greater depth. Hill (1961) revised all the Indo-Australian members of the genus *Tadarida* (*sensu lato*) and recognized three Australasian species of *Mormopterus*. One of these (*becarii*) has been generally recognized as distinct and will be discussed below. The other two (*norfolkensis* and *planiceps*) have presented much more of a problem, in part because of uncertainty as to the type locality of either species. Although the range of *norfolkensis* was given as "Victoria north to Queens-

land," Hill stated that he examined only one specimen besides the type. Three subspecies of *planiceps* were recognized, the nominate form from "South and west Australia": *p. lorae* from Papua, and *p. cobourgiana* from the Northern Territory and northern Queensland (Inkerman). Specimens from northeastern Queensland, which had been identified by Tate (1952a) as *lorae*, are mentioned, but it is not clear whether they should be allocated to *p. lorae* or to *p. cobourgiana*. No mention is made of other northeastern Queensland specimens that Tate referred to *norfolkensis* (= *norfolkensis*) but presumably Hill was inclined to follow Tate in his allocation, since he included Queensland in the range of *norfolkensis*. Felten (1964) adopted a different arrangement. He agreed with Hill in recognizing *norfolkensis* as a distinct species, but allocated Hill's second specimen (from New South Wales) to *planiceps*, leaving *norfolkensis* known only from the type. However *lorae* (with *cobourgiana*) was separated as a species from *planiceps* and a new subspecies (*l. ridei*) was proposed. To this latter subspecies were referred all northern Queensland specimens including those that Tate separated as *norfolkensis* and *lorae* as well as the Inkerman specimen. Felten also allocated specimens from Buchanan's Island (which he places in Shoal Bay, north of Darwin in the Northern Territory) to *l. cobourgiana*, whereas Hill (1961) had identified them as *p. planiceps*. It is therefore evident that the situation is more complicated than simply deciding whether or not *planiceps* and *lorae* are conspecific. The two principal characters by which Felten (1964) distinguished *lorae* from *planiceps* are the less flattened skull and the presence of a gular pouch in males. I have examined all specimens in the American Museum of the *planiceps-lorae* complex, including a number of males in alcohol from northeastern Queensland. I am unable to find anything that I would call a gular pouch. Only three skulls are available from within the range of *planiceps* as given by Felten (1964). The two from Victoria are indeed greatly flattened, the single skull from Western Australia less so. (One of the two Western Australian skulls I previously referred to (Koopman, 1982, p. 24) turns out to be actually *M. beccarii*.) Felten (1964, p. 3) expressed this as a

regression diagram of condylobasal length vs. height of the skull at the posterior margin of the palate. Felten's diagram shows *loriae* and *planiceps* to be well separated, but if I have measured the Western Australian specimen correctly in the American Museum (AMNH 197172 from Contine), it has a condylobasal length of 15.3 and a skull height of 3.5, which places it between *loriae* and *planiceps*. Furthermore, the skulls of four specimens of this group in the National Museum of Natural History from Gloucester (northeastern New South Wales) and Farina (northeastern South Australia), though well within the geographical range of *planiceps* as given by Felten, show the following range of condylobasal lengths and skull heights (as given by Felten): 14.9, 4.1; 15.3, 3.8; 14.9, 3.6; 14.9, 3.3. Only the last (a female from Farina) falls into the *planiceps* range as given by Felten, the other three fall into the *loriae* range. The two American Museum specimens from Victoria likewise fall outside the *planiceps* range (14.8, 4.3; 15.0, 4.1). A specimen in the Field Museum of Natural History from Hermannsburg (southern Northern Territory falls barely inside the *planiceps* range (15.9, 3.5). In short, I cannot duplicate the small skull height that Felten gives for most of his *planiceps* on any Australian *Mormopterus* skull available to me. The ranges of *loriae* and *planiceps* as given by Felten are allopatric (*loriae* in northern Northern Territory and northern Queensland, *planiceps* from New South Wales to southern Western Australia). Hall and Richards (1979, p. 37), however, showed a small area of sympatry in southeastern Queensland (where incidentally they also show *Mormopterus norfolkensis* occurring). If there are really three species of *Mormopterus* in southeastern Queensland, this is extremely interesting and the three taxa should be readily characterized in this limited area. Unfortunately, I have difficulties with the characters of the three species as given by Hall and Richards (1979, p. 33). They separated these three alleged species on the basis of two couplets. First, *planiceps* is separated from the other two by "shafts of ventral fur one continuous color, no neck pouch" vs. "shafts of ventral fur light at base, darker in the center and lighter at the tips; neck pouch may be present." Secondly, *loriae* is separated from

norfolkensis by "wing membrane attaches near ankle joint; forearm 28–34 mm. "vs." wing membrane attaches approximately $\frac{1}{3}$ of tibia's length from the ankle; forearm 34–40 mm." This is supplemented by additional information in the text in that the neck pouch is stated to be present in males but rudimentary in females of both *loriae* and *norfolkensis*. The wing membrane is stated to arise from "mid leg" in *planiceps*, whereas in *norfolkensis* the wing membrane is confusingly stated to arise from the ankle. The forearm length is stated to be 32–38 mm. in *planiceps*. The important characters to check would therefore seem to be presence or absence of banding on ventral hairs, presence or absence of a gular pouch in males, place of attachment of the wing membrane, and forearm length. All American Museum material is clearly within the geographical range of either *planiceps* alone (three from Victoria) or *loriae* alone (50 from northeastern Queensland). I have checked all these specimens for the above characters, skins for ventral hair color, alcoholics for gular pouch and wing membrane attachment, and both for forearm length. As stated above, I have been unable to find a gular pouch in any of them. The two Victorian skins do agree fairly well with Hall and Richards's (1979) color characterization of *planiceps*, but those from northeastern Queensland show considerable variation, the skins Tate (1952a) referred to *norfolkensis* (Mossman, Cairns) showing a pronounced ventral hair banding, whereas those he referred to *loriae* (Helenvale) having it poorly developed. In the single Victorian alcoholic, while the wing membrane attachment could hardly be called "mid leg," it is definitely above the ankle. The northeastern Queensland alcoholics on the other hand show considerable variability. Most show an attachment at the ankle, several show an attachment higher up, and there is a certain amount of arbitrariness in scoring. All the specimens I have studied have a forearm length of less than 34 mm. so none seems to conform to *norfolkensis*. All three Victorian specimens have forearms of slightly more than 32 mm. and seem to be good *planiceps*. The northeast Queensland specimens, however, though on geographical grounds clearly within the range of *loriae ridei*, show considerable variability

in and in part discrepancy from the characters which Hall and Richards have assigned to *loriae*. Taking account of my problems with the delimitation of *loriae* from *planiceps* as given by Felten (1964) and by Hall and Richards (1979), I remain skeptical of their distinction, particularly as sympatric reproductively isolated species. Until an analysis of the situation in southeastern Queensland is made showing two (or three) clearly distinct species within this critical area I will continue to include *loriae* in *M. planiceps* and thus find myself in agreement with Winter and Allison (1980, p. 34). I am still not clear about the status of *norfolkensis*, but at least *sensu* Hall and Richards (1979), its range does not extend north of the Tropic of Capricorn. This leaves two tropical Australian *Mormopterus* species to be considered, *M. planiceps* and *M. beccarii*.

Mormopterus planiceps: As discussed above, Tate (1952a) allocated material of this species from northern Queensland to two species, "*Nyctinomys norfolcensis*" and "*Nyctinomys loriae*." Combining his records for these two, we have four localities. The American Museum also has specimens from China Camp and Lord's Prayer (both south of Cooktown and collected by J. Roberts in 1951), Grasstree (J. Roberts in 1952), and Gordonvale (R. F. Peterson in 1959). All these are from northeastern Queensland and are, I believe, referable to *M. p. ridei*. I might add that, as indicated above, the skins Tate allocated to the two species do differ in color, and furthermore all "*norfolcensis*" have forearms longer than 30 mm. and all "*loriae*" have forearms shorter than 30 mm. I can make no such separation in the large Ship-ton's Flat series of alcoholics and am unable to understand how Tate divided the part of this series that was then available to him. Though the American Museum has no specimens to document this, *M. planiceps* extends across the Northern Territory to Western Australia (McKenzie et al., 1977; Kitchener, 1978). In the north, two subspecies are recognized, *p. ridei* (in northeastern Queensland) and *p. cobourgiana* (in northwestern Northern Territory). Allocation of other northern populations are, however, at present uncertain. The only area north of the Tropic of Capricorn from which the southern

p. planiceps is definitely known is in southern Northern Territory, where Parker (1973, p. 36) shows *planiceps* (which he distinguished from *loriae*) extending almost to 22°S. Bannister (1969, p. 70) records *planiceps* from the Yannarie River (in the Pilbara region of Western Australia), just north of the Tropic of Capricorn. However, the *Mormopterus*, specimen we have from that locality (part of the same collection that Bannister reports) is, as explained below, actually *M. beccarii*. On the other hand, Kitchener and Vicker (1981) list specimens identified as *planiceps*, *loriae*, and cf. *beccarii*, all from the Pilbara region. So this area, like southeastern Queensland, would repay further analysis. Except for these two areas, however, there appears to be a broad gap between the ranges of *p. ridei* and *p. cobourgiana* to the north and *p. planiceps* to the south.

Mormopterus beccarii: Until recently (Hill, 1961; Koopman, 1982), this species was known only from the Moluccas and New Guinea (including the Louisiades). Winter and Allison (1980, p. 34) record this species from two localities on the Cape York peninsula (as I would define it), Hill (1983) mentions two Queensland localities, one in the southeast, just south of the Tropic of Capricorn, and Kitchener and Vicker (1981) list 22 specimens from the Pilbara district. Nevertheless, the first specimen that I have definitely identified is a single female from Yannarie River (Western Australia, Pilbara district). This specimen (obtained by W. H. Butler in 1965) was previously misidentified as *planiceps* by both Bannister (1969, p. 70) and myself (Koopman, 1982, p. 24). It differs from *planiceps* and agrees better with *beccarii* in its larger skull, higher braincase, and more inflated rostrum. It does show differences from available New Guinea material of *beccarii*, however, in its longer forearm, smaller skull, and less-reduced anterior upper premolar (indistinguishable from that of *M. planiceps*). Measurements of the Yannarie River female (AMNH 197749) to be compared with Hill's (1961, p. 47) are: forearm (39), condylobasal length (15.7), "interorbital" width (4.1), braincase width (7.4), m^3 - m^3 width outside alveoli (7.4), c^1 - c^1 width outside alveoli (4.3), c - m^3 length outside alveoli (5.7), pm^4 - m^3 length outside alveoli

(4.7). It is evident that the Yannarie River specimen has a considerably longer forearm than any of the Amboina or New Guinea material but is shorter in all skull dimensions. While there are, therefore, rather pronounced differences from either of the two currently recognized subspecies of *M. beccarii*, I would allocate the Yannarie River specimen to this species. The Field Museum has a series of *Mormopterus* from the Kimberley district, previously identified as *loriae*. With condylobasal lengths of 15.6 to 17.0, m^3 - m^3 widths of 7.2-7.9, and c - m^3 lengths of 5.8-6.3, it is evident that they are much too large for *loriae* but agree well with the Yannarie River *beccarii*. Furthermore, I have measured, but not critically compared, a skull in the Museum of Comparative Zoology from Coen on the Cape York Peninsula (MCZ 29109). This is a male with a condylobasal length of 17.8, an m^3 - m^3 width of 8.4 and a c - m^3 length of 6.7. Hill's (1983) measurements of a Queensland male and female are: condylobasal (17.9, 16.9), m^3 - m^3 width (8.2, 7.3), c - m^3 length (6.5, 6.2). The MCZ skull is considerably larger than the Yannarie River female skull and thus agrees best with a Fergusson Island male skull (see Koopman, 1982, p. 24) with the same condylobasal length. I have been unable to compare the two skulls, however. Probably, the specimen from Coen does represent a population of *beccarii* closely related to those of New Guinea. (Hill, 1983, allocates his Queensland specimens tentatively to *b. astrolabiensis*.) Waithman (1979) records *beccarii* from two localities in the Western province of Papua, New Guinea, just across Torres Straits from Cape York, but he gives no measurements.

Tadarida australis: I previously (Koopman, 1982) presented evidence for treating the New Guinea *kuboriensis* as a subspecies of the chiefly southern Australian *T. australis* and follow Hill (1961) in synonymizing *atratus* with *T. a. australis*. Incidentally, this removes the presence of a white flank stripe as a diagnostic character of *T. a. australis* (vs. *a. kuboriensis*) since Thomas (1924), in his description of *atratus*, states that the type lacks "any trace of the whitish line along the edge of the body below," thus leaving size as the only constant character separating the two subspecies. Most of tropical Australia lies in

the broad hiatus between them. *Tadarida a. australis* barely extends north of the Tropic of Capricorn in Queensland (Hall and Richards, 1979), Northern Territory (Parker, 1973), and Western Australia (several Pilbara localities listed by Kitchener and Vicker (1981). All American Museum specimens are from farther south in Victoria, southwestern Queensland (Birdsville), and southern Western Australia (Elduna; Malura Sork; "wheat belt"; Shark Bay Turnoff).

Chaerephon jobensis: Tate (1952a) recorded this species under the name of "*Nyctinomus colonicus*" from two localities in northern Queensland. The American Museum also has specimens from Lucinda collected by L. D. Crossan in 1959. There are also numerous specimens from tropical Western Australia: 25 mi. n. Hall's Creek (Butler in 1965); Mt. Anderson (Butler in 1965); Woodstock (Butler in 1965); Derby (Butler in 1965 and 1973); Willie Wollie Spring, ca. 20 mi. wnw. Poonda (Nelson, Butler, and Rosen in 1969). This is the only species of *Chaerephon* in the Australian region. Felten (1964) recognized four subspecies ranging from New Guinea and Western Australia to the Fijis. In Australia, *C. jobensis* appears to be confined to areas, north of the Tropic of Capricorn (Hall and Richards, 1979; Parker, 1973; Bannister, 1969), though Kitchener and Vicker (1981) record a specimen from barely south of it. The only possible exceptions are old, doubtful records from South Australia (Aitken, 1975). The American Museum of Natural History also has an old specimen from the Wood Jones collection (AMNH 160320) labeled only "South Australia." As Aitken (1975) pointed out, these Wood Jones specimens were probably collected at a time when the Northern Territory (where the species is well known) was part of South Australia. In Australia, the distribution of *C. jobensis* is therefore largely allopatric with *Tadarida australis* (though both species occur in New Guinea). Currently all Australian populations of *C. jobensis* are allocated to *C. j. colonicus* and comparing specimens from as far apart as Lucinda on the Pacific coast of Queensland, Woodstock, and Willie Wollie Spring in northwestern Western Australia reveals no significant differences. *Chaerephon jobensis colonicus* seems therefore to be an

endemic subspecies, widespread across tropical Queensland, Northern Territory, and Western Australia.

DISCUSSION

Having taken up the various families, genera and species of tropical Australian bats, I would now like to discuss their distributions and relationships under several headings. These are the distributional patterns within tropical Australia and with the three major adjoining areas: temperate Australia, New Guinea (particularly its south central lowlands), and the Lesser Sunda Islands (particularly their largest, nearest, and best worked island, Timor; see Goodwin, 1979). In the following analyses, I am omitting three species supposed to have come from tropical Australia and discussed in the accounts above (*Pteropus brunneus*, *Myotis* sp. (near *australis*), *Pipistrellus javanicus*). All are too poorly known, at least in Australia, for anything very useful to be said.

GEOGRAPHICAL RELATIONSHIPS WITHIN TROPICAL AUSTRALIA

Since tropical Australia extends some 800 mi. north-south and over 2000 mi. east-west and exhibits a variety of environments from rain forest to desert, it is not surprising that its 49 species analyzed here should show a great variety of distributional patterns. Aside from 11 widespread species, most of the remainder may be said to center on Cape York, which was probably an important part of the corridor through which a majority of the Australian bats reached their present distributional areas. These 26 species which occur on Cape York are taken up as a group, though as will be pointed out, many extend far from Cape York either to the south or the west. Among the 12 species of tropical Australian bats that do not reach Cape York, I have recognized a "western mesic" group of three species, a "southern marginal" group of four species (which form a group transitional to that of the few exclusively temperate species that are discussed in the following section), and finally two species that I have not been able to fit into any distributional pattern.

WIDESPREAD SPECIES: Eleven species have

an extensive distribution in Australia, going across the entire continent, extending from at least the base of the Cape York Peninsula to at least some distance south of the Tropic of Capricorn. Five species (*Pteropus alecto*, *P. scapulatus*, *Nyctophilus gouldi*, *Mormopterus planiceps*, *Chaerephon jobensis*) also occur in New Guinea. The only other way I know of in which distributions of this group can be classified is between those species that tend to avoid the really arid areas (*Pteropus alecto*, *Nyctophilus gouldi*, *Chaerephon jobensis*) and those that do not (*Pteropus scapulatus*, *Taphozous georgianus*, *Saccolaimus flaviventris*, *Macroderma gigas*, *Eptesicus pumilus*, *Chalinolobus gouldii*, *Nyctophilus geoffroyi*, *Mormopterus planiceps*). As would be expected for such widespread species, the latter category predominates.

CAPE YORK SPECIES: Of the 25 species which are not widespread in tropical Australia but occur on at least part of the Cape York Peninsula, only six (*Dobsonia moluccensis*, *Saccolaimus mixtus*, *Rhinolophus philippinensis*, *Hipposideros cervinus*, *H. semoni*, *Murina florium*) are confined to Cape York in the sense that they do not occur south of Townsville nor appreciably west of the Great Dividing Range. Two others (*Pteropus conspicillatus*, *Taphozous australis*) are similarly confined to the eastern tropics (assuming that all more western records of *T. australis* are misidentified), but do extend south of the Cape York Peninsula. Five additional species are likewise strictly eastern but reach farther south to southeastern Queensland (*Nyctimene robinsoni*), New South Wales (*Syconycteris australis*, *Nycticeius ruppellii*, *Miniopterus australis*) or Victoria (*Rhinolophus megaphyllus*). Two species (*Saccolaimus saccolaimus*, *Hipposideros diadema*) though not extending south of the Cape York Peninsula, do have apparently isolated populations in the northern part of the Northern Territory. Four additional species (*Macroglossus minimus*, *Hipposideros ater*, *Pipistrellus tenuis*, *Miniopterus schreibersi*) have a similar distribution except that they also reach the Kimberley region (northeastern Western Australia). None extend appreciably south of the Cape York Peninsula except for *Miniopterus schreibersi* that extends all the way to Victoria. Of the remaining species, all except

Mormopterus beccarii are vespertilionids and the known range of *M. beccarii* (Cape York, southeastern Queensland, Kimberley and Pilbara regions of Western Australia) does not fit any known pattern. Of the remaining six species, two (*Nycticeius influatus*, *Kerivoula papuanus*) are Queensland endemics (except that *K. papuanus*, but not *N. influatus*, also occurs in New Guinea). Both occur on the Cape York Peninsula (*N. influatus* apparently only marginally), but barely extend south of the tropics, and both occur in relatively arid regions in northwestern Queensland. Both are also known only by a few specimens which may explain some of their apparent resemblances and differences. Of the remaining four species, all are fairly widespread. *Myotis adversus*, *Chalinolobus nigrogriseus*, and *Nycticeius greyii* (the latter only marginally in the Cape York Peninsula) are similar in that all occur across tropical Australia and extend south of the Tropic of Capricorn in the east but not (apparently) in the west. Finally, *Nycticeius balstoni* occurs in both tropical Queensland and tropical Western Australia and across temperate Australia, but apparently not across tropical Australia.

WESTERN MESIC SPECIES: Three species (*Taphozous kapalgensis*, *Eptesicus douglasi*, *Nyctophilus walkeri*, all Australian endemics) are absent from Queensland but are confined to mesic areas in extreme northern Northern Territory and, except for *T. kapalgensis*, also in the Kimberley region (extreme northeastern Western Australia). Except for the fact that they are absent from Cape York, their distributions in Australia are quite comparable with those of *Macroglossus minimus*, *Saccolaimus saccolaimus*, *Hipposideros ater*, *H. diadema*, and *Pipistrellus tenuis* mentioned above. Three additional species (*Hipposideros stenotis*, *Rhinonycteris aurantius*, *Nyctophilus arnhemensis*) have somewhat similar distributions except that they extend into somewhat more arid regions (but not into the desert), thus reaching northwestern (but not northeastern) Queensland and, in the case of *Rhinonycteris*, also the Pilbara region of northwestern Western Australia. *H. stenotis* is closely related to the Cape York *H. semoni*.

SOUTHERN MARGINAL SPECIES: Besides a few species which are confined to temperate

Australia (south of the Tropic of Capricorn), there are four (*Pteropus poliocephalus*, *Chalinolobus picatus*, *C. morio*, *Tadarida australis*) which extend a relatively short distance into tropical Australia. Except for *T. australis*, these extensions are only in the east and indeed two (*P. poliocephalus*, *C. picatus*) are confined to eastern Australia. Presumably the absence of desert barriers in the east has facilitated northward spread of southern elements.

MISCELLANEOUS SPECIES: Two species (*Taphozous hilli*, *Nyctophilus timoriensis*) cannot be fitted into any of the above patterns at present. In the case of *N. timoriensis*, this may be resolved once the confusion in the records between it and *N. gouldi* is disentangled. Until this is done, little can be said about the distributional pattern. *Taphozous hilli*, however, does seem to present a unique pattern. It is the only Australian bat that appears to be confined to arid areas, avoiding more mesic regions to the north, east, and south.

GEOGRAPHICAL RELATIONSHIPS WITH TEMPERATE AUSTRALIA

Excluding the poorly understood *Mormopterus norfolkensis*, five species (*Pipistrellus tasmaniensis*, *Eptesicus vulturnus*, *E. regulus*, *E. sagittula*, *Chalinolobus dwyeri*) are confined to the large part of Australia south of the Tropic of Capricorn. As indicated above, four other species (*Pteropus poliocephalus*, *Chalinolobus picatus*, *C. morio*, *Tadarida australis*) are largely confined in Australia to the temperate zone. Since both *P. poliocephalus* and *T. australis* have close (and in the case of *Tadarida* conspecific) relatives in New Guinea, it is evident that with the exception of *Eptesicus* and *Chalinolobus*, temperate Australia has not been an important evolutionary center for bats. Of the 24 remaining species of bats that occur south of the Tropic of Capricorn, three also belong to the genera *Eptesicus* and *Chalinolobus* (*E. pumilus*, *C. nigrogriseus*, *C. gouldii*). Temperate Australia may have been involved in the endemic Australian radiations of *Taphozous* (*T. georgianus*, *T. hilli*) *Nycticeius* (*N. greyii*, *N. balstoni*, *N. influatus*, *N. rueppelli*), and *Nyctophilus* (*N. gouldi*, *N. timoriensis*, *N. geoffroyi*), though the last almost certainly

also involved tropical Australia and even New Guinea. The remaining 13 species all have their closest (usually only congeneric) relatives to the north and are represented in temperate Australia only by peripheral populations. *Pipistrellus tasmaniensis* is a special case. It is a very isolated species, not at all closely related to the tropical *P. tenuis* and of highly uncertain relationships within its almost cosmopolitan genus.

GEOGRAPHICAL RELATIONSHIPS WITH NEW GUINEA

New Guinea has a rich tropical bat fauna of some 70 species (see Koopman, 1982), much of which occurs in the southern lowlands, separated from Cape York and north-eastern Northern Territory (Arnhemland) only by the shallow Torres Straits and Arafura Sea. These were dry land at various low sea level periods during the Pleistocene epoch, the most recent ending only about 10,000 years ago. Thus a broad land connection, presumably with a varied environment (wetter in the east and dryer in the west) connected the two now separate land masses. It should be pointed out that it was, of course, a lowland connection so that species confined to mountains would not be able to use it. After each reunion following a period of separation, however, lowland species would be expected to disperse in both directions. Since the original vegetation of New Guinea was chiefly forest and the original vegetation of Australia chiefly savanna and grassland, dispersal from the north mainly has involved forest elements, whereas dispersal from the south mainly has involved savanna elements.

Of the 49 tropical Australian species here discussed, 27 also occur in New Guinea, though *Pteropus alecto* and *P. scapulatus* barely get across Torres Straits. I am not including *Taphozous australis* in this figure since the single New Guinea record (Port Moresby) is almost certainly accidental or erroneous. Four additional species are represented in the New Guinea region by close relatives: *Pteropus poliocephalus* (*P. macrootis*), *Nyctimene robinsoni* (*P. major*), *Nyctophilus arnhemensis* (*N. microtis*), and *N. geoffroyi* (*N. microdon*). All species that are shared between New Guinea and Australia occur on

the Cape York Peninsula with the exception of *Nyctophilus timoriensis* and *Tadarida australis*. As mentioned above, the true distribution of *N. timoriensis* is poorly known but it almost certainly does not occur on the Cape York Peninsula. It may have used the western part of the land bridge since it is known from both the Northern Territory and New Guinea. *Tadarida australis* is, as discussed above, represented by widely separated populations in Australia (*a. australis*) and New Guinea (*a. kuboriensis*) and the precise nature of the former connection is unknown. As mentioned above, five New Guinea species (*Dobsonia moluccensis*, *Saccolaimus mixtus*, *Hipposideros cervinus*, *H. semoni*, *Murina florum*) have only a limited distribution on Australia (Cape York Peninsula). Five other species (*Macroglossus minimus*, *Saccolaimus saccolaimus*, *Hipposideros ater*, *H. diadema*, *Pipistrellus tenuis*) occur also in tropical areas to the west (Northern Territory, Western Australia). *Mormopterus beccarii* might also be included in this category since, though poorly known in Australia, it does occur on the Cape York Peninsula and in northern Western Australia, but also in southeastern Queensland. Yet another species (*Pteropus conspicillatus*) is confined to tropical eastern Queensland but does extend south of the Cape York Peninsula. For all the species mentioned above except for *Pteropus alecto*, *P. scapulatus*, *Nyctophilus timoriensis*, and *Tadarida australis*, the main distributional areas as well as the ranges of related species are to the north of Australia so dispersal from New Guinea to Australia is strongly indicated.

Besides *Pteropus alecto* and *scapulatus*, there are four species (*Chalinolobus nigrogriseus*, *Nycticeius balstoni*, *Nyctophilus gouldi*, *N. timoriensis*), which have a much more restricted distribution in New Guinea than in Australia. It is therefore probable that all six species reached New Guinea from Australia. As mentioned above, *C. nigrogriseus* and *N. balstoni* are each part of an Australian radiation. The radiation of *Nyctophilus* involved both areas since each has endemic species lacking in the other (*N. walkeri*, *N. arnhemensis*, *N. geoffroyi*, in Australia; *N. microtis*, *N. microdon*, in New Guinea).

Some eight cases require more extensive

discussion. *Syconycteris australis* has an extensive Australian distribution from Cape York to northeastern New South Wales but only a single subspecies occurs. North of New Guinea, the species has a range from the Moluccas to the Bismarcks and East Papuan Islands with considerable geographical variation. Moreover a second species (Ziegler, 1982) has been described from New Guinea. A northern origin with southward dispersal is therefore indicated. *Rhinolophus megalophyllus* has an even more extensive Australian distribution, from Cape York to Victoria. However, as explained above, I believe there is only a single subspecies throughout this area. While the known New Guinea range is small, the species occurs in the Bismarcks and East Papuan Islands and three well-marked subspecies can be recognized. Furthermore, several closely related species (*simplex*, *keyensis*, *borneensis*) are known from islands to the west of New Guinea. Again, northern origin and southward dispersal are indicated. *Myotis adversus* has a still more extensive Australian distribution from Cape York south to Victoria and also west to northeastern Western Australia, but with only one subspecies. North of Australia, *M. adversus* has an extensive range from southeastern Asia to the New Hebrides in which there are several subspecies. Furthermore, there are several close relatives (e.g., *M. hasselti*, *M. horsfieldi*) on the islands of the Sunda shelf. Again, northern origin and southward dispersal are indicated. *Miniopterus schreibersi* (as I delimit this species) has a very extensive range from Europe and Africa at least as far east as the Solomon Islands. Within this area, numerous subspecies are recognized and other related species (e.g., *M. magnater*) also occur. In Australia, there is (according to my view) only a single species, with two well-marked subspecies, and a fairly extensive continental distribution. *Miniopterus schreibersi* tends to avoid the dryer areas, however, and is therefore absent from large areas of the south and west. It also has no very close relatives in Australia, *M. australis* belonging to a somewhat different group within the genus. Again, northern origin and southward dispersal seems indicated. *Miniopterus australis* has a distribution very similar to that of *Syconycteris australis* and like

it has only a single Australian subspecies. The subspecies situation to the north of Australia is confused, but there are related species (*M. paululus*, *M. pusillus*) which are present in the north but absent in Australia. Again, a northern origin and subsequent dispersal to the south seems the most likely explanation. *Kerivoula (Phoniscus) papuanus* is known by only a few specimens from eastern New Guinea and northeastern Australia. However, its closest relatives (*K. atrox* and *K. jagorii*) are confined to the Sunda and Wallacean portions of the Indo-Malayan region. Again, northern origin followed by southward dispersal is most likely. *Mormopterus planiceps* presents a more complicated problem. Since it has an extensive Australian and (apparently) a restricted New Guinea distribution, southern origin seems most probable. However, its closest relatives are *norfolkensis* (if indeed this is a distinct species) and *becarii*. Both are poorly known from a distributional standpoint, so there is some doubt as to how to treat *Mormopterus planiceps*. Finally, there is *Chaerephon jobensis*, which has an extensive tropical Australian distribution, but representing a single subspecies. The species also has an extensive northern distribution, extending from New Guinea to the Fijis and in this area is represented by three subspecies. Furthermore, its closest relative is *C. plicata* of the Indo-Malayan region. A northern origin and southward dispersal is therefore most probable. Thus we see that of the 27 species shared between tropical Australia and New Guinea, only *Pteropus alecto*, *P. scapulatus*, *Chalinolobus nigrogriseus*, *Nycticeius balstoni*, *Nyctophilus gouldi*, *N. timoriensis*, and perhaps *Mormopterus planiceps* and *Tadarida australis* are likely to have moved from Australia. For the remaining 19 species, a New Guinea origin is most probable. This is, of course, to be expected since bats show greatest diversity in wet tropical areas and New Guinea is much richer than Australia in wet tropical habitats.

GEOGRAPHICAL RELATIONSHIPS WITH THE LESSER SUNDAS

The Lesser Sunda Islands, the area which approaches Australia to the northwest, is here

defined as all the islands from Lombok to Tanimbar (=Timorlaut). This area is somewhat arbitrarily defined since the more western islands show closest mammalogical affinity with Java, whereas the easternmost islands (particularly Tanimbar) have their closest affinity with New Guinea. However, there is no evidence that any of these islands have been connected with either of the two large land masses of the Sunda and Sahul shelves. Goodwin (1979) recognized 22 species of bats as almost certainly occurring on Timor and there appear to be some 15 additional species not known from Timor, but reliably recorded from other Lesser Sunda Islands. Many of these 37 species have no close relatives in Australia. In the following discussion only those species which either occur or are represented in Australia are considered.

Pteropus alecto: Besides Australia and extreme southern New Guinea, this species occurs on several islands from Bawean (on the Sunda shelf) and Celebes to Sawu (=Savu, just west of Timor), over this area being represented by three subspecies, whereas all Australian (and New Guinea) populations are referable to *P. a. gouldi*. This seems to be a clear instance of derivation of the Australian (and through them the New Guinea) populations from the Lesser Sundas.

Macroglossus minimus (=lagochilus): As mentioned above, this species has an extensive distribution from the Malay Peninsula to the Solomons, including Timor. Goodwin (1979) referred Timor specimens to *M. m. lagochilus*, whereas Australian specimens are here referred to *M. m. nanus* (=pygmaeus). These subspecies are distinguished by Andersen (1912) primarily by the narrower molars and premolars of *nanus*. This distinction seems to hold (although with considerable variation), the few adult Australian skulls I have seen agreeing with those from New Guinea in having narrower cheek teeth than the few skulls I have seen from Timor. While a revision of the genus is certainly in order, derivation of the Australian populations from Timor seems considerably less likely than from New Guinea.

GENUS *Taphozous*: With the exception of a single record (probably accidental) of *T. australis*, all four Australian species are endemic to that continent. Since, with the above

exception, there are no species in New Guinea, but two in the Lesser Sunda Islands, the latter seems the most probable source for the Australian species. *Taphozous melanopogon* is recorded (Goodwin, 1979) from as far east as Timor and there is also a specimen in the American Museum from the Kei Islands. *Taphozous longimanus leucopleurus* was described from Flores and, as mentioned above, was compared in the original description of *T. kapalgensis*. Males of *T. melanopogon* have long, usually black, hair in the gular region and no trace of a gular sac in either sex. This condition is unknown in any of the Australian species. Males of *T. longimanus*, on the other hand, have a naked gular area with a well-developed sac, a condition found in three of the four Australian species (*hilli*, *kapalgensis*, *australis*). It also shares small skull size with *hilli*, broad sphenoid pits with *australis*, and a weak anterior mandibular emargination with *kapalgensis*. Therefore, there do seem to be special relationships between *T. longimanus* and at least three of the Australian species. Whereas radiation of a single stock into four species subsequent to reaching Australia is most probable, this stock would seem to have been either *T. longimanus* or a close relative and to have come from the Lesser Sunda Island area.

GENUS *Saccolaimus*: As discussed above, there are three species of this genus in Australia, one endemic (*flaviventris*) and two shared with New Guinea (*mixtus*, *saccolaimus*), the latter also having an extensive Indo-Malayan range, including the Lesser Sunda Islands, where it is the only species of *Saccolaimus*. As mentioned above in the New Guinea section, clearly there has been recent interchange between Australian and New Guinea involving *T. mixtus* and *T. saccolaimus*, but the ultimate derivation of the Australasian species is less certain. Certainly the endemic Australian *T. flaviventris* is the most distinctive of the three species and could have had a separate origin from *S. saccolaimus* or a close relative coming into Australia from the Lesser Sundas. *Saccolaimus saccolaimus* itself could have entered Australia from either the Lesser Sundas or New Guinea (or even perhaps both) since it is now known from the Northern Territory as well as Cape York. *Saccolaimus mixtus*, however, judged

by its very restricted Cape York distribution in Australia and its much more extensive New Guinea distribution, almost certainly did not enter Australia from the Lesser Sundas.

Rhinolophus megaphyllus Subgroup: Besides *megaphyllus*, this subgroup (called the *simplex* subgroup by Tate and Archbold, 1939) includes, in the Lesser Sundas, *R. simplex* of Lombok, Sumbawa, and Komodo (specimen in the American Museum) and *keyensis annectens* of Wetar. Though this group is in need of taxonomic revision, it is evident that neither of these two taxa is as closely related to *m. megaphyllus* (= *ignifer*) as the three New Guinea subspecies. This, plus the absence of *m. megaphyllus* from west of the Great Dividing Range makes it unlikely that *R. megaphyllus* reached Australia from the Lesser Sundas.

Rhinolophus philippinensis: Known records for this species are very spotty. Besides *R. p. robertsi* of Cape York, there is *R. p. achilles* of the Kei Islands, and the newly described *R. p. montanus* of Timor (Goodwin, 1979, p. 112), together with several subspecies from farther north. The species has not, as yet, been recorded from New Guinea. The distances are so great among these separate areas that it seems impossible, at this time to decide by what route *R. p. robertsi* reached its present range.

Hipposideros diadema: This widespread species is represented by *H. d. diadema* in the islands from Java to Timor. As mentioned above, this subspecies is quite different from either of the two Australian subspecies. Furthermore, the subspecies closest to Timor (*H. d. inornatus*) is particularly different from it, whereas *H. d. reginae* of Cape York is very similar to *H. d. pullatus* of the New Guinea mainland. Derivation of the Australian populations from the Lesser Sundas is highly improbable.

Myotis (Selysius): As discussed above, this subgenus probably does not occur in New Guinea but is represented by *M. muricola* in the Lesser Sundas (east to Flores and Sumba). It is therefore likely that the very poorly known *australis* and the Kimberley species were derived from the Lesser Sundas.

Pipistrellus tenuis: I have discussed this species at length above. Although the sub-

species on Cape York (*P. t. papuanus*) almost certainly came from New Guinea, *P. t. westralis* of Western Australia probably came from the Lesser Sundas. The two lineages have evidently come together in the Northern Territory and hybridized, since I would interpret the two specimens I have seen from the Northern Territory as intergrades.

Murina florium: In the Lesser Sundas, this species is known from Sumbawa and Flores. Too little is known about geographical variation in this species to say whether the Cape York population is more closely related to those of New Guinea or to the Lesser Sundas. The known Australian distribution, however, makes Lesser Sunda derivation highly improbable.

Nyctophilus timoriensis: There is still considerable doubt as to whether or not this species really occurs on Timor (see Hill and Pratt, 1981). Even if this old unsubstantiated record is correct it would obviously have nothing to do with the origin of the otherwise endemic Australia-New Guinea genus *Nyctophilus*.

This concludes the species or species groups that are shared between Australia and the Lesser Sundas. Of these only two (*Pteropus alecto* and *Pipistrellus tenuis sewelanus-westralis*) show clear evidence of recent derivation of Australian populations from conspecific ones on the Lesser Sundas. For two others (*Taphozous*, *Myotis (Selysius)*), an earlier derivation with subsequent speciation on Australia seems the most likely explanation. For all others, either derivation from the Lesser Sundas is improbable, or the evidence is equivocal.

THE ORIGIN OF THE AUSTRALIAN BAT FAUNA

It is now generally agreed (see e.g., Hallam, 1981) that early in the Cenozoic, Australia lay far to the south of its present position and close to if not actually joined with Antarctica. Both the monotremes and the marsupials clearly have had a long history in Australia. The former may even have been in Australia since the breakup of Pangaea in the Jurassic, judged by the extreme distance of their relationship with other mammals and their re-

striction (as far as we know) to Australia and New Guinea (the southern part of which was part of Australia before it moved northward), either as living animals or fossils. From known fossil evidence, it is likely that the marsupials did not reach Australia much before the beginning of the Cenozoic. If so, they probably had to get across at least one (albeit narrow) water gap from South America via Antarctica, since otherwise it is difficult to understand why edentates and South American ungulates (which also occurred in South America at the beginning of the Cenozoic) did not also reach Australia. Between the beginning of the Eocene and sometime in the Miocene (some 30 million years) it is probable that monotremes and marsupials were the only land mammals in Australia.

Starting sometime in the Miocene, however, Australia (including what is now southern New Guinea) came close to a northern chain of islands extending from southeastern Asia through what is now northern New Guinea and beyond. Whereas a number of groups of placental mammals presumably occurred at the western end of this chain, only the murid rodents and five families of bats occurred on the more eastward islands with which the Australian plate became associated. This is shown by the absence of any other placentals from the Moluccas, New Guinea, or the Bismarcks with the exception of recent human introductions. Both the bats and the murid rodents had reached Australia by the Pliocene and, as we shall see, at least one bat species is now known as fossil from the Miocene.

One characteristic of both the rodent and bat faunas of Australia (and also New Guinea) is the low level of endemism, which hardly goes above the tribal level even when the Bismarcks, Solomons, and Moluccas are added. Thus, among the bats, the tribe Nyctophilini (including *Nyctophilus* and *Pharotis*), which is almost endemic to Australia and New Guinea, is probably the most distinct. As mentioned above, there are only two endemic Australian genera of bats (*Macroderma*, *Rhinonycteris*); only three in New Guinea (*Aproteles*, *Paranyctimene*, *Pharotis*); and no additional genera endemic to Australia and New Guinea together. To me this makes any

hypothesis that some part of the Australian bat fauna was there when Australia commenced its northward drift in the Eocene (or reached there across broad expanses of open ocean afterward) highly improbable. Rather a percolation of numerous species across a series of relatively narrow water gaps from the north and west, starting in the Miocene, seems indicated. Some of these species that reached Australia relatively early either differentiated into endemic genera or radiated out into a group of endemic species (*Taphozous*, *Eptesicus*, *Chalinolobus*, *Nycticeius*). In the case of *Taphozous*, there is still a related species on islands nearby, whereas in the other three (as also with *Nyctophilus* whose radiation surely also involved New Guinea), there is now a wide gap between the ranges of the Australian species and their closest Asian (or African) relatives.

Prior to 1982, the few known pre-Pleistocene fossil bats were represented by too little material to determine their affinities. Sigé et al. (1982), however, have now described a Miocene species from northwestern Queensland which they refer to the otherwise French Miocene subgenus *Hipposideros* (*Brachhipposideros*). What is more, they point out a special resemblance between this subgenus and the living endemic Australian genus *Rhinonycteris*. I have compared their figures with skulls of the three groups of *Hipposideros* now in Australia, together with the three other Australian region hipposiderines (*Anthops*, *Aselliscus*, *Rhinonycteris*) and agree with them. Thus it would appear that we can now trace the origin of one of the two endemic Australian bat genera back to the Miocene when it was still referable to an apparently widespread Old World subgenus. Furthermore, Hill (1982) has regarded *Rhinonycteris* as being specially related to the African *Cloeotis* and *Triaenops*. Therefore, all three genera could have been derived from the widespread Miocene *Brachhipposideros*. *Macroderma*, the other endemic Australian bat genus, is most closely related to the Indo-Malayan *Megaderma*, which extends east at least to Celebes and perhaps to the Moluccas, but is not known from either the Lesser Sundas or New Guinea. *Macroderma* is known fossil from the Pleistocene, when it occurred

farther south in Australia than today (Hamilton-Smith, 1966), but it is not known how long it has been in Australia.

Of the other endemic Australian species, I have already discussed *Pteropus poliocephalus* (an Australian representative of the New Guinea *P. macrotis*), *Nyctimene robinsoni* (an Australian representative of *N. major* of the New Guinea area), the species of the genus *Taphozous*, *Saccolaimus flaviventris*, *Hipposideros stenotis* (a dry country representative of the mesic Australia-New Guinea *H. semoni*), and *Myotis australis* and its Kimberley representative. I have no idea what is the closest relative of the endemic southern Australian *Pipistrellus tasmanienensis*. This leaves the endemic Australian representatives of the genera *Eptesicus*, *Chalinolobus*, *Nycticeius*, and *Nyctophilus*.

As discussed above, though the Australian *Eptesicus* seem to be closely related among themselves; their relationship to other *Eptesicus* is far from clear. They show no special relationship to the geographically closest species (in mainland southeast Asia) and may be more closely related to the *Eptesicus capensis* group of Africa (see Koopman, 1975, p. 405). In view of our ignorance of *Eptesicus* relationships, it is difficult to say. Another possibility is that in view of the probably polyphyletic origin of *Eptesicus* (see Koopman, 1975, p. 406), Australian "*Eptesicus*" are really independently derived from a small *Pipistrellus* such as *P. tenuis*, which would explain its wide geographical separation from other *Eptesicus*.

I previously (Koopman, 1971) discussed my reasons for uniting *Glauconycteris* of Africa with *Chalinolobus* subgenerically. The subgenus *Chalinolobus* is, of course, not endemic to Australia but also occurs in southeastern New Guinea and on three Pacific islands (New Caledonia, Norfolk, New Zealand). There is, however, a great gap between Australia and Africa where there is at present no member of the genus *Chalinolobus*, though, if I am correct, there almost certainly were representatives in southern Asia at one time, which have since disappeared.

I previously (Koopman, 1978) discussed the Australian species of *Nycticeius* in relation to other members of the genus. Briefly, the Australian (and New Guinea) species be-

long to two endemic sugenera (*Scoteanax* and *Scotorepens*). The subgenus *Nycticeius* includes the remaining species but these are widely separated from those of Australia and from one another. In Africa and extreme southwestern Asia there is *N. (N.) schlieffeni* whereas in North America and Cuba there is the *N. (N.) humeralis* group. As with *Chalinolobus*, this is obviously a relict distribution with occurrence at one time in southern and eastern Asia including the Malay archipelago.

Nyctophilus (along with its close endemic New Guinea relative, *Pharotis*) has generally been associated taxonomically with the North American and Cuban *Antrozous* and the Middle American *Bauerus* (Engstrom and Wilson, 1981). A closely related early Pleistocene genus, *Anzanycteris*, from North America has also been described (White, 1969). However, considerable doubt has been expressed as to whether the North American and the Australasian genera are really each others closest relatives or whether instead they are independently derived from Nycticeini. It has even been suggested (see Pine, Carter, and LaVal, 1971) that the *Antrozous* group is specially related to the Palearctic nycticeine genus *Otonycteris*, to which it bears a strong external resemblance. In any case, it is clear that the *Nyctophilus* group has no close relatives in the Indo-Malayan region at present. It has been in New Guinea and Australia long enough to have undergone a considerable adaptive radiation, including the evolution of a New Guinea endemic (*Pharotis imogene*) that is currently regarded as a separate genus.

APPENDIX: LOCALITIES OF TROPICAL AUSTRALIAN BATS IN THE AMERICAN MUSEUM OF NATURAL HISTORY

Pteropus alecto gouldi

QUEENSLAND: no locality (AMNH 108867–108868); Brown's Creek, Pascoe River (AMNH 154550–154553, 155005); Coen (AMNH 108860–108863); Lockerbie, 10 mi. wsw. Somerset (AMNH 154547); Normanton (AMNH 183581); Portland Roads (AMNH 155548–155549).

WESTERN AUSTRALIA: Kalumburu (AMNH 197132); Mitchell River (AMNH 236505–236508); Parry Creek (AMNH 197123–197131); Tambrey (AMNH 197133–197135); Tunnel Creek (AMNH 197136–197138, 236510–236511).

Pteropus conspicillatus conspicillatus

QUEENSLAND: locality uncertain (AMNH 156963, 156966–156967); Babinda Creek (AMNH 66150–66155); Coen (AMNH 108864); Cooktown (AMNH 155318); Julattan (AMNH 154242–154246); Lake Barrine (AMNH 107332–107334); Peach River (AMNH 154565–154568, 154570); Shipton's Flat (AMNH 155303–155317, 155319–155324).

Pteropus scapulatus

QUEENSLAND: Byfield (AMNH 162661–162662); Coen (AMNH 108865–108866, 153500, 154571–154572); Cooktown (AMNH 155318); Flaggy (AMNH 156964–156965); Green Hills (AMNH 156989–156708); Hann River (AMNH 154573–154577); Helenvale (AMNH 154579–154585); Peach River (AMNH 154564, 154569); Shipton's Flat (AMNH 154578, 156968–156988); Wenlock, Batavia River (AMNH 154554–154563).

WESTERN AUSTRALIA: Frazier Downs (AMNH 197139–197142); Ningbing (AMNH 197143–197149); Parry Creek (AMNH 197150–197152); Stockade Creek (AMNH 236509).

Dobsonia moluccensis magna

QUEENSLAND: Coen (AMNH 154589); Iron Range (AMNH 154586–154588); Peach River (AMNH 154590–154591).

Nyctimene robinsoni

QUEENSLAND: Captain Billy Creek, "Heathlands" (AMNH 222758–222759); Mission Beach (AMNH 196643–196644); Portland Roads (AMNH 154759); Shipton's Flat (AMNH 196630, 222726).

Macrogllossus minimus nanus

QUEENSLAND: Seagren's Farm (AMNH 154741–154743).

WESTERN AUSTRALIA: Mitchell River (AMNH 236512–236514).

Syconycteris australis australis

QUEENSLAND: no locality (AMNH 108843, 108845, 108848, 108856–108857, 108859); Shipton's Flat (AMNH 222725).

Taphozous australis

QUEENSLAND: no locality (AMNH 153516); Albany Island (108826–108828); Cairns-Mossman Road, Rex's Lookout (AMNH 154850–154851); Coen (AMNH 154729–154731, 154852–154855); Cowie Bay Cave (AMNH 156946–156958); Newcastle Bay (AMNH 154716); Port-

land Roads (AMNH 154717–154719); Possession Island (AMNH 154714–154715); Wenlock, Batavia River (AMNH 154723–154728).

Taphozous georgianus troughtoni

QUEENSLAND: Chillagoe Caves (AMNH 66145, 154847–154849, 183556–183557); Lappa Junction (AMNH 183558–183560); Mungana Caves (AMNH 183551–183555); Rifle Creek, Mt. Isa (AMNH 162707–162708); Pentland (AMNH 107727, 107769–107770, 109268–109269); Quamby (AMNH 107720–107725, 107731, 107733–107737, 107740–107741, 107746–107754, 107761, 109263–109267); Mt. Etna, Rockhampton (AMNH 162706).

NORTHERN TERRITORY: 3 mi. n. Katherine (AMNH 160387–160390, 220075); 18 mi. n. Wollgorang (AMNH 183437–183440, 183537–183550).

Taphozous georgianus georgianus

WESTERN AUSTRALIA: Barrow Island (AMNH 197558); Black Elvire River (AMNH 197176–197177); 20 mi. n. Callowa (AMNH 236515); Inglis Gap (AMNH 197559); Kalumburu (AMNH 197179–197180); King Edward River (AMNH 236525–236529); Manning Creek (AMNH 236530–236536); Mt. Anderson (AMNH 197175, 236537); Napier Downs (AMNH 236538–236540); Ningbing (AMNH 197181); Parry Creek (AMNH 197182); Peawah, Mundabulungana (AMNH 197183–197185); Tambrey (AMNH 197186–197188, 197560, 236516–236518); Tunnel Creek (AMNH 197189–197190, 236541–236542); Whim Creek (AMNH 197191–197193); Willie Wollie Spring (AMNH 216130–216132); Wittenoom Gorge (AMNH 236519–236524); Woodstock (AMNH 197194–197199); Yardie Homestead (AMNH 197200).

Taphozous hilli

NORTHERN TERRITORY: Tennant Creek (AMNH 160450).

Saccolaimus mixtus

QUEENSLAND: Brown's Creek, Pascoe River (AMNH 154720–154722).

Saccolaimus saccolaimus nudicluniatus

QUEENSLAND: Babinda Creek (AMNH 66144).

Saccolaimus flaviventris

QUEENSLAND: Malbon (AMNH 107729, 107742); Pentland (AMNH 107755–107760).

WESTERN AUSTRALIA: Inglis Gap (AMNH 197174); Ningbing (AMNH 197201–197202).

Macroderma gigas (incl. *saturata*)

QUEENSLAND: Mt. Etna, Rockhampton (AMNH 162669–162674).

NORTHERN TERRITORY: 18 mi. w. Wologorang (AMNH 183435).

WESTERN AUSTRALIA: Kalumburu (AMNH 197210); Koolan Island (AMNH 197203–197209, 236543); 20 mi. s. Marble Bar (AMNH 197211); Tunnel Creek (AMNH 236544–236546).

Rhinolophus megaphyllus megaphyllus
(incl. *ignifer*)

QUEENSLAND: no locality (AMNH 108829–108836, 108839–108842, 108844, 108846–108847, 108849–108850, 108852, 108854–108855, 108858); Mt. Carbine (AMNH 107365); Coen (AMNH 108818–108825, 154959–154996, 220076); Cairns (AMNH 154592–154593); Julattan-Mossman Road (AMNH 154594–154595, 154904–154908); Portland Roads (AMNH 154596–154600); Iron Range (AMNH 154601–154615, 154909–154952); Pascoe River, Brown's Creek (AMNH 154616); upper Nesbit River (AMNH 154617–154620); upper Peach River (AMNH 154621–154624); Laura (AMNH 154626); Mt. Finnigan (AMNH 154627–154630, 154997–154999); Shipton's Flat (AMNH 154631–154632, 155000, 155251–155255, 155257–155259, 155261–155269, 155271, 155273, 155275, 155277–155280, 155282, 155284–155285, 155287–155288, 155291, 155293, 155295–155298, 155302); Walter Hill range (AMNH 154664); Irvine Bank (AMNH 154898–154903); Wenlock (AMNH 154953–154958); Cooktown-Laura railroad (AMNH 155001–155003); Collingwood (AMNH 155256, 155260, 155276, 155299); Home Rule (AMNH 155270, 155283, 155286, 155290, 155301, 157009–157011); Grass Tree (AMNH 155272, 155274, 155281, 155292, 155294, 155300, 155407–155414); Helenvale (AMNH 155289); Boiling Springs (AMNH 155404–155405); Mt. Poverty (AMNH 155406); Stucky's Gap (AMNH 157012); Wyalla (AMNH 157013); Green Hills (AMNH 157014); Ayton (AMNH 156924, 157015–157018); Middle Normanby (AMNH 157019–157021); Mt. Amos, Phoenician (AMNH 157022–157053); Lappa Junction (AMNH 183445–183446, 183515–183520); Chillagoe (AMNH 183509); Mt. Cook (AMNH 194155–194158); Endeavor Bridge (AMNH 194159–194170); McIvor (AMNH 194171–194172); Innisfail (AMNH 194230–194238); Mt. Etna (AMNH

162663–162666); Cromarty (AMNH 162667–162668); Lyndhurst Station (AMNH 183510–183514).

Rhinolophus philippinensis robertsi

QUEENSLAND: Helenvale (AMNH 157034); Mt. Amos, Phoenician (AMNH 157055–157071).

Hipposideros ater aruensis

QUEENSLAND: Lockerbie (AMNH 155666–155668); Shipton's Flat (AMNH 155394, 194173, 196631); Bramston Beach (AMNH 194224–194229).

Hipposideros ater gilberti

NORTHERN TERRITORY: 13 mi. s. Katherine (AMNH 160376–160377).

WESTERN AUSTRALIA: Koolan Island (AMNH 197212).

Hipposideros cervinus cervinus

QUEENSLAND: Newcastle Bay (AMNH 154669); Somerset (AMNH 154670–154685, 154857–154878); Thursday Island (AMNH 154686–154687); Iron Range (AMNH 154691–154696, 154708, 154881–154883, 154885–154888); Coen (AMNH 154889–154897).

Hipposideros semoni

QUEENSLAND: no locality (AMNH 108851); Coen (AMNH 154709); Cooktown (AMNH 154856); Iron Range (AMNH 154707); Upper Nesbit River (AMNH 154710–154712).

Hipposideros stenotis

NORTHERN TERRITORY: 18 mi. w. Wologorang (AMNH 183441–183442, 183563–183564).

Hipposideros diadema reginae

QUEENSLAND: Coen (AMNH 108853); Cairns (AMNH 154665); Chillagoe (AMNH 183565–183578); Iron Range (AMNH 154688–154690, 154697–154706, 154879–154880, 154884); Shipton's Flat (AMNH 160284, 194174–194175).

Rhinonycteris aurantius

NORTHERN TERRITORY: 16 mi. s. Katherine (AMNH 199979–199980).

WESTERN AUSTRALIA: Koolan Island (AMNH 197213–197216).

Myotis adversus macropus

QUEENSLAND: Cairns (AMNH 154635–154636, 155010).

WESTERN AUSTRALIA: Mitchell River (AMNH 236547–236577).

Pipistrellus tenuis papuanus

QUEENSLAND: Archer River (AMNH 154655); Brown's Creek (AMNH 154654); Upper Peach River (AMNH 154656).

Pipistrellus tenuis westralis

WESTERN AUSTRALIA: Cape Bossut (AMNH 216134–216137).

Eptesicus pumilus pumilus

QUEENSLAND: Alderbury, 25 mi. out on Cooktown-Laura Railway (AMNH 154659); Black Mountain, 15 mi. s. Cooktown (AMNH 154657–154658); Chillagoe (AMNH 154760–154762); China Camp, south of Cooktown (AMNH 194176–194185); Helenvale, south of Cooktown (AMNH 156959–156962); Iron Range (AMNH 154651–154653); Irvinebank (AMNH 154772–154774, 155015); Lappa Junction (AMNH 183536); Lock-erbie, 8 mi. wsw. Somerset (AMNH 155012); Mungana caves (AMNH 183534–183535); Pentland (AMNH 107728, 107790–107795); Koombooloomba Creek, 30 mi. s. Ravenshoe (AMNH 183383, 183495–183496).

Eptesicus pumilus caurinus

QUEENSLAND: Mount Isa (AMNH 162702–162705); Quamby (AMNH 107726, 107732, 107739, 107772–107789, 109270–109273).

NORTHERN TERRITORY: 3–5 mi. n. Katherine (AMNH 160378–160386, 160391–160400, 220084–220085).

WESTERN AUSTRALIA: Inglis Gap (AMNH 197575); Kalumburu (AMNH 197577–197586); Parry Creek (AMNH 197622–197630); King Edward River (AMNH 236597); Koolan Island (AMNH 236598–236603); Napier Range (AMNH 236611–236621); Tunnel Creek (AMNH 236622–236623); Peawah, Mundabullangana (AMNH 197631–197636); Tambrey (AMNH 197637–197642, 236632–236639); Whim Creek (AMNH 197643); Woodstock Station (AMNH 197644–197650, 197705–197709); 20 mi. n. Callowa (AMNH 236624–236631); Wittenoom Gorge (AMNH 236640–236642).

Eptesicus pumilus ssp.

WESTERN AUSTRALIA: Barrow Island (AMNH 197570–197573, 197699–197704,

197727); Montebellos, Hermite Island (AMNH 197698, 197702); Nodswell Creek (AMNH 197621); 6 mi. ne. Yardie Homestead (AMNH 197710–197726).

Eptesicus douglasi

WESTERN AUSTRALIA: Inglis Gap (AMNH 197596); Langey Crossing (AMNH 197598–197620); Mt. Anderson (AMNH 197566–197569, 236604–610); Derby (AMNH 236578–236596).

Chalinolobus nigrogriseus nigrogriseus

QUEENSLAND: Seagren's Farm (AMNH 154661–154663); Shipton's Flat (AMNH 155230, 155232–155234, 155401–155402); Karumba (AMNH 160243).

Chalinolobus nigrogriseus rogersi

QUEENSLAND: 24 mi. s. Burketown (AMNH 183431).

NORTHERN TERRITORY: 18 mi. w. Wologorang (AMNH 183432, 183579); 12 mi. e. Coolibah (AMNH 216194).

WESTERN AUSTRALIA: Ningbing (AMNH 196711, 197261–197262); Parry Creek (AMNH 196710); North Creek (AMNH 216195–216196).

Chalinolobus gouldi venatoris

QUEENSLAND: Pentland (AMNH 107764–107765, 107800, 109275); Malbon (AMNH 109274).

WESTERN AUSTRALIA: Inglis Gap (AMNH 197248); La Grange Dam (AMNH 107250–107251); Cape Bossut (AMNH 216183–216193).

Nycticeius greyi

QUEENSLAND: Pentland (AMNH 107796–107798, 109278); Malbon (AMNH 109279); 24 mi. s. Burketown, Gregory River (AMNH 183429); between Camooweal and Mt. Isa (AMNH 196642).

NORTHERN TERRITORY: 18 mi. w. Wologorang (AMNH 183430, 183432–183433); 12 mi. e. Coolibah, Victoria River (AMNH 216138).

WESTERN AUSTRALIA: Cape Bossut (AMNH 216141–216146, 216150–216157, 216161–216166, 216168–216174, 216176–216179, 236645).

Nycticeius balstoni sanborni

QUEENSLAND: Seagren's Farm, 10 mi. w. Cooktown (AMNH 154660); Cooktown (AMNH 154775).

Nycticeius balstoni caprenus

WESTERN AUSTRALIA: Frazier Downs (AMNH 197263); La Grange (AMNH 197264–197267); Ningbing (AMNH 197268); Yannarie River (AMNH 197269–197271); Cape Bossut (AMNH 216139–216140, 216147–216149, 216158–216160, 216167, 216175, 216180, 236643–236644); Yeeda Creek (AMNH 216181).

Nycticeius rueppelli

QUEENSLAND: Ravenshoe, Koombooloombah Creek (AMNH 183376).

Miniopterus schreibersi oceanensis

QUEENSLAND: Cunjeboi (AMNH 107340–107352); Mt. Spurgeon (AMNH 107353–107364); Pentland (AMNH 107766–107768, 107799, 109276); Port Stuart (AMNH 108805–108816); Somerset (AMNH 108817); Cairns (AMNH 154633–154634); Thursday Island (AMNH 154637–154650, 154776–154826); Walter Hill Range (AMNH 154744); Possession Island (AMNH 154745, 154751–154753, 154835–154846); Chillagoe (AMNH 154827–154834); Lockerbie (AMNH 155011, 155013); Shipton's Flat (AMNH 155226, 194190–194191); Mt. Amos, Phoenician (AMNH 156904–156923); Ayton (AMNH 156925–156945); Koombooloomba Creek (AMNH 183374–183375, 183468–183471); Lyndhurst Station (AMNH 183478–183479); Green Hills (AMNH 194188); Cooktown (AMNH 194189); Bramston Beach (AMNH 194240–194241); Ingham (AMNH 194242–194245); 5 mi. se. Coen (AMNH 220088).

Miniopterus schreibersi orianae

NORTHERN TERRITORY: Kintore Cave, north of Katherine (AMNH 220087).

WESTERN AUSTRALIA: Ningbing (AMNH 197272–197274); Parry Creek (AMNH 197275–197276); Mitchell River (AMNH 236752–236779); Port Warrender (AMNH 236780).

Miniopterus australis australis

QUEENSLAND: Port Stuart (AMNH 108804); Upper Peach River (AMNH 157754); Shipton's Flat (AMNH 154755, 155231, 194186–194187); 4 mi. s. Lappa (AMNH 154763–154771); Cowie Bay (AMNH 156903); 10 mi. n. Rockhampton (162679–162701); Chillagoe (AMNH 183472–183475); 3 mi. w. Mt. Garnet (AMNH 183476–183477); Mungana (AMNH 183480–183483); Innisfail (AMNH 194239).

Kerivoula (Phoniscus) papuensis

QUEENSLAND: Shipton's Flat (AMNH 155403).

Nyctophilus arnhemensis

QUEENSLAND: 24 mi. s. Burketown (AMNH 183436).

NORTHERN TERRITORY: Adelaide River, Tortilla Flats (AMNH 222760).

WESTERN AUSTRALIA: Cape Bossut (AMNH 216197–216200, 216682–216685).

Nyctophilus gouldi bifax

QUEENSLAND: Ravenshoe (AMNH 66147); Atherton Tableland, 9 mi. sse. Ravenshoe (AMNH 66146); Mt. Finnegan (AMNH 154749); Upper Nesbit River (AMNH 154746); Shipton's Flat (AMNH 154747–154748, 154750, 155227–155229, 155395–155397, 160244, 194192–194194, 222727); Jackaroo (AMNH 155398–155400).

Nyctophilus gouldi daedalus

WESTERN AUSTRALIA: Willie Wollie Spring, ca. 20 mi. wnw. Poonda (AMNH 216686–216687).

Nyctophilus geoffroyi pallescens

QUEENSLAND: Pentland (AMNH 109277).

Nyctophilus geoffroyi geoffroyi

WESTERN AUSTRALIA: Yarraloola (AMNH 197279).

Mormopterus planiceps ridei

QUEENSLAND: Cairns (AMNH 154736–154740, 155014); Helenvale (AMNH 154756–154758); Mossman (AMNH 154732–154735); Shipton's Flat (AMNH 155235–155250, 155419–155432); Grasstree (AMNH 155415–155418); Lord's Prayer, south of Cooktown (AMNH 194195); China Camp, south of Cooktown (AMNH 194196); Gordonvale (AMNH 183589).

Mormopterus beccarii ssp.

WESTERN AUSTRALIA: Yannarie River (AMNH 197749).

Chaerephon jobensis colonicus

QUEENSLAND: Lucinda (AMNH 160294–160295); Pentland (AMNH 109281); Malbon (AMNH 107762–107763, 107801–107804, 109280).

WESTERN AUSTRALIA: Derby (AMNH 197155–197170, 236787–236798; 25 mi. n. Hall's Creek (AMNH 197173); Mt. Anderson (AMNH 197154); Woodstock (AMNH 197171); Willie Wollie Spring (AMNH 216688–216691).

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