AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3024, 27 pp., 9 figures, 14 tables November 26, 1991

Biological Observations on a Collection of New Guinea *Syconycteris australis* (Chiroptera, Pteropodidae) in the American Museum of Natural History

MARIE A. LAWRENCE[1]

ABSTRACT

The AMNH collection of *Syconycteris* from mainland New Guinea was studied to determine species identity, mainland distribution, and ecological and breeding data. The 442 adults are identified as *Syconycteris australis.* Collection sites range in altitude from sea level to 2770 m but are mainly at the foothills and mid-montane levels. Only Southern Highlands and Enga provinces in New Guinea and Sorong, Fakfak, Merauke, and Jayapura districts of Irian Jaya are not sampled. Data indicate that the species breeds throughout the year. Twin fetuses are reported, and six stages of fetal development are described. Limited ecological data are discussed.

INTRODUCTION

Syconycteris australis, a macroglossine, is one of the smallest of the megachiroptera. It is known from the island of New Guinea, D'Entrecasteaux, Trobriand, central Moluccas, Aru, Kai Islands, and the Bismark and Louisiade Archipelagos, as well as Queensland and New South Wales in Australia. Relatively common in recently made collections from the Australian region, the species appeared to be scarce before mist nets were used for collecting. Accounts of its natural history and biology are rare in the professional literature. Although Lidicker and Ziegler (1968), McKean (1972), Koopman (1979, 1982), Hill (1983), Ziegler (1982), and Rozendaal (1984) have published on the taxonomy of the genus, there is little in the literature about reproduction, ecology, or behavior.

The published accounts have usually been of the Australian subspecies, *Syconycteris australis australis,* the Queensland blossom bat (Bartholomew, et al., 1964; Robinson, 1980; Dobat, 1985; Irvin and Driscoll, 1986; Milledge, 1987; Norberg and Raynor, 1987) or do not reveal whether, *Syconycteris australis papuana,* the New Guinea form or the Australian form was studied (Hood, 1989). Except for Irvin and Driscoll's (1986) prelim-

[1] Senior Scientific Assistant, Department of Mammalogy, American Museum of Natural History.

 ISSN 0003-0082 / Price $3.40

Fig. 1. *Syconycteris australis.* Profile showing tongue extension.

inary abstract on feeding research, the Norberg and Raynor (1987) studies of flight morphology, the metabolism research of Bartholomew et al., (1964), and Hood's (1989) study of female reproductive tract morphology, reports have been mainly anecdotal accounts of feeding behavior.

There is extensive literature on chiropteran reproduction dating from Duval (1895) to the present. Much of this research has focused on seasonality, ovulation, implantation, and the earliest embryonic stages. The postembryonic stages of development in bats have been ignored. There have been no studies of reproduction in *Syconycteris.*

Between 1933 and 1974, The American Museum of Natural History (AMNH) acquired a collection of 632 specimens of *Syconycteris australis* from 64 localities on mainland New Guinea. The locales range from sea level to 2770 m and sample the Vogelkop, central and eastern Irian Jaya, and every province of New Guinea except Southern Highland and Enga. These bats were collected by expeditions where the goal was to sample the flora and fauna of the then little explored regions of New Guinea (Archbold and Rand, 1935; Rand and Brass, 1940; Archbold et al., 1942; Brass, 1964; Diamond, 1969; Van Deusen, 1978). The accomplishments of earlier collectors make it possible now to formulate and test hypotheses about particular animals.

From this large series of *Syconycteris* at the American Museum of Natural History, I can report: identification of the species and distribution in mainland New Guinea; ecological relationship to vegetation; seasonality of reproduction; and fetal development.

Materials and Methods

The collection consists of 493 specimens judged to be adult by degree of metacarpal-phalangeal fusion, tooth wear, or skull sutures. There are 346 specimens preserved in fluid, 77 skins and skulls, 5 skins with skull and carcass, 53 skulls only, and 12 skins only. The variety of preparations made obtaining comparable statistical data a challenge. I took all measurements with dial calipers graduated to 10 mm. The measurements that included the most specimens for comparative purposes were **forearm length** (taken from tip of elbow to proximal end of carpals) and **condylobasal length** (taken from posterior edge

of condyles to anterior edge of incisors). Other measurements taken were **greatest length of cranium** (from posteriormost occiput to most anterior point of premaxilla), **lachrymonasal length** (from anterior midline point of nasals to anterior rim of lachrymal foramen), and **lower canine to third molar length** (from most anterior face of lower canine crown to posterior of lower third molar crown).

Reproductive tracts of males were examined to determine breeding condition. Testes diameter was measured and slide smears made of epididymal contents. Female reproductive organs were examined for possible pregnancies. Uterine horns of immature or apparently nongravid females were 0.5 mm wide. When a horn was enlarged, the side (right or left), as well as length and width of the enlargement were noted. The length of embryos and fetuses was estimated by subtracting 0.3 mm from the length and 0.3 mm from the width of the uterine enlargement. There were 42 pregnancies where both length and width of the uterine enlargement measured more than 5.0 mm. These were excised. The method of selection is biased toward fetuses rather than embryos. Though gross, the method preserves the material for future study with minimal destruction.

Measurements taken from the excised specimens were lengths of **crown to rump** (top of crown to end of rump), **forearm** (point of elbow to proximal end of carpals), and **crown to snout** (top of crown to distal end of muzzle).

External developmental stages were noted and compared with the compilation of mammalian embryo developmental stages published by Butler and Juurlink (1987). These authors used as a standard the "Carnegie stages 9 to 23 of human embryos" (Butler and Juurlink: p. v) and calibrated the embryonic development of a range of taxa against that standard. The mammals described included the primates man, baboon, rhesus monkey, common marmoset, and lesser galago; the rodents mouse, rat, chinese hamster, golden hamster, and guinea pig; as well as rabbit, sheep, pig, and tree shrew.

The *Syconycteris* embryos that, on the basis of external characters, were at Carnegie stages 12 through 23 are described and any differences from the Carnegie scale are noted. The external character development of the fetuses is described in six stages ranging from after Carnegie 23 to near term.

Acknowledgments

I sincerely thank Patricia Freeman, Thomas Griffiths, Guy Musser, Karl Koopman, and John Wahlert who critically reviewed the manuscript at various stages; Carla Kishinimi, Bishop Musuem, who graciously supplied locality information, and Len Marino, New York Botanical Garden, who provided information about New Guinea *Ficus*. The text has been made vivid by Patricia Wynne's fetus illustrations, Ed Heck's map, and Peter Goldberg's prints of habitat photographs which were taken originally by members of various Archbold Expeditions.

LOCALITIES AND SPECIMENS

Irian Jaya

MANOKWARI

1. Oransbari, sea level, Dec. 1962, Jan./Feb. 1963
   Skins/skulls: 221937, 221941, 221943
2. Kebar Valley, 550 m, 16, 19, 20 Jan. 1962
   Alcohol: 221839–221842 (skull extracted 221842)

YAPAN WAROPEN

3. Yapen Island, 5 km NE Sumberbaba, sea level, 27 Oct. 1962
   Skins/skulls: 221936
   Dawai River, 22 Oct., 2 Nov. 1962
   Skins/skulls: 221949, 221951

PANIAI

4. Gebroeders, Weyland Range, 1525 m, 8 July 1933
   Skin/skull: 101947
5. Enarotali, 1830 m, 12, 13, 14, 27 July 1962, 4–5, 9, 12, 15, 17 Aug. 1962
   Skins only: 221782–221785, 221787–221789, 221791–795

JAYAWIJAYA

6. Bokondini, 40 km N Baliem Valley, 1400 m, 17 Nov. 1961
   Alcohol: 221844, 221845
7. Balim River, 1600 m, 13 Dec. 1938
   Skins/skulls: 109953, 109954

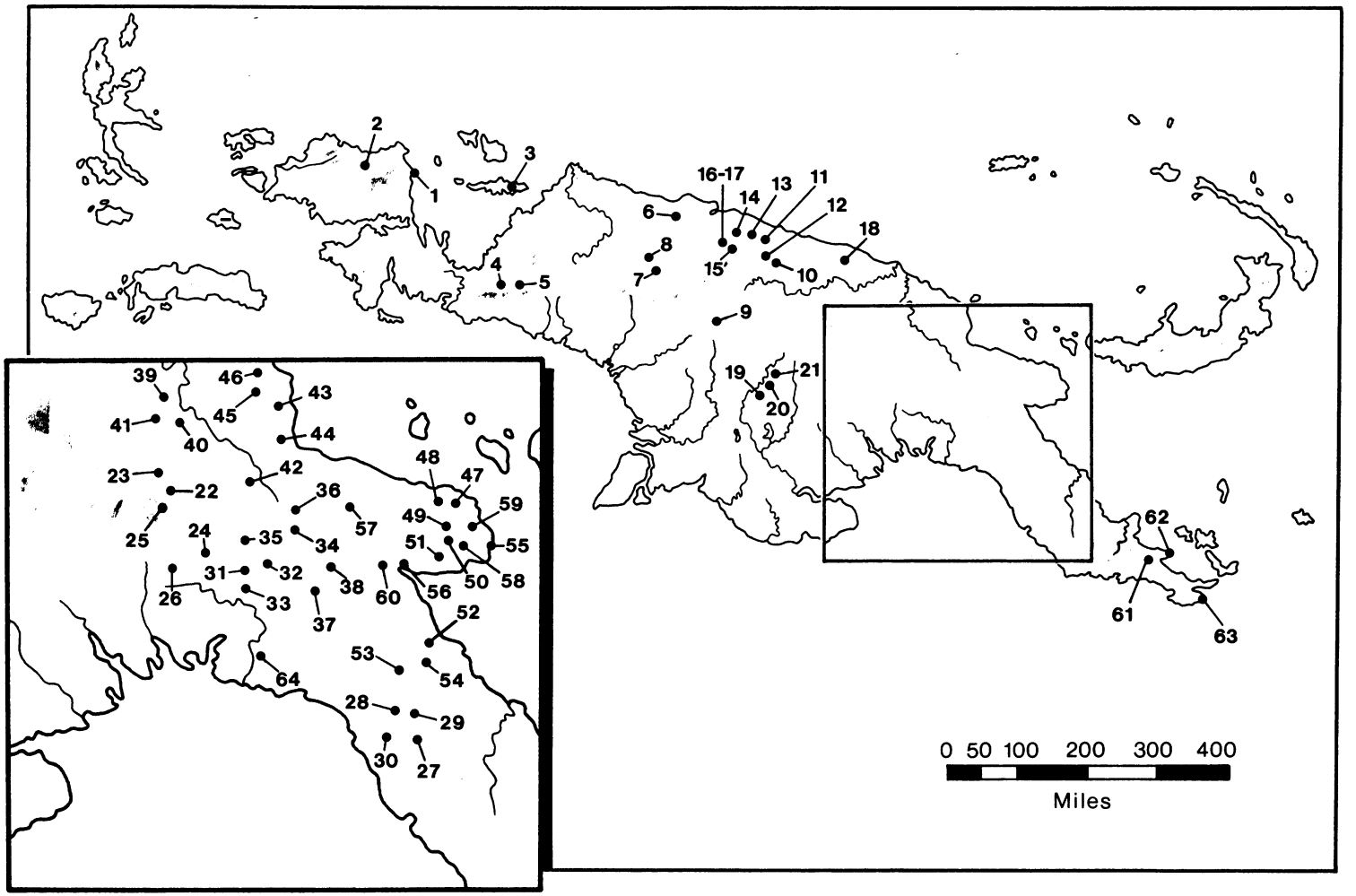

Fig. 2. Map of mainland New Guinea collection localities. Numbers correspond to those in Locality and Specimen List.

8. Archbold Lake, 760 m, 1 Dec. 1961
   Alcohol: 221843
9. Sibil Valley, Star Mtns., 1250 m, Oct./Nov. 1961
   Alcohol: 221874–878, 221880, 221882–886, 221888–890, 221892

Papua New Guinea

SANDUAN (West Sepik)

10. Mt. Nibo, 12 mi NE Lumi, Torricelli Mtns., 1465 m, 12, 13, 14 July 1966
    Alcohol: 198331–335, 198337, 198338–342, 245606, 245608–609
    1067 m, 15 July 1966
    Alcohol: 198344, 198346–350
    857 m, 17 July 1966
    Alcohol: 198352
11. Miliom, 2 mi E Lumi, Torricelli Mtns., 457 m, 21–26 July 1966
    Alcohol: 198355–362, 198364–375, 198377, 198379
12. Mt. Somoro 7 mi NE Lumi, Torricelli Mtns., 945–1128 m, 5, 6, 7 July 1966
    Alcohol: 198381–383, 198385–392, 198395, 198397–398, 198400
    1342–1403 m, 8 July 1966
    Alcohol: 198403–407, 198409–411, 198413–420
    945–1189 m, 4 July 1966
    Alcohol: 198309–317, 198319–198330
13. Utai, Bewani Mtns., 198 m, 20–25 Aug. 1966
    Alcohol: 198421–422, 198424, 198426–434, 198436–437, 198439–450, 198452
    Skulls only: 198069–070, 198166, 198168–171, 198174–198176, 198180–182, 198186–190, 198192–198199, 198245
14. Mt. Menawa, 10 mi NE Utai, 854–1037 m, 2 Aug. 1966
    Alcohol: 198455–458, 198460–462, 198524, 198526
    854–1098 m, 3 Aug. 1966
    Alcohol: 198464–465, 198467, 198468, 198470–471, 198473–479, 189482
    845–1128 m, 4, 5 Aug. 1966
    Alcohol: 198486–487, 198490, 198492, 198495–499, 198501, 198505–506
    845–1128 m, 6 Aug. 1966
    Alcohol: 198508–509, 198512
    884–1128 m, 7, 8 Aug. 1966
    Alcohol: 198514–515, 198519, 198522
    1220–1647 m, 9, 10 Aug. 1966
    Skulls only: 198148, 198150–153, 198156–157, 198160, 198163
15. Biip, 2/3 mi SE Ravit, 503 m, 9, 10, 11 Aug. 1966
    Alcohol: 198574–575, 198577–579, 198581, 198583–588, 198592–597
16. Ravit, 533 m, 5 Sept. 1974
    Alcohol: 196763
17. Maimbel River nr. Ravit, 305 m, 17, 18 Aug. 1966
    Alcohol: 198598–599, 198601, 198603

EAST SEPIK

18. Mt. Turu, Prince Alexander Range, 915–1143 m, 7, 8, 9, 10 Sept. 1966
    Skulls only: 198200–201, 198206, 198208, 198210, 198211–213, 198216, 198218, 198221–226, 198228–229

WESTERN

19. Upper Fly River, 5 mi below Palmer Jct., 50 m, 26, 28, 30 May, 3, 4 June 1936
    Alcohol: 105076–080, 108640
20. Upper Fly River, 1 mi below Black River, 100 m, 15, 24 June 1936
    Skin/Skull: 105087, 105088
21. Upper Fly River, 2 mi below Black River and Palmer Jct., 100 m, 18 July 1936
    Alcohol: 108696

WESTERN HIGHLANDS

22. Kondiu, across Wahgi River from Kup, 1525 m, Aug. 1955
    Alcohol: 160293
23. Nondugl, 1830 m, 6, 11 Aug. 1959
    Alcohol: 183597–598, 183600, 183602–603

SIMBU (CHIMBU)

24. Bomai, 1067 m, 6, 7, 9 July 1965
    Alcohol: 197823–839
25. Kup, Camp #1, foot of Kubor Mtns., 1525 m, 15, 16 Apr. 1952
    Alcohol: 160015–160018

26. Karimui, 1067 m, 1, 2, 3, 4 July 1965
Alcohol: 197843–859, 197862–867
10 July–6 Aug. 1965
Alcohol: 197778, 197787–791

CENTRAL

27. Kagi, Kagoda Road, 1100 m, 12 Mar. 1937
Skin/skull: 108532
28. Mave, Tafa Range, 2225 m, 7 Sept. 1933
Skin/skull: 104024
29. Mt. Albert-Edward, 2165 m, 20 Aug. 1969
Skin/skull: 221475
30. Mafulu, 1253 m, 16 Oct. 1933
Skin/skull: 104025

EASTERN HIGHLANDS

31. Okasa, nr. Okapa, 1281 m, 22, 24 June 1965
Alcohol: 197774–777
32. Okapa, 1952 m, 14–17 June 1965
Alcohol: 197792–794, 197796, 197798, 197800–801, 197803–804, 197808–809, 197815, 197818–820
33. Purosa, nr. Okapa, 1950 m, 21–24, 26, 27 Sept., 1 Oct. 1959
Skins/skulls: 191264, 191266, 191268–269
Alcohol: 192784–790
34. Irumbofoie, 9 mi S, 10 mi W Goroka, 2013 m, 10–13 July 1964
Alcohol: 195240
35. Mt. Michael, 1982 m, 10 Sept. 1959
Skin/skull: 191252, 191255, 191259
Alcohol: 192782, 192783
36. Mt. Otto, Collins Sawmill, 2196 m, 12, 16 Aug. 1959
Skin/skull: 191251
Alcohol: 192781
37. Arau, Kratke Mtns., 1400 m, 7, 8, 10, 14, 15 Oct. 1959
Skin/skull: 191270–271, 191274, 191278–279
Alcohol: 192254, 192791–792, 192794–795, 192797, 192799–800
38. Kassam, Kratke Mtns., 1350 m, 6 Nov. 1959
Alcohol: 192802, 192803

MADANG

39. Gobnem, Kaironk River, 1891 m, 12 Nov. 1963
Alcohol: 193915
40. Upper Kaironk Valley, 1738 m, 1 Dec. 1963
Alcohol: 193916
41. Aynung, mid Kaironk, 1616 m, 10 Aug. 1964
Alcohol: 193917
42. Mt. Wilhelm, 2770 m, 30 June, 20, 23–27, 29 July 1959
Skin/skull: 191243–246, 191248–249
Alcohol: 192766–773
12 June 1950
Alcohol: 156308
Dinugo, SE slopes, 26 July 1959
Alcohol: 192775–777
Umbamambano, 29 July 1959
Alcohol: 192778
Gumana, 30 July 1959
Alcohol: 192779–780
43. Sempi, sea level, 4 July 1959
Alcohol: 220015
44. Nr. Madang, sea level, 2 May–21 June 1971
Alcohol: 222745
45. Wanuma, Adelbert Mtns., 671 m, 21–23 Oct. 1967
Skin/skull: 198757–759, 198763
46. Atitau, 1159 m, 8, 9 Oct. 1967
Skin/skull: 198754–755

MOROBE

47. Mt. Ulur, Mannasat, 2379 m, 6, 7, 12 Aug. 1964
Skin/skull: 194844, 194846
Alcohol: 195237
48. Mt. Upasenga, 2440 m, 31 Aug. 1964
Skin/skull: 194847
49. Nr. Avengu, 1555 m, 28 July 1964
Alcohol: 195236
50. Nr. Siu, 1525 m, 28 July 1964
Skin/skull: 194843
51. Gang Creek, 1311 m, 11, 13, 23 June 1964
Skin/skull: 194840–842
52. Bulolo, Sawmill Creek, 1067 m, May 1959
Alcohol: 192765

53. Wau, 1200 m, 13, 26 Dec. 1961, 6, 26, 29 Jan. 1962
    Skin/skull: 221766, 221772–776
54. Sandy Creek, 1067 m, 20 Sept. 1962
    Skin/skull: 221930
55. Finschhafen, sea level, 23, 25 Sept. 1964
    Alcohol: 195238–239
56. Lae, sea level, 28 Mar., 9 Apr. 1959
    Skin/skull: 191235–237
57. Umi, Upper Markham, 475 m, 27 Nov. 1959
    Skin/skull: 191283
    450 m, 27 Nov. 1959
    Skin/skull: 191284
58. Masba Creek, 640 m, 19 May 1964
    Skin/skull: 194837–838
59. Pindiu, 845 m, 25–28 Apr. 1964
    Skin/skull: 194827–828, 194830–835
60. Oomsis Creek, 100 m, 19, 26, 27 Apr. 1959
    Skin/skull: 191238–240, 191242
    Alcohol: 192758, 192763

MILNE BAY

61. Mt. Dayman, Bottom Camp, 700 m, 23, 26 July 1953
    Skin/skull: 157376–377
    Alcohol: 158824
62. Menapi, Cape Vogel, 25 m, 1, 2 Apr. 1953
    Skin/skull: 157374–375
63. Mornouna, 50 m, 2 Dec. 1956
    Skin/skull: 159156

GULF

64. Weiana, 457 m, 29 Sept. 1967
    Alcohol: 222673

IDENTIFICATION AND VARIATION

IDENTIFICATION: The AMNH collection was assembled before 1980, and there was the possibility that it might include unidentified examples of *Syconycteris hobbit* described by Ziegler in 1982. The material was examined to determine if any specimens possessed the suite of characters Ziegler listed for *S. hobbit* (table 1). All but 16 of the skins had medium to pale brown pelage that was silky rather than woolly and lacked silvery dorsal guard hair. All dorsal metatarsi were thinly haired, and plantar surfaces were relatively pale and fleshy. The ear pinnae tended to be long, bluntly pointed and without pale fleshy rims. All possessed a rudimentary uropatagium and calcar. The terminal phalanx of digit III and the forearm were not above average length for the genus.

TABLE 1
Differential Diagnostic Characters for *S. hobbit* and *S. australis*

S. hobbit	*S. australis*
1. Very dark brown pelage, some silver guard hair, woolly	Pale brown pelage, no silver hairs, silkier
2. Dorsal metatarsus hairy	Dorsal metatarsus bare or sparsely haired
3. No uropatagium, tail, or calcar	Rudimentary calcar and uropatagium
4. Plantar surface dark, not fleshy	Plantar surface pale and fleshy
5. Ear pinna short, distally rounded with thickened light rim	Ear pinna long, bluntly pointed without thickened rim
6. Forearm 45 to 50 mm	Forearm less than 44 mm
7. Terminal phalanx of digit III more than 30 mm	Terminal phalanx of digit III less than 26 mm
8. Hind digits short and thick	Hind digits relatively long
9. Lacrimonasal not over 6.2 mm	Lacrimonasal 5.5 to 8.8 mm
10. Lower canine to third molar 7.8 to 8.4 mm	Lower canine to third molar length 8.1 to 10.2 mm

The 16 dark specimens lacked the woolly pelage and occasional silver guard hairs of *S. hobbit* and did not have any of the other distinguishing characters of that species (table 1). All the AMNH skulls had a long nasolacrimal length and long lower canine through last molar length when compared with Ziegler's ranges and means for *S. hobbit* (table 2). All of the specimens examined belonged to *Syconycteris australis* (fig. 1).

VARIATION: The *P* value of males versus females for both condylobasal and forearm means was between 0.9 and 0.8. As there was

TABLE 2

Selected Means (mm) of Adults *S. hobbit* and *S. australis*

(Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range.)

	S. hobbit[a]	*S. australis*	*P* value
Greatest length	24.90 ± .25 (5) 24.2–25.4	25.51 ± .68 (115) 24.2–27.6	<.2
Condylobasal length	23.15 ± .36 (4) 22.1–23.7	23.97 ± .75 (119) 21.3–26.2	<.1
Lacrimonasal length	5.74 ± .14 (5) 5.3–6.1	6.67 ± .61 (126) 5.5–8.8	**<.02**
Length $c_1 - m_3$	8.16 ± .11 (5) 7.8–8.4	9.20 ± .40 (117) 8.1–10.2	**<.001**
Forearm length	47.2 ± .75 (6) 45–50	42.30 ± 1.78 (74) 37.6–46.0	**<.001**

[a] Figures from Ziegler (1982).

no significant difference, the data for both sexes are combined (table 4).

Because the collecting localities ranged from sea level to 2770 m, I looked for morphologic and morphometric differences by altitude. The mean values of measurements of specimens collected above 1500 m did not differ significantly from those taken below 1500 m (table 5).

The only difference, already noted, was the darker pelage of 16 specimens. These darker specimens came from seven localities in Central, Madang, Eastern Highlands, and Morobe provinces (table 6). One of these came from an altitude below 1500 m and six from altitudes above 2200 m (table 6). Although noticeably darker than most *S. australis* specimens, they are not as dark as *S. hobbit* and have none of the latter species' other characters.

The dark pelage may be linked with a mossy habitat. Van Deusen (1978) did not describe vegetation for Mt. Upasenga or Gang Creek. The description of the camp at Mt. Ulur focused on the grass plain and did not describe the adjoining forest. In the same publication, a photo was included (1978: p. 13) of the heavily mossed forest at Gang Creek. The descriptions of Mave (Archbold and Rand, 1935), as well as Mt. Wilhelm, Purosa, and Mt. Otto (Brass, 1964) indicated that the collecting environment was "mossy." However at Mt. Wilhelm, Purosa, Mt. Otto, and Mt. Ulur the darker bats were captured with pale-pelage conspecifics. These darker bats were captured in the months of June through October in 1933, 1959, and 1964. The condylobasal and forearm measurements of dark-pelage specimens do not differ significantly from those of the rest of the sample (table 3).

TABLE 3

Comparison Among Means (mm) of Samples of *Syconycteris australis* and *Syconycteris hobbit*

(Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed.)

	S. australis			*S. hobbit*[a]	
	Pale	*P*	Dark	*P*	
Forearm	41.96 ± 1.54 37.5–46.1 (413)	>.9	41.92 ± 1.47 37.9–44.0 (16)	<.001	47.2 ± .75 45–50 (6)
Condylbasal	24.18 ± .84 22.0–26.2 (55)	>.4	24.0 ± .56 23.2–25.2 (16)	<.05	23.1 ± .36 22.1–23.7 (4)

[a] Values for *S. hobbit* from Ziegler (1982: 12).

TABLE 4

Forearm and Condylobasal Means (mm) of Adults, *Syconycteris australis*

(Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed.)

	Males	*P* value	Females	Combined
Forearm	41.94 ± 1.4 38.5–46.0 (215)	>.8	41.97 ± 1.6 37.5–46.1 (214)	41.96 ± 1.5 37.5–46.1 (429)
Condylobasal	24.6 ± .74 22.4–25.7 (36)	>.8	24.11 ± .84 22.0–26.2 (35)	24.1 ± .79 22.0–26.2 (71)

Koopman shared his unpublished data on the northeast coast specimens he reported in 1982. As all of his sample was included in my material, and only one of his specimens came from a locality above 1500 m, I removed Koopman's nine specimens from my lowland sample and compared the two sets of lowland specimens (table 7). My measurements for the same specimens are consistently smaller than Koopman's. The probability that the northeast coast sample is the same species is between 30 and 40 percent.

DISTRIBUTION AND ECOLOGY

Specimens were taken at altitudes ranging from sea level to 2770 m. The distributional pattern of the collection is concentrated in the upland regions that form the central spine of New Guinea, and in the north coastal ranges of Papua New Guinea and Irian Jaya (fig. 2). Twenty-one of the 64 localities are between 1500 and 2800 m, and were considered lower montane forest by Paijmans (1975). I characterized them as mid-montane forest following Brass (1964). Thirty-three localities are inland lowland or foothill sites between 100 and 1499 m.

Sea level coastal sites are limited to Lae (56), Finschhafen (55), Madang (44), Sempi (43), and Mornouna (63) in the east and to Oransbari (1) and Yapen Island (3) in Irian Jaya. The numbers correspond to the localities in figure 2. Flannery (1990) labeled the southern lowland the Austral Zoogeographic Zone and included in it the Trans-Fly plains, the Port Moresby region, and the coastal grasslands to the southeast, as well as the northeast coast to Popondetta. The only localities within this zone are on the upper reaches of the Fly River (localities 19, 20, 21), at the Palmer and Black rivers at altitudes of approximately 100 m.

Habitats in New Guinea are varied, and there have been attempts to classify them according to altitude and vegetation (Lane-Poole, 1925; Archbold et al., 1942; Brass, 1964), by vegetational structure and community (Paijmans, 1975), and by zoogeographic province (Schodde and Calaby, 1972; Flannery, 1990). However, it is Steven's (1989) view that the flora of New Guinea is

TABLE 5

Comparison of Means (mm) between Lowland (below 1500 m) and Highland (1500 m and above) *Syconycteris australis*

(Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range.)

	Lowland	*P* value	Highland
Forearm	41.91 ± 1.47 38.1–46.1 (306)	>.6	42.11 ± 1.66 37.5–46.0 (123)
Condylobasal	24.11 ± .84 22.0–26.2 (50)	>.7	24.19 ± .67 23.0–25.5 (21)

TABLE 6

Number of Specimens, Date of Collection and Altitude (m) of Dark Pelage *Syconycteris australis* by Locality

Locality	Date	Altitude	Number of specimens
Mave, Tafa Mts.	Sept. 1933	2226	1
Mt. Wilhelm	June 1959	2770	1
	July 1959	2770	5
Purosa, nr. Okapa	Sept. 1959	1952	1
	Oct. 1959	1952	1
Mt. Otto	Aug. 1959	2196	1
Gang Creek	June 1964	1311	3
Mt. Ulur	Aug. 1964	2379	2
Mt. Upusenga	Aug. 1964	2379	1

one of the most poorly collected in the tropics and its diversity and ecology little understood. He noted that intense study had been concentrated in high-altitude areas and that mid and lower montane vegetation had been subject only to broad survey such as that of Paijmans (1975).

I follow Brass' (1964) vegetation and altitude categories (table 8) because of the detail he provided for the collecting localities of the Archbold Expeditions, the source of many of the bats in this study. The following definitions are a compilation of various locality descriptions by Brass and the general summaries of Womersley (1978):

Savanna is defined as an open tree layer over a ground cover of grasses or grasslike plants. There are *Eucalyptus, Melaleuca,* and a combination of mixed savannas in New Guinea (fig. 3).

Mixed Rain Forest is lowland forest rich in tree species. The upper canopy trees often reach 30 to 45 m but at higher altitudes may be only 25 to 30 m. Strangler figs and tall palms are common at lower altitudes. The shrub layer may include fan palms, tall gingers, and Marantaceae. The herb layer consists of varieties of ferns and tree and palm seedlings. Climbing rattans are dense in forest openings, and epiphytes are profuse in canopy crowns (fig. 4).

Mid-montane Forest often is an oak-*Castanopsis* forest and may include conifers such as *Podocarpus* or *Araucaria* (fig. 5). The shrub layer is dense; palms and rattans are rare, and

TABLE 7

Comparison of Condylobasal Means (mm), Lowland and Koopman (1982) Samples[a]

(Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range are listed.)

Lowland	*P* value	Koopman
24.18 ± .80	>.3	24.45 ± .72
22.4–26.2		23.2–25.7
(45)		(9)

[a] Lowland sample without specimens used by Koopman (1982).

woody lianes are less abundant. Scrambling bamboos are common as is *Pandanus.* Mosses and tree ferns are numerous and conspicuous.

Nothofagus Forest is composed of southern beeches, *Nothofagus species,* mixed hardwoods, and conifers (fig. 6). As altitude increases the conifers become dominant.

Mossy Cloud Forest has one tree layer, composed mainly of Myrtaceae and conifers, with heavy bryophyte cover in locations where slopes are generally under cloud cover by midday (fig. 7). It should be noted that due to prevailing winds and rains, moss can be heavy in lowland and mid montane forests as well.

Subalpine Forest is an impoverished vegetation community, with gnarled trees of thin trunks and flat twiggy crowns (fig. 8). Conifers are dominant. Ericaceae are common in the scrub layer. Toward the tree limit the trees grade into dense scrub or a low open woodland.

Alpine Grassland lies above the natural tree limit and is characterized by low shrub or herbaceous communities. Ericaceae are common shrubs. Tussock grassland gives way to low grassland, and mountain herbs are common. In the wetter sites cycadlike tree ferns are locally abundant among the grasses and sedges. As might be expected lichens, bryophytes, and mountain herbs become more important elements with increased altitude.

The altitudinal overlap of vegetation types (table 8) indicates that they often intergrade. The vegetation patterns are affected not only by altitude, but by degree of daily cloud cover, prevailing winds and rains, and extent of disturbance. River flooding with silt depo-

Fig. 3. Savanna forest. Gaima, Western Province, New Guinea. November 1936.

Fig. 4. Rain forest: *Pandanus* on right and a small fan palm left foreground. Diene, Central Province. May 1933.

sition, as along the Upper Fly, creates areas of quick-growing, flood-resistant secondary growth forest. Human garden settlements or plantations as at Mornouna (63), Menapi (62), Pindiu (59), Arau (37), Balim River (7), and commercial logging activity at Oomsis Creek (60), Mt. Michael (35), and Mt. Otto (36) have either greatly altered or decimated the foothill and mid montane primary forests.

Most of the collection sites are in lowland mixed rain forest or mid montane forest or their remnants. Table 9 summarizes Brass' descriptions of locales. Complete descriptions can be found in accounts of the Archbold Expeditions (Archbold and Rand, 1935; Rand and Brass, 1940; Archbold et al., 1942; Brass, 1964).

Although Brass reported the vegetation of the Archbold itineraries in detail, he seldom indicated the precise habitat where animals were captured. I have botanical association only for *Syconycteris* specimens from Arau,

Fig. 5. Mid-montane *Castanopsis* forest with *Araucaria.* Balim River valley, 1850 m, Irian Jaya. 1938.

Pindiu, Oomsis Creek, and Lae. Brass (1964) reported for Arau, "netted in *Ficus pungens*" (p. 202); Oomsis Creek, "*Syconycteris* taken in mist nets set in *Ficus pungens,* a common tree in second growth forest" (p. 181); and Lae, "*Syconycteris* caught in mist nets in Botanic garden" (p. 179). Van Deusen (1978: 6) noted that at Pindiu, "*Syconycteris* caught in sago swamp below village."

Some information may be gleaned from

Fig. 6. *Nothofagus* forest. Mt. Tafa, Central Province, New Guinea; ridges above 2400 m. August/September 1933.

Fig. 7. Upper montane moss forest: Myrtaceae trees with epiphytic *Rhododendron* (upper center) and leaves of young *Pandanus* in foreground. Mt. Tafa, 2400 m, Central Province, New Guinea. 1933.

remarks written on collector's specimen labels: "Sleeps under big leaves about gardens" (AMNH 160018, Kup); "Caught in dry submontane *Araucaria* dominated forest" (AMNH 192765, Bulolo); "shot in *Macaranga* tree" (AMNH 193916, Upper Kaironk Valley); "visiting a banana at night" (AMNH 193817, Aynung). Ralph Bulmer, who collected the last two specimens, wrote that *Syconycteris* in the Upper Kaironk Valley was found "in garden areas, where it comes to the banana blossom and in the forest," and "makes nests of leaves in branches of trees and thickets not very far above the ground"

Fig. 8. Subalpine scrub forest and tussock grass. East slopes of Mt. Wilhelm, Lake Piunde-Aunde area, about 4040 m.

(Majnep and Bulmer, 1977). This is the only statement I have found about roosting behavior and, if true, is unusual for a fruit bat.

These notes associate *Syconycteris australis* with *Musa, Ficus,* gardens, *Macaranga,* sago palm, and dry *Araucaria* forest. They also suggest that *S. australis* feeds on banana, *Musa* sp., and possibly on *Ficus pungens.* Whether sago palm, *Macaranga,* and *Araucaria* are sources of food or merely near a food source is not known. Both cultivated and wild bananas occur in New Guinea. The banana, *Musa* sp., has an aseasonal flowering habit, with a small number of flowers per night, but it remains in bloom continuously or for long periods of time. There are numerous species of *Ficus* on New Guinea, many with an aseasonal flowering habit similar to that of the banana (Len Marino, N.Y. Botanical Garden, personal commun.). From these two plants alone there is the possibility of a food supply throughout the year.

In New Guinea there are three species of nectar-feeding bats *Syconycteris australis, S. hobbit,* and *Macroglossus minimus.* The relative distributions of the three are beginning to emerge, although *S. hobbit* has been known only since 1982. An examination of AMNH specimens revealed that *S. australis* and *M. minimus* were captured together at Finschhafen, Sempi, Lae, and near Madang at sea level; at Ravit, between 500 and 533 m; and at Bulolo, 1067 m. *Macroglossus* was not taken with *S. australis* in this collection above Bulolo, 1067 m. The two species were captured together at Mt. Turu but the altitude given is an imprecise "between 915 and 1144 meters."

Flannery and Seri (1990) reported *S. hobbit* and *S. australis* sympatric in the upper Sol River Valley at 2300 m, and Ziegler (1982) observed that the two species were sympatric at Mt. Kaindi, 2300 m. From the data available now, *Macroglossus minimus* ranges from sea level to 1067 m; *Syconycteris australis* from sea level to approximately 3000 m; and *S. hobbit* from 2300 m upward (the upper limits of its distribution are not yet known). *Syconycteris australis*' altitudinal distribution overlaps both of the other species but *M. minimus* and *S. hobbit* are not sympatric.

Three species of macroglossines also occur in West Malaysia and each utilizes different food resources (Start and Marshall, 1976): *Eonycteris,* known to travel as much as 38 km to forage, feeds on plants that flower seasonally in flushes with a great number of blossoms per night; and *Macroglossus minimus* and *M. sobrinus,* which "roost in the vicinity of their food source." Each feed on plants that bloom continuously for long periods of time but have a small number of flowers per night. *Syconycteris australis* feeds on plants with the same blossoming habit. There is no information about food plant partitioning by macroglossines on New Guinea.

TABLE 8
Mainland New Guinea Vegetation by Altitude (m) following Brass (1964)

Savanna and savanna forest	0–1700
Mixed rain forest	0–2400
Mid montane forest	480–2350
Nothofagus forest	850–3100
Mossy cloud forest	1500–3200
Subalpine forest	3000–4500
Alpine grassland	2900–up[a]

[a] Permanent snowline.

Macroglossus minimus, present on New Guinea and West Malaysia, is closely associated in West Malaysia with the mangrove genus *Sonneratia*; it was never recorded away from mangrove areas, though banana was noted as part of its diet (Start and Marshall, 1976). In New Guinea, however, that species has been "recorded in rain forest, sago swamp, mangroves, and paperback woodland" (Flannery, 1990). Although my study associates *Syconycteris australis* with *Ficus pungens* and *Musa* sp., I do not know if these are the staples of its diet. There is no published information on the diet of *Syconycteris hobbit.* The altitudinal distribution and the sympatry of *Syconycteris australis* with the other two species suggest that partitioning of food resources is probable on New Guinea but somewhat different from that in West Malaysia.

Breeden (1964) noted that the Australian form of *Syconycteris australis* thoroughly groomed itself of pollen after feeding. Irvin and Driscoll (1986) found "significant quantities" of pollen in the blossom bat's feces. Howell's (1974) classic study found that the glossophagine *Leptonycteris* was able to ex-

TABLE 9
Habitat Descriptions Condensed from Brass and Van Deusen Archbold Localities
(Numbers in parentheses refer to Localities in fig. 1.)

Locality	Altitude (m)	Habitat
Lae (56)	SL	Botanic garden
Menapi (62)	25	Mixed rain forest, 2nd growth forest, gardens
Mornouna (63)	50	Cocoa plantation, gallery mixed rain forest, mangrove stand along beach
Upper Fly River (19, 20, 21)	100	Mixed rain forest, flood resistant 2nd growth plants on banks
Oomsis Creek (60)	118	Heavily logged Dipterocarp forest, patches of wild banana
Umi, Upper Markham River (57)	490	Mixed rain forest without oaks; former gardens = Macaranga forest; cane grass on flood banks
Masba Creek (58)	610	Undisturbed upper limit of mixed rain forest
Mt. Dayman, Bottom Camp (61)	700	Just below juncture of mixed rain forest and mid montane oak–*Castanopsis* forest. Cloud zone marked contact line of the 2 forest types
Pindiu (59)	845	Mostly garden plots, sago palm swamp below village, little forest in this sector of valley
Mafulu (30)	1254	Heavy rain forest with areas of open light forest with low ferns, grass around camp
Kassam (38)	1350	Oak–*Castanopsis* grassland ecotone; relic gallery strips of oak–*Engelhardia* forest through grassland; *Musa ingens* at roadsides
Arau (37)	1400	Coffee plantation in remnants of oak–*Castanopsis* forest; from ridge tops to 1525 m; undisturbed forest transition from oak–*Castanopsis* to *Nothofagous* forest
Balim River (7)	1600	Primary forest out of collecting range; 2nd growth *Casuarina* with low growths of *Ficus* and climbing *Piper*; gardens and grass
Purosa (33)	1952	Primary montane mixed rain forest on ridges (@ 150 m higher) stands of mossy *Castanopsis*
Mt. Michael NE slopes, Kimi Creek (35)	1982	*Nothofagus/Castanopsis* with sprinkling of oaks and other trees; herbaceous undergrowth rich in ravines
Mt. Otto, Kotuni Sawmill (36)	2196	Deforested by logging. Relics of rich montane broadleafed forest; above logging area (2600 m) *Nothofagus* heavily laden with moss; in ravine at 1830 m relic clumps of mid-mountain *Castanopsis*
Mave, W. slopes Mt. Tafa (28)	2226	Ridge forest: rather mossy and without bamboo, trees 15–20 m tall; lower forest: trees 20–30 m, much trailing bamboo, some moss only on limbs
Mt. Ulur (47)	2379	Camp at junction of Kunai grass plain and forest
Mt. Wilhelm, Pengagl Creek (42)	2770	Lower montane rain forest–broadleaf gymnosperm alliance, moist, bryophytes abounded. Subalpine and alpine elements in open areas

tract the amino acids it needed from the pollen of the plants it visited. Though it has not been demonstrated, pollen is probably the source of protein for *Syconycteris*.

Richards (1983) considered *Syconycteris australis* "an important pollinator of the tropics." The evidence for this is not clear, as Faegri and van der Pijl (1966: 117) pointed out, unless it is assumed that any nectar feeder must perforce assist pollination. Because the data on food plants of *Syconycteris australis* of new Guinea are scanty, and knowledge of New Guinea mid-montane vegetation and its propagation is limited, the assumption that this bat is a pollinator is premature.

TABLE 10
Breeding Condition of Males Listed by Month

Month	Number	With sperm	Without sperm
Jan.	3	2	1
Feb.	—	—	—
Mar.	—	—	—
Apr.	2	1	1
May	1	0	1
June	13	12	1
July	74	65	9
Aug.	61	57	4
Sept.	5	5	0
Oct.	7	5	2
Nov.	5	3	2
Dec.	—	—	—
Total	171	150	21

TABLE 11
***Syconycteris australis* By Month of Capture**

Month	Adult ♂	Adult ♀	Juv	Spirit ♀	Embryos
Jan.	4	5	0	1	1
Feb.	1	—	1	1	1
Mar.	1	1	—	—	—
Apr.	13	8	7	4	1
May	6	2	7	1	—
June	16	13	15	9	5
July	77	91	23	83	48
Aug.	68	60	53	53	40
Sept.	8	13	25	8	8
Oct.	15	19	15	12	14[a]
Nov.	8	4	5	4	4
Dec.	3	5	2	2	2
Total	220	221	153	177	123

[a] An embryo from skin and skull carcass and a set of twins.

REPRODUCTION AND FETAL DEVELOPMENT

Reproductive tract data suggest that *Syconycteris australis papuana* breeds throughout the year. Intact sperm were found in 150 of the 171 adult males preserved in alcohol. At least 10 males originally classed as immature on the basis of epiphyseal cartilage and forearm length were found to have enlarged testes and epididymal sperm. The kind of preservation (fixed in 10% formalin and transferred to 70% ethanol) and length of time in fluid apparently do not destroy sperm. The distribution of breeding capable males through the year can be seen in table 10; in every sample greater than one, at least 50 percent were producing sperm. The testes diameter of sperm-producing males was usually 3.9 to 6.0 mm. One sperm-producing adult, AMNH 183597, with a forearm length of 40.1 mm, had testes 2.9 mm in diameter.

There are pregnancies from every month in which there is more than one female preserved in alcohol (table 11). The large number of pregnancies in July, August, and October cannot be attributed to seasonal breeding peaks because 86 percent of the specimens were collected during those months. Ten females which I classed as immature on the basis of epiphyseal cartilage and forearm length were pregnant.

Fetal length varies considerably in each month (table 12). Prenatal specimens collected in one day at one locality also show a wide range in length (table 13). Only the July 4 series from Mt. Somoro does not show much variation in length.

Although the monthly samples are small, the breeding readiness of the males, the presence of embryos and fetuses every month, the range of fetal length during any single month, and even on one day at one locality, support the hypothesis that *Syconycteris australis* breeds throughout the year in New Guinea.

There was no indication of uterine horn dominance in the sample of 40 embryos and fetuses studied for development. Seven fetuses had been removed by the collector and there were no data on uterine horn location.

TABLE 12
Embryo Length (mm) Listed By Month

Month	Number	Observed range
Jan.	1	(4.1)
Feb.	—	—
Mar.	—	—
Apr.	1	(19.6)
May	—	—
June	5	3.2–9.6
July	48	1.2–27.0
Aug.	40	1.5–17.4
Sept.	8	1.0–19.6
Oct.	14	2.8–29.2
Nov.	4	4.2–21.3
Dec.	2	2.5–10.7

TABLE 13
Fetal Length (mm) of Samples Captured on Same Day and Same Locality
(Mean plus or minus one standard deviation, specimen number in parentheses, and observed range are listed.)

Locality, date	Length
Mt. Somoro	
4 July 1966	4.4 ± .5 (9) 3.6–5.2
Miliom	
25 July 1966	7.9 ± 4.6 (3) 3.2–12.4
26 July 1966	8.2 ± 2.2 (4) 5.9–10.5
Mt. Wilhelm	
26 July 1959	17.3 ± 9.8 (2) 10.4–24.3
Mt. Menawi	
3 August 1966	5.7 ± 3.5 (5) 3.0–11.6
Utai	
22 August 1966	8.2 ± 4.3 (5) 4.3–15.5
Arau	
7 October 1959	14.7 ± 11.1 (5) 2.8–29.2

Of the remaining 33, 16 pregnancies were located in the right horn and 17 in the left. All but one were single pregnancies. The exception, AMNH 191279 collected in October at Arau, carried a 16.4 mm fetus in the left horn and a 13.5 mm fetus in the right. Although somewhat compressed, both appear normal. This is the first record of a multiple pregnancy for this species.

The external development observed in the 40 embryos and fetuses is presented below. The time of conception is not known for these wild caught bats, nor is actual gestation length known for the species. Therefore, prenatal development cannot be calibrated against either of these standards. Instead each specimen is placed, by level of development of external characters, in either a Carnegie mammal embryo stage or in a newly designated *Syconycteris* fetal stage. (There are not enough data on fetal development in bats to label the fetal stages either chiropteran or pteropodid.)

Carnegie Mammal Embryo Stage 12 (AMNH 198465)
21 to 29 pairs of somites
Caudal neuropore closes
C-shaped embryo
Three branchial bars visible
Beginning pectoral limb buds

Carnegie Mammal Embryo Stage 16 (AMNH 192771)
Retinal pigment visible
Hind limb footplate
Nasal plates face ventrally
AMNH 192771 has the above plus unfused ear auricle hillocks and forelimb handplate. These two characters appear in Carnegie mammal stage 15.

Carnegie Mammal Embryo Stage 17 (AMNH 198375)
Finger rays
6 distinct auricle hillocks
Nasolacrimal groove
AMNH 198375: Both limb plates present, faint finger rays; auricle hillocks beginning to fuse; nostrils present; lower jaw visible, recessed, and turtlelike.

Carnegie Mammal Embryo Stage 18 (AMNH 193096)
Notched handplate
Elbow present
Toe rays
Beginning eyelids
Vibrissae
Mammary buds
AMNH 193096: Vibrissae primordia and mammary buds not visible; auricle hillocks fused to small pineal flap; finger and toe rays present; elbow present; lower jaw not recessed.

Carnegie Mammal Embryo Stage 20 (AMNH 198597, 198433)
Forelimbs longer and elbow bent
Forelimb digits separating
Hind limb digits visible
Eyebrow follicles appear
AMNH 198597 and 198433: Elbow bent and wrist bent; plagiopatagium from foredigit V to shin region; propatagium beginning from shoulder to wrist; fore- and hind limb digits separating; manus digit III longer than II or IV; vibrissae primordia on eyebrow and snout; eyelid distinct; auricles small flaps that do not cover meatus.

Carnegie Mammal Embryo Stage 21 (AMNH 221843, 191278)
Forelimb digits longer and with touchpads

Feet approach each other
Pinna of ear without helix

AMNH 221843 and 191278: Plagiopatagium and propatagium as in last stage; forelimb digit III clearly longer than II and IV; metacarpals visible; feet approach each other; muzzle blunt, mandible markedly recessed; tongue visible; pinnae almost cover meatus; umbilical hernia obvious (fig. 9A, AMNH 191278).

Carnegie Mammal Embryo Stage 23 (AMNH 198370, 221878)
Fusion of secondary palate
Limbs longer and more developed than Stage 22 (or 21)
All digits completely separated
Eyelids cover most of eye
Definitive shape of auricle
Hair follicles on body

AMNH 198370 and 221878: Secondary palate not seen; only snout and eyebrow follicles present; pinnae small triangular flap without helix; limbs and digits longer, more developed than in earlier stage but without claws; pro-, chiro-, and plagiopatagia distinct and taut; eyelid covers most of eye.

Syconycteris Fetal Stage 1 (AMNH 198372, 198366, 193097, 192803, 198471, 198368)
Crown-rump 9.3–13.1 mm, forearm 3.6–5.6 mm
Forearm raised toward head, elbow clearly seen
Digits spread, chiropatagium taut
Translucent claws on manus digits I and II and all pedal digits
Manual digit III slightly longer than II and IV
Eyelids closed (fig. 9B, AMNH 192803)

Syconycteris Fetal Stage 2 (AMNH 193094, 198498, 221884, 198363, 198575)
Crown-rump 11.0–15.5 mm, forearm 4.7–6.7 mm
Pigment on eyelid edge, inner rim of pinnae, distal end of clawed digits
Nacreous band midline of all claws
Manual digit III lengthened a centimeter
Distal phalanx of manual digit III soft, curved cartilage (fig. 9C, AMNH 198363)

Syconycteris Fetal Stage 3 (AMNH 198580, 193100b, 192780, 198428, 198442)
Crown-rump 13.9–16.4 mm, forearm 6.1–6.7 mm
Pigment along distal edge of chiropatagium
Plagiopatagiales appear
Chiropatagium expanded laterally
Claws opaque
Forearm muscles visible

Syconycteris Fetal Stage 4 (AMNH 193917, 191244, 198452, 193098, 193100a, 193095)
Crown-rump 16.7–20.3 mm, forearm 6.4–8.9 mm
Pigment dots on eyelids, snout, forearms, shins, and dorsum of feet
Forearm upright, carpals resting between shoulder and pinnae
Digit I usually extending behind neck
Wrist flexed downward; digits II through IV not spread
Patagia very full, folds often hiding digits
Torso skin taut

Syconycteris Fetal Stage 5 (AMNH 198602, 192798, 195235)
Crown-rump 18.1–19.6 mm, forearm 7.8–9.5 mm
Faint pigment over cranium
Two phalanges of digit III visible
Lower canines erupting through gum
Skin of torso appears loose

Syconycteris Fetal Stage 6 (AMNH 221845, 192776, 192781)
Crown-rump 19.0–25.4 mm, forearm 8.9–11.6 mm
Dark pigment on outer rim of pinnae
Pigment pronounced on shins, forearms, carpals, and dorsal pes
Entire patagium darkened
Metacarpals not translucent; phalanges not translucent
Upper and lower canines erupted
Older specimens: vibrissae visible on snout and eyelids; fine brown hairs on occiput, nape, and back; colorless hairs on feet and muzzle (fig. 9D, AMNH 192781).

Syconycteris australis showed some deviation from the Butler and Juurlink Carnegie mammal embryo stages. Ear auricles began to fuse and nostrils formed earlier (stage 17). Forelimb digits developed earlier (stage 21). Patagia were visible as early as stage 20. However hair on body appeared later than in the Carnegie mammal schedule.

During the blossom bat's fetal development the pinnae acquire species' shape and size, claws form, digit III lengthens, the patagium gradually expands laterally and acquires muscle fibers; and pigment appears first on edge of eyelid, inner rims of pinnae, and at distal ends of clawed digits. Pigment then appears along the distal edge of patagium, and next on the rest of eyelid, forearms, shins, and dorsum of feet. Finally outer rims of pinnae and all of patagium become pigmented. Near term, vibrissae emerge from follicles on

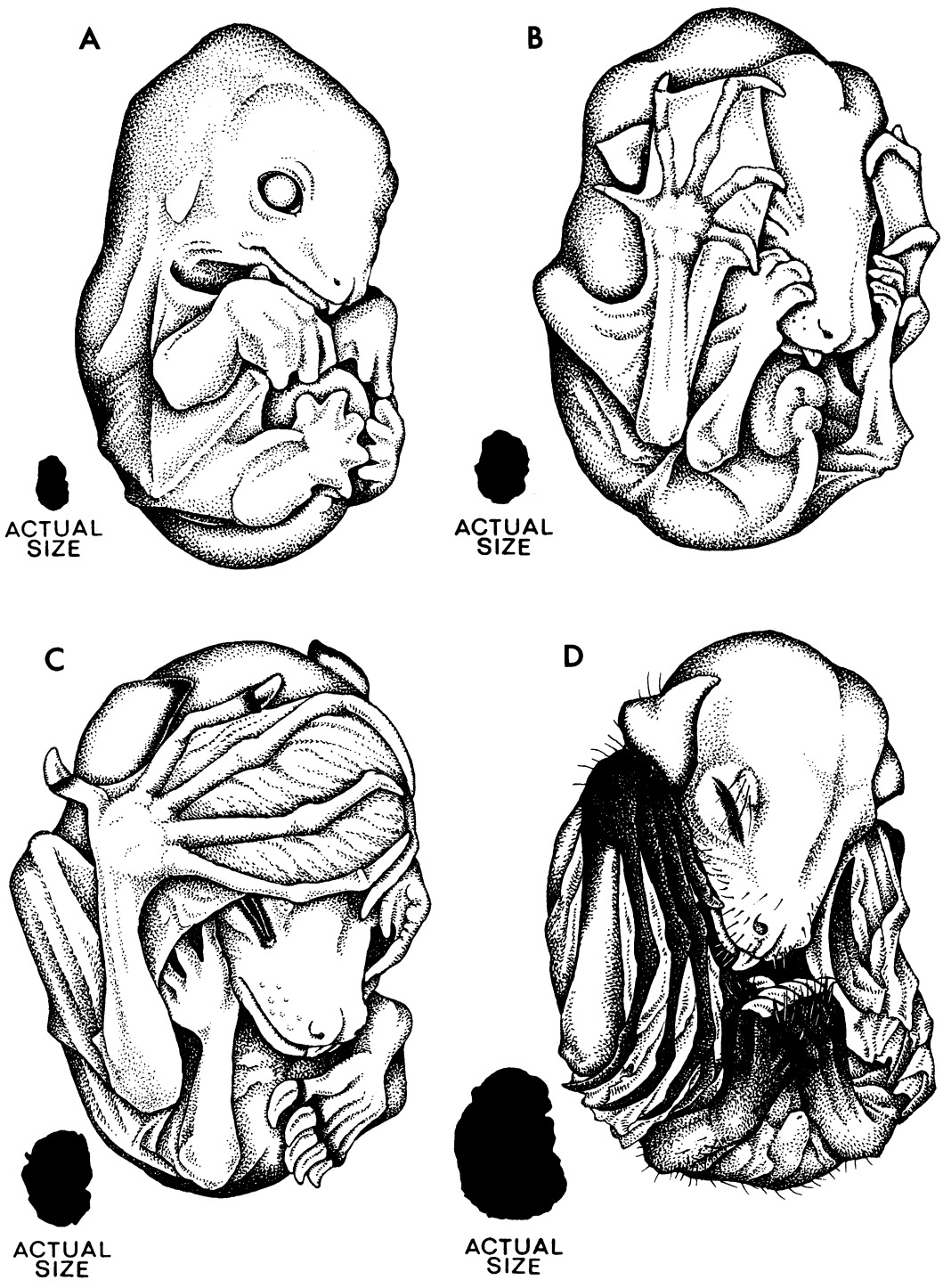

Fig. 9. Some prenatal stages of *Syconycteris australis*: **A.** Carnegie embryo stage 21, AMNH 121278; **B.** *Syconycteris* fetal stage 1, AMNH 192803; **C.** *Syconycteris* fetal stage 2, AMNH 198363; **D.** *Syconycteris* fetal stage 6, AMNH 192781.

TABLE 14
Means (mm) for *Syconycteris* Fetal Stages
(Mean plus or minus one standard deviation, number of specimens in parentheses, and observed range listed.)

Stage	Crown–rump	Forearm	Crown–snout
I	10.9 ± 1.4 (6)	4.7 ± .68 (6)	7.4 ± .65 (6)
	9.3–13.1	3.6–5.6	6.8–8.7
II	13.5 ± 1.8 (5)	5.8 ± .75 (5)	9.5 ± .31 (4)
	11.0–15.5	4.7–6.7	9.2–9.9
III	14.9 ± 1.1 (5)	6.3 ± .25 (5)	10.9 ± .49 (5)
	13.8–16.4	6.1–6.7	9.7–10.9
IV	18.0 ± 1.2 (6)	7.7 ± .89 (6)	11.4 ± .53 (3)
	16.7–20.3	6.4–8.9	10.6–12.0
V	18.96 ± .77 (3)	8.56 ± .86 (3)	12.46 ± .49 (3)
	18.1–19.6	7.8–9.5	11.9–12.8
VI	23.1 ± 3.6 (3)	10.8 ± 1.6 (3)	14.7 ± 1.1 (3)
	19.0–25.4	8.9–11.6	13.4–15.6

snout, above eyes, and on eyelids; very fine, pale body hair appears on occiput, nape, and back. During stage five, lower canines begin to erupt. In stage 6, upper and lower canines have erupted but no other teeth.

Support for the assumption that stage 6 is almost at term is derived from Hill and Smith's (1984) observation that megachiropterans are 20 to 30 percent of adult size at birth. The forearm range and mean of my stage 6 fetuses (table 14) are about 25 percent of those of the adults in table 4. Moreover, AMNH 198765, a "nursing young of AMNH 198764" (collector's label note), has a forearm measuring 14.8 mm or about 35 percent of the forearm mean for adult *Syconycteris.* The range of forearm measurements for stage 6 is 8.9 to 12.0 mm with a mean of 10.8 mm.

Using Sowler's (1980) tooth eruption scale for the pteropodid *Epomophorus,* I place the age of AMNH 198765 between birth and 14 days old. All of the fully erupted teeth are deciduous, caniniform, and recurved. The formula is 2/2, 1/1, 1/1 with two molariform cheekteeth just erupting through the bone. In the mandible, alveoli of permanent teeth are visible between the canine and first deciduous cheektooth and between that tooth and the erupting second deciduous cheektooth.

There is considerable overlap between stages in crown rump measurements and very little overlap in forearm and head measurements (table 14). Crown-to-rump measurements of embryos and fetuses are widely used, but are unreliable. Changes in spinal curvature and differences of in utero positions alter measurements considerably for specimens of the same developmental stage. It is my view that the relatively rigid elements from which forearm and crown snout measurements are taken are more reliable indicators of growth.

Comparisons of embryonic development were made with the data published by Butler and Juurlink (1987) for the lesser bushbaby, *Galago senegalensis,* and the tree shrew, *Tupaia belangeri.* Of the animals reported by Butler and Juurlink, Scandentia and Primates are phylogenetically closest to Chiroptera (Novacek, 1990; Novacek et al., 1988). No Dermopterans were reported. The Carnegie mammal embryo stages are calibrated to internal organ development, making it the same for all animals at each stage. Data on external development permit comparison of the tree shrew and blossom bat at stage 16 and the lesser bushbaby and the blossom bat at stage 18. External developmental data for the three species were available at stages 20 and 23.

At stages 16 and 18, the blossom bat is more advanced in limb development then either the bushbaby or tree shrew. The bat has acquired both hand and foot plates at stage 16, while only hand plates are beginning at this stage in the tree shrew. At stage 18, finger rays, elbow, and toe rays are visible on the blossom bat. The bushbaby has none of

these characters at stage 18. At this stage the blossom bat's pinna is a small flap but the auricle hillocks of the bushbaby are just starting to fuse. The blossom bat's limb development is markedly more advanced than that of either the bushbaby or the tree shrew at stage 20, but at stage 23 the three animals have clearly defined limbs and digits.

Vibrissae primordia are visible in both the tree shrew and the blossom bat at stage 20. The eyelid at the last embryo stage has closed in the tree shrew and bat, and is beginning to descend in the bushbaby. The data on development of vibrissae and pigmentation were compared with that reported by Klima and Gaisler (1968). Their sample of the pteropodids *Rousettus* and *Casinycteris* was small. They observed that the vibrissae are the first hairs to emerge, early during fetal life. Pelage also appears during prenatal life, and they inferred that pelage appeared first on dorsum of head and body (Klima and Gaisler, 1968: 219). In our specimens, vibrissae primordia appear on the snout and above the eyes in embryo stage 20 and vibrissae are visible in fetal stage 6. Very fine blond hair appeared on the occiput, nape, and back in the two most mature fetuses of stage 6, AMNH 192776 and AMNH 192781.

CONCLUSIONS

The AMNH collection of *Syconycteris* is composed entirely of the species *S. australis.* Although the Mt. Upusenga (Morobe Province), and Mt. Wilhelm (Madang Province) localities are above 2300 m and within the altitude range of *Syconycteris hobbit,* that species is absent from the collection. The Flannery and Seri (1990) record of *S. hobbit* collected at 2300 m in the upper Sol River valley (southern West Sepik Province) raises questions about the distribution of that species. Does *S. hobbit* have a disjunct distribution and if so, why? Is the species a seasonal migrant? The specimens that Ziegler (1982) reported were captured in June, July, and August. Flannery and Seri did not give the month in which their specimen was taken.

Our collection shows an altitudinal distribution for *Syconycteris australis* from sea level to 2770 m. A majority of collecting sites are in upland regions of the central and north coastal ranges of New Guinea and Irian Jaya. This may be a collection artifact rather than a limitation in distribution of *Syconycteris australis.* In order to establish the limits of distribution in mainland New Guinea, collections are needed from the southern coastal plain, Flannery's Austral Zoogeographic Zone, and from unsampled areas of Irian Jaya.

The collection reveals no sexual dimorphism for the species on the mainland of New Guinea. It does have a pale and dark color phase. Flannery (1990) observed that the darker colored individuals appeared at higher altitudes. In the AMNH collection, darker individuals were only taken from 1311 m (Gang Creek, Morobe) to 2770 m (Mt. Wilhelm, Madang) and seemed to be associated with mossy vegetation, and were collected during the months of June through October. More data are needed on the conditions under which the darker specimens are found in order to understand the two color phases.

The collectors' notes for AMNH specimens suggest a strong association with wild and cultivated banana, *Musa,* and with the wild fig, *Ficus.* The diversity of vegetation communities in which *Syconycteris australis* was caught could mean that this bat feeds on a wide variety of flowering plants, or that it feeds on a few plants that are ubiquitous. In either case, its food sources are abundant enough to support reproduction throughout the year.

Sympatry of *Syconycteris australis* with *Macroglossus minimus* in various habitats below 1100 m suggests resource partitioning. *Macroglossus minimus* in New Guinea seems less restricted in habitat than in West Malaysia. There appears to be some geographic variation in its abundance relative to *Syconycteris australis.* In the Trans-Fly plains, part of Flannery's Austral zoogeographic province, *Macroglossus* has been reported more abundant than *S. australis* (Waithman, 1979). In southern West Sepik (Flannery and Seri, 1990) and in central Morobe (Ziegler, 1982), *S. australis* has been reported more abundant than *M. minimus.* The true limits of both species and their relative abundance will not be clear until collections are made in unsampled areas and precise botanical associations are noted throughout the year.

The number of males and females in breed-

ing condition (including specimens reproductively active prior to skeletal maturity), the presence of pregnant females in every month for which there are spirit specimens, and the wide range of fetal size from females taken at one time and place, support the hypothesis that *Syconycteris australis papuana* breeds throughout the year.

However, because of the narrow range of length of fetuses from a single day from Mt. Somoro, we must be cautious. Not only is this the largest sample for a single locality and day, but it is the earliest in the year (July 4) and the most uniform in fetal length with a range of 3.6 mm to 5.2 mm and a 0.5 mm standard deviation from the mean. Heideman (1988) reported a mechanism of delayed postimplantation growth in *Haplonycteris fischeri* so that parturition coincides with local patterns of resource abundance. As precise knowledge of *Syconycteris* diet and of low- to mid-altitude nectarous plants is lacking; and the same day/same locality samples are too small to draw reliable conclusions, the possibility of delayed embryonic growth should not be overlooked. *Syconycteris*' ovarian cycle may be complex. Ovarian histological and hormone studies are needed.

In the 122 observed pregnancies in the AMNH collection, the one double pregnancy is the first reported for this species. The significance of equal distribution of pregnancies between the left and right horns is not known.

I used the Carnegie embryo stages to calibrate the embryos from this collection, but a logical flaw in using this scale for most mammals should be stressed. The Carnegie stages are based on human embryos and assume that the rate and sequence of development of this highly derived primate is the standard for all mammals. The fallacy of this assumption limits our understanding of the differences in sequence or rate of development for mammals other than primates. The Carnegie stages can be most useful for those sequences that prove to be the same for all mammals: the appearance of the pectoral limb bud prior to that of the caudal limb bud, for example. The concept of prenatal stages based on the sequence of development can be useful when studying wild-caught animals where time of conception is not known. Ideally, these stages should combine and correlate the sequences of bone ossification, internal organ, and external character development. Such studies of prenatal development have not been published.

The traditional practice of not considering the development of prenatal organisms after internal organ systems are in place has limited our knowledge of character derivation. Relatively early forelimb development of blossom bat embryos is not surprising since chiropterans are animals defined by their specialized forelimbs. Research on the fetal limb and limb membrane development in dermopterans and the flying squirrels would be of interest for comparison.

Data are needed on the distribution of *Syconycteris australis* in Irian Jaya and in the unsampled regions of Papua New Guinea. Further clarification of the relative distribution of *S. australis* and *Macroglossus minimus* would also be valuable. In order to obtain this information, not only collection but careful reports on roosting sites, vegetation of foraging areas, and observations on food plants visited are necessary. Knowledge of New Guinea flowering plants and their natural history is also needed in order to understand fully the ecological and co-evolutionary relationships of macroglossines and plants. Finally, laboratory research on ovarian histology, embryological organ development, and fetal ossification sequence of specimens in existing collections would be profitable.

Specimens in museum collections are used to test hypotheses about phylogeny, classification, and zoogeography. Systematists are aware of the information available in variously preserved specimens. However, the data presented and the questions raised in this report show the broader use that biologists may make of existing collections.

REFERENCES

Archbold, R., and A. L. Rand
1935. Results of Archbold Expeditions no. 7. Summary of the 1933–1934 Papuan expedition. Bull. Am. Mus. Nat. Hist. 68(8): 527–579.

Archbold, R., A. L. Rand, and L. J. Brass
1942. Results of Archbold Expeditions no. 41. Summary of the 1938–1939 New Guin-

ea expedition. Bull. Am. Mus. Nat. Hist. 79(3): 197–288.

Bartholomew, G. A., P. Leitner, and J. E. Nelson
1964. Body temperature, oxygen consumption, and heart rate in three species of Australian flying foxes. Physiol. Zool. 37(2): 179–198.

Brass, L. J.
1964. Results of Archbold Expeditions no. 86. Summary of the Sixth Archbold expedition to New Guinea. Bull. Am. Nat. Hist. 127(4): 145–216.

Breeden, K.
1964. Dwarf among the fruit bats. Animals 4(16): 456–459.

Bulmer, R. N. H., and J. I. Menzies
1972. Karam classification of marsupials and rodents. J. Polynesian Soc. 81(4): 472–479.

Butler, H., and B. H. J. Juurlink
1987. An atlas for staging mammalian and chick embryos. Boca Raton: CRC Press, 218 pp.

Diamond, J.
1969. Preliminary results of an ornithological exploration of the North Coastal Range, New Guinea. Am. Mus. Novitates 2362: 57 pp.

Dobat, K.
1985. Blüten und Fledermäuse. Bestäubung durch Fledermäuse und Flughunde (Chiropterophilie). Senckenberg-Buch 60. Frankfort am Main: W. Kramer. 370 pp.

Duval, M.
1895. Etudes sur l'embryologie des chéiroptères. J. Anat. Physiol. Paris 31: 94–160, 427–474.

Faegri, K., and L. van der Pijl
1966. The principles of pollination ecology. Oxford: Pergamon Press, 284 pp.

Flannery, T. F.
1990. The mammals of New Guinea. Carina, Queensland, Robert Brown, 439 pp.

Flannery, T. F., and L. Seri
1990. The mammals of southern West Sepik Province, Papua New Guinea: their distribution, abundance, human use and zoogeography. Rec. Australian Mus. 42: 173–208.

Heideman, P. D.
1988. The timing of reproduction in the fruit bat *Haplonycteris fischeri* (Pteropodidae): geographic variation and delayed development. J. Zool. London 215: 577–595.

Hill, J. E.
1983. Bats (Mammalia: Chiroptera) from Indo-Australia. Bull. Br. Mus. Nat. Hist. (Zool.) 45(3): 103–208.

Hill, J. E., and J. D. Smith
1984. Bats: a natural history. Austin: Univ. Texas Press, 243 pp.

Hood, C. S.
1989. Comparative morphology and evolution of the female reproductive tract in macroglossine bats (Mammalia, Chiroptera). J. Morphol. 199: 207–221.

Howell, D. J.
1974. Bats and pollen: physiological aspects of the syndrome of chiropterophily. Comp. Biochem. Physiol. 48(2A): 263–276.

Irvin, B., and P. V. Driscoll
1986. Seasonal changes in the diet of the Queensland blossom bat (*Syconycteris australis*) in coastal vegetation on Bribie Island. Macroderma 2(1): 22. (Abstract).

Klima, M., and J. Gaisler
1968. Study of growth of juvenile pelage in bats, IV. Desmodontidae, Pteropidae. Zool. Listy 17(3): 211–220.

Koopman, K. F.
1979. Zoogeography of mammals from islands off the northeastern coast of New Guinea. Am. Mus. Novitates 2690: 17 pp.
1982. Results of Archbold Expeditions no. 109. Bats from Eastern Papua and the east Papuan islands. Ibid., 2747: 34 pp.

Lane-Poole, C. E.
1925. The forest resources of the Territories of Papua and New Guinea. Melbourne, Government Printer, Commonwealth of Australia, 209 pp.

Lidicker, W. Z., Jr., and A. C. Ziegler.
1968. Report on a collection of mammals from eastern New Guinea, including species keys for fourteen genera. Univ. California Publ. Zool. 87: 1–64.

Majnep, S., and R. Bulmer
1977. Birds of my Kalam country. Auckland: Auckland Univ. Press, 219 pp.

McKean, J. L.
1972. Notes on some collections of bats (Order Chiroptera) from Papua-New Guinea and Bougainville Island. CSIRO, Div. Wildl. Res. Tech. Pap. 26: 1–35.

Milledge, D. R.
1987. Predation of a mist-netted Queensland blossom-bat *Syconycteris australis*. Macroderma 3(2): 30–31.

Norberg, U. M., and J. M. V. Raynor
1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strat-

egy and echolocation. Philos. Trans. Roy. Soc. London 316B: 335–427.

Novacek, M. J.
1990. Morphology, paleontology, and the higher clades of mammals. *In* Hugh H. Genoways (ed.), Current mammalogy 2: 507–543. New York: Plenum.

Novacek, M. J., A. R. Wyss, and M. C. McKenna
1988. The major groups of eutherian mammals. *In* M. J. Benton (ed.), The phylogeny and classification of tetrapods. Systematics Assoc. Spec. Vol. 35B: 31–71. Oxford: Clarendon Press.

Paijmans, K.
1975. Explanatory notes to the vegetation map of New Guinea. CSIRO Land Res. 35: 1–25.

Rand, A. L., and L. J. Brass
1940. Results of Archbold Expeditions no. 29. Summary of the 1936–1937 New Guinea expedition. Bull. Am. Mus. Nat. Hist. 77(7): 341–380.

Richards, G. C.
1983. Queensland blossom bat, *Syconycteris australis*. *In* R. Strahan (ed.), The Australian Museum complete book of Australian mammals, p. 289. Sydney: Angus & Robertson.

Robinson, M.
1980. Field observations on some North Queensland Megachiroptera. North Queensland Natur. 45(177): 2–3.

Rozendaal, F. G.
1984. Notes on Macroglossine bats from Sulawesi and the Moluccas, Indonesia, with the description of a new species of *Syconycteris* Matschie, 1899 from Halmahera (Mammalia: Megachiroptera). Zool. Meded. 58(13): 187–212.

Schodde, R., and J. H. Calaby
1972. The biogeography of the Australo-papuan bird and mammal faunas in relation to the Torres Straits. *In* D. Walker (ed.), Bridge and barrier the natural and cultural history of the Torres Strait, Publ. BG/3: 257–300. Canberra: Australian National Univ.

Sowler, S. G.
1980. Tooth eruption in known age specimens of *Epomophorus wahlbergi*. S. African J. Wildl. Res. 10(3/4): 112–117.

Start, A. N., and A. G. Marshall
1976. Nectivorous bats as pollinators of trees in West Malaysia. *In* J. Burley and B. T. Styles (eds.), Tropical trees: variation, breeding and conservation. Linnean Soc. Symp. Ser. 2: 141–150. London: Academic Press.

Stevens, P. F.
1989. New Guinea. *In* David G. Campbell and David Hammond (eds.), Floristic inventory of tropical countries: the status of plant systematic collections, vegetation, plus recommendations for the future, pp. 122–132. New York: Botanical Garden.

Van Deusen, H. M.
1978. Results of the Archbold Expeditions no. 101. Summary of the seventh Archbold Expedition to New Guinea (1964). Am. Mus. Novitates 2660: 21 pp.

Waithman, J.
1979. A report on a collection of mammals from southwest Papua, 1972–1973. Australian Zool. 20(2): 313–326.

Whitmore, T. C.
1984. Tropical rain forests of the Far East. 2nd ed. Oxford: Clarendon Press, 352 pp.

Womersley, J. S. (ed.)
1978. Handbooks of the flora of Papua New Guinea. Carleton, Victoria: Melbourne Univ. Press, 1 vol.

Ziegler, A. C.
1982. The Australo-Papuan genus *Syconycteris* (Chiroptera: Pteropodidae) with the description of a new Papua New Guinea species. Occas. Pap. Bernice Bishop Mus. 25(5): 1–22.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates, Bulletin,* and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.