Mammals of the Lowland Rain-Forest of North Borneo

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INTRODUCTION

THIS REPORT is an account of all mammals known to occur in the lowland areas of the Colony of North Borneo. Above 3,000 feet on the massifs of Kinabalu and Trus Madi the mammalian fauna is so different that it forms an essentially distinct problem, and one that to me at least is far less interesting than that of the rich fauna of the lowland tropical rain-forest.

This work is based largely on specimens and field data collected by three field parties from Chicago Natural History Museum that visited North Borneo between 1929 and 1956. These data were supplemented by material borrowed from other American museums and by an examination, unfortunately very cursory, of North Bornean material in the National Museum in Singapore and the Sarawak Museum in Kuching. I have tried to include all pertinent published information in order to bring our knowledge of this fauna up to date.

Borneo is of unusual biological interest. Here the rich flora and fauna of the Oriental tropics are less disturbed by man than in any other area of comparable size. Thousands of square miles of continuous rain-forest provide what is perhaps the most favorable terrestrial environment on earth for both plant and animal life. Among mammals, some of the most generalized of living forms flourish side by side with some of the most specialized. The island lies in the area that has long been recognized as presenting the most complex and difficult of all zoogeographic problems.

It is unlikely that any species of North Bornean mammal remains undiscovered; no valid new species has been described since 1938, no species of non-flying mammal since 1903. This indicates that the first step in understanding the mammals of Borneo—the primary inventorying of the fauna—has been completed. Attention may now turn to other facets of the problem—testing and synthesizing the taxonomic hypotheses and exploring the ecological relationships of the mammals. This report is a first attempt at such an orientation.

ACKNOWLEDGEMENTS

Much indispensable assistance was provided during our field work in Borneo. The Chicago Natural History Museum is deeply obligated to the Forestry Department of North Borneo, particularly to Messrs. G. S. Brown and F. V. Webster in 1950, and to Messrs. G. Carson and G. H. S. Wood in 1956, for innumerable favors to Museum personnel. The Bombay Burmah Trading Corporation, Ltd., provided facilities and transportation both in 1950 and 1956, and we are further grateful to Messrs. O. C. Finch, John Shelley, and J. D. H. Hedley for many personal favors. Mr. Lai Foo Kim, of United Timbers, Ltd., provided transportation to and from the Deramakot camp and facilities at the camp. Mr. Tom Harrisson, Curator of the Sarawak Museum, provided us with a trained Iban collector in 1950 and again in 1956, in addition to many personal kindnesses. Messrs. M. F. W. Tweedie and C. A. Gibson-Hill, formerly of the National Museum, Singapore, were helpful during our stay in Singapore and granted permission to study materials under their care.

The U.S. National Museum and the Museum of Comparative Zoology loaned certain specimens for use in this study. Prof. C. G. G. J. van Steenis, Rijksherbarium, Leiden, identified plant materials submitted to him. Mr. Harry Nelson, Roosevelt University, Chicago, and Mr. Henry S. Dybas, Associate Curator of Insects, Chicago Natural History Museum, identified arthropod fragments in stomach contents. Dr. Alan Solem, Assistant Curator of Lower Invertebrates, Chicago Natural History Museum, identified molluscs from the stomachs of mammals. My assistant, Miss Phyllis Wade, prepared the drawings illustrating this report and was helpful in many other ways. I am indebted to Mr. Philip Hershkovitz, Curator of Mammals, Chicago Natural History Museum, for assistance and for stimulating discussions during the course of the study. Dr. Karl F. Koopman read the manuscript and made many valuable suggestions.

METHODS

During our field work in both 1950 and 1956 data in addition to the standard skin and skull were collected. A running diary was kept of all mammals observed, including any pertinent ecological data. In addition to standard flesh measurements, the weight

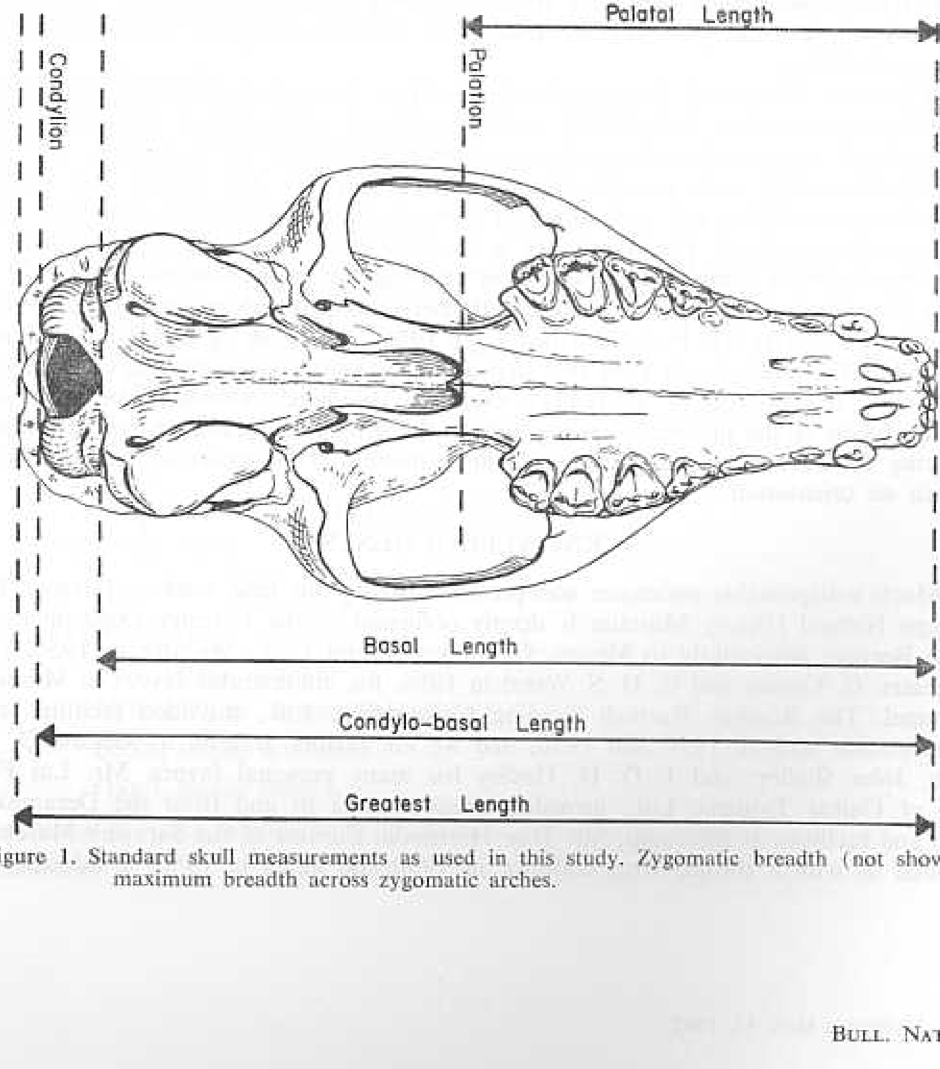


Figure 1. Standard skull measurements as used in this study. Zygomatic breadth (not shown) is maximum breadth across zygomatic arches.

of each collected mammal was recorded. Weights were made with spring balances checked for accuracy before they were taken into the field. Each individual was examined for ectoparasites, which were preserved separately. All food-containing stomachs were preserved, and all females were examined for pregnancy or signs of lactation, and all pregnant uteri preserved.

All measurements used in this study, both flesh and bone dimensions, were made by me unless otherwise stated. Skull measurements up to 150 mm. were made with the same Vernier calipers graduated to 0.1 mm. The smallest skulls were measured under a binocular microscope. Lengths beyond 150 mm. were measured with a large calipers and meter stick. Tooth measurements were made at the alveoli, not at the crown. The nomenclature used for skull measurements is that recommended by Thomas (1905, *Proc. Biol. Soc. Wash.*, 18; see also fig. 1). "Greatest length" is the distance between lines *perpendicular to the toothrow*, taken not farther divergent from the midline than either condylion.

When the sample is large enough (usually 10 or more specimens), important measurements are expressed as the mean, the standard error of the mean, and the observed range, written, e.g., 30.3 ± 0.21 (28.1–32.4). The standard error of the mean is the range on either side of the sample mean that may be expected to include 67 per cent of any sample means drawn from the same population.

For the most part, colors are described in general terms. In a few instances Ridgeway names are used for colors, and such names are capitalized.

Stomach contents were washed by placing the material on fine-meshed cheesecloth and running a stream of water through it for a few minutes. The washed material was then placed in water in a finger bowl and sorted under a 9-power binocular microscope. After sorting, the relative bulk of each item or food category was estimated by eye; the bulk of the entire food organism, rather than the fragments actually recovered, was used in making estimates. Except in a few instances it was impractical to identify prey animals down to the species level.

Nomenclature in general follows Chasen's *Handlist of Malaysian Mammals* (1940). I have not attempted to compile complete synonymies. In most instances only the original description and the first appearance of the currently accepted combination are cited, except where my views differ from those of Chasen. In the latter case the name or combination appearing in the *Handlist* are also given.

HISTORY OF WORK ON NORTH BORNEAN MAMMALS

North Borneo has been less fortunate, from the standpoint of faunal research, than the adjoining colony of Sarawak. The existence of the Sarawak Museum in Kuching, plus the active collecting activities of such colonial officials as A. H. Everett and Charles Hose, have resulted in a considerable accumulation of specimens and information on the mammalian fauna of Sarawak. In North Borneo the lofty isolated massif of Mt. Kinabalu, easily accessible from the coast, has long acted as a magnet to collectors, but the lowland rain-forest has received little attention.

Recorded knowledge of the mammals of the North Bornean rain-forest may be said to begin with Magellan's visit in 1521; Pigafetta, his chronicler, reported the existence of elephants. Systematic work on the fauna, largely by the staff of the British Museum, began about the middle of the last century. J. E. Gray, Albert Günther, and particularly Oldfield Thomas, described 15 North Bornean forms between 1846 and 1902. Collections were made in the vicinity of Sandakan by W. B. Pryer in 1881, on Mt. Kinabalu by John Whitehead in 1887–1888, and at various points along the coast

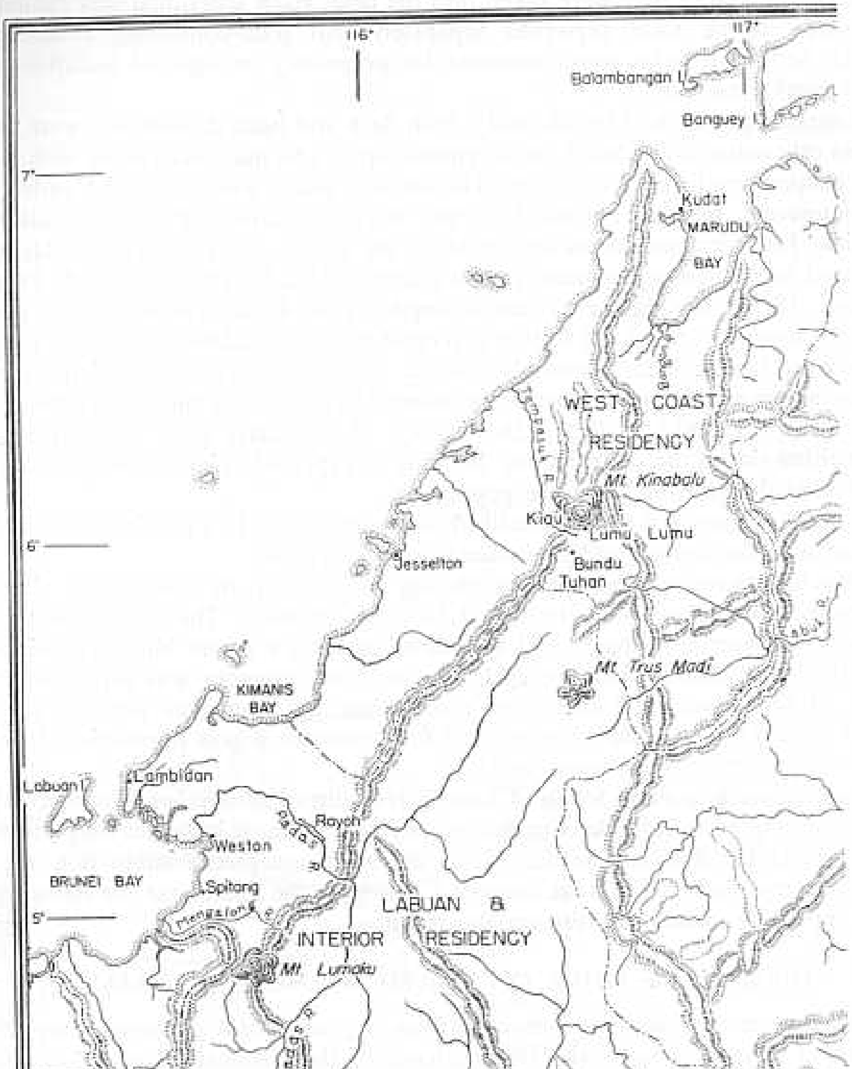
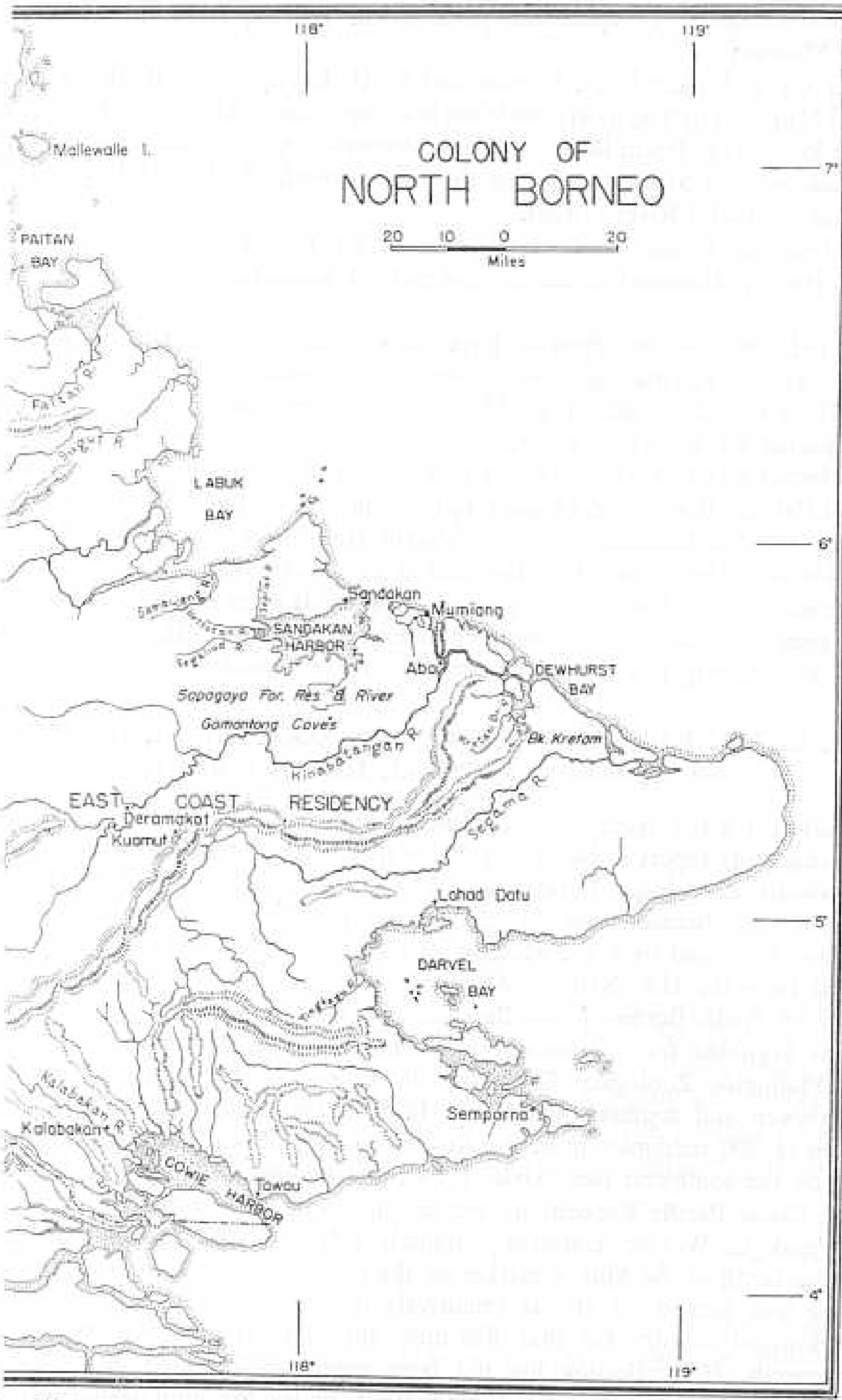


Figure 2. Colony of North Borneo, showing



localities where mammals have been collected.

by A. H. Everett in 1892–1893. A small selection of the historically important Everett collections, including 17 specimens from North Borneo, is in the Chicago Natural History Museum.

In 1927 and 1928 F. N. Chasen and C. B. Kloss, of the Raffles Museum (now National Museum) in Singapore, made the first important modern collections of mammals from the lowlands of North Borneo. Their collections, which totaled about 575 specimens, were made west of Sandakan and on the islands north of Marudu Bay (1927) and at Rayoh on the Padas River (1928).

In 1929 the Crane Pacific Expedition of the then Field Museum (now Chicago Natural History Museum) collected mammals at Sandakan over a period of about a month.

In 1937 the Asiatic Primate Expedition collected mammals on Mt. Kinabalu, at Abai on the Kinabatangan River (exclusively primates), and on the Kalabakan River. These collections are in the Museum of Comparative Zoology at Harvard; they were reported on by Allen and Coolidge (1940). Chicago Natural History Museum has a selected series of 16 specimens collected by this expedition on Mt. Kinabalu.

In 1950 the Bornean Zoological Expedition of Chicago Natural History Museum worked at several localities in eastern North Borneo. A second Bornean Zoological Expedition in 1956 collected at Deramakot and Kalabakan.

The mammalian fauna of the interior of North Borneo has not yet been investigated, and even in the coastal areas between Sandakan and Brunei Bay, and from Dewhurst Bay south to Cowie Harbour, the mammals are very inadequately known.

THE CRANE PACIFIC AND BORNEAN ZOOLOGICAL EXPEDITIONS OF CHICAGO NATURAL HISTORY MUSEUM

Except for a few specimens the Museum has acquired over the years by purchase or exchange, this report is based largely on the collections made by the Crane Pacific and Bornean Zoological Expeditions of Chicago Natural History Museum. This material was supplemented by 22 selected specimens collected by the Asiatic Primate Expedition, borrowed from the Museum of Comparative Zoology, and a few specimens borrowed from the U.S. National Museum. A total of about 850 mammals from the lowlands of North Borneo forms the basis for this report.

Also available for comparison were the extensive Philippines collections made by the Philippine Zoological Expedition in 1946–47, which includes much material from Palawan and southern Mindanao. From neighboring areas in Borneo I had a collection of 200 mammals from the Kelabit country of Sarawak, which adjoins North Borneo on the southwest (see Davis, 1958), and another of 150 from Kuching.

The Crane Pacific Expedition operated in North Borneo during July and August, 1929. Frank C. Wonder collected mammals July 4–9 and August 10–29. A camp was set up north of the Mile 8 marker on the road running west out of Sandakan, and collecting was carried on almost exclusively in the immediate vicinity of the camp. This is lowland country less than five miles inland from the coast. Wonder collected 106 mammals. His collection has not been previously reported on.

The Bornean Zoological Expedition 1950, under the joint leadership of Robert F. Inger and myself, operated in North Borneo from early April to early September.

A trained Iban collector was with us throughout our stay. A total of 352 mammals was collected. Two main field stations were established. During May and June a station was maintained in a logging camp at Bukit Kretam, situated at the mouth of the Kretam Kechil (Little Kretam) River, which flows into the south end of Dewhurst Bay. The area consisted almost entirely of undisturbed primary rain-forest, with a section of nipa-mangrove association immediately adjacent along the bay and the river. Elevation varies from sea level along the bay shore to about 450 feet on the highest ridges. The lowland soil is damp, whereas the ridges are well drained and the soil relatively drier. A network of about ten miles of 50-foot logging roads had been cleared through the forest, preliminary to large-scale logging operations, and this, together with several well-marked trails, made about ten square miles of primary forest readily available.

A second station was established in the Sapagaya Forest Reserve, where field work was carried on from July 13 to August 12. The Sapagaya Forest Reserve is situated on the west bank of the Sapagaya River, about ten miles above its mouth. There is no important relief, and elevation is near sea level. The area consisted of rain-forest that had been logged about fifteen years previously. Most of the large trees were removed, and as a result the forest canopy was not continuous. Smaller trees bearing pulpy fruits were much more numerous than in the undisturbed forest at Bukit Kretam. Large woody lianas and large trees of no commercial value (e.g., *Ficus*) were being systematically removed by the Forestry Department. Primary forest was accessible immediately north of the camp site and also directly across the river, but most of our field work was carried out in the logged area.

The Bornean Zoological Expedition 1956, under the leadership of Robert F. Inger, was in the field in North Borneo from April 22 to June 28, 1956. A trained Iban collector worked on mammals throughout this period. Two field stations were set up, the first at Deramakot on the Kinabatangan River, about six airline miles below Kuamut and about 80 airline miles from the mouth of the river (April 22–May 18), and the second on the Kalabakan River about two miles above the village of Kalabakan (June 2–28). A total of 121 mammals was collected.

The Deramakot area is low and relatively flat, estimated by Dr. Inger at no more than 100–150 feet above sea level. Numerous ridges, varying in different parts of the area from 150 to 850 feet in elevation, rise above the flatland. Soil is damp and clayey in the flatland, whereas the ridges are well drained and the soil is sandy. Both the lowland and the ridges support dense tropical rain-forest, mostly undisturbed by man, with large trees sufficiently numerous to form a canopy. The lowland forest is rich in vines and undergrowth; vines are less common and the undergrowth thinner on the ridges.

The Kalabakan camp was situated at the mouth of the Sungei Tibas, a small tributary of the Kalabakan River. The region is low but with very rugged relief, some ridges reaching an elevation of a thousand feet. The area immediately surrounding the camp site was being or had been logged; practically all the large trees had been removed, leaving the remaining forest without a canopy. A patch of primary forest, similar in physiognomy to the forest at Bukit Kretam and Deramakot, was available about half a mile upstream from the Sungei Tibas camp. Most mammal collecting was in the logged-over area.

THE PHYSICAL ENVIRONMENT

The colony of North Borneo lies between 7° 2′ and 3° 42′ N. latitude, and has an area of about 31,000 square miles. The colony is divided by a group of north-south mountain ranges into a larger eastern part and a smaller western part. The most conspicuous physical feature is the lofty massif of Mt. Kinabalu, which rises to 13,455 feet, and lies at the northern tip of the Crocker Range. The second highest elevation is Mt. Trus Madi, approximately 8,000 feet. The eastern area consists of a series of river basins, with a general northeast orientation, separated from each other by ranges of hills. The largest of these basins is that of the Kinabatangan River. The western area, west of the Crocker Range, consists of a narrow coastal plain about 25 miles wide extending along the west coast. It is drained by numerous short rivers flowing in a general northwesterly direction into the South China Sea. Maps show a large interior plateau lying between the Crocker and Maitland mountain ranges, draining south into the Sembakong River. This interior plateau has not been explored zoologically.

In the eastern area the native peoples are seafarers or hunters and foodgatherers, and the population is thinly distributed. On the west coast the aborigines practice a primitive shifting agriculture and the population is much denser.

Tropical rain-forest extends from sea level to an elevation of about 3,000 feet. Above 3,000 feet the tropical forest is replaced by montane rain-forest, including mossy forest, and finally by subalpine forest and alpine scrub. The character of the fauna varies with this altitudinal zonation (Pendlebury and Chasen, 1932). Only the tropical rain-forest (the Lowland Zone of Pendlebury and Chasen) is considered here.

Tropical ever-green[1] rain-forest originally covered by far the greater part of North Borneo. This primary cover has been disturbed somewhat by man, much less so in the East Coast Residency than in the west. In the west the forest has been seriously damaged by the aborigines, who cut and burn large tracts of forest in connection with a destructive system of shifting agriculture (Plate 1). Here the original forest has been replaced by secondary forests with entirely different predominant vegetational elements (Keith, 1947). Aerial reconnaissance of the East Coast Residency, from Sandakan south to Lahad Datu and west beyond Kuamut, indicated that in 1950 remaining forest of original type was practically continuous and uninterrupted. The head of the Forestry Department at Sandakan estimated, however, that about five per cent of the land area of North Borneo had been logged, and probably more interfered with by aborigines in one way and another (personal communication).

STRUCTURE OF THE FOREST

The North Bornean rain-forest forms a three-dimensional matrix within which the associated animal life lives. The ecological relationships of the mammalian fauna must be considered in relation to this matrix. The forest is composed of some 3,000 species of trees (Browne, 1955), stratified in three layers, a distinct and easily recognizable top story and less easily separable middle and lower stories (fig. 3).

The top story.—The forest is dominated by huge trees of many species, from 100 to 200 feet or more in height and with trunks three to seven feet in diameter. Although numerous in species, they are remarkably uniform in general appearance. The crowns of these trees form the forest canopy, although they are usually well separated from each other and do not form a continuous layer. Their boles rise straight and unbranched for

[1] This term is used in the botanical sense, which refers to absence of a season during which trees are bare. It has no relation to coniferous forest.

80 feet or more, usually supported at the base by plank-like buttresses. These trees are chiefly dipterocarps (family Dipterocarpaceae), an essentially Indo-Malayan family, and the forest type is commonly called Ever-green Dipterocarp Forest. According to Keith (1947) dipterocarp species make up 60 per cent of the (commercial) timbers in this area. Richards (1952) found that dipterocarps formed at least 44 per cent of all trees 16 inches or more in diameter in the Mt. Dulit region in Sarawak.

Strangling figs (various species of *Ficus*, Plate 3) are of no commercial importance and were not considered by Keith, but they are numerous and form an important element of the forest. Adult stranglers reach tremendous size, their crowns participating in forming the canopy. The fruits of the several species of *Ficus* are extremely important to frugivorous mammals and birds. In general pomiferous fruits are not numerous.

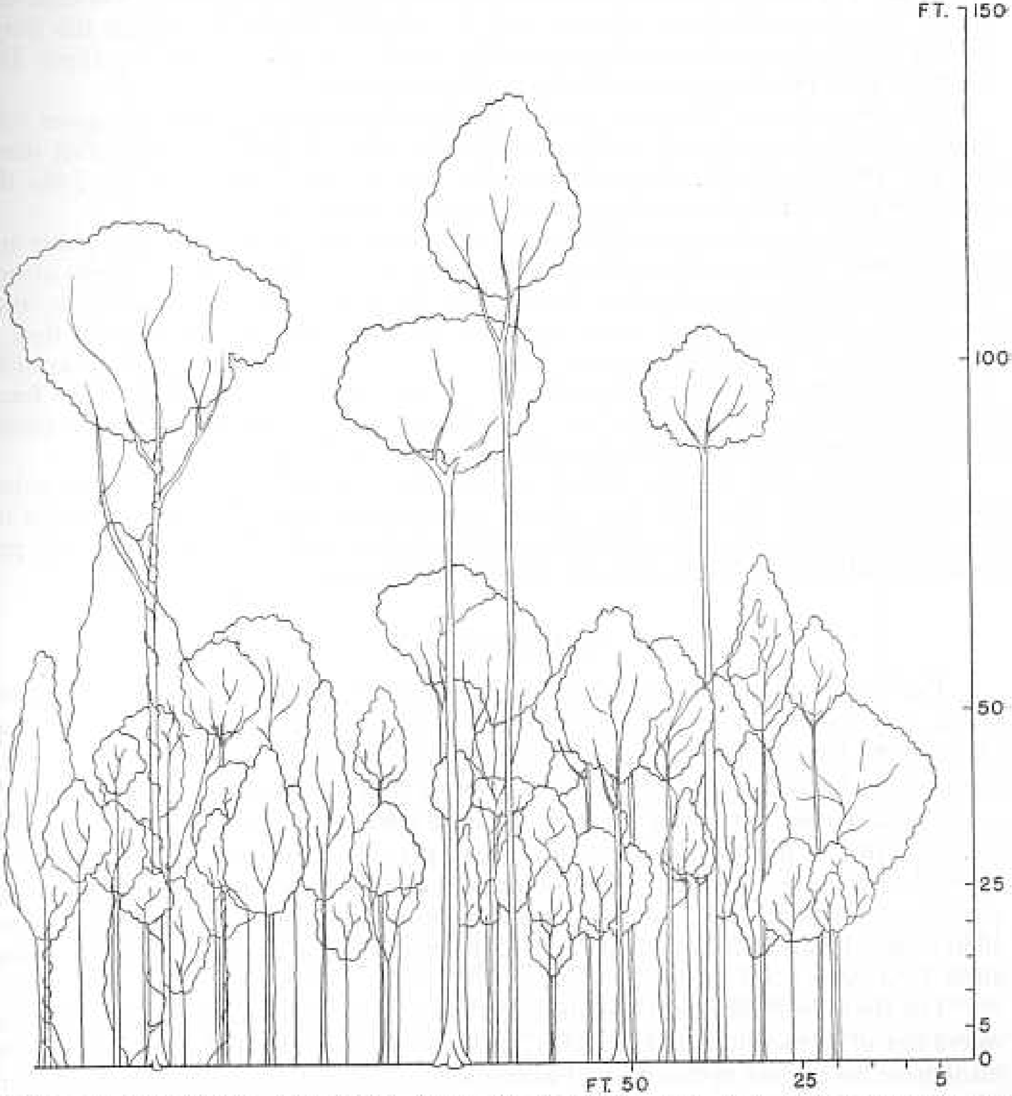


Figure 3. Profile diagram of Bornean dipterocarp rain-forest. Only trees over 25 feet high are shown. Slightly modified from Richards 1952.

The crowns of these trees are heavily infested with epiphytic ferns, some of which attain immense size, and orchids and bromeliads are present to a lesser extent. Woody lianas of various sizes, some thicker than a man's thigh, hang down from the canopy, and more slender vines and other climbing plants are common. These climbers tie the forest together, forming important and much-used highways along which arboreal animals travel. They are less prominent in undisturbed dipterocarp forest than in disturbed forests where other tree species predominate (Keith, 1947).

The middle story.—Beneath the top story is a middle story composed of smaller trees whose tops reach approximately to the underside of the canopy. Immature individuals of the giant trees are represented, but this layer is composed chiefly of various species of trees of smaller size, representing many families. This zone extends from about 60 feet down to about 25 feet, and is dense and nearly continuous, the crown of each tree usually in contact with those adjacent to it. Lianas and vines pass through this story, forming a conspicuous element much used by small mammals for moving about. The middle story is not sharply separable from the lower story.

The lower story.—This zone consists largely of young trees, partly of mature individuals of various species of small trees 25 feet or less in height, representing many families. The species differ from those of the middle story. The lower story, like the middle story, forms a dense and continuous zone of vegetation.

Below this there is a ground layer of scattered shrubs and herbaceous plants and seedling trees. There is no moss stratum on the ground, and grasses are entirely absent. The forest floor is covered with a thin litter of dead leaves, barely sufficient to cover the ground, mixed with dead twigs and branches, and rotting trunks of fallen trees.

Nowhere in undisturbed primary forest is the undergrowth dense enough to make walking difficult. The interior of the forest is open, often almost park-like. The forest roof is not so dense that sunlight does not get through; direct sunlight reaches the ground in small scattered patches, even where the canopy is continuous.

Many permanent streams, of various sizes, flow through the forest. The smallest streams are usually clear, but they become increasingly muddy as they flow toward the sea, and the rivers are coffee-and-cream colored from suspended matter. The only permanent standing water in the forest is in the form of oxbows.

CLIMATOLOGY

The dense canopy of the tropical rain-forest is remarkably effective in holding within very narrow limits the meteorological features of the environment it encloses (Allee 1926, Paulian 1947). The measurements of Allee, Paulian, and others show that temperature, humidity, light, and wind velocity form vertical gradients within the forest —that the climate near the ground is quite different from that in the canopy. Thus animals living at different levels in the forest exist under different conditions. Warm-blooded vertebrates are certainly far less sensitive to such variations than are the smaller, cold-blooded invertebrates, or even than amphibians and reptiles. Nevertheless these climatological differences are important to mammals, even if only indirectly as they affect food supply and predators.

The Bornean Zoological Expedition of 1950 was not equipped to make continuous recordings of temperature and humidity, and only spot readings of these factors were made near the ground in forest and clearing with a wet-and-dry bulb thermometer and a sling psychrometer. The Bornean Zoological Expedition of 1956 was equipped with a Bristol Recording Thermohumidigraph, which was used to chart temperature and humidity at Deramakot and Kalabakan. The thermohumidigraph was calibrated in the field by means of a sling psychrometer.

Rainfall.—Two sets of rainfall data are available for Sandakan: daily records for the 23-year period 1918–1940, made by H. G. Keith; and data for the 8-year period 1947–1955, from Malayan Meteorological Service records. Means of the Keith records are significantly higher than those of the Meteorological Service, but since they represent the longest available continuous series of readings I have used them in preference to the more recent figures. For Jesselton, records are available only for the 1947–1955 period.

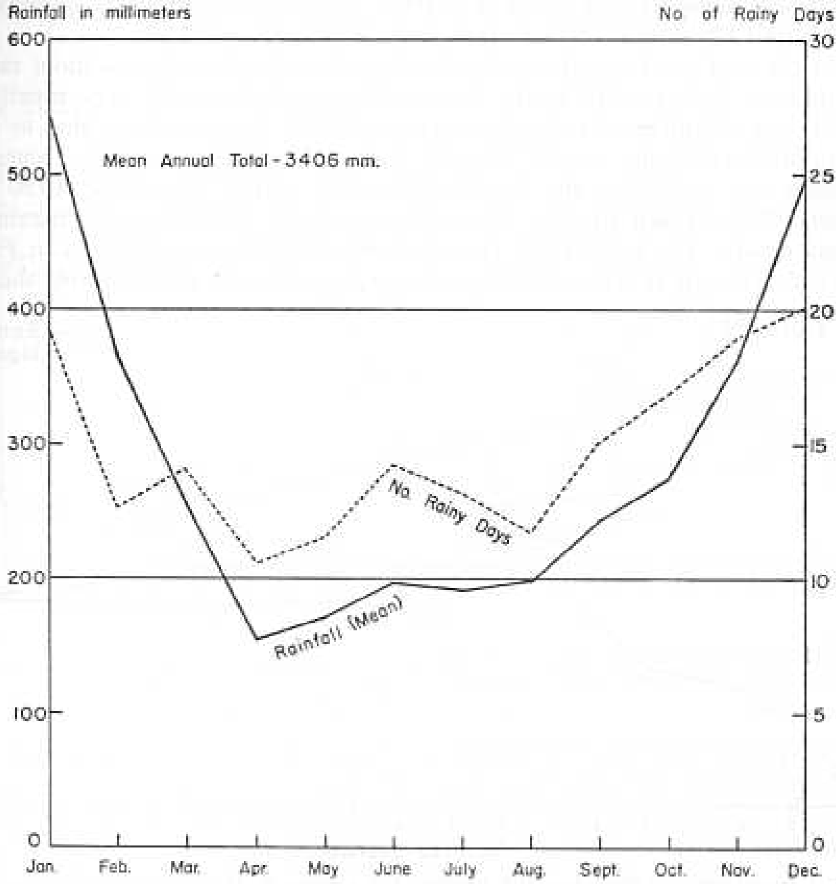


Figure 4. Mean monthly rainfall at Sandakan, North Borneo, for the 23 years 1918–1940. From rainfall records in Forestry Department, Sandakan.

At Sandakan mean annual rainfall was 3406 mm. (134 inches) from 1918 to 1940, with a maximum of 4431 mm. (1918) and a minimum of 2205 mm. (1919). The mean from 1947 to 1955 was 3023 mm., maximum 3313 (1950), minimum 2507 (1949). There is no dry season, although rainfall follows a definite seasonal pattern. The north-east monsoon brings a maximum of precipitation in December-January, and the minimum occurs in April-August (fig. 4). The mean number of rainy days per year for

1918–1940 was 178, maximum 211 (1935), minimum 131 (1930); for 1947–1955 the mean was 181, maximum 232 (1954), minimum 139 (1947). The temperature-rainfall relations for Sandakan are shown in the accompanying graph (fig. 5).

Jesselton has slightly less rain than Sandakan: the mean 1947–1955 was 2845 mm. (112 inches), maximum 3429 (1954), minimum 2337 (1951). Mean number of rainy days 1947–1955 was 199, maximum 251, minimum 162. The seasonal pattern is the reverse of that at Sandakan, with maximum precipitation in the period June-November, and the minimum January-March.

Rainfall appears to be significantly less in North Borneo than farther south in Sarawak. The 1947–1955 mean for Kuching was 3871 mm. (152 inches), with an average of 263 rainy days per year. For these years rainfall increases steadily toward the south, from Jesselton to Miri to Bintulu to Kuching.

From the ecological standpoint the number of consecutive days without rain is far more important than rainfall totals, because the forest desiccates very rapidly in the absence of rain. Number of rainy days per month (fig. 4) provides a clue to distribution of rainfall within the month, but only daily rainfall figures supply accurate data. Such figures are available only for the 28-month period from June 1950 through September 1952 at Bukit Kretam. They give an average of 4.8 days for maximum dry period per month. The longest dry period during this time was 14 days in February-March 1952, a drouth that exceeded by six days any other dry period during this time.

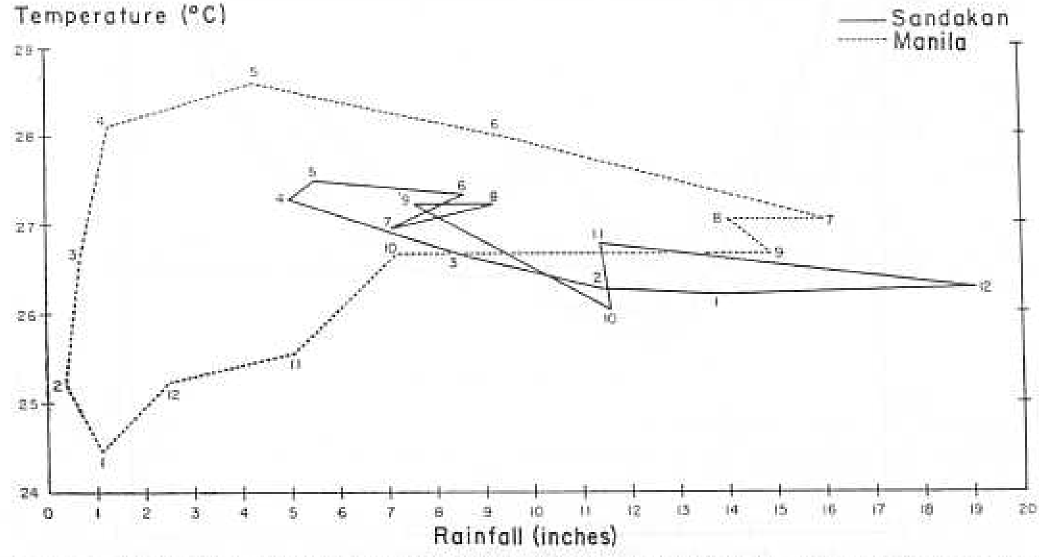


Figure. 5. Climographs for Sandakan and Manila. The climate at Manila is much less uniform that at Sandakan. The numerals 1–12 on the graphs refer to the months of the year. Sandakan data for the years 1947–54; Manila data from Allee 1926.

Humidity.—Mean relative humidity at Sandakan in 1954 was 86.0 per cent, with a mean range of 33.8. The corresponding figures for Jesselton are 84.4 per cent, mean range 30.9.

Autographic charts were made inside the primary rain-forest at Deramakot on April 25–30, 1956. The first three days the Thermohumidigraph was placed 5 feet above ground, in the lower story; the following three days 50 feet above ground, in the middle story of the forest. The usual precautions were taken against exposing the instrument to direct rays of the sun. The means of the resulting readings are shown in fig. 6. In the lower story the diurnal range of mean humidity was 8 per cent (89–96), with the minimum at 2:00 p.m. and the maximum at 10:00–11:00 a.m. In the middle story the range was 37 per cent (55–91), with the minimum at 2:00 p.m. and the maximum at 5:00–7:00 a.m. Relative humidity varied inversely with temperature.

Parallel spot readings of relative humidity in rain-forest and adjoining clearing were made with a wet-and-dry bulb thermometer at Bukit Kretam in June, 1950. Twelve such readings, made over a period of seven days and at various hours between 8:00 a.m. and 10:30 p.m., show a mean difference between forest and clearing of 10 per cent, with a minimum of 0 per cent (10:30 p.m.), and a maximum of 18 per cent (3:30 p.m.).

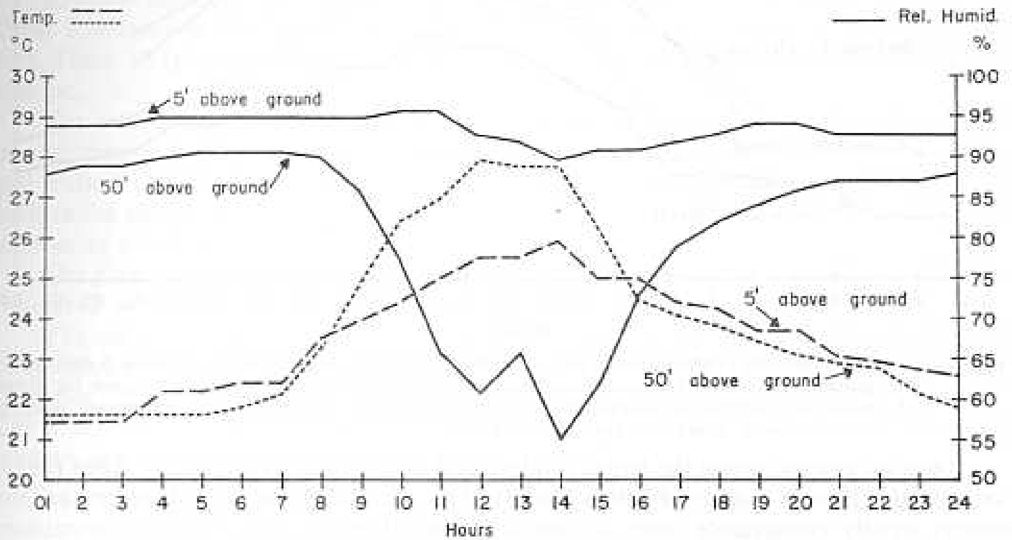


Figure 6. Temperature and humidity relations in primary forest at Deramakot, North Borneo. Each line represents an average of three consecutive days. Data from Bristol Thermohumidigraph charts. April 25–May 1, 1956.

Temperature.—The mean annual temperature at Sandakan for the years 1951–1954 was 26.9°C (80.6°F), with a mean total variation of monthly mean temperature during the year of 2.9°F. The corresponding figures for Jesselton are 26.8° and 3.2°F. Percentage of possible sunshine during the years 1953–1954 was 56 at Sandakan and 57 at Jesselton.

Diurnal temperature variation inside the rain-forest at Deramakot is shown graphically in fig. 6. In the lower story of the forest the mean diurnal range was 4.4°C; at fifty feet, in the middle story, 6.3°C. The difference between the stories is most pronounced during the middle hours of the day; at noon the middle story averaged 4° warmer than the lower story.

Comparative temperatures near ground level in primary forest and adjoining clearing at Deramakot and Kalabakan are shown in fig. 7. Daytime temperatures run consistently higher in the clearings, and have a greater range of diurnal variation than in the forest. The maximum difference, at noon, was about 10°F. At Deramakot the daytime clearing temperatures were also consistently higher and had a greater range than 50 feet above ground in the adjacent forest; the maximum difference, at noon, was about 6°F.

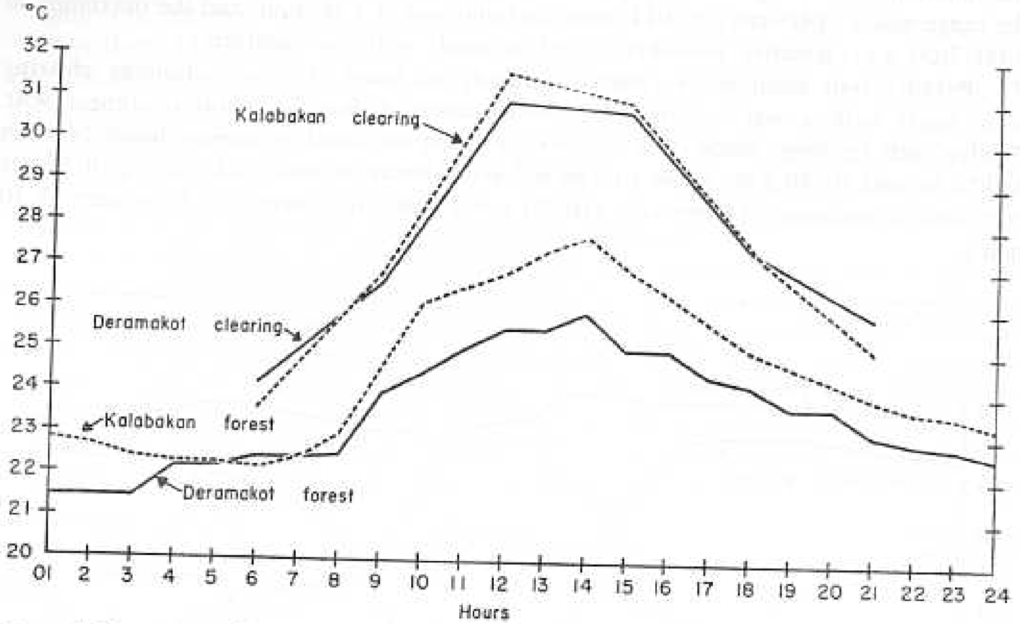


Figure 7. Temperature in primary forest 5–6 feet above ground and in forest clearing 6 feet above ground. Each line represents an average of several consecutive days. Curves for forest based on continuous autographic readings, those for clearings on thermometer readings at three-hour intervals. April–June, 1956.

Data on climate inside the tropical rain-forest are given for Panama by Allee (1926) and for the Ivory Coast by Paulian (1947). The data of these two observers are not always strictly comparable *inter se,* nor with our Bornean data. Where comparisons can be made, agreement among the Neotropical, Ethiopian, and Oriental rain-forests is astonishingly close. Mean diurnal temperature at approximately the same height above ground varies slightly, but the pattern of the daily temperature cycle and the daily range within the cycle are very similar. Data are much more fragmentary for relative humidity, but here too the patterns and ranges at similar levels above ground appear to agree closely.

THE NIPA-MANGROVE ASSOCIATION

The only important lowland formation besides the dipterocarp forest is the nipa-mangrove association, which occupies the tidal lowlands and fringes the coastal rivers as far upstream as the banks are inundated at high tide (Plate 5). In sharp contrast to the adjacent dipterocarp forest, the nipa-mangrove forest is gregarious. It is composed chiefly of nipa palm (*Nipa fruticans*); and mangroves representing several families (*Rhizophora, Avicennia, Sonneratia, Brugeira, Carapa*), all of similar habit. Pure stands of nipa may cover acres, or even square miles as for example along the Trusan Kinabatangan. On the landward side the transition from nipa-mangrove to dipterocarp forest is abrupt; this is especially evident from the air (Plate 2).

The face of the mangrove forest presents a continuous wall of vegetation down to the high-water line, but within the forest it is relatively open, with a dense leafy canopy overhead. Stands of the trunkless nipa palm are difficult to penetrate because of the treacherous footing.

The periodic flooding of this zone by tidal movements creates a habitat unfavorable to mammals, but several species are more or less intimately associated with the nipa-mangrove formation. The proboscis monkey (*Nasalis*) and the crab-eating macaque (*Macacus irus*) are characteristic of this zone. Colonies of flying foxes usually roost in nipa, moving into the dipertocarp forest at dusk to feed. Carnivores are known to enter nipa in search of prey, and nipa is an element in the diet of the elephant.

GENERAL ECOLOGY OF RAIN-FOREST MAMMALS

Relative numbers of species.—The fauna of the lowland rain-forest in the East Coast Residency of North Borneo includes 77 known species of mammals exclusive of bats. These 77 species represent the mammalian element of a typical Oriental rain-forest biotope.

For comparison with this rain-forest fauna I have selected the mammalian fauna of a temperate deciduous forest in southeastern United States, using the data of Handley and Patton (1947). There are 40 species of forest-inhabiting mammals (exclusive of bats) in the mammalian fauna of Virginia as listed by these authors, or 54 per cent of the number in the Bornean forest.

The figures for bats are dramatically different: 58 species in the rain-forest fauna, compared with only 11 in the temperate forest.

The only comparable lowland tropical rain-forest area for which data on number of species are readily available is Panama (Goldman, 1920, *Mammals of Panama*, p. 27). Goldman lists 79 species of non-flying mammals from the Lower Tropical Zone. The following species in Goldman's list are not forest animals, but brushland and savanna forms:

Odocoileus chiriquensis	*Sigmodon hispidus*
Odocoileus rothschildi	*Macrogeomys dariensis*
Zygodontomys cherrei	*Macrogeomys pansa*
Zygodontomys seorsus	*Liomys adspersus*

Eliminating these 8 species leaves a total of 71, a number that is astonishingly close to the 77 species recorded from the North Bornean rain-forest.

Occupation of habitat zones.—Comparison of the rain-forest fauna with the temperate forest fauna reveals notable differences in distribution among the major habitat zones of the forest, as is shown in the following tabulation.

	Tropical Rain-forest		*Temperate Forest*	
	No. of species	*% of total*	*No. of species*	*% of total*
Terrestrial	40	52	29	72
Arboreal	35	45	6	15
Fossorial	0	0	2	5
Aquatic	2	3	3	8
	77	100	40	100

The most conspicuous difference here is the much more extensive occupation of the arboreal zone in the rain-forest, with a corresponding reduction in number of terrestrial species. This is accounted for only in part by the absence of primates in the temperate forest. The primates represent 13 per cent of the total Bornean species, but even if they are omitted more than 30 per cent of the remaining mammalian fauna is arboreal.

Diurnality vs. nocturnality.—Further comparison of these two faunas with respect to times of daily activity of mammals is shown in the following tabulation. Data for temperate forest mammals are taken largely from Hamilton (1943, *The Mammals of Eastern United States*).

	Tropical Rain-forest		*Temperate Forest*	
	No. of species	*% of total*	*No. of species*	*% of total*
Diurnal	23	30	5	12.5
Nocturnal	37	48	19	47.5
Both	17	22	16	40
	77	100	40	100

These figures indicate a more even ratio between diurnal and nocturnal forms in the rain-forest than in the temperate forest. Our observations also indicate a sharper division into diurnal and nocturnal groups in the tropics, with fewer species that do not show a pronounced daily rhythm. In the tabulation above, the diurnal component of the tropical forest fauna is accounted for entirely by treeshrews, primates, and squirrels, all obligatory diurnal animals. All of these except two species of treeshrews and one terrestrial squirrel are arboreal animals. The nocturnal component of the tropical forest fauna is made up largely of obligatory or near-obligatory nocturnal forms: 20 of the 36 species are cats, civets, flying squirrels, and other forms such as *Tarsius* and *Nycticebus*, that are strongly adapted morphologically for nocturnalism. In contrast, only 4 or 5 species in the temperate forest fauna show comparable morphological adaptations for nocturnalism. In the tropical forest all individuals of *Rattus* observed by us were seen at night, and all trapped specimens were taken at night, and I have therefore listed all *Rattus* as nocturnal.

Park (1940) made a similar comparison of the mammalian faunas of the Chicago area and the Panama rain-forest, dividing the faunas only into the two components "diurnal" and "nocturnal." After eliminating the bats to make his data comparable with mine, I find his percentages are: *tropical rain-forest*, diurnal, 40 per cent, nocturnal 60 per cent; *temperate forest*, diurnal 46 per cent, nocturnal 54 per cent. These figures differ widely from mine, for both tropical and temperate forest, and Park's statement that "the general ratio of nocturnal to diurnal species is constant for two widely different geographic areas" is not supported by my data.

Diet.—How do the food habits of the tropical and temperate forest mammals compare? In the following tabulation the data for American mammals are taken from the summaries in Hamilton (*loc. cit.*) and Burt (1946, *The Mammals of Michigan*). Data for Bornean mammals are largely our own.

	Tropical Rain-forest		Temperate Forest	
	No. of species	% of total	No. of species	% of total
Twigs, leaves, buds	15	20	8	20
Fruits and nuts ...	6	8	3	7.5
Mixed fruits, nuts, leaves, buds ...	2	3	2	5
Mixed plant and invertebrate ...	14	18	5	12
Arthropods and other invertebrates ...	10	13	7	17.5
Termites	1	1	0	0
Mixed invertebrate and vertebrate	4	5	2	5
Vertebrate	7	9	6	15
Omnivorous	11	14	7	17.5
Unknown	7	9	—	—
	77	100	40	99.5

Agreement between the mammalian faunas of the tropical and temperate forests in major dietary habits appears to be astonishingly close. There is no category, except the very specialized one of termite-feeding, in which the percentages seem to differ significantly.

A few tentative generalizations may be made on relations between diet and the ecology and morphology of Bornean mammals. Differentiation in food habits among closely-related forms is clearly evident in instances where enough data are available. This is notably true among the squirrels (p. 73) and treeshrews (p. 45), less evident, perhaps because of insufficient data, for the civets (p. 103). The treeshrew situation is further interesting because the diurnal *Tupaia tana* (a treeshrew) and the nocturnal *Echinosorex* (an erinaceid insectivore) seem to be exploiting the same food niche on a "double shift" basis, whereas the two terrestrial treeshrews, *Tupaia tana* and *T. glis*, both diurnal, operate in different food niches. Orthopteroids[2] form a disproportionately large fraction of the insects entering the diets of many insect-eating mammals. They were heavily predominant in the stomachs of *Tarsius* and the civets, less so for treeshrews, and still less so for *Echinosorex*. Orthopteroids were scarcely represented, by contrast, in stomachs of the heavily insectivorous squirrel *Sundasciurus lowi*, the only insect-eating rodent for which we have data. Often there is little or no correlation between dentition and diet among closely-related mammals. Among the squirrels, for example, there appears to be wide variation in diet from species to species, with little associated variation in the dentition (p. 73). The civets, on the other hand, exhibit a wide range of variation in both dentition and diet, but these are correlated in only the most general way (p. 102).

2. Orthoptera *sensu latu*, including also Phasmidae, Mantidae, and Blattidae.

A notable correlation is the tendency for mammals that include a significant proportion of earthworms in their diet to have the snout attenuated. This is evident in *Echinosorex*, *Tupaia tana*, and *Hemigalus derbyanus*. It is interesting that the rostral region is elongated in *Rattus manipulus* of Assam and Burma, a species in which according to Roonwal (1949, *Trans. Nat. Inst. Sci. India*, 3: 102) earthworms form a large proportion of the diet.

Breeding season.—All adult female mammals, except bats, collected by the Bornean Zoological Expeditions 1950 and 1956 were examined for pregnancy and lactation. Data on 201 adult females collected between April 9 and August 15 were recorded. Of these, 51 were pregnant. These data were studied by Wade (1958). She divided the mammals into two groups: those with a gestation period greatly exceeding 60 days, and those with a gestation period of 60 days or less. In both groups the onset of breeding coincided with the period of minimum rainfall, the pregnancy rate reaching a maximum in July and August. For the collection as a whole, the pregnancy rate rose steadily from 0 in April to 44 per cent of all adult females in August. The picture between the middle of August and the end of March, which includes the period of maximum rainfall, is of course unknown because we were not in the field during that period.

Harrison (1952, 1955) concluded that there is no breeding season among rodents and insectivores in Malaya, but only irregular fluctuations in pregnancy rate that are broadly related to amount of rainfall in any given month.

We may conclude from the preceding data that the Bornean rain-forest supports almost twice as many species of mammals as a temperate forest, that the percentage of arboreal species is notably greater in the tropical forest, and that the proportion of strictly diurnal species in much greater with fewer species not showing a pronounced daily activity rhythm. Despite wide disparity in the taxonomic composition of the two faunas, the proportion of each that falls into each of the several dietary categories is very similar. There appears to be a breeding season in the Bornean fauna, but it is correlated with rainfall, and not with day length as in the temperate forest.

ZOOGEOGRAPHY OF NORTH BORNEO

A good, though brief, account of the zoogeography of Bornean mammals was given by Chasen (1940: xiii–xiv). My conclusions agree substantially with his.

There is evidence of at least two poorly-defined faunal areas in the lowlands of North Borneo. These two regions appear to be separated by the north-south mountain ranges lying south of Mt. Kinabalu. Region 1 is much the larger. It embraces the area east of a line drawn south from Marudu Bay, and includes the basins of the Sugut, Labuk, Kinabatangan, and Segama rivers. Region 2 is the area west of this line, which includes the basins of several short rivers flowing west into the South China Sea. Region 2 continues southward into Sarawak for an unknown distance; the Baram River seems to mark an approximate southern boundary.

Five species of mammals are represented in Regions 1 and 2 by forms distinct enough to be given subspecific status. These are: *Echinosorex gymnurus*, *Tupaia minor*, *Presbytis* *hosei*, *Callosciurus prevosti*, and *Sundasciurus hippurus*. In three of these the coloration is paler in the eastern region than in the western, in one (*Callosciurus prevosti*) it is darker, and the fifth (*Presbytis hosei*) is distinguished by head coloration.

There is some indication that North Bornean mammals tend to be slightly dwarfed compared with their counterparts farther south, and that southern Philippine forms in turn tend to be smaller than those of North Borneo.

In only five instances do we have adequate population samples of the same species from North Borneo and from a more southern Bornean locality. In four of these (*Tupaia tana*, *Callosciurus notatus*, *Sundasciurus hippurus* and *Rattus mulleri*), skull measurements of the North Bornean form are slightly but significantly smaller than skull measurements of the same species from Kuching, Sarawak. In the fifth species (*Tragulus javanicus*), on the contrary, the North Bornean form is distinctly larger than its counterpart in Indonesian Borneo (p. 122).

Adequate samples for comparing North Bornean with southern Philippine forms are at hand for four species. In three of these the Philippine representative is smaller in skull dimensions: *Tupaia glis* > *Tupaia palawanensis*, *Tarsius bancanus* > *Tarsius syrichta*, *Mydaus javanensis* > *Mydaus marchei*. In the fourth (*Paradoxurus hermaphroditus*) the Philippine representative is larger (p. 100).

Endemism.—The Bornean mammalian fauna is more specialized than anywhere else in the Malaysian subregion. Borneo has four (perhaps five) endemic genera of mammals, all monotypic. Two of these (*Nasalis* and *Rheithrosciurus*) are very distinctive. *Nasalis* is related to the snub-nosed monkeys of western China, Tonkin, and the Mentawi Islands, and thus appears to be a relict. The relationships of *Rheithrosciurus* are unknown; Moore (1961) believed the presence of two septa in the auditory bulla and of four pairs of mammae ally it to the Holarctic *Sciurus*, but much more evidence is needed before so improbable a relationship can be accepted. Both *Nasalis* and *Rheithrosciurus* are lowland forms.

The three remaining genera (*Paralariscus*, *Glyphotes*, and *Diplogale*) represent a quite different situation. Each differs only slightly from a common and more widely distributed genus. *Glyphotes* and *Diplogale* are montane forms. These three genera may have differentiated in Borneo.

Too little is known of the inter-relationships among species in the Malaysian subregion to permit generalization. Species have been described from each of the larger land masses, but there has been little attempt to synthesize these analytical data. Careful comparison of the North Bornean with the Philippine fauna is extremely desirable but has been hampered by political factors. Students and collections of the Philippine fauna have been chiefly American, of the Malaysian fauna chiefly British and Dutch, and the artificial political boundaries have tended to act as barriers to zoological thinking.

SYSTEMATIC ACCOUNT OF THE MAMMALS OF NORTH BORNEO

A total of 144 forms, representing 135 species, is recognized in the following account. Of these, 60 forms representing 58 species are bats, leaving a total of 84 forms and 77 species of non-flying mammals in the North Bornean fauna.

The distribution of species and subspecies among the various orders is shown in the following table. Four of the ten orders account for 90 per cent of the species.

	Number of species	*Number of species and subspecies*
Insectivora	3	4
Dermoptera	1	1
Chiroptera	58	60
Primates	16	21
Pholidota	1	1
Rodentia	28	29
Carnivora	20	20
Proboscidea	1	1
Perissodatyla	1	1
Artiodactyla	6	6
	135	144

INSECTIVORA

The insectivores are represented in Borneo only by the gymnures and shrews. Moles (Talpidae) occur in the Malay Peninsula, but are not found in any of the East Indian islands.

GYMNURES

Family ERINACEIDAE, Subfamily ECHINOSORICINAE

This group contains some of the most primitive and generalized of living placental mammals. Only *Echinosorex* is found in the lowland forest. The short-tailed lesser gymnure (*Hylomys*) is present on Mt. Kinabalu above 3,000 feet.

Echinosorex gymnurus albus Giebel. Gymnure or Moon Rat, *Ticus bulan*. (Plates 6, 7).

Gymnura alba Giebel, 1863, Zeitschr. Ges. Nat., 22: 277.—Banjermasin, South Borneo.
Echinosorex gymnurus albus Chasen, 1934, Bull. Raffles Mus., 9: 87.—suggests Banjermasin as type locality.

General appearance rat-like, with a long scaly naked tail and a long pointed muzzle. Pelage white above and below, with a few scattered black-tipped hairs on the dorsal surface; the black-tipped hairs may tend to form a patch on the nape. Nose and ears pink. Tail white throughout.

Mean and extreme head and body lengths of 8 adult specimens from the Sapagaya Forest Reserve 366 (335–396); tail 248 (207–292); hind foot 69.5 (68–75). Mean and extreme measurements of six skulls are: greatest length 87.8 (85.5–90.5), condylobasal length 87.6 ± 1.09 (85.3–90.5), zygomatic breadth 43.3 (41.8–45), palatal length 53.4 (51.4–55), upper tooth row, including all teeth, 48.0 ± .39 (46.5–48.9). All these measurements, both flesh and skull, run somewhat higher than those given by Chasen and Kloss (1931) for seven specimens from Bettotan.

PERISSODACTYLA

Family Rhinocerotidae

Didermocerus sumatrensis Fischer. Sumatran Rhinoceros.

Rhinoceros sumatrensis Fischer, 1814, Zoogn. ed. 3, vol. 3, p. 301.—Sumatra.

Didermocerus sumatrensis Brookes, 1828, Cat. Anat. Zool. Mus. of J. Brookes, London, p. 75.

The smallest of living rhinoceroses, measuring about 4 feet at the shoulder (Hose, 1893). Color dark brown to black, the body thinly covered with long dark hairs, longer on ears and tail. Two horns on the rostrum.

This animal is widely but very thinly distributed throughout Borneo. It is well known in North Borneo, but the only North Bornean specimen I have seen is a mounted head exhibited in the Singapore National Museum and labelled Tingkayu, N. Borneo, 1927; Tingkayu is a river on the east coast, emptying into Darvel Bay.

Banks (1931) wrote of its habits: "It is a browser, feeding on twigs and leaves, knocking down small saplings, making a great noise about its feeding and leaving a broad path of broken trees and trampled undergrowth . . . They are said to be fond of a muddy bath by the river side, and I have seen the tracks where they and many pigs wallowed in the hollows of a mountain ridge."

The horns of this animal are greatly prized by the Chinese for medicinal purposes, and the rhinoceros has been greatly persecuted to supply the market with these. Its numbers appear to have been much reduced during the past hundred years.

Locality records.—Tingkayu (Singapore National Museum).

ARTIODACTYLA

Family Suidae

The common Bornean wild pig is *Sus b. barbatus*. The species is represented in Sumatra, the Malay Peninsula, and many of the smaller islands by the closely related *Sus barbatus oi*. A dwarf race, *Sus barbatus ahoenobarbus*, occurs on Balabac, Palawan, and the Calamianes in the Philippines; condylobasal length in adult male 308–327.

A supposed giant pig (*Sus gargantua* Miller, 1906, *Proc. U.S. Nat. Mus.*, 30: 743) was described from southeastern Borneo on the basis of a single skull, and Tucker (*Proc. Zool. Soc. London*, 1931: 487) assigned a second specimen, from the Baram district, to this species. It is very probable that *Sus gargantua* is merely an aberrant form of *Sus barbatus*.

Sus barbatus barbatus Müller. Bearded Pig, *Babi utan*. (Plate 22).

Sus barbatus Müller, 1838, Tijdschr. Nat. Geschied. Physiol., 5: 149.—Banjermassin, South Borneo.

Sus barbatus barbatus Lydekker, 1915, Cat. Ungulate Mam. Brit. Mus., vol. 4, p. 340.

A large pig characterized by a prominent fleshy protuberance, covered with long bristles directed upward and forward, on either side of the snout above and slightly behind the tusk; a conspicuous "beard" of long bristles along the edge of the jowls; and a mane of backwardly-directed bristles extending along the dorsal midline to about the middle of the back. Body thinly haired.

According to Banks (1931) the color varies from "chalky white" through gray to yellowish. An adult male collected by us at Bukit Kretam is reddish above, the mane conspicuously so, dark brown to black below, and black on lower legs and feet; the bristles of the beard are buff at the base, reddish brown at the tip. The scalp of a second male, collected in the Sapagaya Forest Reserve, is much darker; the bristles of the beard are black proximally and bright reddish brown distally. An adult female from near Sandakan is even blacker. According to Banks sucklings are dark brown with three pale longitudinal stripes on the flanks and traces of a fourth and fifth "near the elbow joint." Pfeffer (1959) says that the young are usually not striped.

Measurements of an adult male from Bukit Kretam are: head and body 1,365, tail 225, hind foot 280, ear 85, shoulder height 890. An adult female from near Sandakan measured: head and body 1,220, tail 230, hind foot 290, shoulder height 890. Pfeffer gives the measurements of an adult male "of average size" as: head and body 1,760, tail 230; adult female, head and body 1,500, tail 280.

Mean and extreme measurements of four adult male skulls from Bukit Kretam and the Sandakan Bay area are: greatest length 420 (410–425), condylobasal length 389 (379–397), zygomatic breadth 156 (147–168), palatal length 296 (287–302), maxillary toothrow 129.8 (128–131), M^3 37.3 (36–38) in length, 21.6 (20.5–23.5) in breadth. Skull measurements of an adult female from Kalabakan are: greatest length 367, condylobasal length 347, zygomatic breadth 126, palatal length 265, maxillary toothrow 122.5, M^3 36 in length, 20 in breadth. Where comparable, these measurements are very similar to those given by Lyon (1911) for pigs from the coastal area and adjacent islands just south of Pontianak in Indonesian Borneo. Lyon's figures for the maxillary toothrow in 13 adult males are 130.3 (120–146).

The bearded pig appears to be abundant in all parts of Borneo, and is often a nuisance. Places where they had been rooting were a common sight in the forest at Bukit Kretam. They range up to an elevation of 7,000 feet on Mt. Murud. They are essentially crepuscular and nocturnal, but are sometimes active during the day, especially if it is raining. During the heat of the day an individual usually rests on a bed of twigs and branches that it has cut with its teeth and arranged into a litter. Bearded pigs swim rivers readily, and Abbott (in Lyon, 1911) even reported droves of pigs attempting to swim across Klumpang Bay. Various observers (e.g., Pfeffer, 1959) have reported massive regular migrations of these animals. According to Banks their feeding consists of "rooting in the ground, tearing open rotten logs, picking up fruit, gnawing roots, and consuming any carrion handy." Their greatest enemies are crocodiles.

According to Abbott the numbers of fetuses found in five pregnant females were 4, 7, 9, 10, and 11, respectively.

Specimens examined.—Total 8. Bukit Kretam, 1 skin and skull, 1 skull only; Sandakan mi. 8, 1 skin and skull; Sapagaya Forest Reserve, 1 skull and scalp; Gomantong Forest Reserve, 1 skull only; Deramakot, 1 skull only; Kalabakan, 2 skulls only.

Family TRAGULIDAE

Two species of mouse deer occur in Borneo. Both are represented by very slightly differentiated Bornean races of widely distributed species. The smaller *Tragulus javanicus* ranges over the whole Malaysian Subregion and north into Indochina and Siam, while the larger *T. napu* is restricted to the Malaysian Subregion. The numerous described races are based almost entirely on color and pattern differences. Neither species occurs in the Philippines; the genus *Tragulus* is represented there only on Balabac Island.

Tragulus javanicus klossi Chasen. Small Mouse Deer, *Pēlandok*. (Plate 23).

Tragulus kanchil klossi Chasen, 1934, Bull. Raffles Mus. 9: 98.—Bettotan, near Sandakan, North Borneo.

A small mouse deer with very slender legs. Color above dark brown washed with reddish; individual hairs gray at base, followed by a band of reddish buff, and tipped with dark brown. Flanks without the reddish wash, grizzled buff and dark brown. Belly white with a poorly-defined central area of buff; a narrow brown stripe from throat to about the middle of the belly. Legs bright reddish brown. A narrow black nuchal stripe from occiput to shoulders. Gular chevron marking dark brown. The young are unspotted.

Measurements.—Mean and extreme measurements of four adults of both sexes from the Sapagaya Forest Reserve and Bukit Kretam are: head and body 469 (455–483), tail 81 (70–93), hind foot 137.5 (135–140). Eleven adult skulls from the same region measure: greatest length 98.8 (97–100.4), condylobasal length 91.8 ± .4 (90.0–94.0), zygomatic breadth 44.1 (42.5–46), palatal length 60.6 (59.0–63.0), upper cheek teeth 34.45 ± .36 (33.0–37.2), upper canine of 11 males 15.2 (12–17.5), of 6 females 4.8 (4.0–6). Except for canine length there is no statistically significant sexual dimorphism in these measurements. Mean and extreme weights of 4 adult males were 2,220 (2,000–2,500) grams, of 3 non-pregnant adult females 2,320 (2,200–2,500) grams.

No comparable data are available for *T. j. hosei* of Sarawak. Measurements of a series of 10 specimens from the Kendawangan River in northwestern Indonesian Borneo, identified by Lyon (1911: 68) as *T. j. longipes*, run slightly smaller than *T. j. klossi*, as shown in the following table.

Comparative Mean Measurements of *Tragulus javanicus*

	T. j. klossi	*T. j. longipes* (*data from Lyon*)
No. of specimens	11	10
Hind foot	137.5	130.4
Condylobasal length	91.8	87.1
Upper cheek teeth	34.5	31.9

The small mouse deer is one of the commonest mammals in both primary and secondary forest. We found it active both day and night. We usually observed them as isolated individuals, although they were occasionally seen in pairs, or as a female accompanied by a partly-grown young.

The posture of this animal is not at all deer-like. It stands with the back arched and the rump curved downward. Locomotion is surprisingly suggestive of a rabbit. A startled animal moves off in a bouncing stiff-legged gallop that superficially resembles the saltation of a rabbit. After running a short distance the animal stops. Despite their small size and delicate appearance the flesh of these animals is coarse, far inferior to that of the muntjac or sambhur deer.

Of 14 females collected between 24 April and 8 August 6 were pregnant. Dates of pregnancy were May 9, June 5, July 26 (3), and August 8. Each doe carried a single young.

Specimens examined.—Total 30. Sandakan mi. 8 (5), Sapagaya Forest Reserve (5), Bukit Kretam (3), Deramakot (10), Kalabakan (7). Chasen and Kloss record it from Samawang and Bettotan, and Lyon (1911) from the Kinabatangan River.

Tragulus napu borneanus Miller. Large Mouse Deer.

Tragulus borneanus Miller, 1902, Proc. Biol. Soc. Wash., 15: 174.—North Borneo, Suanlamba River (flowing into south end of Sandakan Bay).

Tragulus javanicus borneanus Kloss, 1918, Jour. Fed. Malay States Mus., 7: 248.

Somewhat larger than *Tragulus javanicus* and with much heavier legs. Color above dark brown washed with buffy-red along the back; individual hairs on the back are gray at the base, followed by a band of buffy red, and tipped with dark brown. Flanks paler than back, the buffy gray under color showing through to produce a mottled effect. Belly white fore and aft, with a central area lightly washed with brown. Legs reddish brown. The dark nuchal stripe seen in *T. javanicus* is typically absent, although two individuals in our series have a poorly-defined dark line running back from the occiput. Gular chevron marking dark brown, coarsely flecked with red. There is much individual variation in the intensity of coloration.

Measurements.—Mean and extreme measurements of eight adults of both sexes from eastern North Borneo are: head and body 529 (527–557), tail 87 (78–105), hind foot 151 (142–165). Seven adult skulls measure: greatest length 110.4 (104.8–120), condylobasal length 104.8 (99.8–114), zygomatic breadth 50.1 (48.3–53.3), palatal length 70.5 (66–77), upper cheek teeth 37.9 (36.5–39.4). Two adult males weighed 3,625 and 4,000 grams, a non-pregnant female 3,500 grams.

As is true of *T. javanicus*, specimens of *T. napu* from eastern North Borneo are slightly larger than specimens from Indonesian Borneo, based on Lyon's measurements of the latter.

Little is known of the habits of this mouse deer. It appears to be less common than the smaller *T. javanicus*. It has been taken at an altitude of 3,700 feet in the Kelabit country of Northern Sarawak.

Of 4 females collected between 5 June and 2 August, 3 were pregnant. These were collected June 15, July 17, and August 2, and each contained a single young.

Specimens examined.—Total 8. Sandakan mi. 8 (2), Sapagaya Forest Reserve (3), Kalabakan (3). Chasen and Kloss record it from Bettotan and Rayoh, and Lyon from the Suanlamba and Kinabatangan Rivers.

Family CERVIDAE

Muntiacus muntjak pleiharicus Kohlbrugge. Barking Deer, *Kijang*. (Plate 22).

Cervulus pleiharicus Kohlbrugge, 1895, Natuurk. Tijdschr. Neth.-Indies, 55 (2): 192.—Pleihari, Southeast Borneo.

Muntiacus rubidus Lyon, 1911, Proc. U.S. Nat. Mus., 40: 73.—Pamukang Bay, southeastern Borneo.

General color reddish buff, darker along the midline where an admixture of brown forms an indistinct dorsal line, darkest and most clearly marked on the neck. Top of head brown, face buffy brown, chin and throat whitish. Under surface pale reddish buff, becoming lighter on the abdomen. Axillary and inguinal regions whitish, the light color extending halfway or more down the inner sides of legs. Outer sides of legs colored like sides of body. Tail white (buff in one individual), with a narrow dorsal stripe of dark brown. There is some color variation in our series, mostly in the intensity of the brown along the dorsal midline and in the amount of red in the pelage.

The fawn has "two rows of sometimes almost continuous white spots down the back and two or more irregular rows on each flank" (Banks, 1931).

Antlers.—The antlers apparently vary greatly with age. In old males (*rubidus* of authors) the pedicel is heavy, there is a prominent burr, the antlers curve sharply inward at the tip, and there is a short basal spine. No measurements of fully developed antlers are available. The antlers vary greatly in form, and exhibit many individual anomalies. In younger but fully adult males (*pleiharicus* of authors) the pedicel is more slender, there is little or no burr, and the antlers are short simple spikes, 50–75 mm. long. All three of our males have antlers of the *pleiharicus* type, although all are fully adult.

Measurements.—Three adult males measure: head and body 860, 905, 894; tail 200, 135, 142; hind foot 288, 275, 256; skull, greatest length 192, 185, 176; condylobasal length 174, 175, 169; palatal length —, 111, 107; zygomatic breadth 84, 82, 79; maxillary toothrow 57, 57, 49; canine length 20, 21, 18.5. Weights of these three animals were 17.7, 15, and 13.5 kilograms. Three adult females measure: head and body 920, 897, 908; tail 150, 153, 155; hind foot 275, 282, 260. Skull, greatest length 185, 191, 171; condylobasal length 171, 183, 164; palatal length 113, 119, 105; zygomatic breadth 79, 77.5, 75; maxillary toothrow 56.5, 54.2, 51.5. Weights of two non-pregnant females were 15.6 and 14.5 kilograms.

The seven animals collected by us were in pairs, except for one female in an advanced stage of pregnancy. This bears out Banks' statement that "it is usual to find them in pairs." All were in primary forest, and one pair was shot in late afternoon, another in mid-morning. The "barking" of this species was heard during daylight hours in both primary and old logged forest.

According to Banks the antlers are shed in May and renewed in August, "though it is doubtful if the shedding is annual." Our three males, collected June 8, June 11, and July 28, all had well developed antlers. Females collected on June 11 and June 26 were pregnant; each contained a single young.

Specimens examined.—Total 7. Bukit Kretam (2), Sapagaya Forest Reserve (2), Kalabakan (3). Chasen and Kloss record this species from Rayoh.

Cervus unicolor brookei Hose. Sambar Deer, *Rusa.*

Cervus brookei Hose, 1893, Ann. Mag. Nat. Hist. (6) 12: 206.—Mt. Dulit, Sarawak.
Cervus unicolor brookei Gyldenstolpe, 1920, K. Svenska Vet. Akad Handl., 60, no. 6, p. 50.

A young male from Bukit Kretam may be described as follows. General color gray-brown, washed with rufous on the nape, back, and hind quarters; the red is brightest on the buttocks. Individual hairs gray at the base, followed by a broad band of brown, a narrower band of buff or hazel, and tipped with black. A narrow black stripe begins in front of the shoulders and extends along the dorsal midline onto the tail. Tail black above and below. Underside brown, becoming cream on posterior belly. Legs cream on inner surface to wrist and ankle, below wrist and ankle buffy cream with a narrow brown line on anterior surface.

Antlers.—The antlers of *brookei* are distinctly shorter than those of *equinus* from the Malay Peninsula (Lyon 1907: 585). There are the three tines typical of this species: a brow tine coming off the main beam at an acute angle, and a single terminal forking of the main beam. The inner tine of the terminal fork is smaller than the outer, which appears to be a direct continuation of the beam.

Measurements of the right antler of an individual taken 8 miles north of Sandakan are: length along outside curve 478 mm., burr to tip of brow tine along convexity 186, circumference above burr 133, circumference above brow tine 115. The largest antler measured by Lyon (1911: 70) was from Pulo Laut; the right antler measured 562 mm. along the outside curve.

Measurements.—The upper cheek teeth of the above male from near Sandakan measure 100 mm.

Sambar appeared to be common in the Sandakan Bay and Dewhurst Bay areas. They are nocturnal and therefore rarely seen. According to Hose this species "feeds on grass, especially the green grass near water, and various wild fruits, of which it is very fond, but it also browses greatly on shoots and leaves of trees."

Specimens examined.—Bukit Kretam (1), Sandakan mi. 8 (1 skull and antlers only).

Family Bovidae

Bos javanicus lowi Lydekker. Temadau.

Bos sondaicus lowi Lydekker, 1912, Proc. Zool. Soc. London, 1912: 902.—Sarawak.
Bibos javanicus Hooijer, 1956, Zool. Meded. Rijksmus. Leiden, 34: 223.

We did not collect this species, and I have had no opportunity to examine specimens. There appear to be no North Bornean records of the temedau, although it is well known to the inhabitants and unquestionably occurs in the colony.

The descriptions given by Lyon (1911) and Banks (1931) of specimens from southeastern Dutch Borneo and Sarawak, respectively, may be summarized as follows. General color of male glossy black; cheeks, axillary and inguinal regions, and a small area at base of tail chocolate brown; feet dirty white to above wrist and ankle; belly dirty white; a white patch on hind quarters; tail brown at base, becoming black toward the tip. General color of female reddish brown above, becoming paler posteriorly, dark brown below; a narrow black stripe along the dorsal midline from shoulder to base of tail; stockings and buttock patch dirty white; tail the color of body proximally, the terminal third black.

According to Lydekker the Bornean race of *B. sondaicus* is distinguished from the Javan race by its stouter, less curved, and more upright horns.

Lyon gives the following measurements of an adult female from Pamukang Bay, southeastern Borneo: head and body 2060, tail 670, hind foot 560, height at shoulder 1280; skull, condylobasal length 405, zygomatic breadth 175, maxillary toothrow 128. Weight of cut-up carcass, without entrails, 176 kilos (386 pounds).

Dried manure of the temadau was present in the camp clearing in the Sapagaya Forest Reserve when we arrived, but the animals were gone. The area had been occupied by Forestry Department personnel for a month before our arrival.

According to Banks the temadau is partial to secondary growth rather than primary forest. The same author says they travel in herds of 8 or 10 individuals.

Locality records.—None.

LOCALITIES IN NORTH BORNEO AT WHICH MAMMALS HAVE BEEN COLLECTED[18]

Locality.	*District.*	*Co-ordinates.*	*Collector.*
Abai	Sandakan	5° 42′ N, 118° 23′ E	Schultz & Washburn 1937.
Balembangan Island		7° 16′ N, 116° 53′ E	Chasen & Kloss 1927.
Banggi Island		7° 15′ N, 117° 10′ E	Chasen & Kloss 1927.
Baturong Caves	Lahad Datu	5° 02′ N, 118° 20′ E*	P. Orolfo 1930.
Benoni	Jesselton	6° N, 116° 05′ E*	
Berhala Island	Sandakan	5° 52′ N, 118° 09′ E	P. Orolfo 1930.
Bettotan	Sandakan	5° 48′ N, 117° 50′ E	Chasen & Kloss 1927.
Bongon	Kudat	6° 33′ N, 116° 50′ E	A. H. Everett 1893.
Bukit Kretam	Kinabatangan	5° 30′ N, 118° 33′ E	D. D. Davis 1950.
Bundu Tuhan	Jesselton	5° 58′ N, 116° 32′ E	J. A. Griswold 1937.
Deramakot	Kinabatangan	5° 17′ N, 117° 33′ E	R. F. Inger 1956.
Dewhurst Bay	Kinabatangan	5°39′ N, 118° 37′ E	D. D. Davis 1950.
Gomantong Caves	Kinabatangan	5° 33′ N, 118° 04′ E	F. N. Chasen 1929.
Jesselton	Jesselton	5° 59′ N, 116° 05′ E	J. A. Griswold 1937.
Kalabakan	Tawau	4° 25′ N, 117° 29′ E	H. G. Deignan 1937. R. F. Inger 1956.
Kinabalu, Mt.	Jesselton	6° 05′ N, 116° 33′ E	A. H. Everett 1892. J. Whitehead 1887-8. J. A. Griswold 1937.
Kinabatangan River	Kinabatangan	5° 39′ N, 118° 37′ E	R. F. Inger 1956.
Kretam Besar River	Kinabatangan	5° 32′ N, 118° 32′ E	D. D. Davis 1950.
Kretam Kechil River	Kinabatangan	5° 31′ N, 118° 33′ E	D. D. Davis 1950.
Kuamut	Kinabatangan	5° 14′ N, 117° 30′ E	R. F. Inger 1956.
Kudat	Kudat	6° 53′ N, 116° 51′ E	Chasen & Kloss 1927.
Labuan Island		5° 20′ N, 115° 15′ E	J. Motley, pre-1855. A. H. Everett 1892.
Lahad Datu	Lahad Datu	5° 02′ N, 118° 20′ E	
Lambidan	Beaufort	5° 23′ N, 115° 22′ E	
Lumu Lumu	Jesselton	6° 02′ N, 116° 34′ E*	J. A. Griswold 1937.
Madai Caves	Lahad Datu	5° 02′ N, 118° 20′ E*	P. Orolfo.
Malawali Island		7° 04′ N, 117° 17′ E	Chasen & Kloss 1927.

[18]. Boundaries as shown on U.S. Army Map Service, Borneo series, T532, dated 1945. District boundaries have changed slightly since 1945. Co-ordinates marked with an asterisk (*) are approximate.

Locality.	*District.*	*Co-ordinates.*	*Collector.*
Mengalong River	Beaufort	5° 02′ N, 115° 27′ E	
Merutai Besar River	Lahad Datu	4° 26′ N, 117° 46′ E	H. G. Deignan 1937.
Mumiang	Sandakan	5° 49′ N, 118° 20′ E	D. D. Davis 1950.
Paitan River		6° 32′ N, 117° 27′ E	A. H. Everett 1892.
Rayoh	Beaufort	5° 15′ N, 115° 50′ E*	Chasen & Kloss 1928.
Samawang River	Sandakan	5° 54′ N, 117° 46′ E	Chasen & Kloss 1927.
Sandakan	Sandakan	5° 50′ N, 118° 05′ E	W. B. Pryer 1881. F. C. Wonder 1929. D. D. Davis 1950.
Sapagaya Forest Reserve	Sandakan	5° 37′ N, 118° 04′ E	D. D. Davis 1950.
Sapagaya River	Sandakan	5° 37′ N, 118° 04′ E	
Segaliud River	Sandakan	5° 45′ N, 117° 50′ E	D. D. Davis 1950.
Semporna	Lahad Datu	4° 29′ N, 118° 37′ E	J. A. Tubb 1948.
Sepilok Forest Reserve	Sandakan	5° 48′ N, 117° 56′ E	D. D. Davis 1950. R. F. Inger 1956.
Sipitang	Beaufort	5° 05′ N, 115° 33′ E	A. H. Everett 1892.
Suanlamba River	Sandakan	5° 40′ N, 118° 07′ E	
Sungei Tibas	Tawau	4° 26′ N, 117° 29′ E	R. F. Inger 1956.
Tapadong Caves	Lahad Datu	5° 02′ N, 118° 20′ E*	P. Orolfo.
Tingkayu River	Lahad Datu	4° 50′ N, 118° 10′ E	
Tuaran	Jesselton	6° 12′ N, 116° 14′ E	J. A. Griswold 1937.
Weston	Beaufort	5° 13′ N, 115° 36′ E	

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