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Distributional Patterns of Indo-Malayan Bats (Mammalia: Chiroptera)

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ABSTRACT

The bats of southeastern Asia and its islands (northeastern India, southern China, and the Riukiu islands to the Philippines, Sulawesi, and the Lesser Sundas) are enumerated with relevant taxonomic and distributional remarks. Some 254 species occur in this area. A majority of the species occur either in the Indochinese region (north of the Isthmus of Kra) or else in Malaya and the islands of the continental shelf. In each of the portions of this continental area, endemism is relatively low, even though some islands, such as Borneo, are very species-rich. Endemism is much higher in Sulawesi and the Philippines, which have a depauperate bat fauna but a much higher percentage of endemism. The indications from the bat fauna are very strong that the continental islands (separated by relatively shallow water) were recently connected to the mainland, whereas other islands were not.

INTRODUCTION

The area to be discussed (fig. 1) has a particularly rich bat fauna, some 254 species (between a quarter and a third of the world total), 60 genera, and 9 families (all of those in the Eastern Hemisphere except the Myzopodidae and Mystacinidae). The area I will cover is the entire Southeast Asian continent (including extreme northeastern India, Burma, and the southern Chinese lowlands north to the Yangzte River) and continental islands (Taiwan, Sumatra, Java, Borneo, Palawan, etc.). When I use the name "Malaya," it will refer to what is politically "west Malaysia" plus Singapore. Also the following oceanic islands (those off the continental shelves): Riukius, Andamans, Nicobars, Mentawai islands (in a very broad sense, including all offshelf islands of the West Sumatra chain from Simeulue south to Engano), the Palawan group of the Philippines, and the three portions of Wallacea west of Weber's line (Lesser Sundas, Sulawesi and its islands including the Sangihes and Talauds, and the Philippines, excluding the continental islands of the Palawan group). Note that this does not include the Moluccas, whose mammal fauna is predominantly Australasian.

I will first discuss the various genera which

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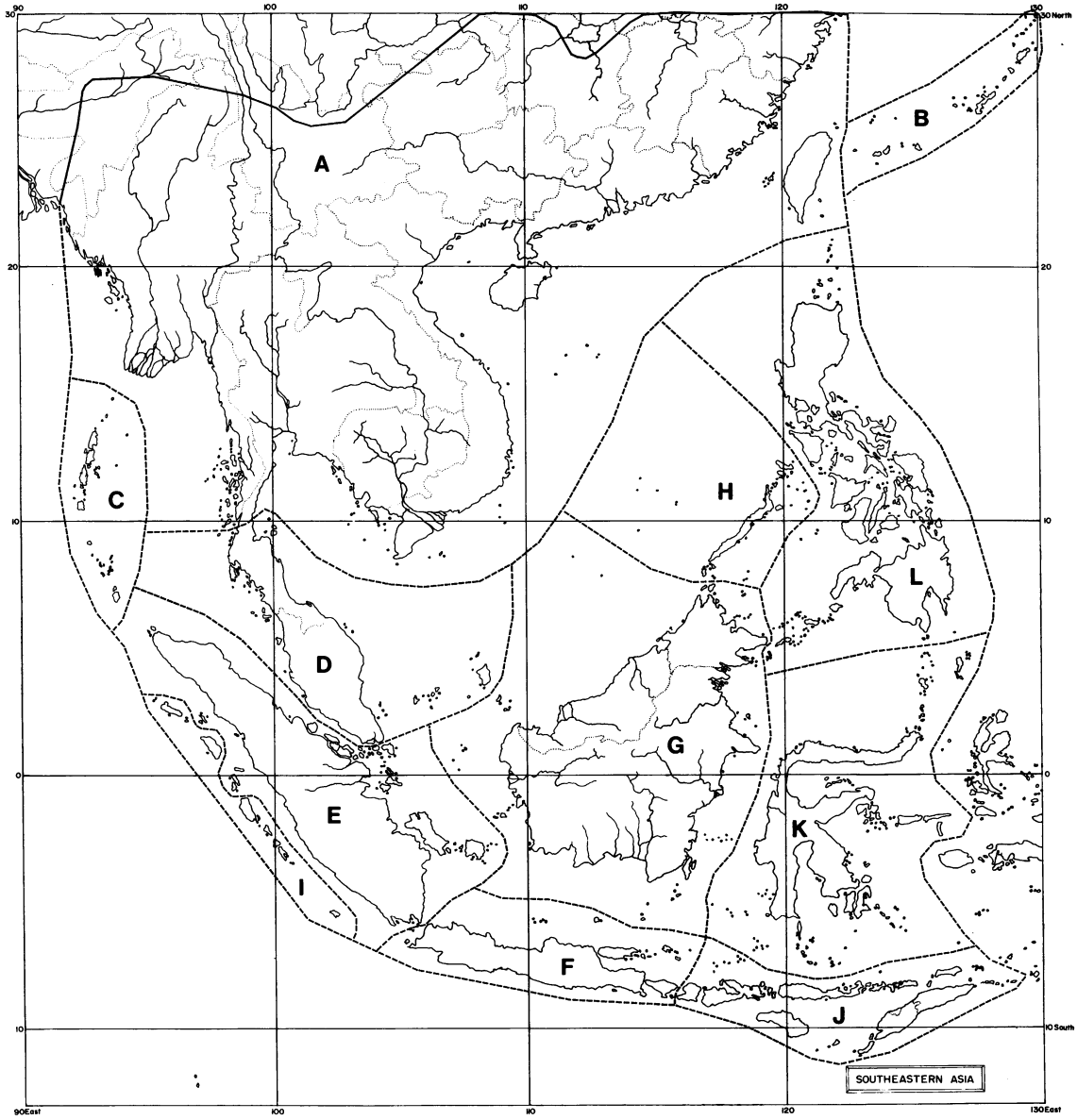

Fig. 1. The area covered in this paper together with the boundaries of the 12 subdivisions referred to in table 1. The Isthmus of Kra is the portion of the mainland across which the boundary between **A** and **D** runs.

occur in this area and the general distribution of the species of each. This will be followed by a general discussion in which I will try to determine the distributional patterns within the area. In general, I follow Payne et al. (1985) for Borneo; I follow Heaney et al. (1987) for the Philippines. I would like to thank Mr. John Hill for access to specimens in the British Museum (Natural History) in London and, as usual, much stimulating discussion. Dr. Lawrence Heaney of the Field Museum of Natural History and Dr. Thomas Griffiths of

Illinois Wesleyan University have each carefully read over the manuscript and made valuable suggestions.

DISTRIBUTIONAL SURVEY OF BAT GENERA IN THE AREA

Pteropodidae

Rousettus (see Rookmaaker and Bergmans, 1981): This is a widespread genus ranging from Africa to the Solomons with four species in our area. *R. leschenaulti* extends from India to peninsular Thailand, Vietnam, and southern China, reappearing in Sumatra and Java and even reaching Simeulue in the Mentawis. *R. amplexicaudatus* has an extensive range from Thailand to the Solomons. The newly described *R. spinalatus* is known only from Sumatra and Borneo, while *R. celebensis* is endemic to the Sulawesi area.

Boneia: This monotypic genus (*B. bidens*) is endemic to northern Sulawesi and is derived from *Rousettus*. In fact, Bergmans and Rozendaal (1988) include it in *Rousettus*.

Pteropus: This is another widespread genus (chiefly on islands) extending from the western Indian Ocean to the central Pacific. While there are many taxonomic and distributional problems, 16 species are currently recognized in the area. *P. hypomelanus* extends from southern Asia to the Solomons, mostly on small peripheral islands. Five closely related species (*P. pumilus, P. speciosus, P. griseus, P. faunulus, P. dasymallus*) occur in the Philippines, small islands around Borneo, Sulawesi, the Lesser Sundas, Nicobars, Taiwan, and the Riukius. (See Klingener and Creighton, 1984, for status of some of the Philippine species.) *P. mariannus* is a Micronesian species that reaches the Riukius. *P. caniceps* is endemic to Sulawesi and the Moluccas. *P. melanotus* occurs on several islands from the Andamans to Christmas (in the northern Indian Ocean). *P. lombocensis* is endemic to the Lesser Sundas, but has a relative (*molossinus*) in Micronesia. *P. leucopterus* is endemic to the Philippines, but also has relatives (*pselaphon, pilosus*) in Micronesia. Three species related to one another are found on the mainland of Southeast Asia: *P. lylei* is confined to Thailand, Cambodia, and Vietnam; *P. giganteus* ranges from India to Burma and is probably conspecific with *P. vampyrus,* which extends from Tenasserim (if *intermedius* is included; see Lekagul and McNeely, 1977: 77) and Vietnam to the Lesser Sundas and Philippines. Finally, *P. alecto* ranges from Bawean and Kangean islands on the Sunda Shelf through Sulawesi and the Lesser Sundas to Australia.

Acerodon: This genus is very closely related to *Pteropus* and is almost confined to Western Wallacea. The one exception (*A. leucotis*; see Musser et al. 1982) is endemic to the Palawan group of the Philippines. *A. celebensis* is endemic to Sulawesi, *A. mackloti* to the Lesser Sundas, *A. humilus* to the Talauds, and *A. lucifer* and *A. jubatus* to the main (oceanic) portion of the Philippines.

Neopteryx and *Styloctenium*: These two monotypic (*N. frosti* and *S. wallacei*) genera are endemic to Sulawesi. Both are offshoots of *Pteropus*.

Dobsonia (see Bergmans, 1978; Jong and Bergmans, 1981; Bergmans and Rozendaal, 1988, for recent taxonomic and distributional changes): This genus is almost entirely Wallacean and Australasian in distribution. *D. minor,* a New Guinea species, has recently been recorded from Sulawesi (see Bergmans and Rozendaal, 1988). The otherwise endemic Lesser Sunda *D. peroni* almost reaches the Sunda shelf on Nusa Penida, a small (and apparently oceanic) island off the southeast corner of Bali. *D. viridis* (= *crenulata*) is chiefly Moluccan but has colonized Sulawesi and some of its small islands. (See Bergmans and Rozendaal, 1988, for an alternative interpretation.) *D. chapmani* is endemic to the Philippines and *D. exoleta* is endemic to Sulawesi.

Harpyionycteris: This genus is confined to Sulawesi and the Philippines. Laurie and Hill (1954) recognized a single species, but Peterson and Fenton (1970) separated *H. celebensis* from the Philippine *H. whiteheadi.* However, Hill (1983) has shown that several of the alleged characters show considerable variation within series; I believe that they are best considered to be conspecific.

Cynopterus: This genus has an extensive Indo-Malayan (including western Wallacean) distribution. Hill (1983) has made extensive taxonomic changes and for the most part, I

follow his treatment. *C. sphinx* ranges from India to southern China and south through Malaya and Sumatra, with a probable record from Borneo, including the Nicobars and Mentawais. *C. titthaecheilus* (formerly included in *C. sphinx*) occurs with it in Sumatra and also reaches Java and the Lesser Sundas as well as the Mentawais. *C. brachyotis* (which has frequently been confused with *C. sphinx*) ranges from Burma and Vietnam to Java, Sulawesi, and the Philippines, as well as the Andamans and Mentawais. There is also a specimen in the American Museum from Lombok in the Lesser Sundas. *C. horsfieldi* (including *harpax,* which is apparently the oldest available name for the subspecies known as *minor* or *lyoni*) has a very limited range in Thailand but from there its range extends to Java and Borneo. Hill (1983) recognized two additional species, each known only from the holotype, *C. minor* of Sulawesi and *C. archipelagus* of the Philippines. Each appears to be only an aberrant specimen of *C. brachyotis,* the only other *Cynopterus* species known from either of these areas (the type of *minor* is very young). See Bergmans and Rozendaal (1988) for the status of *minor* and Heaney et al. (1987) for the status of *archipelagus.*

Megaerops: Four species are now recognized in this Indo-Malayan genus. *M. ecaudatus* ranges from Thailand (and possibly Vietnam) to Sumatra and Borneo. *M. niphanae* has recently been described (Yenbutra and Felten, 1983) from Thailand, the American Museum has specimens from Vietnam, and the British Museum has a specimen from northeastern India. *M. kusnotoi* occurs in Java (Hill and Boeadi, 1978). Finally, *M. wetmorei* is known from Borneo and the Philippines.

Ptenochirus: Two species are currently recognized in this genus, both confined to the Philippines. *P. jagori* is confined to the main (oceanic) islands, while the newly described *P. minor* (Yoshiyuki, 1979) has also been recorded from Palawan.

Dyacopterus: The single species (*D. spadiceus*) of this genus is known only from Malaya, Sumatra, Borneo, and the Philippines (see Kock, 1969a).

Chironax: The single species, *C. melanocephalus,* is known from Malaya, Sumatra, Java, Borneo, Nias (in the Mentawai islands), and Sulawesi (see Hill, 1983).

Thoopterus: The single species, *T. nigrescens,* is endemic to Sulawesi and the Moluccas with a doubtful record from the Philippines.

Sphaerias: The single species, *S. blanfordi,* has a limited range from northern India to Thailand and southwestern China.

Balionycteris: The single species, *B. maculata,* is known only from Malaya and Borneo.

Aethalops: The single species, *A. alecto,* ranges from Malaya through Sumatra to Java and Borneo (Hill, 1983).

Penthetor: The single species, *P. lucasi,* is, like *Balionycteris,* known only from the Malay Peninsula and Borneo.

Alionycteris, Otopteropus, and *Haplonycteris*: These three monotypic genera (*A. paucidentata, O. cartilaginodus, H. fischeri*) are all confined to the Philippines. Only *Haplonycteris* has also been recorded from the Palawan group (Kock, 1969b, 1969c).

Nyctimene: This genus is centered in New Guinea and only three species are known west of Weber's line. *N. cephalotes* extends from the New Guinea region west to Sulawesi and Timor; *N. minutus* is endemic to the Moluccas and Sulawesi. The newly described *N. rabori* (see Heaney and Peterson, 1984) occurs in the Philippines.

Eonycteris: This is a widespread Indo-Malayan genus ranging from India east to the Philippines, Sulawesi, and the Lesser Sundas, including the Andamans and the Mentawais. There are probably only two good species. *E. spelaea* occupies the entire range of the genus except the Mentawais (see Hill, 1983), whereas *E. major* (including *robusta*; see Tate, 1942: 344, though Heaney et al., 1987, disagree) is known only from Borneo, the Mentawais, and the Philippines. I have seen the type and only known specimen of *E. rosenbergii* from Sulawesi and cannot distinguish it (except for the absence of the third lower molar) from *E. spelaea,* though Rozendaal (1984) considered it a separate species. However, Bergmans and Rozendaal (1988) made *rosenbergii* a subspecies of *E. spelaea.*

Macroglossus: This is a widespread genus extending from Burma to the Solomons and northern Australia. Hill (1983) discussed and

considerably clarified the nomenclature and distribution of the two species. (I agree with Heaney and Rabor, 1982, that the Philippine *fructivorus* is a synonym of *M. minimus.*) *M. minimus* (the species previously called *lagochilus*) ranges from Thailand and Vietnam through Malaya and the Sumatran area to the Philippines, Solomons, and Australia. *M. sobrinus* (the species formerly called *minimus*) has a more restricted distribution from Burma to Java, including the Mentawais. While I am inclined to follow Hill (1983), there are certain problems. The most serious of these is that all American Museum specimens from Java (26 specimens from 6 localities in both East and West Java) and Bali seem all to belong to one species and, while somewhat intermediate between the two species as represented by mainland material, agree better with *M. sobrinus.* This contrasts with Javan material at the British Museum which separates neatly into two species. More work is needed to distinguish the two species clearly.

Rhinopomatidae

Rhinopoma: This is a widespread, chiefly southwestern Palearctic genus that is only marginally represented in our area. *R. microphyllum* (including *sumatrae*) is definitely known from Sumatra, but it is uncertain whether records from Burma and peninsular Thailand pertain to this species or to *R. hardwickei* (Hill, 1977). Both species occur in India.

Craseonycteridae

Craseonycteris: This recently described monotypic genus (Hill, 1974) is known only from a small area of west central Thailand.

Emballonuridae

Emballonura: This is a widespread genus, ranging, chiefly in insular areas, from Madagascar to the central Pacific. *E. monticola* is the only continental species, extending barely north of the isthmus of Kra and south through Malaya, Sumatra, Java, and Borneo to Sulawesi, as well as the Mentawais. *E. alecto* is known from Borneo, Sulawesi, the Philippines and east to the Moluccas. *E. nigrescens* is found, in our area, only in Sulawesi, but ranges east to the Solomons. (See Hill, 1983, on Sulawesi records of *Emballonura.*)

Taphozous: This is another widespread tropical and subtropical Old World genus. Five species occur in our area. *T. longimanus* ranges from India and the Southeast Asian mainland through Malaya and Sumatra to Borneo and Java and also reaches the Lesser Sundas. Another species, *T. melanopogon,* has a somewhat similar range but also occurs on the Andamans, Sulawesi, and east to the Moluccas (Hill, 1967, 1983; Koopman, 1984). A closely related species (*T. philipinensis*) is confined to the Philippines (including the Palawan group), but is probably conspecific with *T. melanopogon. T. theobaldi* is confined to India and the Southeast Asian mainland except for some specimens from Java (see Hill, 1983). There are no records from Malaya or Sumatra. The last species, *T.* (*Liponycteris*) *nudiventris* (including *kachensis*; see Felten, 1962), has an extensive African and southern Asian distribution but in our area occurs only in Burma. A Malayan record is apparently erroneous (see Medway, 1969).

Saccolaimus: Two species of this widespread Old World tropical genus are currently recognized from our area. *S. saccolaimus* has an extensive distribution from India through Southeast Asia, Malaya, and Sumatra to Java and Borneo. It is also known from the Nicobars (Hill, 1967), from Sulawesi and the Lesser Sundas (Hill, 1983), and on to Australia and the Solomons. *S. pluto* (= *capito*) is confined to the Philippines, but is probably conspecific with *S. saccolaimus.*

Nycteridae

Nycteris: Two well-marked species occur in our area, though they have frequently been combined. *N. tragata* ranges from Burma and Thailand through Malaya to Sumatra and Borneo. *N. javanica* is confined to Java, Kangean, and Bali. Records of the genus from Timor and Sulawesi require confirmation. All other species of the genus are African.

Megadermatidae

Megaderma: This genus is confined to the Indo-Malayan region and has two species. *M. spasma* ranges from India and Southeast Asia through Sumatra and Borneo to Java, Sula-

wesi, and the Philippines, also the Andamans and Mentawais: *M. lyra* occurs only on the mainland, ranging from India and southern China to Malaya.

Rhinolophidae

Rhinolophus: This is a large, widespread Old World genus that is particularly well represented in the Indo-Malayan region, 42 species being currently recognized in our area. However, many of these species are poorly known and there are still many taxonomic problems. Reference should here be made to a number of papers by Hill and co-authors, particularly Hill (1983), which gives references to earlier papers. I will therefore only summarize the species and their ranges, without giving all the subspecies and synonyms, many of which have been recognized as full species in various checklists and other recent papers. Starting with the *ferrumequinum* group, *R. simplex* is endemic to the Lesser Sundas; the closly related *R. keyensis* is mainly Moluccan but also reaches the Lesser Sundas. *R. borneensis* has a limited Indochinese range and also occurs on Java and Borneo, while the closely related *nereis* is endemic to the Anambas and North Natunas. *R. celebensis* occurs on Java, the Lesser Sundas, and Sulawesi, while the closely related *virgo* is endemic to the Philippines (including the Palawan group). *R. malayanus* occurs in Indochina south to Malaya. *R. ferrumequinum* is chiefly a Palearctic species but reaches southern China. *R. stheno* ranges from Thailand through Malaya and Sumatra to Java; *R. anderseni* is endemic to the Philippines, including the Palawan group. *R. rouxi* is an Indian species that extends eastward to southern China and Indochina; *R. thomasi* is endemic to the Indochinese subregion. *Rhinolophus affinis* has an extensive range from India and southern China through Malaya and Sumatra to Java and Borneo and also the Andamans, Mentawais, and Lesser Sundas. *R. robinsoni* ranges from northern Thailand to the Malay Peninsula.

Introducing the *pusillus* group, *R. acuminatus* ranges from Indochina through Malaya and Sumatra to Java and Borneo, also Palawan, the Mentawais, and Lesser Sundas. *R. lepidus* ranges from India and southern China through Malaya to Sumatra; *R. pusillus* from India to southern China, also Malaya, Borneo, Java, and the Mentawai islands. *R. cornutus* occurs in Japan, the Riukius, and possibly southeastern China. Two additional forms treated by Hill and Yoshiyuki (1980) as separate species are *monoceros* of Taiwan (clearly very close to *cornutus*) and the more distinct *imaizumii* of the Riukius. The last two members of the *pusillus* group are *R. subbadius* of northeastern India and Indochina and *R. cognatus* of the Andamans. However, *R. osgoodi* of southwestern China also evidently belongs in this group.

Two species generally placed in the *philippinensis* group are *R. pearsoni* (ranging from India to Malaya) and *yunanensis* (confined to the Indochinese subregion. *R. philippinensis* extends from Borneo, the Philippines, and the Lesser Sundas to Australia; *R. macrotis* from northern India and southern China to Sumatra and also in the Philippines. *R. rex* is endemic to southwestern China, *R. marshalli* and *R. paradoxolophus* to Indochina. *R. trifoliatus* ranges from northeastern India to Java and Borneo including the Mentawais. *R. sedulus* is confined to Malaya and Borneo. Finally, to conclude the *philippinensis* group, *R. luctus* ranges from India and southern China to Java and Borneo.

Two species best placed in the *arcuatus* group are *R. coelophyllus* and *R. shameli,* both confined to Indochina and Malaya. *R. arcuatus* is known from Sumatra, Borneo, the Lesser Sundas, and the Philippines east to New Guinea, but is not known from Sulawesi. *R. subrufus* and *R. inops* are endemic to the Philippines. *R. creaghi* is known from Java and Borneo, the related *R. canuti* from Java and the Lesser Sundas. Finally, *R. rufus* is endemic to the Philippines and *R. euryotis* occurs in Sulawesi and ranges east to the Bismarcks.

Hipposideros: This is another widespread Old World genus, particularly well represented in the Indo-Malayan region. Fortunately the genus was well revised by Hill (1963) and there have been relatively few taxonomic changes since then (Jenkins and Hill, 1981; Hill and Yenbutra, 1984; Hill et al., 1986).

There are 29 species currently recognized in our area. More than half belong to the

bicolor group. *H. bicolor* occurs on the Malay Peninsula, Sumatra, and Borneo, as well as the Mentawais, Lesser Sundas, and Philippines. *H. pomona* extends from India and southern China to Malaya. *H. macrobullatus* is found from the Kangean islands and Sulawesi to the Moluccas. *H. ater* occurs in India, but is absent from all but the southern edge of the Indochinese subregion and seems to be of extremely limited occurrence on the Malay Peninsula; it also occurs in Sumatra, Java, and Borneo, in the Nicobars, Sulawesi, and Philippines and east to the Bismarcks and Australia. *H. fulvus* ranges from India into Burma (though Hill et al. doubt its occurrence from Burma or even northeastern India); *H. cineraceus* from India through southeastern Asia and Malaya to Borneo and possibly the Philippines (if, as Hill and Francis suggest, *wrighti* is a form of *H. cineraceus* rather than of *H. ater*); the recently described *H. halophyllus* is confined to central Thailand. *H. nequam* is endemic to Malaya; *H. coronatus* to the Philippines; *H. ridleyi* is confined to Malaya and Borneo; *H. dyacorum* is known from Borneo and also occurs in Malaya (J. E. Hill, in litt.); *H. pygmaeus* to the Philippines. *H. galeritus* occurs in India, but in Indochina only in a limited part of Thailand, and also ranges from the Malay Peninsula to Java and Borneo. *H. cervinus,* which has been split off from *H. galeritus* (Jenkins and Hill, 1981) ranges from Malaya through Sumatra, Borneo, Sulawesi, and Philippines east to the New Hebrides as well as on the Mentawai islands; *H. breviceps* is endemic to the Mentawais; *H. crumeniferus* (a doubtful form) is known only from the Lesser Sundas. *H. coxi* is endemic to Borneo; *H. sabanus* in Malaya as well as in Sumatra and Borneo. *H. doriae* (which may be a senior synonym of *sabanus*) is known only from Borneo; *H. obscurus* is endemic to the Philippines.

In the *pratti* group, there are only two species, *H. pratti* and *H. lylei,* both of which extend from the Indochinese subregion into Malaya.

The *armiger* group also includes two species, *H. armiger,* which ranges from India to Malaya, and *H. turpis,* which is known only from the Riukius and Malaya. The *speoris* group is probably represented in our area only by *H. larvatus,* which ranges from the Indochinese subregion through Malaya, Sumatra, Borneo, and Java to the Lesser Sundas and also in the Mentawais.

Finally, four species of the *diadema* group are known from our area. *H. diadema* is the most widespread, ranging from the Indochinese subregion through Malaya, Sumatra, Java, and Borneo to the Lesser Sundas, Sulawesi, and Philippines, and east to Australia and the Solomons as well as on the Nicobars and Mentawais. *H. dinops* occurs only in Sulawesi and the Solomons; *H. lekaguli* is confined to a limited area of southern Thailand south into Malaya; *H. inexpectatus* is endemic to Sulawesi.

Aselliscus: There are only two species in this genus and one is confined to the Australasian region. *A. stoliczkanus,* however, is confined to the Indochinese subregion and Malaya.

Coelops: There are two species in this genus, *C. frithi* in the Indochinese subregion, Malaya, and Java; *C. robinsoni* (including *hirsuta*) in Malaya, Borneo, and the Philippines (see Hill, 1983).

Paracoelops: The single, poorly known species of this genus, *P. megalotis,* is known only from Vietnam.

Vespertilionidae

Myotis: This is a large cosmopolitan genus with some 18 species in our area. (See Hill, 1983, on this genus, though I disagree with him on some points.)

Starting with the members of the subgenus *Selysius,* we have *M. montivagus,* which ranges from northern China to Malaya and Borneo. *M. muricola* (including *ater, browni,* and *herrei,* but which may include more than one species) ranges from northern India through Indochina, Malaya, Sumatra, Java, and Borneo to the Mentawais, Lesser Sundas, Sulawesi, and Philippines and east at least to the Moluccas. *M. siligorensis* extends from northern India, through Indochina and Malaya to Borneo. *M. annectans* and *M. altarium* are each confined to parts of the Indochinese subregion. *M. frater* is chiefly eastern Palearctic but reaches southern China; *M. oreias* is endemic to Malaya. Finally, we have two closely related species, *M. rosseti* confined to Indochina and *M. ridleyi* occurring

in Malaya, Sumatra, and Borneo. (See Hill and Topal, 1973, for allocation of these two species to *Myotis.*

Starting the subgenus *Leuconoe, M. daubentoni* is a Palearctic species that reaches southern China; *M. fimbriatus* also occurs in southern China, though its status as a separate species from *capaccinii* or *macrodactylus* is uncertain. *M. adversus* is known from Malaya, Sumatra, Java, Borneo, and Sulawesi east to the New Hebrides, also Taiwan (since I believe *taiwanensis* is a subspecies). *M. horsfieldi* (assuming that *deignani, peshwa, dryas,* and *jeannei* are all conspecific with it) ranges from India through the Indochinese subregion, Malaya, Borneo, and Java to Sulawesi and the Philippines as well as the Andaman islands. *M. hasselti* occurs in Indochina through Malaya and Sumatra to Java and Borneo as well as the Mentawai islands. Finally, *M. macrotarsus* is confined to Borneo and the Philippines (including the Palawan group) and *M. ricketti* is endemic to southern and eastern China.

The subgenus *Myotis* has only two species in our area: *M. chinensis* is confined to the Indochinese subregion, whereas *M. formosus* ranges from the eastern Palearctic through Indochina and also on Sumatra, Java, Sulawesi, and the Philippines (including the Palawan group).

Eudiscopus: The single species, *E. denticulus,* is known only from Burma and Vietnam.

Pipistrellus: This is another very widespread genus represented by 19 species in our area. (See Francis and Hill, 1986, for a review of the Bornean species.)

Several groups can be recognized (Koopman, 1973, but see also Hill and Harrison, 1987, for an alternative arrangement), of which the most primitive is the *pipistrellus* group. This includes first the widespread *P. javanicus,* which extends from the eastern Palearctic through Indochina, Malaya, Sumatra, Java, and Borneo to Sulawesi and the Philippines at least, as well as on the Riukius and Nicobars. *P. peguensis* is endemic to Burma, *P. coromandra* extends from Afghanistan to southeastern China and northern Thailand (including the Nicobars); *P. mimus* from Afghanistan to Indochina. *P. tenuis* ranges from Malaya through Sumatra, Java, and Borneo to the Lesser Sundas, Sulawesi, and the Philippines and east to the New Hebrides; *P. paterculus* from northeastern India to Thailand. The poorly known *P. imbricatus* is known only from Java and Borneo, though it has been recorded from the Philippines. *P. babu* ranges from Afghanistan to Burma and southwestern China.

Of the five species of the *affinis* group, *P. affinis* occurs from India to southwestern China; *P. pulveratus* is endemic to the Indochinese subregion; *P. kitchneri* to Borneo. *P. petersi* occurs in Borneo, Sulawesi, the Philippines, and the Moluccas, while *P. lophurus* is known only from southern Tenasserim (just north of the isthmus of Kra). *P. mordax,* which may also belong to this group, is endemic to Java (the Indian records are referable to *affinis*).

P. ceylonicus, the only member of the *ceylonicus* group, occurs in India and Indochina, also in Borneo.

Of the two species of the *savii* group in our area, *P. macrotis* (including *vordermanni* and *curtatus*) extends from Malaya through Sumatra to Bali and Borneo, as well as the Mentawai islands, while *P. cadornae* is known from northeastern India, Burma, and Thailand.

There are three species in the *circumdatus* group, of which *P. circumdatus* occurs in Burma, southwestern China (see Wang, 1982), Malaya, and Java; *P. societatis* is endemic to Malaya; the newly described *P. cuprosus* (see Hill and Francis, 1984) is endemic to Borneo.

P. minahassae, the only species of its group, is endemic to Sulawesi.

Nyctalus: I include the *stenopterus* group here rather than in *Pipistrellus* (where Hill and Harrison, 1987, place it) since its resemblances to *Nyctalus* are in its derived characters. There are three species in this group, *N. anthonyi* and *N. joffrei* being known only from Burma, whereas *N. stenopterus* ranges from Malaya through Sumatra and Borneo to the Philippines. *N. noctula,* the only member of its group in our area, extends from the Palearctic through Indochina to Malaya.

Ia: The single species in this genus, *I. io,* ranges from northern China through Indochina.

Glischropus: Two species are currently recognized in this genus. *G. tylopus* extends from

Indochina through Malaya and Sumatra to Borneo and the Palawan group, as well as the Moluccas, whereas *G. javanus* is endemic to Java.

Eptesicus: This is an almost cosmopolitan genus, but is poorly represented in our area. *E. pachyotis* is only known from northeastern India and Thailand, whereas *E. demissus* has only been recorded from peninsular Thailand. In addition, the widespread Palearctic *E. serotinus* extends into southern China.

Vespertilio: This is a small, chiefly Palearctic, genus. One species (*V. orientalis*) extends from Korea to southern China.

Philetor: The single species of this genus *P. brachypterus* is known from various areas extending from Nepal to the Bismarcks (see Koopman, 1983). In our area, it has been recorded from Malaya, Sumatra, Borneo, and the Philippines.

Tylonycteris: Two species are currently recognized in this genus. *T. pachypus* extends from India through Indochina, Malaya, Sumatra, Java, and Borneo to the Lesser Sundas and the Philippines, as well as the Andamans. *T. robustula* ranges from the Indochinese subregion through Malaya, Sumatra, Java, and Borneo to Sulawesi, the Lesser Sundas, and the Philippines.

Hesperoptenus: This genus with five currently recognized species is confined to the Indo-Malayan region. Two quite distinct subgenera are currently recognized (Hill, 1976), *H. doriae* is the only species of the nominate subgenus, known only from Malaya and Borneo. The subgenus *Milithronycteris* includes the remainder: *H. tickelli* ranging from India to Indochina and the Andamans, *H. tomesi* known only from Malaya and Borneo, the newly described *H. gaskelli* (Hill, 1983) endemic to Sulawesi, and *H. blanfordi* also known only from Malaya and Borneo.

Scotomanes: The single species in this genus, *S. ornatus,* ranges from northeastern India to Indochina.

Scotophilus: This is a widespread Old World tropical genus with two or three species in our area. *S. kuhli* ranges from India through Indochina, Malaya, Borneo, and Java to the Lesser Sundas, Sulawesi, and the Philippines, as well as the Nicobars. *S. heathi* extends from India across Indochina and perhaps barely south of the Isthmus of Kra, while the closely related (and possibly conspecific) *celebensis* is endemic to Sulawesi.

Barbastella: This is a small, chiefly Palearctic, genus, of which one species, *B. leucomelas,* reaches southwestern China and perhaps somewhat farther.

Miniopterus: This is a fairly large Old World genus, currently in considerable taxonomic confusion. (See Hill, 1983, for a recent discussion of this.) I am inclined to recognize seven species in our area, which—running from smallest to largest—are as follows. *M. paululus* is known from Java, Balembangan off the north coast of Borneo, the Lesser Sundas, and the Philippines with scattered records east to the New Hebrides. The closely related *M. australis* is known from Borneo and Sulawesi east to Australia and the Solomons. *M. pusillus* ranges from India through Indochina, on to the Nicobars, but not known from Malaya, also Sumatra through Java and Borneo to the Lesser Sundas, Sulawesi, possibly from the Philippines and with some records farther east as far as the New Hebrides. *M. fuscus* (including *medius*) is known from the Indochinese subregion, Malaya, Java, Borneo, Sulawesi, the Philippines and east to New Guinea, as well as the Riukius. *M. schreibersi* has an extensive Old World distribution which extends through the Indochinese subregion, Malaya, Java, and Borneo to Sulawesi and the Philippines and east to Australia and the Solomons. *M. magnater* ranges from the Indochinese subregion through Malaya, Java, and Borneo to the Lesser Sundas and east to New Guinea. Finally, *M. tristis* is known in our area only from Sulawesi and the Philippines, but extends east to the New Hebrides.

Murina: This is a rather large genus confined to the eastern Palearctic, Indo-Malayan, and Australian regions (see Koopman and Danforth, 1989). About a dozen species have been recognized in our area. *M. aurata* extends from northeastern India to southwestern China and northern Thailand. The next three species are very closely related and are probably conspecific: *M. tubinaris* in India and Indochina; *M. suilla* (including *balstoni* and *canescens*) in Malaya, Sumatra, Java, Borneo, and Nias (an oceanic island west of Sumatra); *M. florium,* from the Lesser Sun-

das and Sulawesi east to New Guinea and Australia. *M. leucogaster* ranges from the eastern Palearctic into southern China. *M. huttoni* extends from northern India through Indochina to Malaya; the related *M. cyclotis* from Ceylon and northeastern India through Indochina, Malaya, and Borneo to the Philippines. Also related is *M. puta* known only from Taiwan. Finally, *M. aenea* occurs in Malaya and Borneo and the newly described *M. rozendaali* (see Hill and Francis, 1984) is endemic to Borneo.

Harpiocephalus: Of the two currently recognized species of this genus (see Hill and Francis, 1984), *H. harpia,* ranges from India through Indochina and also in Sumatra, Java, and Borneo. *H. mordax* is known only from Burma and Borneo.

Kerivoula: This is a fairly large Old World tropical genus with nine species in our area. There are two quite distinct subgenera (often called genera), the first seven species in *K. (Kerivoula)* and the last two in *K. (Phoniscus)*. *K. whiteheadi* is known from Malaya, Borneo, and the Philippines. *K. picta* ranges from India through Indochina, Malaya, Sumatra, Java, and Borneo, to the Lesser Sundas and also in the Moluccas. Both *K. minuta* and the newly described *K. intermedia* (Hill and Francis, 1984) are confined to the Malay peninsula and Borneo. *K. pellucida* extends from Malaya through Sumatra, Java, and Borneo to the Philippines. *K. hardwickei* ranges from India through Indochina, Malaya, Sumatra, Java, and Borneo to the Lesser Sundas, Sulawesi, and the Philippines and also in the Mentawais. *K. papillosa* extends from the Indochinese subregion through Malaya, Sumatra, Java, and Borneo to Sulawesi.

Of the two species of the subgenus *Phoniscus, K. jagorii* is known from Java, Borneo, Sulawesi, and the Philippines, *P. atrox* from Malaya, Sumatra, and Borneo.

Molossidae

Mormopterus: This is a fairly small genus with a spotty distribution in the tropics of both hemispheres. The single species in our area, *M. doriae,* is confined to Sumatra.

Tadarida: In its present restricted sense, this is a fairly small but almost cosmopolitan genus. The only species in our area, *T. teniotis,* is chiefly Palearctic, but does reach southern China.

Chaerephon: This is a fairly large Old World tropical genus with only two species in our area, one of which, *C. johorensis,* is confined to Malaya and Sumatra. *C. plicata* ranges from India through Indochina, Malaya, Sumatra, Java, and Borneo to the Philippines.

Mops: This is a fairly large African and Indo-Malayan genus but with only two species in our area. *M. mops* is known from Malaya, Sumatra, Borneo, and possibly Java, while *M. sarasinorum* (including *lanei*) occurs on Sulawesi and the Philippines.

Otomops: This is a small Old World tropical genus with a single species, *O. formosus,* in our area which is endemic to Java.

Cheiromeles: This genus consists of two very closely related Indo-Malayan forms previously regarded as separate species, but which are here considered to be conspecific. *C. torquatus* (includes *parvidens*) occurs on the Malay Peninsula, Sumatra, Java, Borneo, the Mentawais, Sulawesi, and the Philippines.

DISCUSSION

The distributional patterns are summarized in table 1. Of the 253 species listed, 127 are known from the Indochinese subregion. Of these, 27 are endemic, the others being shared with the eastern Palearctic, the Indian subregion, or the Sunda area. There are 67 species that are shared between the Indochinese subregion and the Malay Peninsula (with its islands), of which 15 do not extend beyond Malaya. There are 101 Malay species, of which only 5 are endemic (one only on the Anambas and North Natunas); 139 species on the Sunda shelf, of which 37 occur on all four large units (Malaya, Sumatra, Java, Borneo) of the Sunda shelf. There are 80 species that are shared between Malaya and at least one of the Sunda shelf islands, 54 shared between Malaya and Sumatra, 73 shared between Malaya and Borneo. Sumatra has 63 species (only one endemic), 44 shared with Java and 54 with Borneo. Java has 66 species, only 5 endemic, and 52 shared with Borneo. Borneo has 98 species, of which only 5 are endemic. The Palawan group has 30 species, of which one is endemic, 23 are shared with

TABLE 1

Species of Bats in the Indochinese and Malayan Subregions and Their Outliers

(Subregions are spelled out at end of table)

	A	B	C	D	E	F	G	H	I	J	K	L
Rousettus												
leschenaulti	+	−	−	+	+	+	−	−	+	−	−	−
amplexicaudatus	+	−	−	+	+	+	+	+	+	+	+	+
spinalatus	−	−	−	−	+	−	+	−	−	−	−	−
celebensis	−	−	−	−	−	−	−	−	−	−	+	−
Boneia bidens	−	−	−	−	−	−	−	−	−	−	+	−
Pteropus												
hypomelanus	(+)	−	−	(+)	−	−	(+)	+	+	−	+	+
pumilus	−	−	−	−	−	−	−	−	−	−	−	+
speciosus	−	−	−	−	−	−	(+)	−	−	−	−	+
griseus	−	−	−	−	−	−	−	−	−	+	+	?
faunulus	−	−	+	−	−	−	−	−	−	−	−	−
dasymallus	(+)	+	−	−	−	−	−	−	−	−	−	−
mariannus	−	+	−	−	−	−	−	−	−	−	−	−
caniceps	−	−	−	−	−	−	−	−	−	−	+	−
melanotus	−	−	+	−	−	−	−	−	+	−	−	−
lombocensis	−	−	−	−	−	−	−	−	−	+	−	−
leucopterus	−	−	−	−	−	−	−	−	−	−	−	+
lylei	+	−	−	−	−	−	−	−	−	−	−	−
giganteus	+	−	+	−	−	−	−	−	−	−	−	−
vampyrus	+	−	−	+	+	+	+	+	+	+	−	+
alecto	−	−	−	−	−	(+)	−	−	−	+	+	−
Acerodon												
leucotis	−	−	−	−	−	−	−	+	−	−	−	−
celebensis	−	−	−	−	−	−	−	−	−	−	+	−
mackloti	−	−	−	−	−	−	−	−	−	+	−	−
humilus	−	−	−	−	−	−	−	−	−	−	(+)	−
lucifer	−	−	−	−	−	−	−	−	−	−	−	+
jubatus	−	−	−	−	−	−	−	−	−	−	−	+
Neopteryx frosti	−	−	−	−	−	−	−	−	−	−	+	−
Styloctenium wallacei	−	−	−	−	−	−	−	−	−	−	+	−
Dobsonia												
minor	−	−	−	−	−	−	−	−	−	−	+	−
peroni	−	−	−	−	−	−	−	−	−	+	−	−
viridis	−	−	−	−	−	−	−	−	−	−	+	−
chapmani	−	−	−	−	−	−	−	−	−	−	−	+
exoleta	−	−	−	−	−	−	−	−	−	−	+	−
Harpyionycteris whiteheadi	−	−	−	−	−	−	−	−	−	−	+	+
Cynopterus												
sphinx	+	−	+	+	+	−	+	−	+	−	−	−
titthaecheilus	−	−	−	−	+	+	−	−	+	+	−	−
brachyotis	+	−	+	+	+	+	+	+	+	+	+	+
horsfieldii	(+)	−	−	+	+	+	+	−	+	−	−	−
Megaerops												
ecaudatus	+	−	−	+	+	−	+	−	−	−	−	−
niphanae	+	−	−	−	−	−	−	−	−	−	−	−
kusnotoi	−	−	−	−	−	+	−	−	−	−	−	−
wetmorei	−	−	−	−	−	−	+	−	−	−	−	+
Ptenochirus												
minor	−	−	−	−	−	−	−	+	−	−	−	+
jagorii	−	−	−	−	−	−	−	−	−	−	−	+
Dyacopterus spadiceus	−	−	−	+	+	−	+	−	−	−	−	+

TABLE 1
Continued

	A	B	C	D	E	F	G	H	I	J	K	L
Chironax melanocephalus	−	−	−	+	+	+	+	−	+	−	+	−
Thoopterus nigrescens	−	−	−	−	−	−	−	−	−	−	+	?
Sphaerias blanfordi	+	−	−	−	−	−	−	−	−	−	−	−
Balionycteris maculata	−	−	−	+	−	−	+	−	−	−	−	−
Aethalops alecto	−	−	−	+	+	+	+	−	−	−	−	−
Penthetor lucasi	−	−	−	+	−	−	+	−	−	−	−	−
Alionycteris paucidentata	−	−	−	−	−	−	−	−	−	−	−	+
Otopteropus cartilaginodus	−	−	−	−	−	−	−	−	−	−	−	+
Haplonycteris fischeri	−	−	−	−	−	−	−	+	−	−	−	+
Nyctimene												
minutus	−	−	−	−	−	−	−	−	−	−	+	−
cephalotes	−	−	−	−	−	−	−	−	−	+	+	−
rabori	−	−	−	−	−	−	−	−	−	−	−	+
Eonycteris												
spelaea	+	−	+	+	+	+	+	+	−	+	+	+
major	−	−	−	−	−	−	+	−	−	−	−	+
Macroglossus												
sobrinus	+	−	−	+	+	+	−	−	+	−	−	−
minimus	+	−	−	+	+	+	+	+	−	+	+	+
Rhinopoma												
microphyllum	?	−	−	?	+	−	−	−	−	−	−	−
hardwickei	?	−	−	?	−	−	−	−	−	−	−	−
Craseonycteris thonglongyai	+	−	−	−	−	−	−	−	−	−	−	−
Emballonura												
monticola	(+)	−	−	+	+	+	+	−	+	−	+	−
alecto	−	−	−	−	−	−	+	+	−	−	+	+
nigrescens	−	−	−	−	−	−	−	−	−	−	+	−
Taphozous												
longimanus	+	−	−	+	+	+	+	−	−	+	−	−
melanopogon	+	−	+	+	+	+	+	−	−	+	+	−
philippinensis	−	−	−	−	−	−	−	+	−	−	−	+
theobaldi	+	−	−	−	−	+	−	−	−	−	−	−
nudiventris	+	−	−	−	−	−	−	−	−	−	−	−
Saccolaimus												
saccolaimus	+	−	+	+	+	+	+	−	−	+	+	−
pluto	−	−	−	−	−	−	−	−	−	−	−	+
Nycteris												
javanica	−	−	−	−	−	+	−	−	−	−	−	−
tragata	+	−	−	+	+	−	+	−	−	?	?	−
Megaderma												
spasma	+	−	+	+	+	+	+	+	+	−	+	+
lyra	+	−	−	+	−	−	−	−	−	−	−	−
Rhinolophus												
simplex	−	−	−	−	−	−	−	−	−	+	−	−
keyensis	−	−	−	−	−	−	−	−	−	+	−	−
borneensis	+	−	−	−	−	+	+	−	−	−	−	−
nereis	−	−	−	(+)	−	−	−	−	−	−	−	−
celebensis	−	−	−	−	−	+	−	−	−	+	+	−
virgo	−	−	−	−	−	−	−	+	−	−	−	+
malayanus	+	−	−	+	−	−	−	−	−	−	−	−
ferrumequinum	+	−	−	−	−	−	−	−	−	−	−	−
stheno	+	−	−	+	+	+	−	−	−	−	−	−
anderseni	−	−	−	−	−	−	−	+	−	−	−	+

TABLE 1
Continued

	A	B	C	D	E	F	G	H	I	J	K	L
rouxi	+	−	−	−	−	−	−	−	−	−	−	−
thomasi	+	−	−	−	−	−	−	−	−	−	−	−
affinis	+	−	+	+	+	+	+	−	+	+	−	−
robinsoni	+	−	−	+	−	−	−	−	−	−	−	−
acuminatus	+	−	−	+	+	+	+	+	+	+	−	−
lepidus	+	−	−	+	+	−	−	−	−	−	−	−
osgoodi	+	−	−	−	−	−	−	−	−	−	−	−
pusillus	+	−	−	+	−	+	+	−	+	−	−	−
cornutus	?	+	−	−	−	−	−	−	−	−	−	−
subbadius	+	−	−	−	−	−	−	−	−	−	−	−
monoceros	(+)	−	−	−	−	−	−	−	−	−	−	−
cognatus	−	−	+	−	−	−	−	−	−	−	−	−
imaizumii	−	+	−	−	−	−	−	−	−	−	−	−
pearsoni	+	−	−	+	−	−	−	−	−	−	−	−
yunanensis	+	−	−	−	−	−	−	−	−	−	−	−
philippinensis	−	−	−	−	−	−	+	−	−	+	+	+
macrotis	+	−	−	+	+	−	−	−	−	−	−	+
coelophyllus	+	−	−	+	−	−	−	−	−	−	−	−
shameli	+	−	−	+	−	−	−	−	−	−	−	−
rex	+	−	−	−	−	−	−	−	−	−	−	−
marshalli	+	−	−	−	−	−	−	−	−	−	−	−
paradoxolophus	+	−	−	−	−	−	−	−	−	−	−	−
trifoliatus	+	−	−	+	+	+	+	−	+	−	−	−
sedulus	−	−	−	+	−	−	+	−	−	−	−	−
luctus	+	−	−	+	+	+	+	−	−	−	−	−
arcuatus	−	−	−	−	+	−	+	−	−	+	−	+
subrufus	−	−	−	−	−	−	−	−	−	−	−	+
inops	−	−	−	−	−	−	−	−	−	−	−	+
creaghi	−	−	−	−	−	+	+	−	−	−	−	−
canuti	−	−	−	−	−	+	−	−	−	+	−	−
rufus	−	−	−	−	−	−	−	−	−	−	−	+
euryotis	−	−	−	−	−	−	−	−	−	−	+	−
Hipposideros												
bicolor	−	−	−	+	+	+	+	−	+	+	−	+
pomona	+	−	−	+	−	−	−	−	−	−	−	−
ater	(+)	−	+	(+)	+	+	+	+	−	−	+	+
macrobullatus	−	−	−	−	−	(+)	−	−	−	−	+	−
fulvus	+	−	−	−	−	−	−	−	−	−	−	−
cineraceus	+	−	−	+	−	−	+	−	−	−	−	?
halophyllus	+	−	−	−	−	−	−	−	−	−	−	−
nequam	−	−	−	+	−	−	−	−	−	−	−	−
coronatus	−	−	−	−	−	−	−	−	−	−	−	+
ridleyi	−	−	−	+	−	−	+	−	−	−	−	−
dyacorum	−	−	−	+	−	−	+	−	−	−	−	−
pygmaeus	−	−	−	−	−	−	−	−	−	−	−	+
galeritus	+	−	−	+	−	+	+	−	−	−	−	−
cervinus	−	−	−	+	+	−	+	−	+	−	+	+
breviceps	−	−	−	−	−	−	−	−	+	−	−	−
crumeniferus	−	−	−	−	−	−	−	−	−	+	−	−
coxi	−	−	−	−	−	−	+	−	−	−	−	−
sabanus	−	−	−	+	+	−	+	−	−	−	−	−
doriae	−	−	−	−	−	−	+	−	−	−	−	−
obscurus	−	−	−	−	−	−	−	−	−	−	−	+

TABLE 1
Continued

	A	B	C	D	E	F	G	H	I	J	K	L
pratti	+	−	−	+	−	−	−	−	−	−	−	−
lylei	+	−	−	+	−	−	−	−	−	−	−	−
armiger	+	−	−	+	−	−	−	−	−	−	−	−
turpis	−	+	−	+	−	−	−	−	−	−	−	−
larvatus	+	−	−	+	+	+	+	−	+	+	−	−
diadema	+	−	+	+	+	+	+	+	+	+	+	+
dinops	−	−	−	−	−	−	−	−	−	−	+	−
lekaguli	+	−	−	+	−	−	−	−	−	−	−	−
inexpectatus	−	−	−	−	−	−	−	−	−	−	+	−
Aselliscus stoliczkanus	+	−	−	+	−	−	−	−	−	−	−	−
Coelops												
frithi	+	−	−	+	−	+	−	−	−	−	−	−
robinsoni	−	−	−	+	−	−	+	−	−	−	−	+
Paracoelops megalotis	+	−	−	−	−	−	−	−	−	−	−	−
Myotis												
montivagus	+	−	−	+	−	−	+	−	−	−	−	−
muricola	+	−	−	+	+	+	+	+	+	+	+	+
siligorensis	+	−	−	+	−	−	+	−	−	−	−	−
annectans	+	−	−	−	−	−	−	−	−	−	−	−
altarium	+	−	−	−	−	−	−	−	−	−	−	−
frater	+	−	−	−	−	−	−	−	−	−	−	−
oreias	−	−	−	+	−	−	−	−	−	−	−	−
rosseti	+	−	−	−	−	−	−	−	−	−	−	−
ridleyi	−	−	−	+	+	−	+	−	−	−	−	−
daubentoni	+	−	−	−	−	−	−	−	−	−	−	−
fimbriatus	+	−	−	−	−	−	−	−	−	−	−	−
adversus	(+)	−	−	+	+	+	+	−	−	−	+	−
horsfieldi	+	−	+	+	−	+	+	+	−	−	+	+
hasselti	+	−	−	+	+	+	+	−	+	−	−	−
macrotarsus	−	−	−	−	−	−	+	+	−	−	−	+
ricketti	+	−	−	−	−	−	−	−	−	−	−	−
chinensis	+	−	−	−	−	−	−	−	−	−	−	−
formosus	+	−	−	−	+	+	−	+	−	−	+	+
Eudiscopus denticulus	+	−	−	−	−	−	−	−	−	−	−	−
Pipistrellus												
javanicus	+	+	+	+	+	+	+	+	−	−	+	+
peguensis	+	−	−	−	−	−	−	−	−	−	−	−
coromandra	+	−	+	−	−	−	−	−	−	−	−	−
tenuis	−	−	−	+	+	+	+	−	−	+	+	+
paterculus	+	−	−	−	−	−	−	−	−	−	−	−
imbricatus	−	−	−	−	−	+	+	−	−	−	−	?
babu	+	−	−	−	−	−	−	−	−	−	−	−
mimus	+	−	−	−	−	−	−	−	−	−	−	−
lophurus	(+)	−	−	−	−	−	−	−	−	−	−	−
pulveratus	+	−	−	−	−	−	−	−	−	−	−	−
kitchneri	−	−	−	−	−	−	+	−	−	−	−	−
affinus	+	−	−	−	−	−	−	−	−	−	−	−
petersi	−	−	−	−	−	−	+	−	−	−	+	+
mordax	−	−	−	−	−	+	−	−	−	−	−	−
ceylonicus	+	−	−	−	−	−	+	−	−	−	−	−
macrotis	−	−	−	+	+	+	+	−	+	−	−	−
cadornae	+	−	−	−	−	−	−	−	−	−	−	−
circumdatus	+	−	−	+	−	+	−	−	−	−	−	−
societatis	−	−	−	+	−	−	−	−	−	−	−	−

TABLE 1
Continued

	A	B	C	D	E	F	G	H	I	J	K	L
cuprosus	−	−	−	−	−	−	+	−	−	−	−	−
minahassae	−	−	−	−	−	−	−	−	−	−	+	−
Nyctalus												
anthonyi	+	−	−	−	−	−	−	−	−	−	−	−
joffrei	+	−	−	−	−	−	−	−	−	−	−	−
stenopterus	−	−	−	+	+	−	+	−	−	−	−	+
noctula	+	−	−	+	−	−	−	−	−	−	−	−
Ia io	+	−	−	−	−	−	−	−	−	−	−	−
Glischropus												
tylopus	+	−	−	+	+	−	+	+	−	−	−	−
javanus	−	−	−	−	−	+	−	−	−	−	−	−
Eptesicus												
pachyotis	+	−	−	−	−	−	−	−	−	−	−	−
demissus	−	−	−	+	−	−	−	−	−	−	−	−
serotinus	+	−	−	−	−	−	−	−	−	−	−	−
Vespertilio orientalis	+	−	−	−	−	−	−	−	−	−	−	−
Philetor brachypterus	+	−	−	+	+	−	+	−	−	−	−	+
Tylonycteris												
pachypus	+	−	+	+	+	+	+	+	−	+	−	+
robustula	+	−	−	+	+	+	+	+	−	+	+	+
Hesperoptenus												
doriae	−	−	−	+	−	−	+	−	−	−	−	−
tickelli	+	−	+	−	−	−	−	−	−	−	−	−
tomesi	−	−	−	+	−	−	+	−	−	−	−	−
gaskelli	−	−	−	−	−	−	−	−	−	−	+	−
blanfordi	+	−	−	+	−	−	+	−	−	−	−	−
Scotamanes ornatus	+	−	−	−	−	−	−	−	−	−	−	−
Scotophilus												
kuhli	+	−	+	+	−	+	+	+	−	+	+	+
heathi	+	−	−	?	−	−	−	−	−	−	−	−
celebensis	−	−	−	−	−	−	−	−	−	−	+	−
Barbastella leucomelas	(+)	−	−	−	−	−	−	−	−	−	−	−
Miniopterus												
paululus	−	−	−	−	−	+	(+)	+	−	+	−	+
australis	−	−	−	−	−	−	+	−	−	−	+	−
pusillus	+	−	+	−	+	+	+	−	−	+	+	?
fuscus	+	+	−	+	−	+	+	−	−	−	+	+
schreibersi	+	−	−	+	−	+	+	−	−	+	+	+
magnater	+	−	−	+	+	+	+	−	−	+	−	−
tristis	−	−	−	−	−	−	−	−	−	−	+	+
Murina												
aurata	+	−	−	−	−	−	−	−	−	−	−	−
tubinaris	+	−	−	−	−	−	−	−	−	−	−	−
suilla	−	−	−	+	+	+	+	−	+	−	−	−
florium	−	−	−	−	−	−	−	−	−	+	+	−
leucogaster	+	−	−	−	−	−	−	−	−	−	−	−
huttoni	+	−	−	+	−	−	−	−	−	−	−	−
puta	(+)	−	−	−	−	−	−	−	−	−	−	−
cyclotis	+	−	−	+	−	−	+	−	−	−	−	+
rozendaali	−	−	−	−	−	−	+	−	−	−	−	−
aenea	−	−	−	+	−	−	+	−	−	−	−	−
Harpiocephalus												
harpia	+	−	−	−	+	+	+	−	−	−	−	−
mordax	+	−	−	−	−	−	+	−	−	−	−	−

TABLE 1
Continued

	A	B	C	D	E	F	G	H	I	J	K	L
Kerivoula												
whiteheadi	−	−	−	+	−	−	+	−	−	−	−	+
picta	+	−	−	+	+	+	+	−	−	+	−	−
minuta	−	−	−	+	−	−	+	−	−	−	−	−
intermedia	−	−	−	+	−	−	+	−	−	−	−	−
pellucida	−	−	−	+	+	+	+	+	−	−	−	+
hardwickei	+	−	−	+	+	+	+	+	+	+	+	+
papillosa	+	−	−	+	+	+	+	−	−	−	+	−
jagorii	−	−	−	−	−	+	+	−	−	−	+	+
atrox	−	−	−	+	+	−	+	−	−	−	−	−
Mormopterus doriae	−	−	−	−	+	−	−	−	−	−	−	−
Tadarida teniotis	+	−	−	−	−	−	−	−	−	−	−	−
Chaerephon												
johorensis	−	−	−	+	+	−	−	−	−	−	−	−
plicatus	+	−	−	+	+	+	+	−	−	−	−	+
Mops												
mops	−	−	−	+	+	?	+	−	−	−	−	−
sarasinorum	−	−	−	−	−	−	−	−	−	−	+	+
Otomops formosus	−	−	−	−	−	+	−	−	−	−	−	−
Cheiromeles torquatus	−	−	−	+	+	+	+	+	+	−	+	+
Total number	127	7	20	101	63	66	98	30	28	39	60	66
Number of endemics	27	1	2	5	1	5	5	1	1	5	11	17

A China south of the Yangtze, Burma, Thailand (north of the Isthmus of Kra), Indochina, surrounding islands on the continental shelf (including Taiwan); **B** Riukiu islands; **C** Andaman and Nicobar islands; **D** Malay Peninsula, including surrounding islands on the continental shelf east to the Anambas and North Natunas; **E** Sumatra and adjacent islands on the continental shelf; **F** Java and adjacent islands on the continental shelf, including Bawean, Kangean, and Bali; **G** Borneo and adjacent islands on the continental shelf; **H** the Palawan-Calamiane group of the Philippines; **I** the Mentawai and other west Sumatran islands off the continental shelf, including Nias; **J** the Lesser Sunda islands, including Nusa Penida; **K** Sulawesi and surrounding islands; **L** the Philippines, excluding the Palawan-Calamiane group. **(+)** of very limited occurrence in the area in question (usually on offshore islands); **?** of doubtful occurrence in the area in question.

Borneo, and 27 with the main (oceanic) Philippines.

Comparing areas of Western Wallacea (off the Sunda shelf) with adjacent Greater Sunda islands, we have the Lesser Sundas with 39 species, 5 of which are endemic, and 28 shared with Java and its nearby islands. Sulawesi has 60 species, of which 11 are endemic and 32 are shared with Borneo. The Philippines have 66 species, of which 17 are endemic, 39 are shared with Borneo, and 27 shared with Sulawesi.

It is evident that among the bats, doubtless due to their superior dispersal ability, there are no sharp distributional breaks. While each of the areas has at least one endemic, the percentage is never more than about 30 percent (17 out of 66 species in the Philippines) and is usually much lower. Each area shares species with adjacent areas and, while no species occurs in all areas, a number of species do have quite wide ranges. This sharing is particularly marked among areas that are or recently were connected. The only island areas that have more than 10 percent endemism are those that have not had a recent land connection with southeastern Asia (see also Heaney, 1986).

Since the claim has been made that Borneo is in some sense an oceanic island, we need to look at it more closely. While it has a very rich bat fauna (more species than any other island in our area), the level of endemism is low (only 5 out of 97 species, 5%). To me, this indicates that Borneo is better regarded as a rich, rather peripheral, continental island

rather than an oceanic one. An entirely different picture is seen when Sulawesi (11 out of 60 species, 18%) or the Philippines (17 out of 66 species, 26%) are considered. Here, although the fauna is considerably poorer, the proportion of endemics is significantly greater. I believe that the relatively high endemism for some groups of mammals (tree shrews, langurs, squirrels) may be explained by the large size, diversified ecology, and peripheral position of Borneo. This has enabled it to develop and retain a large number of species, many of which originally occurred more widely on the Sunda shelf, but which have either become extinct (as on Java) or been replaced by invading Indochinese species (as on Malaya, and, to a lesser extent, Sumatra). For the true oceanic islands like Sulawesi and the Philippines, I would visualize a different process in which a limited number of colonizing species reached these islands over water and gave rise to endemic groups that never did occur on the Sunda shelf. Other examples may be found among the macaques of Sulawesi (Fooden, 1969) and the murids of both Sulawesi and the Philippines (Musser, 1987).

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